

# SONG DIALECTS, MIGRATION, AND POPULATION STRUCTURE OF PUGET SOUND WHITE-CROWNED SPARROWS

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**ABSTRACT.**—Baptista's (1977) survey of Pacific Northwest coastal populations of Puget Sound White-crowned Sparrows (*Zonotrichia leucophrys pugetensis*) revealed that Oregon birds sing one sequence of song components, while birds in Washington and British Columbia use another sequence or theme. The form of the terminal trill varies in a manner that defines geographically distinct song dialects. My studies of *pugetensis* breeding at Finley National Wildlife Refuge in the inland Willamette Valley of Oregon in 1977 and 1978 revealed a third southern-theme dialect. This dialect remained stable during my study and was indistinguishable from that of birds recorded in the same area in 1965. By matching songs of *pugetensis* recorded in flocks during spring migration with songs of breeding *pugetensis*, I determined that a single flock may contain birds from many areas of the Pacific Northwest, suggesting that flocks of migrating birds are aggregations of birds, each individual having its own schedule and destination.

A review of the literature on White-crowned Sparrow song indicated that support is equivocal for the hypothesis that there is a particular functional relationship between population and dialect structure and that song dialects are indicators of discrete demes. I concluded that this hypothesis is inconsistent with the observed patterns of geographical variation in *pugetensis* song components. I suggest that these patterns may indicate the existence of some other functional relationship between demes and dialects, or that dialects may not indicate the presence of demes in *pugetensis*. I also note the possibility, suggested by these patterns, that juvenile *pugetensis* may learn songs in a manner different from those documented so far for White-crowned Sparrows. Received 25 August 1980, accepted 29 January 1981.

BAPTISTA'S (1977) breeding-season survey of Pacific Northwest coastal populations of Puget Sound White-crowned Sparrows (*Zonotrichia leucophrys pugetensis*) during 1970 showed that birds in Oregon sing one theme, a particular sequence of song components, while birds in Washington and southern British Columbia sing another theme. These theme populations overlap by approximately 10 km in extreme northwestern Oregon (Fig. 1). The northern theme consists of a whistle, buzz, two identical complex syllables, buzz, and trill (Fig. 2A; terminology after Baptista 1977). The southern theme has a whistle, complex syllable, buzz, and trill (Fig. 2B). Only seven of 295 birds recorded by Baptista had songs with some other component sequencing. Among northern-theme songs, Baptista identified four distinct forms of the trill; southern-theme songs contained two discrete trill types. Because he found very little geographic overlap among trill forms (Fig. 1), he referred to them as song dialects. Within each theme population Baptista found several distinct forms of the complex syllables (six within the southern- and 11 within the northern-theme population) that were used.

Given the poor efficiency of banding studies at determining migration patterns [e.g. 198 returns out of 226,516 (0.087%) White-crowned Sparrows banded over 43 yr, Cortopassi and Mewaldt 1965] and the geographic specificity of *pugetensis* songs, Baptista suggested that the migration pattern of *pugetensis* could be determined by matching songs recorded on the wintering ground or flyway with those recorded on

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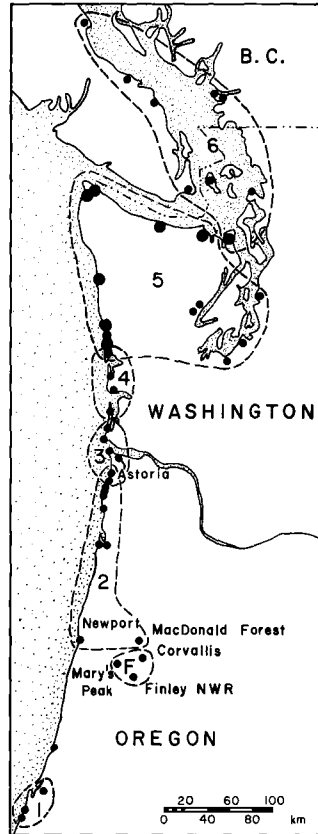


Fig. 1. Map of sampling sites from this study (Finley N.W.R.), Borror 1965 (unpubl. data; MacDonald Forest, Corvallis, Mary's Peak, and Finley N.W.R.), and Baptista's 1970 (Baptista 1977) and 1977 (large dots; unpubl. data) surveys. Sites with birds singing the same dialect are enclosed with dashed lines. Dialects 1, 2, and Finley (F) are southern-theme dialects and 3-6 are northern-theme dialects.

the breeding ground. Baptista recognized three criteria that must be met: (1) sampling of inland populations, (2) demonstration of the temporal stability of a dialect, and (3) filling the gaps in his 1970 sample array (Baptista 1977: Fig 1).

These criteria have been partially met since 1970. In 1977 Baptista and Dennis Martin (unpubl. data) filled a large gap in Baptista's survey by recording songs from birds at eight sites on the Olympic Peninsula, Washington (Fig. 1). I present songs that I recorded in 1977 and 1978 from *pugetensis* breeding in the inland Willamette Valley, Oregon. To assess temporal constancy of dialects, I compare songs recorded in 1977 with songs recorded in 1978, and I compare these to songs recorded in the same area in 1965 (Donald J. Borror unpubl. data). During spring 1978, I recorded songs of *pugetensis* migrating through my study site. To examine the migration pattern of *pugetensis*, I match these songs to songs recorded on the breeding grounds (Baptista 1977, unpubl. data; this study). This approach to the study of migration patterns makes the assumption that a bird's dialect is a marker of its breeding ground. The related assumption, that the dialect is a marker of a bird's natal locality, is a critical component of the hypothesis that song dialects are products or even

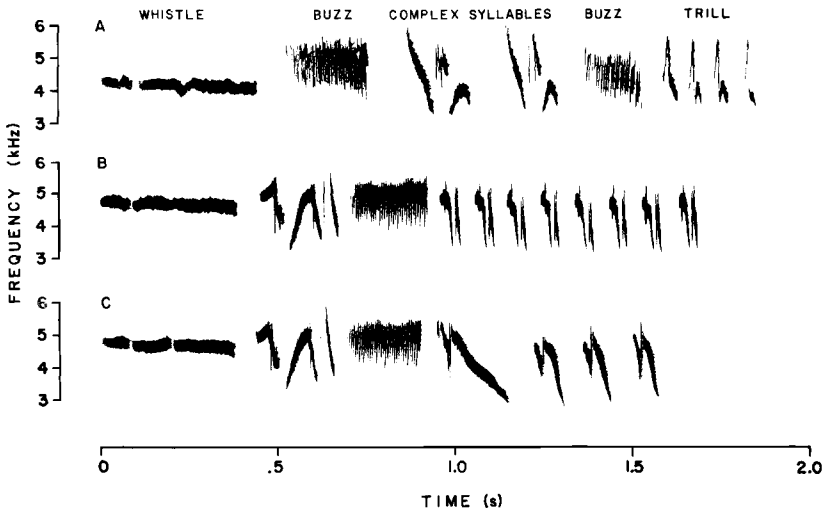


Fig. 2. Sonograms of typical northern (A) and southern (B and C) themes, with song component terminology (after Baptista 1977). Songs B and C were sung by the same bird in 1978 on Bald Top; song B belongs to the Finley dialect and C to Baptista's dialect 2.

producers of a "viscous" population structure (Baker 1975, Baker and Mewaldt 1978; Baptista 1975, 1977). I will evaluate this assumption critically.

#### METHODS

Songs were recorded on and around Finley National Wildlife Refuge, Oregon, which is 65 km east-southeast of Newport, Oregon, one of Baptista's sampling sites (Fig. 1). From 7 June to 15 July 1977, songs of six breeding birds were recorded repeatedly on Bald Top Hill, and single recordings were obtained of two other birds on the hill. In 1978 songs of breeding birds were recorded from 7 April to 14 July, and recordings of migrating birds were made on 16 and 19 April. Of the breeding birds, six were recorded on Bald Top several times over the period, and single samples were obtained from eight birds on Mill Hill (4 km southwest of Bald Top) on 12 April. All songs were recorded with a Sony TC-55 cassette tape recorder and Gibson P-150 parabolic microphone. Songs were audiospectrographed on a Kay 6061A Sonagraph, using the wide band setting, for visual analysis and comparison with sonograms of Baptista (1977, unpubl. data) and Borror (unpubl. data).

Trill types or dialects and complex syllables identified by Baptista are here referred to using his designation—a cardinal number and, in some cases, lower or upper case letter, respectively. Complex syllables identified in this study are designated by a capital letter and, in some cases, subscripted cardinal number.

#### RESULTS

*Breeding birds.*—All the birds breeding at Finley sang the southern theme, but the trills were very different from those of Baptista's dialects 1 and 2 on the Oregon coast (compare Fig. 2B to Baptista 1977: Fig. 5), thus defining a third dialect. During April and May 1978, one individual on Bald Top sang two songs that were identical except in their trills. One was the Finley dialect trill (Fig. 2B), while the other (Fig. 2C) was nearly identical to a variant of dialect 2 that Baptista recorded at Newport, Oregon (1977: Fig. 7, V2). Baptista found five birds that were similarly bilingual. Except for this bird, I could not distinguish any change in the trill morphology of Bald Top songs between 1977 and 1978 beyond what I perceived to be the normal within-year, between-individual variation (Fig. 3). Nor could I distin-

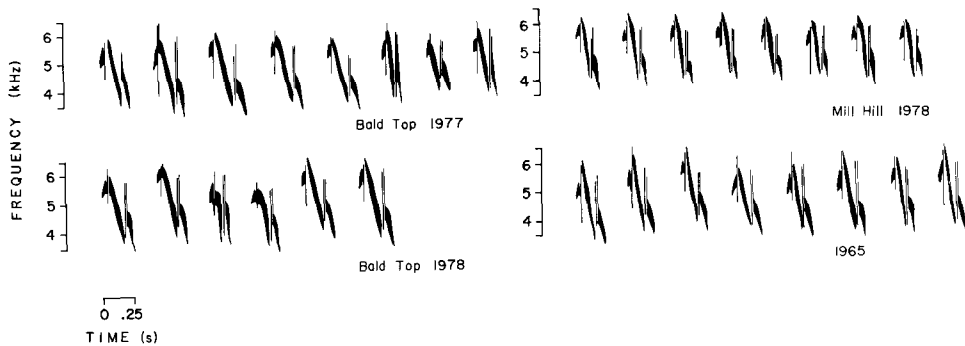


Fig. 3. First syllables of trills from songs of each of the breeding birds recorded in this study and by Borror in 1965 (unpubl. data).

guish any differences between the trills of the Bald Top birds and those of the Mill Hill birds (Fig. 3), which is not surprising given the large geographic extent of the dialects described by Baptista (Fig. 1).

In 1965 Borror (unpubl. data) recorded songs of five birds at Finley, one in Corvallis (20 km north of Finley) and four on Mary's Peak (25 km northwest of Finley), all of which sang the Finley dialect. The trills of these songs were, on the whole, morphologically indistinguishable from those I recorded 12–13 yr later (Fig. 3). Songs of four birds recorded by Borror in or near McDonald Forest (10 km northwest of Corvallis) had trills that were the same as those of dialect 2 (Baptista 1977: Fig. 5, 2d), which 10 of 12 birds at Newport sang.

I identified four major complex syllable types among the Finley birds recorded in this study (Fig. 4); their frequency of use for the different sites and years is given in Table 1. Although dialects 1 and 2 did not share complex syllables (Baptista 1977: Table 4), all the complex syllables used by the Finley birds that I recorded in this study had obvious, although not always identical, counterparts in dialects 1 or 2.

The birds recorded by Borror at Finley used complex syllables  $A_1$ ,  $C_1$ , a variant of  $C_1$ , and a variant of  $B_2$ . Two of the Mary's Peak birds used the  $C_1$  variant, one used the  $B_2$  variant, and the fourth used Baptista's type 14; the Corvallis bird used  $B_1$ . Of the McDonald Forest birds, one used a slight variant of complex syllable  $B_1$ , and the other three used  $B_2$ . With the exception of 3 birds, 2 in this study and 1 from Borror's sample, all birds sang one complex syllable type. The three exceptions each sang two songs differing only in the complex syllable type used.

*Migrating birds.*—On 16 April 1978 near Finley N.W.R. headquarters (1 km southeast of Bald Top), I recorded the songs of approximately 16 migrating *pugetensis* from a mixed-species sparrow flock. On 19 April 1978 I recorded the songs of three birds in a *Zonotrichia* flock that moved about through the territories of the *pugetensis* breeding on Bald Top. The trills and complex syllables from songs of these migrants in most cases could easily be matched with those from Baptista's (1977) study (Table 2).

One song type sung by two birds was unusual in two respects. First, it was a hybrid theme in that the trill identified it as coming from dialect 1 (a southern-theme dialect found at Bandon Beach, Oregon, Baptista 1977: Figs. 1 and 5), but there were two complex syllables (a northern-theme characteristic), and they did not match any known complex syllables. Second, it had a pair of whistles at the beginning,

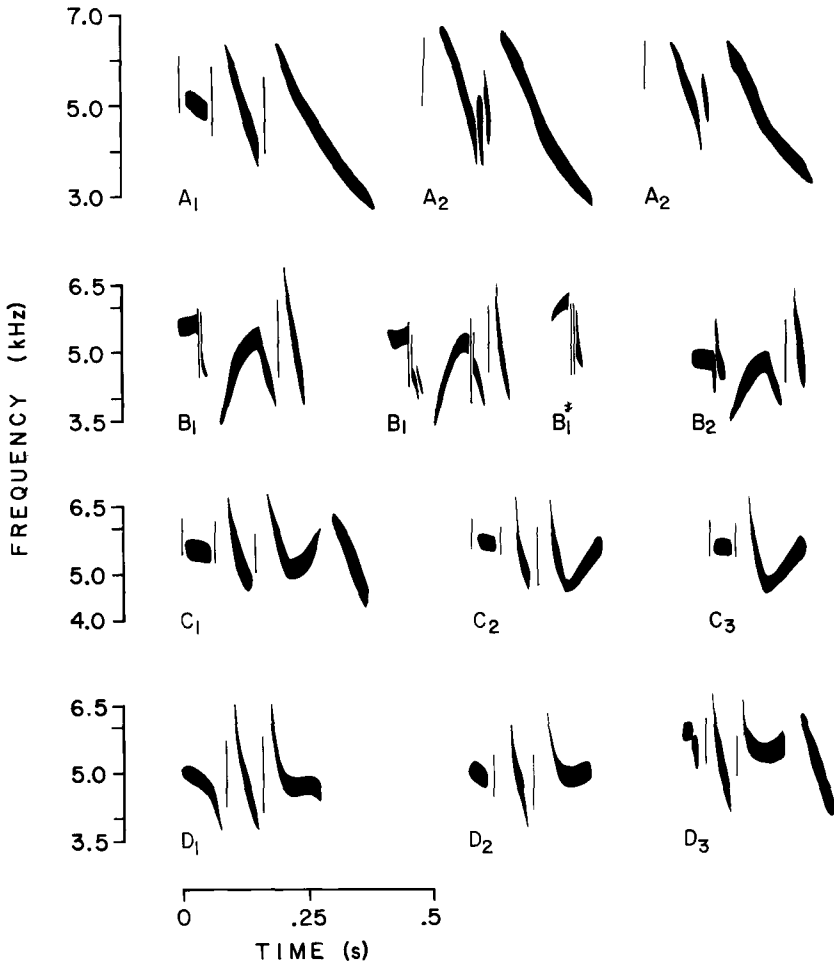


Fig. 4. Complex syllables from breeding birds recorded in this study. Several examples of each type are shown to illustrate the range of individual variation. ‡The latter part of this complex syllable is not shown, as it was the same as that in the first example of B<sub>1</sub>.

the second of which was sung at a higher frequency than the first by one individual and at a lower frequency than the first by the other individual. In both cases the second whistle had a pronounced downward inflection at the beginning. If the second whistle had been replaced by a buzz, the song would have had northern-theme sequencing. Songs with paired whistles have been found in *Z. l. nuttalli* (Baker 1975, Baptista 1975), and Baptista found one *pugetensis* at Astoria, Oregon that sang a remarkably similar song. This bird had a dialect 3 trill as would be expected of a bird breeding at Astoria, but it had a pair of the same unreported complex syllables, and the second trill began with a downward inflection and was lower pitched than the first (Baptista pers. comm.). An unusual northern-theme song had a whistle-buzz, a component found in *nuttalli* (Baptista 1975) but previously unrecorded in *pugetensis* (Baptista 1977).

TABLE 1. The number of songs with a given complex syllable by year and site.

| Location                   | Year  | Complex syllables |   |   |   |
|----------------------------|-------|-------------------|---|---|---|
|                            |       | A                 | B | C | D |
| Bald Top <sup>a</sup>      | 1977  | 4                 | 3 | 1 | 1 |
| Bald Top <sup>a</sup>      | 1978  | 2                 | 4 | 0 | 0 |
| Mill Hill <sup>a</sup>     | 1978  | 4                 | 1 | 3 | 1 |
| Finley N.W.R. <sup>b</sup> | 1965  | 1                 | 1 | 3 | 0 |
|                            | Total | 11                | 9 | 7 | 2 |

<sup>a</sup> This study.  
<sup>b</sup> Berror (unpubl. data).

DISCUSSION

*Sampling gaps.*—The fact that Baptista’s study detected neither the extension of dialect 2 into the Willamette Valley nor the Finley dialect demonstrates the need to sample the songs of *pugetensis* more extensively as a prerequisite to delineating its migration pattern. The fact that the only migrating bird that sang a dialect not detected by Baptista sang the Finley dialect, however, suggests that our knowledge of *pugetensis* dialects is nearly complete. The large geographic extent of the dialects (along as much as 160 km of coastline, Fig. 1) limits the precision with which we can identify a migrant’s breeding ground. That some trill and complex syllable types are somewhat population specific suggests that a greater sampling effort may produce a finer resolution. The current degree of resolution is sufficient, however, to demonstrate whether or not *pugetensis* has a “leapfrog” (Welty 1975: 472) migration pattern (Baptista pers. comm.). Even so, more sampling is needed to determine more precisely the latitudinal extent of the dialects, especially on the Oregon coast, and to establish their longitudinal extent.

*Temporal constancy of dialects.*—An important prerequisite to using dialects in migration studies is a knowledge of the temporal stability of the dialects (Baptista 1977). The results of this study suggest that if there are year-to-year changes, they are not large enough to be detected in a small population over two breeding seasons.

TABLE 2. The number of *pugetensis* migrating through Finley N.W.R. that sang songs that could be matched to those of breeding *pugetensis*.

| Theme:            | Southern |    |        |                    | Northern |                |                       |                | Hybrid               |                |
|-------------------|----------|----|--------|--------------------|----------|----------------|-----------------------|----------------|----------------------|----------------|
|                   | 2        |    | Finley | 5                  | 6        | ? <sup>b</sup> | 3 or 4 <sup>b,c</sup> | ? <sup>b</sup> |                      |                |
| Complex syllable: | 12       | 13 | 14     | 12/14 <sup>a</sup> | 2        | 4              | 4                     | 1              | 10/11/4 <sup>d</sup> | ? <sup>d</sup> |
| Flock             |          |    |        |                    |          |                |                       |                |                      |                |
| Headquarters      | 1        | 1  | 1      | 1                  | 4        | 2              |                       |                | 1                    | 2              |
| Bald top          |          | 1  |        |                    |          |                | 1                     | 1              |                      |                |
| Total             | 1        | 2  | 1      | 1                  | 4        | 2              | 1                     | 1              | 1                    | 2              |

<sup>a</sup> Included notes from complex syllables 12 and 14.  
<sup>b</sup> Not sung in the songs recorded from these individuals.  
<sup>c</sup> The possible trill types given the complex syllable used.  
<sup>d</sup> See text.

Further, the birds at Finley sang the same dialect in 1977 and 1978 that they sang in 1965, with no detectable differences in the trill structure. Similarly, Orejuela and Morton (1975) and Baptista and King (1980) found year-to-year dialect constancy in the migratory Mountain White-crowned Sparrow (*Z. l. oriantha*); Baptista and King (1980) found no songs at Tioga Pass and Mount Lassen not reported by Orejuela and Morton (1975), and Baptista (1975) found that birds in two populations sampled by Marler and Tamura (1962) in 1959–1960 sang the same dialects in 1968–1971.

*Migration pattern.*—The most striking feature of the flocks of migrating *pugetensis* is the co-occurrence of birds of several dialects, from Finley to northern Washington. This lends support to the hypothesis of West et al. (1968) that flocks of migrating birds are not organized units, but rather collections of individuals, each with its own schedule and destination. This was also found to be the case in *Z. l. gambelii* by DeWolfe et al. (1973, 1974). In a species that migrates in a “leapfrog” manner, populations breeding at different latitudes winter at different latitudes and migrate on different schedules. Baptista (1974) found *pugetensis* singing dialects of several areas in the Northwest wintering in the same area. In this study I found similar aggregations of migrating *pugetensis*. These data suggest that *pugetensis* does not migrate in a “leapfrog” fashion.

*Dialects and population structure.*—Baptista (1977) suggested that geographic isolation, oral tradition, and the accumulation of small copying errors, improvisations, or “drift” (Lemon 1975) over time may have produced the themes and dialects observed in *pugetensis*. Implicit in his term “oral tradition” are the assumptions that juveniles learn their song from local birds (i.e. they sing their father’s dialect) and that they are philopatric. These behaviors are thought to produce dialects that correspond to discrete, isolated gene pools. This view of the relationship between dialects and population structure is common among those who work with *nuttalli* (Marler and Tamura 1962, Baker 1975, Baptista 1975, Baker and Mewaldt 1978).

The support for several aspects of this view of the relationship between dialect and population structure in White-crowned Sparrows is equivocal. (1) The evidence for genetic differentiation between dialectal populations in *nuttalli* (Baker 1975) is not solid (Payne in press). (2) Baker and Mewaldt (1978) presented compelling evidence that dialect boundaries act as barriers to juvenile dispersal in *nuttalli*, but Petrinovich et al. (1981) question their techniques and present data suggesting that dialect boundaries are not barriers to dispersal. (3) Baker et al. (1980) presented data suggesting that male-male interactions could operate to inhibit male *nuttalli* from establishing territories in a foreign dialect area, but Petrinovich and Patterson (in prep.) obtained contradictory results. (4) Positive assortative mating by song type has been suggested as a possible mechanism maintaining dialects and reducing gene flow (Baker and Mewaldt 1978); however, recent experiments with *nuttalli* (Petrinovich et al. 1981) and *oriantha* (Baptista and Morton 1980) suggest that positive assortative mating is not occurring. (5) It has long been accepted, based on the work of Blanchard (1941), that fledgling *nuttalli* disperse after day 48 (Baptista 1975) and that the sensitive period for song learning lasts from day 10 to 50 (Marler 1970). A careful reading of Blanchard suggests, however, that juveniles disperse at the latest by day 48, and Marler’s experiments showed that song tutoring could have an effect up to day 100. This creates the potential for song learning from foreign birds, a phenomenon known to occur sporadically in *nuttalli* (Baptista 1974, Baptista and Wells 1975). Further, it is possible that, if Marler had used live tutors, he might

have found a longer sensitive period, as it appears that tape recordings may not provide an adequate song learning model (Baptista and Morton 1981).

Even if these objections prove to be unfounded, I still believe that the application of the song dialect/discrete deme view to *pugetensis* may be invalid for the following reasons. (1) It is not likely that the population structure of the migratory *pugetensis* is the same as that of the sedentary *nuttalli*. (2) *Pugetensis* dialect areas are one to two orders of magnitude larger than *nuttalli* dialect areas. (3) There is no evidence that the dialectal populations of *pugetensis* are the products of isolation or colonization events. (4) Most important, although *pugetensis* can easily be separated into discrete dialectal populations on the basis of the trill, there is extensive sharing of complex syllables among dialects within themes, but none between themes (Baptista 1977: Tables 3 and 4). This last point presents a dilemma. If we take a dialectal song population structure as an indication of little genetic interchange between dialectal populations, then does not sharing of complex syllables among dialects indicate extensive gene flow?

There are two possible solutions to this dilemma within the framework of the song dialect/discrete deme paradigm. (1) Complex syllables may be shared, because each isolate or propagule had most of the types found in the parental population, and those types have been maintained in the daughter populations since the isolation or colonization event with very little change (Baptista pers. comm.). I reject this view for three reasons. First, this hypothesis predicts that complex syllables are temporally constant (i.e. they are subject to very little copying error, improvisation, or "drift"); but complex syllables show the greatest inter-individual variability in form of any song component, which suggests the opposite. Second, this hypothesis cannot account for the complete lack of shared complex syllables between themes. And third, it is not likely that a propagule would carry a large proportion of the complex syllable types found in the parental population. (2) Complex sharing may come about through cultural interchange in zones of dialect overlap. There are two problems with this hypothesis. First, as in *nuttalli* (Baker 1975, Baptista 1975, Baker and Mewaldt 1978), a juvenile raised in the overlap zone may learn both dialects and as an adult sing the song appropriate for the area in which it establishes its territory. While this phenomenon would maintain dialects, it would tend to counteract genetic differentiation of dialectal populations. This hypothesis cannot account for complex syllable sharing if juvenile *pugetensis* learn songs as single units; they would have to learn song components independently. Second, this hypothesis again cannot account for the lack of sharing between themes; and there is a large zone of overlap between the themes (Baptista 1977).

I suggest that this dilemma can be resolved by hypothesizing that juvenile *pugetensis* are exposed to and may learn some components of foreign songs during the sensitive period and that only the natal theme constitutes an acceptable song learning model. I suspect that the first phenomenon comes about because fledglings disperse and/or migrate before the end of the sensitive period. If this is true, then it is difficult to believe that dispersing juveniles raised near the theme boundary would not cross over it and thus be exposed to and learn foreign complex syllables. Yet no complex syllables are shared between themes. Thus, a foreign theme may not be an appropriate learning model for *pugetensis* juveniles, much as Harris' Sparrow (*Z. querula*) or Song Sparrow (*Melospiza melodia*) songs are inappropriate models for *nuttalli* juveniles (Marler 1970).

Trills may be learned only from local birds, because the genetic song "template"



(Marler 1970) may be specific enough to exclude foreign dialects as appropriate models. This seems highly unlikely (Marler 1970, Baptista 1974). Alternatively, different song components may have different sensitive periods, with that of the trill terminating before exposure to foreign songs has occurred. The results of one of Marler's (1970) experiments lend some plausibility to this hypothesis. Two *nutalli* caught between 30 and 100 days and tutored with a foreign dialect sang songs similar to those of the controls (birds caught at the same time but not exposed to a foreign dialect) in some components but different in others.

Direct evidence that juvenile *pugetensis* learn at least part of their songs after dispersal is provided by the two hybrid songs of breeding birds reported in this study and the several found by Baptista (1977). In cases where the trill could be identified (Baptista 1977: Fig. 7, H<sub>1</sub>, H<sub>3</sub>, and H<sub>4</sub>), it was always the same as that sung by the local birds, thus supporting the hypothesis that trills are matched to or learned from local birds only. The birds with hybrid songs incorporated song elements from populations both north and south of, but not necessarily adjacent to, their breeding location. This suggests that juveniles may be learning their song during an extensive premigratory dispersal period or on the common wintering ground in central California (Cortopassi and Mewaldt 1965, Baptista 1974). The song(s) with *nutalli*-like paired whistles (Baptista 1977, this study), whistle-buzzes (this study), or buzz-whistles (Baptista 1977) point to the latter possibility.

An alternative hypothesis for the existence of dialects is that birds are capable of matching their song to the local dialect where they settle to breed. There is some evidence that this occurs in White-crowns. Baptista (1975) and Baker (1975) each recorded bilingual birds that eventually dropped the foreign song from their repertoire. Marler and Susan Peters (pers. comm.) have found that Swamp Sparrows (*Melospiza georgiana*) remember and use in subsong a large number of syllables that are never used in their primary songs. Marler suggests that in some species these unused elements may serve as a reserve for the creation of new songs. I suggest that this process may come into play only when birds encounter a novel dialect (i.e. at the time of territory establishment). Thus, adult birds appear to have the same song for life, either because they show a high degree of site fidelity and never encounter a new song environment or because site-specific studies have little chance of detecting an adult's emigration to a new dialect area and its subsequent switch in song. If juveniles are exposed to and memorize foreign songs and match trills but not complex syllables, then the song-matching hypothesis would account for the existence of trill-defined dialects with an extensive sharing of complex syllables between dialects, as seen in *pugetensis*, even in the presence of extensive gene flow.

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