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## CULTURAL AND GENETIC DIFFERENTIATION OF TWO SUBSPECIES OF WHITE-CROWNED SPARROW

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**ABSTRACT.**—Geographic variation in song, a learned characteristic of White-crowned Sparrows (*Zonotrichia leucophrys*), was compared to variation in morphological, physiological, and allozyme traits across an intergrade between two subspecies. Along the north coast of California, the song structure typical of the southern *Z. l. nuttalli* extended throughout the entire intergrade zones of the other characters. Not until reaching the extreme north end of the intergrade with the northern distributed *Z. l. pugetensis* were any *Z. l. pugetensis* song characteristics encountered. It is at the north end of the intergrade that the birds become migratory (Blanchard 1942) and other workers have identified this as the clear demarcation between subspecies. One possible theory is that if the subspecies met in secondary contact near what is now a fairly abrupt transition between migratory and non-migratory behavior, and this contact was established after the last glacial period, then little erosion has occurred in the cultural transmission of song over many generations. Over the same time scale, however, gene flow has occurred at least 100 km to the south and perhaps farther.

Recent studies argue for a causal relationship between cultural evolution and biological evolution in higher vertebrates (Cavalli-Sforza and Feldman 1981, Lumsden and Wilson 1981, Wyles et al. 1983). Culturally transmitted patterns of learned behavior may be the "... driving force for evolution at the organismal level" (Wyles et al. 1983). Learning one particular cultural model (choice), and not others, allows agents of natural selection to act on the consequence of that choice (Cavalli-Sforza and Feldman 1981). That cultural choices may influence the direction and rate of biological evolution in human populations is readily accepted by recent writers (e.g., Cavalli-Sforza 1974, Lumsden and Wilson 1981).

The phenomenon of song learning, which is characteristic of perhaps as many as 4,000 songbird species (Kroodsma and Baylis 1982), is the best-understood culturally transmitted behavior in non-human vertebrates. Extensive data exist on the details of the transmission process ("inheritance," or learning), as well as on its biological consequences (Kroodsma and

Miller 1982). Rarely, however, has the relationship of cultural differences between populations of a bird species and the genetic properties of the populations been described (Nottebohm and Selander 1972; Handford and Nottebohm 1976; Baker 1981, 1982a, b; Baker et al. 1982).

Along the west coast of North America, a southern non-migratory subspecies, Nuttall's White-crowned Sparrow (*Zonotrichia leucophrys nuttalli*) intergrades through a zone of hybridization with a northern migratory subspecies, the Puget Sound White-crowned Sparrow (*Z. l. pugetensis*). The zone of intergradation is attributable to secondary contact between ancestral populations dating to sometime since the late Pleistocene (Rand 1948, Banks 1964, Selander 1965).

In this paper, we compare the cline in morphological and physiological traits between the two subspecies to the cultural patterns of vocal variation. We address the question: Are patterns of song variation concordant with the variation in other phenotypic characters along

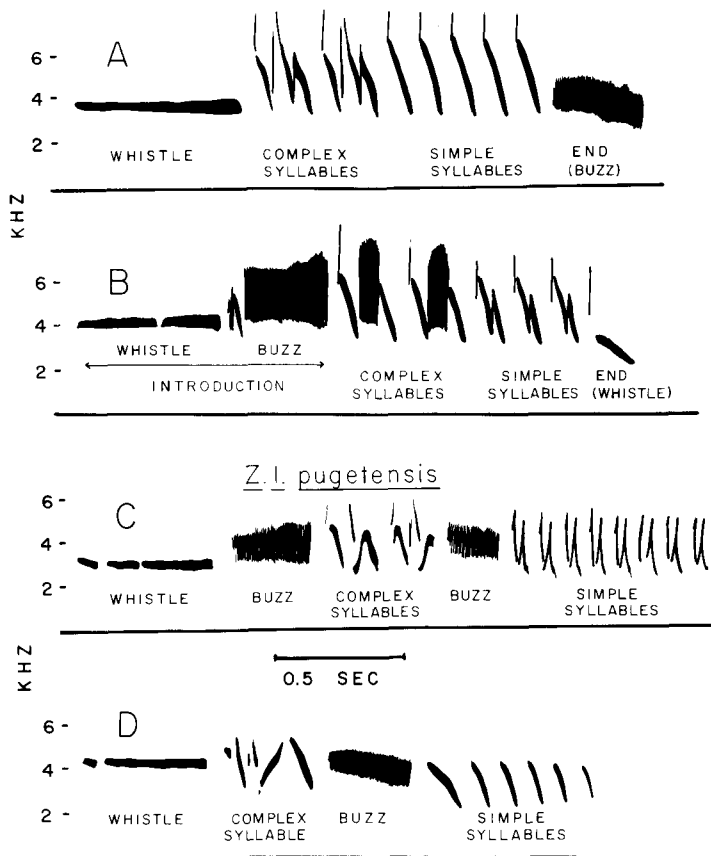


FIGURE 1. Examples of two song dialects of *Z. l. nuttalli* from Point Reyes, California (A and B), and two song "themes" of *Z. l. pugetensis* from Washington (northern theme, C) and Oregon (southern theme, D), with terminology used to describe song patterns. Tracings of spectrograms are from our own recordings of *nuttalli*, and re-drawn from Baptista (1977), for *pugetensis*.

the zone of intergradation? The answer could give us insight into the relationship between biological and cultural evolution.

## MATERIALS AND METHODS

### STUDY SPECIES

*Z. l. nuttalli* and *Z. l. pugetensis* breed in territories of less than a hectare in size, usually as monogamous pairs. Breeding habitat is normally a narrow strip of coastal scrub adjacent to the ocean, but some populations extend a few miles inland, for example into urban areas in the San Francisco Bay region of California.

The southern subspecies, *Z. l. nuttalli*, begins breeding in March and April. Populations of the northern subspecies, *Z. l. pugetensis*, migrate in differing degrees, some populations wintering deep into the range of *Z. l. nuttalli* and migrating into Washington to breed in April (Cortopassi and Mewaldt 1965), whereas others apparently make only short-distance migrations (Blanchard 1942). Reproductive, populational, and behavioral biology were detailed in Blanchard (1941), Mewaldt and King (1977), Baker et al. (1981), Baker (1982a), and Petrinovich and Patterson (1982).

**Song recording.** Songs of 78 territorial males were tape-recorded at six study sites from 3–27 May 1983 using Uher 4200 Stereo IC recorders set at 9.5 cm/s and Uher microphones mounted in 60-cm parabolic reflectors. Our sites corresponded to those used by the authors of published accounts of variation in non-vocal characters. Field tapes were played through a high-pass filter to remove low-frequency background noise and then transformed into audiospectrograms on a Kay Elemetrics 7029A "sonograph" using the wide band (300 Hz) and 80–8,000 Hz frequency range settings.

## RESULTS

### SONG STUDIES

For comparisons discussed later, we provide representative songs (Fig. 1) of two different *Z. l. nuttalli* dialects we recorded at Point Reyes National Seashore (Baker 1975), along with descriptive terminology, and two different *Z. l. pugetensis* "themes" recorded in Oregon and Washington by Baptista (1977). Documentation of the song variations in *Z. l. nuttalli* is in Baker (1975) and Baptista (1975), and that in *Z. l. pugetensis* is in Baptista (1977) and

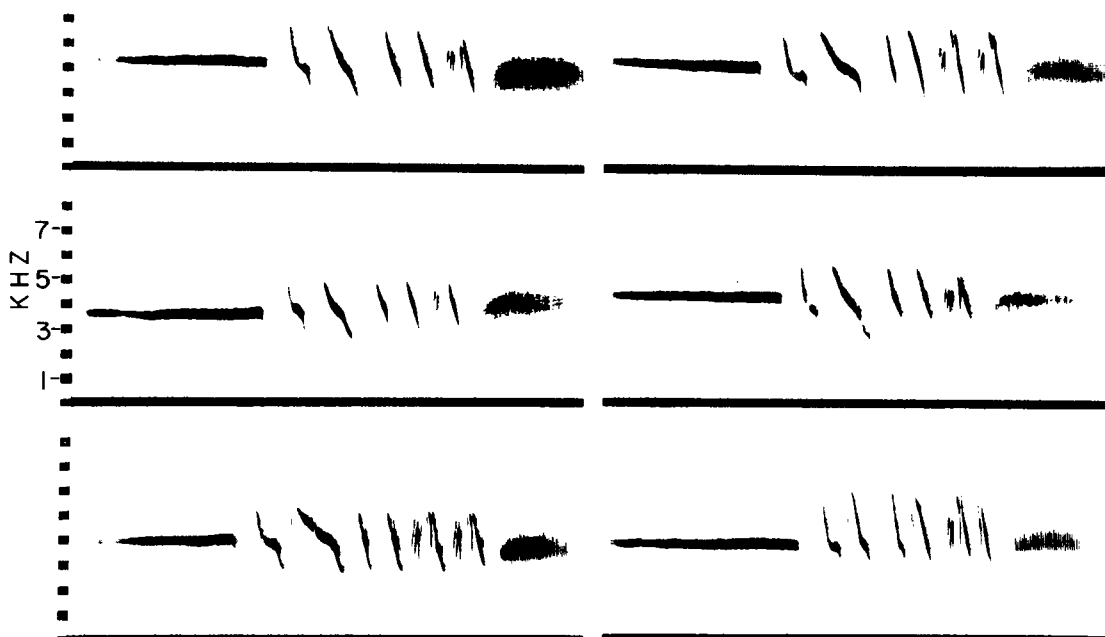


FIGURE 2. Sound spectrograms of six different males constituting one song group at Westport, California. Songs are about 2 s long.

Heinemann (1981). Point Reyes *nutalli* (Fig. 1 A, B) usually have four major components in the song: 1) an introduction, which may consist of a single phrase (whistle) or two phrases, typically a whistle-whistle (W-W) or whistle-buzz (W-B), 2) complex syllables (CS) that are usually paired, 3) simple syllables (SS) that are usually repeated 1–10 times, and 4) an ending note that can be either a descending whistle (W) or a broad-band buzz (B). Complex syllables are often but not always structurally more complex than simple syllables.

The northern “theme” of *Z. l. pugetensis*, occurring as a series of dialects from approximately the Washington–Oregon border northward into British Columbia, is typically a two-phrase introduction (W-B), followed by paired complex syllables, a single buzz, and finally a series of simple syllables (Fig. 1C). The southern “theme” of *pugetensis*, occurring as a series of dialects along most of the Oregon coast, is typically a single phrase introduction, usually a whistle, a complex syllable followed by a buzzy note, and a series of simple syllables (Fig. 1D).

Renditions of the song of a single male are highly stereotyped and a single spectrogram is commonly used to represent the song of an individual (Marler and Tamura 1962, Baptista 1975, example in Baker 1974). Songs of all males recorded in a particular study area can usually be reduced to one or more song groups on the basis of similarity among individuals in a subset of the total sample. To illustrate variation among males in a song group, spec-

trograms of the six males that we classified as having the same song type at our Westport study site are shown in Figure 2. We regard this as a low degree of variation which should be assumed whenever we use a single spectrogram to represent a group of males.

#### GEOGRAPHIC VARIATION SOUTH TO NORTH

We found little variation among individuals at Bodega Bay ( $n = 6$ ) and Fort Ross ( $n = 11$ , Fig. 3, locations in Fig. 5). The Bodega Bay dialect was typical of *Z. l. nutalli*, having a whistle portion, a buzz, paired complex syllables, repeated simple syllables and a buzzy ending (W-B-CS-SS-B). Fort Ross males were similar to those at Bodega Bay in producing a *nutalli* song type but without differentiation of complex and simple syllables. In view of the relatively simple structure and repetition of these trill syllables, we regard them as simple syllables; therefore, the complex syllable structure is absent at Fort Ross. Songs at Albion were more varied than at Bodega Bay and Fort Ross (Fig. 3). All songs at Albion had a typical *nutalli* format: a whistle introduction, paired complex syllables, simple syllables and a buzzy ending. A single whistle introduction was typical of several dialects at Point Reyes (Baker and Thompson, unpubl.) and in the San Francisco Bay region (Baptista 1975). We identified three song groups in the Albion sample, (Albion-1,  $n = 3$ ; Albion-2,  $n = 2$ ; Albion-3,  $n = 8$ ) differing in the morphology of the complex and simple syllables (Fig. 3). One variant (Fig. 3, Albion-2) had two pairs of differing complex

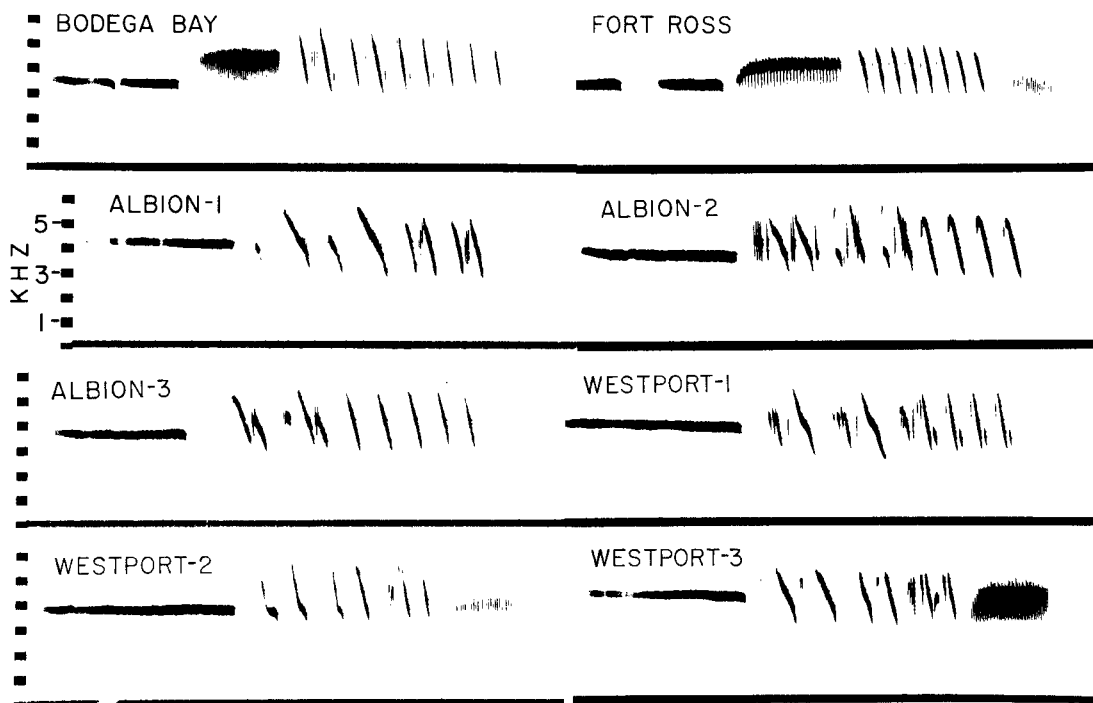


FIGURE 3. Sound spectrograms of song groups found at four study sites along coastal California. Songs are about 2 s long.

syllables, a condition we have infrequently encountered at Point Reyes. All Albion birds had low-amplitude buzzy endings, as is apparent from the faint tracings of these notes in the audiospectrograms. This was a property of the population, not an artifact of recording or reproduction.

At Westport, we again found the typical *Z. l. nuttalli* song pattern. Like Albion birds, those at Westport had a single whistle introduction. There were three different types of complex syllables and two types of simple syllables (Fig. 3: Westport-1,  $n = 4$ ; Westport-2,  $n = 6$ ; Westport-3,  $n = 6$ ). All songs ended with a buzz.

At Cape Mendocino (Fig. 4: Cape M-1,  $n = 4$ ; Cape M-2,  $n = 9$ ; Cape M-3,  $n = 4$ ; locations in Fig. 5) we encountered for the first time in our transect a detectable departure from typical *Z. l. nuttalli* song patterns in the direction of *Z. l. pugetensis*. Even before recording, these songs sounded somewhat odd compared to what we had heard extensively at Point Reyes. In contrast, at the more southern four recording sites the songs sounded typical of those we had heard at Point Reyes. Cape Mendocino songs had a two-phrase (W-B) introduction, which was not unusual, but identifying a complex syllable was problematical. Most of the birds had a single downsweeping (decreasing FM sweep) phrase following the buzzy note of the introduction, but some birds

had a pair of such FM sweeps. All birds had a note composed of a buzzy element with an FM sweep attached, which we call a "flag." The flag was followed by some repeated simple syllables. A few birds had a distinct ending note, a slowly descending FM sweep (Fig. 4, Cape M-3). The general sequence of syllable types in these typical Cape Mendocino songs was reminiscent of patterns seen in some *pugetensis*. In the northern theme of *pugetensis* (Baptista 1977: Fig. 3, bird 6b), the sequence is W-B-CS-B-SS. Our Cape Mendocino birds had a similar pattern W-B-CS-B(flag)-SS. That the Cape Mendocino song patterns were not strongly divergent from those of typical *nuttalli* is supported by the observation that the general pattern of syllables can also be found in pure *nuttalli* populations far to the south (Baptista and King 1980).

At Clam Beach, our most northern study location, we found five different types of songs (Fig. 4: Clam B-1,  $n = 1$ ; Clam B-2,  $n = 5$ ; Clam B-3,  $n = 7$ ; Clam B-4,  $n = 1$ ; Clam B-5,  $n = 1$ ). Most birds in the sample had a whistle-buzz introduction followed by complex syllables that were either paired or unpaired, and a loud buzzy ending. We identified two salient aspects of the Clam Beach songs that represent a departure from the typical *Z. l. nuttalli* even more significantly than we found at Cape Mendocino. Foremost was the occurrence of a territorial male at Clam Beach that sang a pure

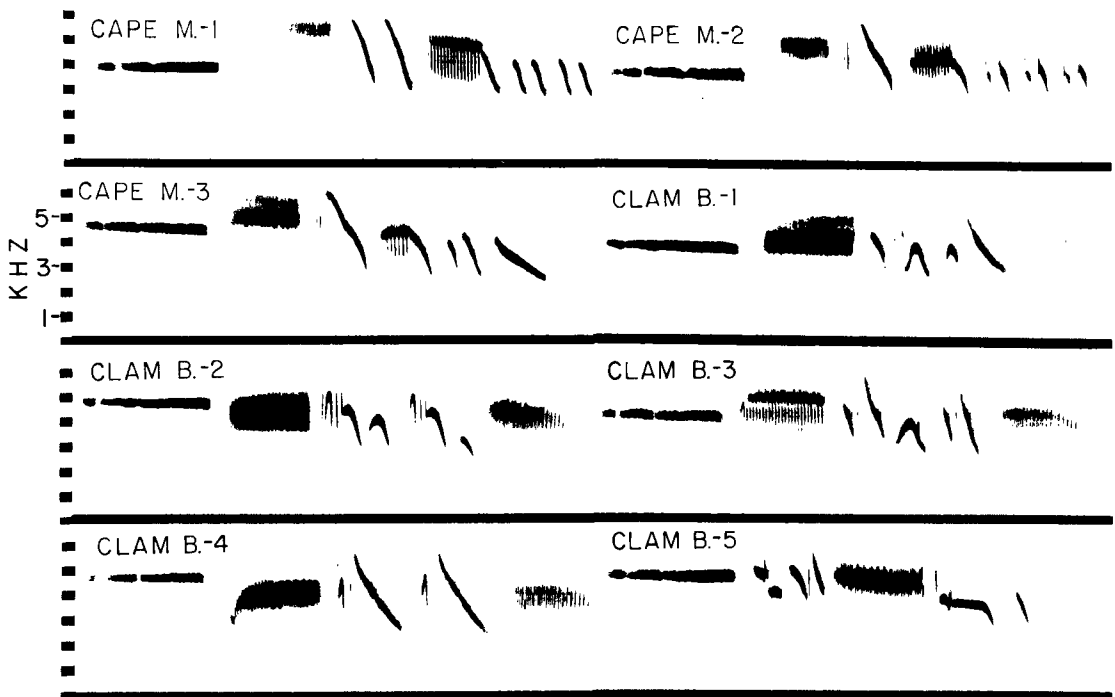


FIGURE 4. Sound spectrograms of song groups found at two study sites along coastal California. Songs are about 2 s long.

*pugetensis* song (compare Fig. 4, Clam B-5, with Baptista 1977: Fig. 5, bird 2a). Second, the general shapes of some of the complex syllables at Clam Beach were similar to those encountered in some *pugetensis* songs (e.g., Baptista 1977: Figs. 4 and 6). On the whole, however, songs at Clam Beach resembled *nuttalli* more than *pugetensis*.

## DISCUSSION

### PREVIOUS STUDIES OF THE INTERGRADE

Five major studies have contributed to our understanding of the zone of character intergradation between the northern subspecies, *Z. l. pugetensis*, and the southern *Z. l. nuttalli* (Grinnell 1928, Blanchard 1942, Banks 1964, Mewaldt et al. 1968, Corbin 1981). On the basis of plumage characters, the two taxa are only weakly differentiated (Grinnell 1928, Banks 1964). However, variation in several other traits across the inclusive range of the two subspecies, from Santa Barbara, California, to Vancouver Island, British Columbia, shows clear evidence of a zone of intergradation.

Grinnell (1928) was not specific on the location of the intergrade, saying only that it was "somewhere" along the coast of Mendocino County. This description refers to a strip of coast running from just south of Manchester to just north of Rockport (Fig. 5). Studying

body weight, tarsal, toe, and bill length, Banks (1964:39) was able to separate the subspecies: "... the major dividing point is in the vicinity of Cape Mendocino, in northern California . . .," the intergrade zone running from about Fort Bragg north to about Eureka (Fig. 5). Banks identified a sharp change in body weight in the Cape Mendocino area that justified the naming of populations to the north as *Z. l. pugetensis* and those to the south as *Z. l. nuttalli*. Corbin (1981:677) re-evaluated Banks' (1964) data on body weight and argued that they indicate the zone of intergradation "... clearly extends at least as far south as his Sonoma County sample and perhaps should include the Marin County samples as well." This would extend Banks' intergrade 40–80 km south of Fort Bragg.

Analyzing a suite of physiological traits associated with migration and breeding (gonadal cycle, molt cycle, locomotor activity, weight), Mewaldt et al. (1968) found that the Westport and Capetown (the latter is equivalent to our Cape Mendocino site) populations had "clearly intermediate" prenuptial molt patterns. On the basis of mean intensity of molt (Mewaldt et al. 1968: Fig. 4), birds at the Westport site exhibited *Z. l. pugetensis* characteristics, Capetown more strongly so, and Clam Beach seemed indistinguishable from more northern *pugetensis*. Analysis of maximum molt intensity (Mewaldt et al. 1968: Fig. 5), showed that

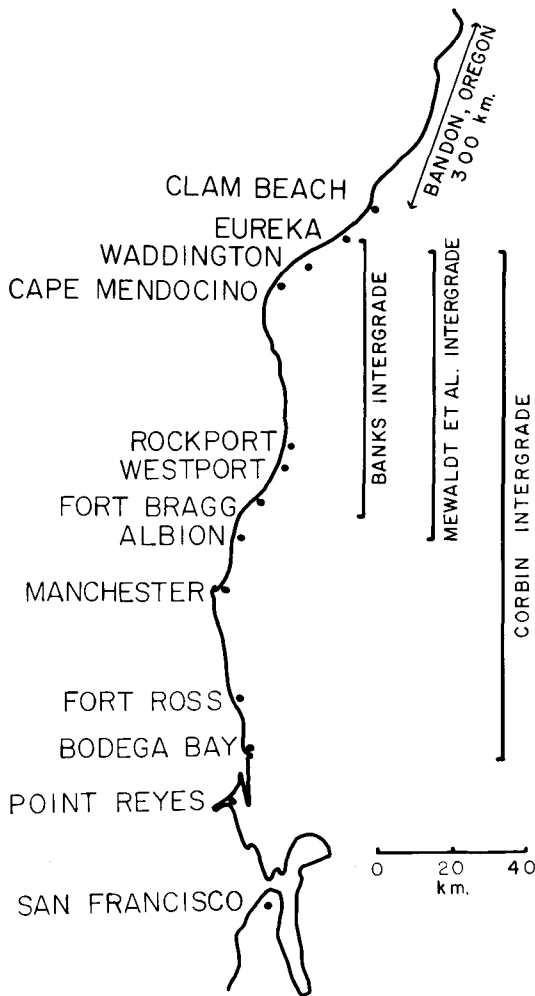


FIGURE 5. Map of sample sites and locations referred to by several authors whose data are discussed in the text. Songs were recorded at Bodega Bay, Fort Ross, Albion, Westport, Cape Mendocino, and Clam Beach. Intergrade zones described in three published studies are indicated.

birds at Point Reyes, Fort Ross, Albion, and Westport all had some evidence of *pugetensis* patterns, Capetown again was more strongly so, and Clam Beach seemed like pure *pugetensis*. Considering molt of central rectrices and secondary remiges #7–9, Mewaldt et al. (1968: Fig. 6) found some evidence of *pugetensis* patterns in the Westport sample, with birds at Capetown and Clam Beach like *pugetensis*. They also identified a sharp division of body weight between Capetown and Clam Beach. Altogether, analysis of the several traits led to the conclusion that the zone of transition covered the area from about Albion to just north of Capetown (Fig. 5), with the "... area of steepest variation and reduced gene flow ... between Capetown and Westport ..." (Mewaldt et al. 1968:29). The traits studied by Mewaldt et al. (1968) were expressed in captivity at a common site (San Jose, California).

In concert with other observations, this led them to conclude that the differences in physiological traits between the study populations reflected genetic differences.

Blanchard (1942) found that the northern limit of the winter range of the White-crowned Sparrow was at Myrtle Point, Oregon, a site just inland from the coastal town of Bandon. She did not determine if any of the individuals at Myrtle Point were year-round residents, only that some birds were found there year-round. The critical data on marked individuals near Waddington, California, 28 km south of Eureka, showed that some birds color-banded in a flock about 15 March bred locally a month later. Others in the local flocks showed all degrees of migratory "instinct," using gonadal physiology and molt as indices, and were from various breeding locations as indicated by song dialects. Blanchard felt certain that these birds had spent the winter locally.

A strict interpretation of Blanchard's data (1942) indicates that birds breeding north of Waddington were migrants and those breeding south of Waddington were non-migrants. The sparrows which bred at Waddington were transsitional individuals that showed only faint evidence of migratory behavior. Thus, Blanchard did not document an intergrade zone of migratory behavior, but rather identified a population in the vicinity of Eureka representing a relatively sharp break between populations that were resident year-round and ones that migrated to more northern breeding areas. Given that at all times of year some White-crowned Sparrows are present farther north at Myrtle Point, it is entirely possible that some of them are permanent residents, but Blanchard did not examine this possibility.

We emphasize, however, that genes which control migratory physiology occur in birds as far south as Albion, California (Mewaldt et al. 1968), but these individuals apparently do not migrate northward to breed. Indeed, Blanchard was clear about her findings in the Eureka area. Referring to the geological past and being suitably cautious, she said "... the front of permanent residence may have crept northward and is now (1942) passing Eureka ..." (Blanchard 1942:62).

More recently, Corbin (1981) analyzed electrophoretic alleles at polymorphic allozyme loci over a major portion of the range of the two subspecies. He suggested that the intergrade zone be extended at least to Manchester, and that his data indicated a major shift in electrophoretic phenotype from *Z. l. pugetensis* to *Z. l. nuttalli* near Albion and Manchester. Moreover, Corbin felt that his data taken together with those of Mewaldt et al. (1968) "...

unequivocally indicate that breeding individuals from as far south along the coast as Albion or Manchester are more similar to *pugetensis* than to *nuttalli*." (Corbin 1981:678). Arguing that heterozygosity should be greatest near the center of the intergrade, he fixed the center of intergradation between Albion and Manchester, with the intergrade running from about Cape Mendocino to Bodega Bay (Fig. 5).

#### INTERPRETATION OF SONG DATA

Our data on variation in song structure over the zone of character intergradation described by previous studies provide an interesting comparison. The morphological, physiological, and allozyme characters are almost certainly attributable to genetic variation. On the other hand, the song differences we describe are learned and are therefore cultural traits. It is conceivable that "innate template" (Marler 1970) differences between *Z. l. nuttalli* and *Z. l. pugetensis* make it easier for each subspecies to learn its own song in comparison to learning that of the other subspecies, but the necessary experiments have not been done. In the only studies available, Baptista (*in* Petrinovich et al. 1981) was able to get a juvenile *nuttalli* to learn a "perfect copy" of the song of an adult *pugetensis* cage mate, and "misimprinted" males of *nuttalli* singing *pugetensis* songs are known from the San Francisco Bay region (Baptista 1974).

Starting in the south, we find *Z. l. nuttalli* song types across virtually the entire intergrade zones of Corbin (allozymes), Grinnell and Banks (weight, morphology), and Mewaldt et al. (migratory physiology and weight). Not until reaching the northern end of the intergrade at Cape Mendocino do we find any indication of *pugetensis* song characteristics. At that site, the evidence is only weakly suggestive. At Clam Beach, we believe songs clearly have *pugetensis* influence; this view is supported by the occurrence of a male with a perfect *pugetensis* song and by the general shapes of the complex syllables in several other birds. Interestingly enough, Clam Beach is near the area that Blanchard (1942) showed to be the northern end of permanent residence of these birds.

Therefore, variation in vocal patterns along the California coast does not predict the genetic variation along the intergrade zone. There is some correspondence, however, between song divergence and the sharply defined northern end of the intergrade, which some authors fix as the clear separation between *Z. l. pugetensis* and *Z. l. nuttalli*. As Corbin (1981) pointed out, this relegates the birds in the intergrade area itself to *nuttalli*. It is not the taxonomic problem that we address, however, but

the interesting lack of concordance between genetic intergradation and song variation between Bodega Bay and Cape Mendocino.

One possible interpretation of the data is that populations ancestral to *Z. l. pugetensis* and *Z. l. nuttalli* met in the area just north of Cape Mendocino/Clam Beach and this is reflected in the sharp song transition as well as the steep gradient in several other characters, including migratory behavior. This view also fits with the condition of the environment in the region of Cape Mendocino noted by Mewaldt et al. (1968). They pointed out that the breeding habitat for White-crowned Sparrows is less suitable there than elsewhere along the coast, consisting of considerable forest and grassland. Hence, they reasoned that in the past the area could have been even more heavily forested, considerably reducing or even precluding gene flow between the two subspecies. Under this northern contact theory, song differences have been maintained over the generations by cultural transmission, and genes of *pugetensis* have gradually migrated southward to produce the observed intergradation in genetic characters.

An alternative southern contact theory is that the ancestral populations met in secondary contact farther south and *Z. l. nuttalli* genes have gradually migrated northward along with the typical *nuttalli* song pattern. Given the intergrade, we would need to make an assumption concerning the symmetry of introgression following secondary contact. Of course, we cannot safely assume that this is a situation of secondary contact, not primary intergradation (Endler 1977), but since previous authors have assumed secondary contact (following Rand 1948), we will do likewise. If the contact was secondary, and gene flow has been symmetrical, the ancestral contact point should be somewhere south of Cape Mendocino, perhaps as far south as the Albion/Manchester area, if we accept Corbin's (1981) interpretations. If this line of speculation is accurate, then the song has followed the introgression of *nuttalli* genes northward, swamping out any trace of *pugetensis* song all the way to the north edge of the zone of intergradation. As far as we can determine, neither the current understanding of song learning nor existing theory of clinal variation helps us decide between these alternatives, but it may be possible to obtain an answer by following the process through time. This may be feasible because parallel situations seem to occur at the level of regional dialect populations.

The symmetry and place of secondary contact aside, we may tentatively accept the hypothesis of secondary contact and calculate the

time since contact occurred, using a theoretical model developed by Endler (1977). This model assumes that the existing intergrade between the subspecies is at equilibrium between gene flow and selection. The calculation uses the width of the intergrade between the points at which the gene frequency in one subspecies is 0.2 and in the other is 0.8, assuming a single-locus genetic model. If we assume that the observed 100-km width (Banks 1964, Mewaldt et al. 1968) represents gene frequencies of 0.0 and 1.0 at each end, and that the intergrade is smooth, then the width to use in the model is 60 km. Also required in the calculation is a gene flow parameter, which we estimate as the mean dispersal distance from hatching to breeding sites, or 584 m (Baker and Mewaldt 1978). Using these values in Endler's equation (1977:153) we calculate

$$T = (0.64)(60,000/584)^2 \\ = 6,755 \text{ generations (12,160 years)}$$

given the generation time of *Z. l. nuttalli* (Baker 1981). Therefore, the contact between these two subspecies appears to qualify as a late Pleistocene event.

If selective regimes differ from one population to another along the coast, then dialect markers in song could act as population identifiers and be used in mate choice, for example, to maintain adaptation to local conditions. Where different song traditions come close together, as at dialect borders, then learning one particular cultural model and not another could have selective consequences for the individuals involved. Without immense sample sizes, such selective consequences could be difficult to identify at the level of local dialect populations, but perhaps would be more obvious at subspecies contacts, and be most apparent at the level of species differences.

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