

# SINGING BEHAVIOR, SONG TYPES ON THEIR WINTERING GROUNDS AND THE QUESTION OF LEAP-FROG MIGRATION IN PUGET SOUND WHITE-CROWNED SPARROWS<sup>1</sup>

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**Abstract.** Singing behavior in *Zonotrichia leucophrys pugetensis* on their wintering grounds in California was studied. Additionally syllables from songs of overwintering birds were compared to syllables in songs recorded previously on their breeding grounds in an effort to identify wintering grounds of dialectal populations. Much singing was recorded from recently arrived birds in the fall. At least some spontaneous singing was recorded every month of the year. However, singing decreased in December and increased in February, probably in response to increasing day lengths. Song development was complete or almost so in some juveniles recorded upon arrival in California. At least some birds responded to playback with singing during all months on the wintering grounds, however, responses peaked during arrival in the fall and before departure for the breeding grounds in the spring. At each wintering locality, several dialects were sung, indicating that more northerly breeding populations do not leap-frog and winter south of more southerly breeding populations. The resident *Z. l. nuttalli* sometimes borrow elements from wintering *Z. l. pugetensis* to construct "hybrid" themes. However, syllables from alien dialects are soon lost from the population due to match-countersinging by *Z. l. nuttalli* males.

**Key words:** White-crowned Sparrows; song dialects; leap-frog migration; *Zonotrichia leucophrys*.

## INTRODUCTION

At north temperate latitudes, singing activity in oscines typically reaches its peak in spring and regresses in late summer (Davis 1958, Bezzel 1988) and birds are usually silent through the fall and winter months. Laboratory studies indicate that fledglings of various oscines learn vocalizations during an early sensitive phase, but song production does not occur until some months later (Konishi 1965, Marler and Peters 1982a, review in Nottebohm 1993). In a field study, Dowsett-Lemaire (1981) studied song ontogeny in European Marsh Warblers (*Acrocephalus dumetorum*) on their wintering quarters in Africa and noted that hatching-year birds memorize allospecific vocalizations for several months until they reach their winter quarters in December or January. At this time stored motifs are first detected (vocalized) as they are incorporated into their "grating juvenile chatter."

The migratory *Zonotrichia leucophrys puge-*

*tensis* breeds in Oregon, Washington and British Columbia in spring and summer, then migrates 500 to 1,900 km to points south to overwinter (Lewis 1975). Songs of breeding populations have been studied in detail (Baptista 1977, Heine-mann 1981) but little is known concerning the singing behavior or song development of this taxon on their wintering grounds. Is there a quiescent period separating acquisition and production of songs? Does subsong first appear in the spring following a silent fall and winter?

In a study of song variation in breeding *Z. l. pugetensis*, Baptista (1977) described two geographically contiguous song themes based on sequencing of song elements (syntax). A northern theme, sung by coastal White-crowned Sparrows breeding north of the Columbia River, typically begins with a whistle (W) followed by a buzz (B) then two complex syllables (CS) followed by another buzz (B) and a terminal trill (SS) or W-B-CS-CS-B-SS (Fig. 1A). A southern theme, sung by birds south of the Columbia River, begins with a whistle (W) followed by a complex syllable (CS), a buzz (B) and a terminal trill, or W-CS-B-SS. The terminal trill may include two com-

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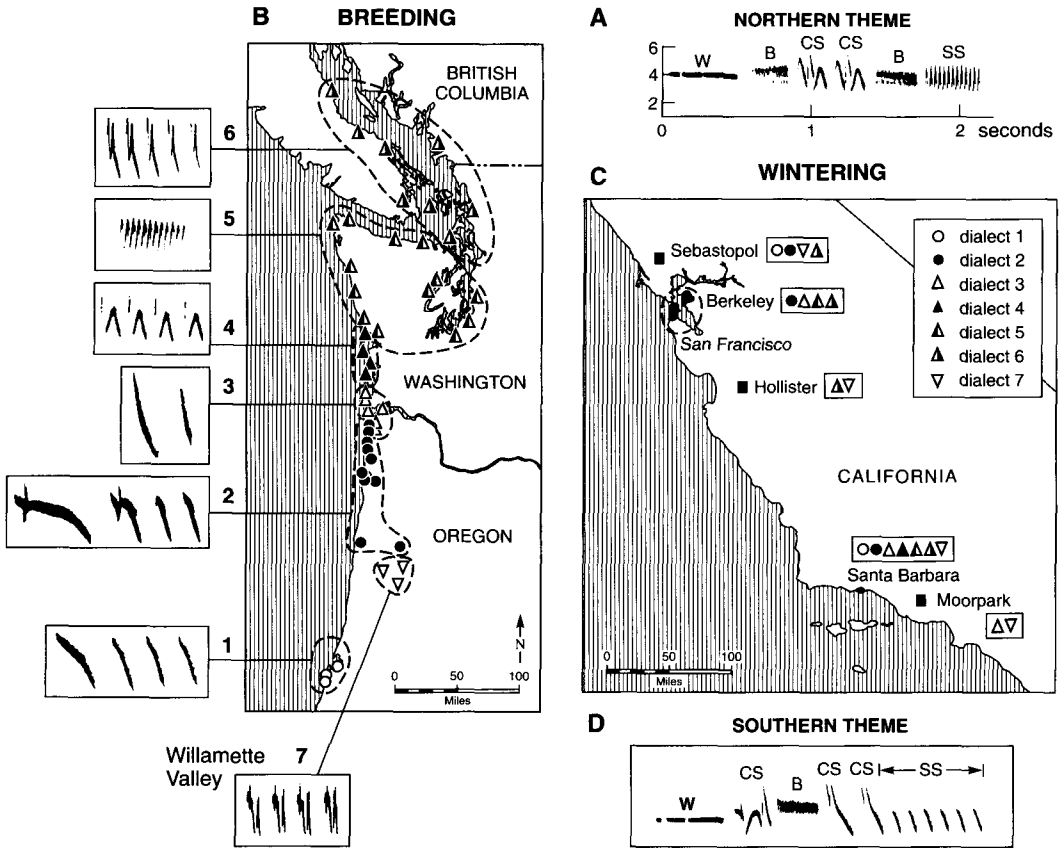


FIGURE 1. A. Terminology and symbols used to describe Northern Theme. W = Whistle. B = Buzz. CS = Complex Syllable. SS = Trill. B. Map showing breeding ranges of dialectal populations of *Z. l. pugetensis*. Each population is designated by terminal trills numbered 1-7. Data from Baptista 1977 and Heinemann 1981. C. Wintering localities sampled. Dialects recorded at each locality are illustrated by symbols next to each locality name. Symbols as in breeding localities in B. D. Terminology and symbols used to describe Southern Theme. Symbols as in A.

plex syllables (W-CS-B-CS-CS-SS), as shown in Fig. 1D.

Some populations breeding south of our southernmost sampled locality at Bandon Beach may sing songs with the syntactical arrangement of elements similar to northern dialects, i.e., W-B-CS-CS-B, but minus the terminal trill complex (Baker 1987). Complex syllables are unlike those sampled by Baptista (1977) or Heinemann (1981).

Within the "northern theme" group, Baptista (1977) identified four different terminal trill types corresponding to four dialectal populations (Fig. 1B). These populations breed in northern Oregon, Washington and British Columbia. Within the "southern theme" group, Baptista (1977) noted two terminal trill types, or dialects, in coastal populations in Oregon and Heinemann

(1981) described a third for the interior Willamette Valley. Because he found only one bird singing a dialect not described by Baptista (1977), Heinemann concluded that our knowledge of song variation in *Z. l. pugetensis* is nearly complete. In summary, seven dialects have been distinguished in breeding populations of *Z. l. pugetensis*: Dialects 1, 2 and 7 in the southern theme group and dialects 3, 4, 5, and 6 in the northern theme group (Fig. 1).

Northern and southern themes may be distinguished by the unaided ear based on sequencing of song elements alone. Because complex syllables within each group are not shared with each other, the form of this element is also a reliable criterion for distinguishing the themes of incomplete songs. Thus the investigator can use either

or both of these criteria to identify the themes of songs sung on the wintering ground (Fig. 1 and Fig. 4).

In contrast to song dialects of *Z. l. nuttalli*, which may occupy only a few kilometers (Marler and Tamura 1962, Baptista 1975, Cunningham et al. 1987), dialects of *Z. l. pugetensis* may range from 60 to 300 km. (see map in Heinemann 1981). When they fly south the birds bring with them the songs of their breeding localities. We do not know how far south a given bird flies. Do breeding populations leap-frog over each other in migration as Swarth (1920) found in subspecies of Fox Sparrows?

Unlike Fox Sparrows, *Z. l. pugetensis* is morphologically similar throughout its range. Color and size differences therefore cannot be used to locate wintering grounds of breeding populations. Hence, we must rely on songs of sparrows recorded on their fall and winter habitat to identify the wintering grounds of dialectal populations. Song structure does not change after the first year (Casey and Baker 1993), so we may expect that overwintering birds will be singing the same song used on their breeding grounds.

Baptista (1974, 1977) found that occasionally *Z. l. nuttalli* learn songs of visiting *Z. l. pugetensis* in the San Francisco Bay Area of California. Fledgling *Z. l. nuttalli* were thought to learn songs only during an early sensitive phase which ends when they are 50 days of age (Marler 1970). Since *Z. l. pugetensis* sing upon arrival on their wintering grounds (Blanchard 1941), it was suggested that only late-hatched *Z. l. nuttalli* would still be within the sensitive period to learn songs and only these birds would be most likely to learn songs from migrants (Baptista 1974). However, recent studies using live tutors indicate that *Z. l. nuttalli* may learn songs beyond 50 days of age (Baptista 1990). Moreover, pilot studies indicate that *Z. l. pugetensis* may sing throughout the fall and winter, increasing the chances for hatching-year *Z. l. nuttalli* to be exposed to alien dialects. Baptista's (1974) schema of how and when *Z. l. nuttalli* may learn alien dialects must be re-examined.

In this paper, we describe singing behavior of *Z. l. pugetensis* on their wintering grounds and examine song development in some hatching-year birds. We analyze complex and simple syllables in songs of flocks at five wintering localities and compare these with songs of breeding populations to see if dialectal populations leap-frog

over each other during migration. Finally we describe instances of sedentary *Z. l. nuttalli* learning songs from *Z. l. pugetensis* and comment on the circumstances leading to "song misimprinting."

## METHODS AND MATERIALS

### RECORDING LOCALITIES

Wintering *Z. l. pugetensis* were studied at five localities in California: (1) Sebastopol at 38°24'N; (2) San Francisco Bay at 37°46'N (includes Berkeley in the east and the city of San Francisco); (3) Hollister at 36°51'N; (4) Santa Barbara at 34°25'N; and (5) Moorpark at 34°17'N.

### RECORDING PROCEDURE AT SANTA BARBARA

Songs from 12 flocks were sampled at seven locations within a radius of 14.4 km. Over 800 visits to flock headquarters were made during five winter seasons between October 1983 and April 1990. It is well known that during the breeding season White-crowned Sparrows will sing in response to playback of recorded song (e.g., Tomback et al. 1983, Catchpole and Baptista 1988). We noted in pilot studies that *Z. l. pugetensis* may sometimes respond to playback with approach and/or song while on their wintering grounds. We conducted playback studies on this subspecies throughout the winter season to quantify changes in this behavior through time in an effort to understand the function(s) of winter song.

On most visits, after all spontaneously uttered patterns distinguishable by ear had been taped, playback was used and the birds' response recorded. If, as sometimes happened in mid-winter, no spontaneous singing occurred within the first five minutes of a visit, playback was started and ensuing songs, if any, recorded.

A tape of dialect number 1 (Fig. 1, southern theme) and a tape of dialect number 5 (northern theme) were used during playback. Only one tape was played at any one recording session at a given site, and order of presentations at a site were randomized. Sparrows did not match playback themes with like themes. Furthermore, those birds singing a northern theme in response to playback of dialect number five responded with any of four northern dialects (i.e., 3, 4 and 6, as well as 5).

No playback was used at one recording site which was kept as a control. Both northern and

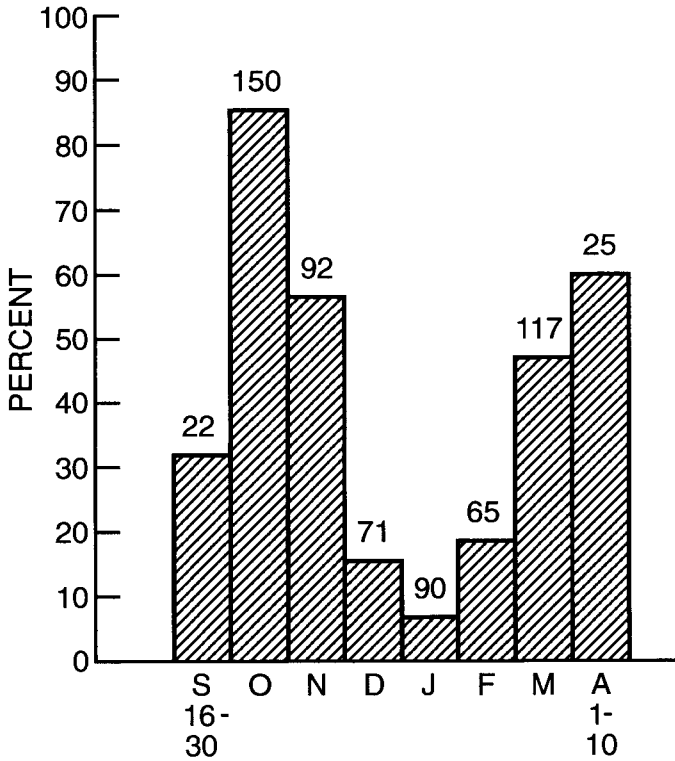


FIGURE 2. Spontaneous singing in *Z. l. pugetensis* during wintering months for five winter seasons. Each bar represents the percentage of site visits when individuals were recorded singing. Numbers above bars are number of site visits. Observations were made during period denoted below bar.

southern themes were recorded here as on the other sites. We are thus confident that our playback activities did not bias our inventories of winter song types.

It might be argued that some *Z. l. nuttalli* may spontaneously sing *Z. l. pugetensis* songs in winter so that we are not always recording songs from migrants. This is a possibility only at one collecting site, namely the coastal San Francisco Bay Area where the two races occur sympatrically in fall and winter. This is unlikely, however, as a population of several hundred color-marked *Z. l. nuttalli* have been followed over a decade and have not been seen to sing alien dialects (e.g., Baptista et al. 1993a). Moreover, *Z. l. nuttalli* do not occur at the other four inland collecting localities so we may be confident that songs recorded are those produced by visiting migrants.

#### EQUIPMENT

DeWolfe used a Sennheiser microphone (ME 80) and Sony cassette-corders TCM 35 and TCM 121. Baptista used a Nagra 4.2 tape recorder cou-

pled with a Sennheiser (ME 20) omnidirectional microphone mounted in a 46 cm plastic parabolic reflector (Sony PBR 330). Songs were graphed on a Kay Elemetrics Digital sonograph (Model 7800) using the wide band-pass filter.

#### RESULTS

##### SINGING BEHAVIOR

*Spontaneous singing.* Migratory populations of *Z. l. pugetensis* arrive in California in mid to late September and depart in late March and early April. Two peaks of singing occur: in October shortly after arrival and in April on the eve of departure for more northerly latitudes (Fig. 2). At these times several birds may sing together in chorus (Blanchard 1941, 1942; DeWolfe 1968, pers. observ.). Chorus singing is rare between these two peaks of spontaneous singing but a few individuals sing in all months including December and January.

*Response to playback.* Response to playback by White-crowned Sparrows consisted of approach to the speaker, raising the crown, and/or

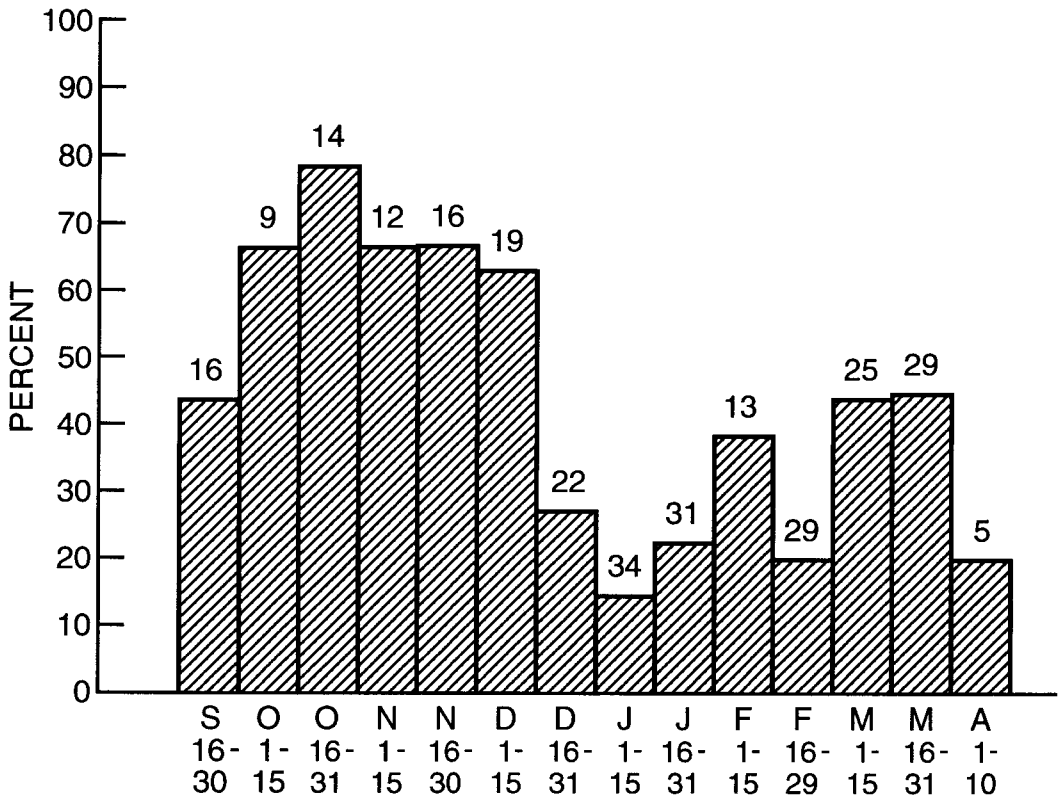


FIGURE 3. Responses to playback by wintering *Z. l. pugetensis*. Each bar represents the percentage of site visits when individuals were noted responding to playback over two-week periods for five winter seasons. Numbers above bars as in Figure 2.

countersinging with playback of conspecific song. At Santa Barbara, at least some birds responded to playback throughout the winter. Figure 3 shows frequency of singing following playback for half-month periods. In April, when chorus singing is at a peak, birds sang in response to playback during only one out of the five visits when playback was used. Except for April 1-10, the seasonal change in response to playback followed approximately that of spontaneous singing. Thus, except in early April, singing could often be evoked with playback even when no spontaneous song was heard.

SONG THEMES SUNG BY WINTERING *Z. L. PUGETENSIS*

Both northern and southern themes were sung by wintering birds at all study localities (Tables 1 and 2, Figs. 1, 4). Birds wintering in the Moorpark area are usually members of the subspecies *Z. l. gambelii*, and *Z. l. pugetensis* are rare. Two

*Z. l. pugetensis* from a mixed flock wintering at Moorpark were captured and identified as males by laparotomy. These individuals were then treated with testosterone to induce song. One sang a northern theme (Dialect 3 of Baptista 1977) and one the southern theme, described by Heinemann 1981 and designated in this paper as Dialect 7 (Fig. 1).

Table 3 shows that at Santa Barbara both northern and southern themes occurred at one or more of the seven recording locations in all eight months, as well as in 12 of the 14 two-week periods of the study. We have 37 examples of birds in the same flock spontaneously singing both northern and southern themes at the same recording session. These data indicate that there was no temporal or spatial separation of birds singing northern or southern themes at all seven Santa Barbara locations. Data for one location indicate that both northern and southern theme singers occur within the same flock throughout

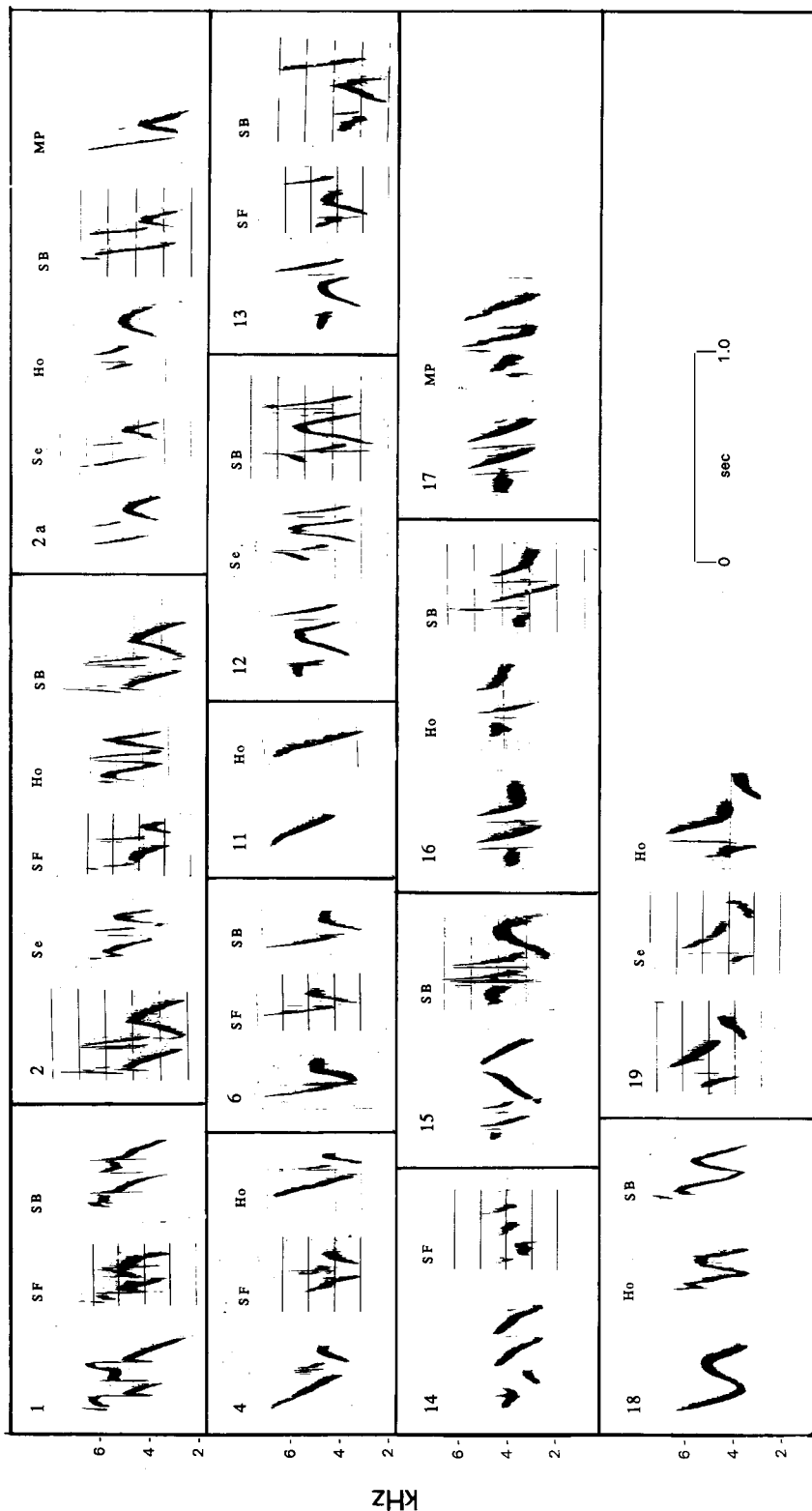


FIGURE 4. Complex syllables from songs of breeding *pugetensis* from various localities compared to syllables recorded on their wintering grounds. Symbols for wintering localities are as follows: SE = Sebastopol, SF = San Francisco Bay, HO = Hollister, SB = Santa Barbara, MP = Moorpark. Complex syllables numbered 1 through 19 are from breeding grounds as in figure catalogues in Baptista (1977) and Heinemann (1981). Complex syllables 1 through 11 are from Northern themes, Complex syllables 12 through 19 are from Southern themes. Complex syllable 2a is considered a variant of 2 and was recorded in Astoria, Oregon (Baptista, unpublished).

TABLE 1. Occurrences of complex syllable types (Fig. 4) in wintering populations of *Z. l. pugetensis*

Locality	Northern themes										Southern themes									
	1	2	2a	3	4	5	6	7	8	9	10	11	12(B1) <sup>1</sup>	13(B2)	14	15(C1)	16(D2)	17	18 <sup>2</sup>	19 <sup>2</sup>
1. Sebastopol		+	+										+							+
2. San Francisco Bay	+	+		+	+		+								+					
3. Hollister	+	+		+							+						+	+	+	
4. Santa Barbara	+	+	+	+			+						+	+		+				
5. Moorpark			+															+		

<sup>1</sup> Letters in brackets denote syllable types in Heinemann (1981) identical to those in Baptista (1977).  
<sup>2</sup> Complex syllable 19 was not encountered by us on the breeding grounds but occurs in a song recorded by Baker (1987) in Big Lagoon, California. Complex syllable 18 is probably a variant of complex syllable 2 but has not been recorded on the breeding grounds.

the wintering months. All seven dialects were recorded from flocks wintering at Santa Barbara (Fig. 1C).

At Sebastopol we also found no temporal separation of northern theme singers from southern theme singers. We did, however, sometimes find some spatial segregation, i.e., birds singing northern themes perched in one tree while southern theme singers sang from a different tree during the same recording session.

SONG DEVELOPMENT IN HATCHING YEAR BIRDS

Hatching year juveniles may be distinguished from breeding adults by the color of the crown which is tan-and-brown striped in juveniles and black-and-white in adults (Blanchard 1941, Parsons and Baptista 1980). Juveniles retain their brown crowns throughout the wintering months. *Z. l. pugetensis* arrive on their breeding grounds in April, so that nestlings do not hatch until late April or May. Young birds are sensitive to learning song from time of fledging at about 10 days of age to at least 100 days (Marler 1970, Petrinovich and Baptista 1987). Young birds are thus exposed to adult song between late April and September when they join adults in flocks migrating to points south.

Juveniles do not develop adult songs instantaneously but go through a series of practice stages during which song quality improves gradually (Marler 1970, DeWolfe et al. 1989). During the initial or "subsung" stages of song development song consists of amorphous whistles not assignable to any population based on sound spectrographs. With practice the juvenile passes on to the "rehearsed" or "plastic" song stage when utterances begin to resemble syllables of known song populations. Songs are said to be "crystallized" when little variation is detected from song to song (Konishi 1965).

We recorded songs of migratory juveniles at San Francisco, Hollister, and Santa Barbara, California in an effort to determine times of the year when juveniles in the wild pass through the different stages of song development. We found juveniles in the late rehearsed song stage upon arrival at their wintering grounds (Fig. 5). Juvenile songs were slightly quavering in quality but bore all the characteristics of adult song. Moreover, we also noted that these juveniles would switch to adult-like songs following fights or when challenged by another bird. These findings indicate

TABLE 2. Occurrences of Terminal Trill Types (Fig. 1) in wintering populations of *Z. l. pugetensis*

Locality	Northern themes				Southern themes		
	3	4	5	6	1	2	7 <sup>1</sup>
1. Sebastopol			+		+	+	+
2. San Francisco Bay	+		+	+		+	
3. Hollister				+			+
4. Santa Barbara	+	+	+	+	+	+	+
5. Moorpark	+						+

<sup>1</sup> Willamette Valley sampled by Heinemann (1981).

that the slight differences between juvenile and adult song are often due to motivation rather than developmental stage. Similar observations were made previously on juveniles of the sedentary *Z. l. nuttalli* (DeWolfe et al. 1989).

A juvenile recorded at Goleta (34°17'N, 119°50'W) near Santa Barbara, California, on September 27, 1987, sang a crystallized song lacking the terminal trill, but comparable in quality to songs of adults (Fig. 5C). The complex syllables in its song (type 5a, Fig. 3 of Baptista 1977) are typical of those used by birds breeding north of the Columbia River, e.g., at Ocean City, Washington (47°04'N, 124°10'W). Juveniles were recorded singing adult-like songs at San Francisco and Hollister as well (Fig. 5).

As White-crowned Sparrow juveniles in the laboratory are not known to sing adult songs until their second spring (Konishi 1965, Marler 1970) we attempt herein to estimate the age of the Goleta juvenile. The earliest of 68 records for eggs laid by *Z. l. pugetensis* in Washington is April 24 (DeWolfe 1968). If we assume that song di-

lect may give some indication of latitude of hatching site, and that the juvenile bird hatched at the earliest the preceding April, then it was not more than four and one-half to five months old when its songs were recorded in September. Song is thus crystallized on the wintering grounds, often soon after arrival hundreds of miles from where the young birds might establish breeding territories next spring.

The above picture presupposes an early hatched bird. However, *Z. l. pugetensis* breed at least into July (Blanchard 1941), so that arriving juveniles may be even younger. In *Z. l. nuttalli* a fledgling has been known to sing almost crystallized song at as early as day 28 while still being fed by its parents (Baptista et al. 1993b).

#### THE INFLUENCE OF *Z. L. PUGETENSIS* ON SONG DEVELOPMENT IN SEDENTARY WHITE-CROWNED SPARROWS

Sedentary White-crowned Sparrows belonging to the subspecies *Z. l. nuttalli* enjoy a long breeding season from late March into September (DeSante and Baptista 1989). *Z. l. nuttalli* fledglings may hear wintering *Z. l. pugetensis* singing early in the breeding season and in the fall upon return of *pugetensis* to *nuttalli* breeding grounds. A few territorial individuals sang songs similar to those of winter visitants. These were identified as *nuttalli* acquiring songs from overwintering migrants (Baptista 1974, Baptista and Wells 1975).

In contrast to the above who acquired alien dialects intact, two territorial White-crowned Sparrows in our study acquired and used syllables from *Z. l. pugetensis* which they combined with elements from *Z. l. nuttalli* song. One bird used a single complex syllable borrowed from a southern *Z. l. pugetensis* theme and inserted it into its San Francisco song (Fig. 6F). Another individual sang a San Francisco, California, *Z. l. nuttalli* theme, and a second theme containing complex syllables 2 and 19 from *pugetensis* songs

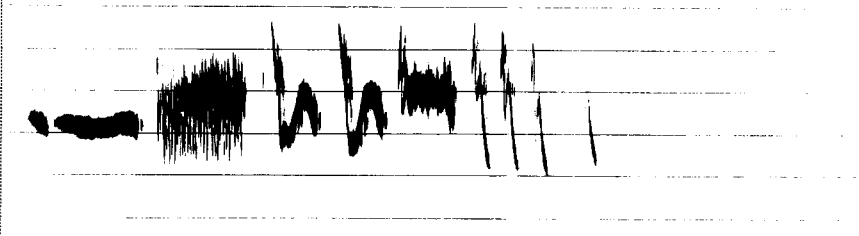
TABLE 3. Spontaneously uttered Northern and Southern themes recorded at Santa Barbara over a two-week period.

One-half month period	Northern	Southern
16-30 Sept.	+	+
1-15 Oct.	+	+
16-31 Oct.	+	+
1-15 Nov.	+	+
16-30 Nov.	+	+
1-15 Dec.	+	+
16-31 Dec.	+	+
1-15 Jan.	-	+
16-31 Jan.	+	+
1-15 Feb.	+	-
16-29 Feb.	+	+
1-15 Mar.	+	+
16-31 Mar.	+	+
1-15 Apr.	+	+

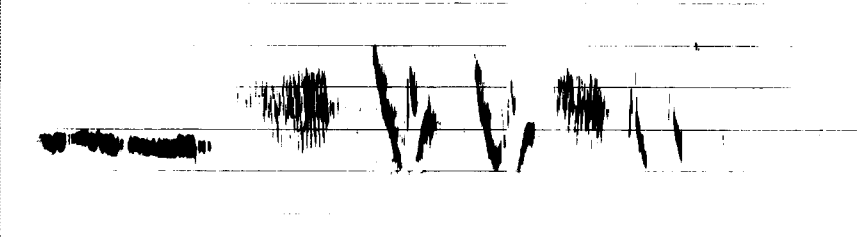


JUVENILES

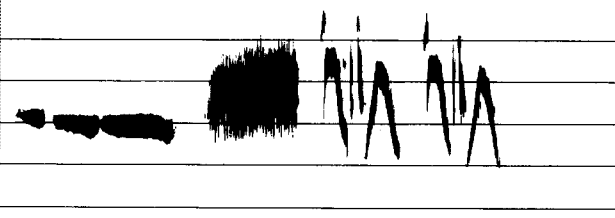
A CAS September 28



B Hollister October 4



C UCSB Campus September 28



ADULT

D CAS November 9

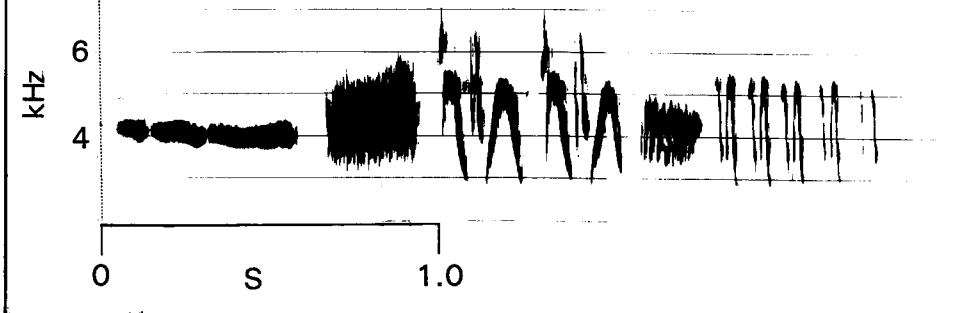


FIGURE 5. A, B, C. Songs of juvenile *Z. l. pugetensis* recently arrived on their wintering grounds in late September or early October. D. Song of an adult *Z. l. pugetensis* recorded in San Francisco, California. CAS = California Academy of Sciences, San Francisco, California.

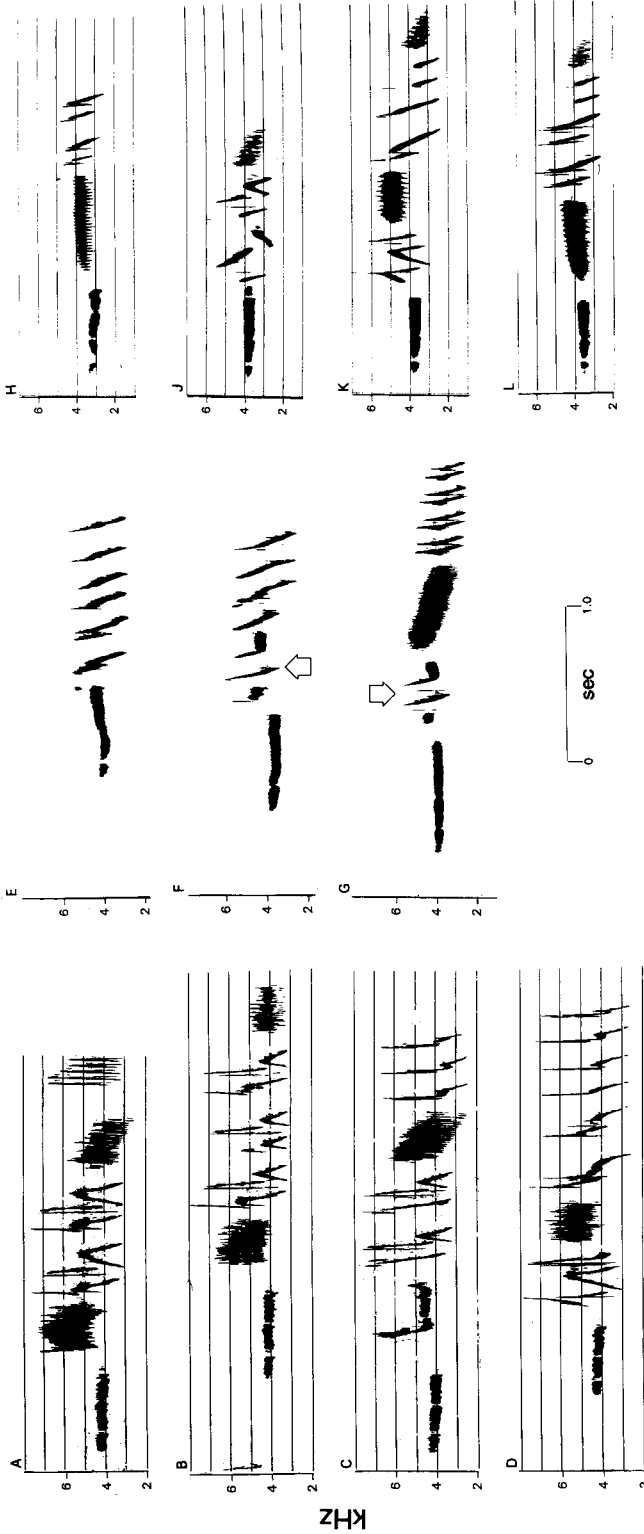


FIGURE 6. A-D are songs of four individuals from a wintering flock of *Z. l. pugetensis* recorded at Sebastopol, California. E-Z. *l. nuttalli* theme from San Francisco, California. F-Z. *l. nuttalli* theme sung by bird E with a *pugetensis* syllable inserted (arrow) in the trill. The *pugetensis* complex syllable is type 16 of Figure 4. G-Z. *l. pugetensis* song from San Francisco illustrating complex syllable (arrow) borrowed by bird E in song F. H-K. Three themes sung by a *Z. l. nuttalli* from San Francisco, California. H is a typical San Francisco song but lacking the terminal trill. J is a theme with complex syllables found in songs typical of wintering *Z. l. pugetensis* migrants (compare complex syllable with types 19 and 2 respectively in Fig. 4). K is a southern theme typical of winter *Z. l. pugetensis*, but containing a terminal downward inflected buzz borrowed from a Lake Merced, San Francisco, theme (L).

as well as a southern *Z. l. pugetensis* theme from Oregon (Fig. 6, H to K). The southern theme ended with a downward inflected vibrato typical of Lake Merced, San Francisco, California.

## DISCUSSION

### THE FUNCTION OF FALL/WINTER SINGING

In this study we confirmed anecdotal observations of earlier workers that wintering *Z. l. pugetensis* sing principally soon after arrival on their wintering grounds in early October and again in March and April when photoperiods lengthen and birds prepare to migrate to their breeding grounds in more northerly latitudes. We also found that some birds may be heard singing throughout the wintering months. Moreover, individuals would respond to playback song with singing throughout these periods.

Winter song may be indicative of behavior with survival value. Song may be used to establish a flock hierarchy as birds first aggregate. Much singing is often heard prior to roosting and may be in the contexts of squabbling for best roosting spots and maintaining individual distances.

Perhaps the slight rise in singing reflects individuals interacting as they establish the peck order. Once ranks in a flock are established, incidences of fighting diminish along with singing.

The second peak in song in early spring probably reflects the rising titres of hormones stimulated by lengthening days (Wingfield and Farner 1986) and functions to stimulate even more hormone production by acting synergistically with spring photoperiods (Morton et al. 1985). The function of testosterone in inducing singing is well documented (Baptista et al. 1987). Kern and King (1972) argue that females sing in early spring because the precursor of estrogen present in their blood is testosterone-like. Morton et al. (1985) have documented copious female song in photostimulated *Z. l. gambelii*. Cheng (1992) observed that devocalized female Ring Doves (*Streptopelia roseogrisea*) did not develop gonads. She concluded that these doves, White-crowned Sparrows and other species sing to self stimulate hormone production and gonadal recrudescence. This may be the function of chorus singing in White-crowned Sparrows preceding spring migration.

### THE QUESTION OF LEAP-FROGGING

Flocks of wintering *Z. l. pugetensis* in our study areas at several latitudes were composed of birds

singing one or more dialects from both northern and southern theme populations (Fig. 1). Indeed, all the dialects recorded by Baptista (1977) and Heinemann (1981) on their breeding grounds were recorded in flocks wintering in Santa Barbara, California (Table 2). Northern and southern themes were recorded from the same flocks throughout the wintering months (Table 3). These data indicate that flocks consist of birds from several different breeding populations in the Pacific Northwest. Thus birds from different latitudes do not winter in separate quarters and populations do not leap-frog over each other during migration as Swarth (1920) found in Fox Sparrows.

### SONG DEVELOPMENT IN JUVENILES

We noted that hatching year birds sing crystallized or close to crystallized songs in late September and early October upon arrival on their wintering grounds. This indicates that the early stages of subsong and rehearsed song were passed on their natal area prior to migration and/or during passage to California. Thus, *Z. l. pugetensis* juveniles are not silent for several months between time of acquisition of song and the actual onset of singing (the motor phase) as has been shown for White-crowned Sparrows in the laboratory (Konishi 1965, Baptista and Petrinovich 1984). Our observations on *Z. l. pugetensis* are similar to those for *Z. l. nuttalli* (DeWolfe et al. 1989, Baptista et al. 1993b) who were also found to crystallize song in the fall.

The difference in results between laboratory and field studies probably lies in the difference in the quality of the social/acoustic environment. Birds in the laboratory go through a long period of non-singing following the molt in July until the following January when photoperiods increase. Birds in the wild sing throughout the fall and winter especially when challenged by another bird (Baptista et al. 1993a). Agonistic behavior in free-living birds is regular and consists of chases, fights and bouts of countersinging. Free-living juveniles thus experience more social interaction with other conspecifics than birds raised in the laboratory. The accelerated song development is probably a result of this richer acoustic and social environment.

Konishi (1965) treated juveniles with testosterone and found that they came into song in October. He concluded that testosterone may function to hasten song ontogeny. Wingfield (1984) found that testosterone titres rose slightly

following fights between two Song Sparrows (*Melospiza melodia*). Agonistic interactions between juvenile White-crowned Sparrows and other adults and juveniles may result in sporadic but regular bursts in testosterone titres which may account for juveniles crystallizing songs earlier in the wild than they do in captivity.

Although syllables are not shared between northern and southern theme groups, there is considerable sharing of complex syllables between dialectal populations within each theme group (Baptista 1977, Heinemann 1981). For example, complex syllable 2 may be found in coastal dialectal populations 4, 5 and 6 (see Fig. 3 in Baptista 1977 for more examples). Heinemann (1981) hypothesized that the terminal trill is learned in the natal area during an early sensitive phase prior to dispersal/migration, and the complex syllables are learned in passage or on their wintering grounds when they encounter birds singing alien dialects. He also postulated a genetic preference to learn the trill of the natal population. A simpler explanation is developed below as follows.

Baptista and Morton (1988) recorded songs of juvenile montane White-crowned Sparrows (*Z. l. oriantha*) using voice-activated microphones and found that during subsong they produce syllables from several dialectal populations uttered in various permutations, combinations and sequences. As adults each individual sang only one theme.

It seems that in White-crowned Sparrows and in Swamp Sparrows (*Melospiza georgiana*) (Baptista and Morton 1988, Marler and Peters 1982b), young birds learn a pool of syllables from adults and as a result of match countersinging select the syllables and syntax used by neighbors at sites settled (Baptista and Morton 1988, Marler and Nelson 1993). Thus any complex syllable may be combined with any terminal trill, the sequence of which is influenced by the singing activities of neighboring males. In the absence of stimulation from immediate neighbors, individuals may sing songs with new combinations of syllables not shared by others in the population.

#### INFLUENCE OF MIGRANTS ON SONG DEVELOPMENT IN *Z. L. NUTTALLI*

In this and in earlier studies (Baptista 1974, 1977), we documented *Z. l. nuttalli* learning songs from visiting *Z. l. pugetensis*. In the earlier studies residents learned entire songs from migrants. In this study we encountered individuals borrowing

portions of songs typical of migrants and incorporating them into their own songs. The circumstances prompting individuals to learn whole songs versus constructing hybrid themes remain to be determined.

Fall arrival of *Z. l. pugetensis* in mid-September is announced by much singing (Blanchard 1941, Davis 1958:334, this study) which is sporadic in November through February. At Berkeley, song was more frequent and louder in late February, four weeks prior to migration (Blanchard 1941, DeWolfe 1968). Because it was once believed that White-crowned Sparrows could learn songs only during a short sensitive phase before juveniles reach 50 days of age, it was postulated that acquisition of song from visiting migrants could take place only during narrow time windows in the fall or early spring (Baptista 1974). Since few birds hatch before April or after July, few individuals would have the opportunity to encounter these song types.

Early song studies were performed using taped-songs as tutor stimuli (Marler 1970, Petrinovich 1985). We now know that by using live tutors naive experimentals may acquire new songs beyond 50 days of age (Petrinovich and Baptista 1987). Thus many more individuals may actually experience songs of migrants. Migrants tend to sing softer (at lower amplitude) than sedentary birds. However, when challenged by another bird, migrants may sing loud and stereotyped song similar to those sung by birds in the breeding season. We have several observations of *Z. l. nuttalli* fighting with *Z. l. pugetensis* and countersinging bouts following these encounters. Playback studies reported herein indicate that loud song could be evoked throughout the wintering months.

Despite ample opportunity for *Z. l. nuttalli* to learn songs from visiting *Z. l. pugetensis*, few records of such song "misimprinting" have been documented. Due to match countersinging with local birds singing *Z. l. nuttalli* songs, *Z. l. pugetensis* themes are not used and are lost from the vocalized *nuttalli* repertoire. This is probably the mechanism whereby local dialects in White-crowned Sparrows are preserved for long periods and songs of migrants prevented from diffusing into the local population in any numbers. Many birds may learn several songs from both subspecies (this study), but because the local *Z. l. nuttalli* dialect is used by the majority, this becomes the preferred song and songs learned from migrants fall into disuse.

In sum, *Z. l. pugetensis* sing throughout the wintering months, although amount of singing waxes and wanes with the seasons. This heightened activity encountered by birds in the wild accelerates song development of hatching-year birds and may result in memes passed on to some of the sedentary birds.

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#### LITERATURE CITED

- BAKER, M. C. 1987. Intergradation of song between two subspecies of White-crowned Sparrows on the west coast of North America. *Ornis Scand.* 18: 265-268.
- BAPTISTA, L. F. 1974. The effects of songs of wintering White-crowned Sparrows on song development in sedentary populations of the species. *Z. Tierpsychol.* 34:147-171.
- BAPTISTA, L. F. 1975. Song dialects and demes in sedentary populations of the White-crowned Sparrow (*Zonotrichia leucophrys nuttalli*). *Univ. Calif. Publ. Zool.* 105:1-52.
- BAPTISTA, L. F. 1977. Geographical variation in song and song dialects of the migratory White-crowned Sparrow, *Zonotrichia leucophrys pugetensis*. *Condor* 79:356-370.
- BAPTISTA, L. F. 1990. Song learning in the White-crowned Sparrow (*Zonotrichia leucophrys*): sensitive phases and stimulus filtering revisited. *Proc. Int. 100. DO-G Meeting, Current Topics Avian Biol., Bonn*, p. 143-152.
- BAPTISTA, L. F., AND H. WELLS. 1975. Additional evidence of song misimprinting in the White-crowned Sparrow. *Bird-banding* 46:269-272.
- BAPTISTA, L. F., B. B. DEWOLFE, AND L. AVERY-BEAUSOLEIL. 1987. Testosterone, aggression, and dominance in Gambel's White-crowned Sparrows. *Wilson Bull.* 99:86-91.
- BAPTISTA, L. F., AND M. L. MORTON. 1988. Song learning in montane White-crowned Sparrows: from whom and when. *Anim. Behav.* 36:1753-1764.
- BAPTISTA, L. F., AND L. PETRINOVICH. 1984. Social interaction, sensitive phases and the song template hypothesis in the White-crowned Sparrow. *Anim. Behav.* 32:172-181.
- BAPTISTA, L. F., D. A. BELL, AND P. W. TRAIL. 1993a. Song learning and production in the White-crowned Sparrow: parallels with sexual imprinting, p. 17-33. *In* C. ten Cate, P.J.B. Slater, and J. Kruijt [eds.], *Proceedings international conference on song learning and imprinting: an inquiry into mechanisms of behavioural development*. Univ. of Groningen, Haren. *Neth. J. Zool.*, 43.
- BAPTISTA, L. F., P. W. TRAIL, B. B. DEWOLFE, AND M. L. MORTON. 1993b. Singing and its functions in female White-crowned Sparrows. *Anim. Behav.* 46:511-524.
- BEZZEL, E. 1988. Die Gesangszeiten des Buchfinken (*Fringilla coelebs*): eine regionalstudie. *J. Ornithol.* 129:71-81.
- BLANCHARD, B. D. 1941. The White-crowned Sparrows (*Zonotrichia leucophrys*) of the Pacific seaboard: environment and annual cycle. *Univ. Calif. Publ. Zool.* 46:1-78.
- BLANCHARD, B. D. 1942. Migration in Pacific coast White-crowned Sparrows. *Auk* 59:47-63.
- CASEY, R. M., AND M. C. BAKER. 1993. Social tutoring of adult male White-crowned Sparrows. *Condor* 95:718-723.
- CATCHPOLE, C. K., AND L. F. BAPTISTA. 1988. A test of the competition hypothesis of vocal mimicry, using Song Sparrow imitations of White-crowned Sparrow song. *Behaviour* 106:119-128.
- CHENG, M. F. 1992. For whom does the female dove coo? A case for the role of vocal self-stimulation. *Anim. Behav.* 43:1035-1044.
- CUNNINGHAM, M. A., M. C. BAKER, AND T. J. BOARDMAN. 1987. Microgeographic song variation in the Nuttall's White-crowned Sparrow. *Condor* 88: 261-275.
- DAVIS, J. 1958. Singing behavior and the gonad cycle of the Rufous-sided Towhee. *Condor* 60:308-336.
- DESANTE, D., AND L. F. BAPTISTA. 1989. Factors affecting the termination of breeding in Nuttall's White-crowned Sparrow. *Wilson Bull.* 101:120-124.
- DEWOLFE, B. B. 1968. Puget Sound White-crowned Sparrow. *In* A. C. Bent and Collaborators, *Life histories of North American cardinals, grosbeaks, buntings, towhees, finches, sparrows, and allies*, part three. *U.S. Natl. Mus. Bull.* 237:1344-1352.
- DEWOLFE, B. B., L. F. BAPTISTA, AND L. PETRINOVICH. 1989. Song development and territory establishment in Nuttall's White-crowned Sparrows. *Condor* 91:397-407.
- DOWSETT-LEMAIRE, F. 1981. The transition period from juvenile to adult song in the European Marsh Warbler. *Ostrich* 52:253-255.
- HEINEMANN, D. 1981. Song dialects, migration, and population structure of Puget Sound White-crowned Sparrows. *Auk* 98:512-521.
- KERN, M. D., AND J. R. KING. 1972. Testosterone-induced singing in female White-crowned Sparrows. *Condor* 74:204-209.
- KONISHI, M. 1965. The role of auditory feedback in the control of vocalization in the White-crowned Sparrow. *Z. Tierpsychol.* 22:770-783.
- LEWIS, R. A. 1975. Reproductive biology of the White-crowned Sparrow (*Zonotrichia leucophrys pugetensis* Grinnell) I. Temporal organization of reproductive and associated cycles. *Condor* 77:46-59.
- 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 M. TAMURA. 1962. Song 'dialects' in three populations of White-crowned Sparrows. *Condor* 64:368-377.
- MARLER, P., AND S. PETERS. 1982a. Long-term stor-

- age of learned birdsongs prior to production. *Anim. Behav.* 30:479-482.
- MARLER, P., AND S. PETERS. 1982b. Developmental overproduction and selective attrition: new processes in the epigenesis of birdsong. *Dev. Psychobiol.* 15:369-378.
- MARLER, P., AND D. A. NELSON. 1993. Action-based learning: a new form of developmental plasticity in bird song, p. 91-103. *In* C. ten Cate, P.J.B. Slater, and J. Kruijt [eds.], *Proceedings international conference on song learning and imprinting: an inquiry into mechanisms of behavioural development*. Univ. of Groningen, Haren. *Neth. J. Zool.*, 43.
- MORTON, M. L., M. E. PEREYRA, AND L. F. BAPTISTA. 1985. Photoperiodically induced ovarian growth in the White-crowned Sparrow (*Zonotrichia leucophrys gambelii*) and its augmentation by song. *Comp. Biochem. Physiol.* 80A:93-97.
- NOTTEBOHM, F. 1993. The search for neural mechanisms that define the sensitive period for song learning in birds. *Neth. J. Zool.* 43:193-234.
- PARSONS J., AND L. F. BAPTISTA. 1980. Crown color and dominance in the White-crowned Sparrow. *Auk* 97:807-815.
- PETRINOVICH, L. 1985. Factors influencing song development in the White-crowned Sparrow (*Zonotrichia leucophrys*). *J. Comp. Psychol.* 99:15-29.
- PETRINOVICH, L., AND L. F. BAPTISTA. 1987. Song development in the White-crowned Sparrow: modification of learned song. *Anim. Behav.* 35:961-974.
- SWARTH H. S. 1920. Revision of the avian genus *Passerella* with special reference to the distribution and migration of the races in California. *Univ. Calif. Publ. Zool.* 21:75-224.
- 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.
- WINGFIELD, J. C. 1984. Environmental and endocrine control of reproduction in the Song Sparrow *Melospiza melodia* II. Agonistic interactions as environmental information stimulating secretion of testosterone. *Gen. Comp. Endocrinol.* 56:417-424.
- WINGFIELD, J. C., AND D. S. FARNER. 1986. The endocrinology of a natural breeding population of the White-crowned Sparrow (*Zonotrichia leucophrys pugetensis*). *Physiol. Zool.* 51:188-205.