SONG "DIALECTS" IN THREE POPULATIONS OF WHITE-CROWNED SPARROWS

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The phenomenon of "dialect" variation in bird song, appearing as a consistent difference in the predominant song type between one population and another of the same species, has a special interest for biologists, serving as a focus for attention in discussion of such diverse topics as speciation (for example, Huxley, 1942; Mayr, 1942), learning (Thorpe, 1954, 1958) and the mechanisms of social communication (Marler, 1959). The White-crowned Sparrow (*Zonotrichia leucophrys*) affords one of the best known cases of such "dialect" variation among North American birds, and it has been commented upon by many who have observed this species (Blanchard, 1941; Peterson, 1941). Before the ontogenetic basis of such local song variation can be assessed and before its evolutionary significance can be satisfactorily determined, careful descriptions of the nature and extent of the variation are required. This paper seeks to provide some of this necessary information by describing song variation in the individual and in a population, both at one time and from year to year, and also by comparing songs in three populations, two adjacent and one distant.

METHODS

The analysis is entirely based on tape recordings, made either with a Magnemite 610-E tape recorder and an Altec 633-A microphone mounted in a parabolic reflector at a tape speed of 15 inches per second, or with a Midgetape 500 tape recorder and an Electrovoice 644 uni-directional microphone at a tape speed of 3¾ inches per second. The response of our Midgetape falls off rapidly with frequencies above 7.5 kc., but below this it is essentially flat. Since we did not study frequencies above this limit, the recordings have been merged with those made on the Magnemite for the purposes of this analysis. The recordings were played back on a Viking 75 deck (15 feet per second) and on a Wollensack T1500 tape recorder (3¾ feet per second) and analyzed on a Kay Electric Company Sonagraph using the "high-shape" and a "wide-band" filter settings. Measurements were made on the sonagrams with the clipboard described in a previous paper (Marler and Isaac, 1960*a*).

The three areas where recordings were made are: (1) Sunset Beach State Park, Santa Cruz County, California, about one hundred miles to the south of Berkeley; (2) the central part of the city of Berkeley, Alameda County, California; (3) the area around Inspiration Point, Contra Costa County, two miles to the northeast from the center of Berkeley. The region between the Berkeley and Inspiration Point areas is more or less continuously occupied by White-crowned Sparrows, while much of that separating these two localities from the Sunset Beach area is only inhabited in a discontinuous fashion, with many extensive gaps. The habitat at Sunset Beach and Inspiration Point is open chaparral, and in Berkeley it consists of town gardens and hedge rows. The birds in this area are all members of the subspecies *Zonotrichia leucophrys nuttalli.*

Unless otherwise stated, measures are given as means plus or minus one standard deviation.

GENERAL DESCRIPTION OF THE SONG

A White-crowned Sparrow song is about two seconds in duration with a pattern described as several plaintive whistled notes followed by a husky trilled whistle (Peterson, 1941). All the songs we have studied conformed to this description. As Peterson

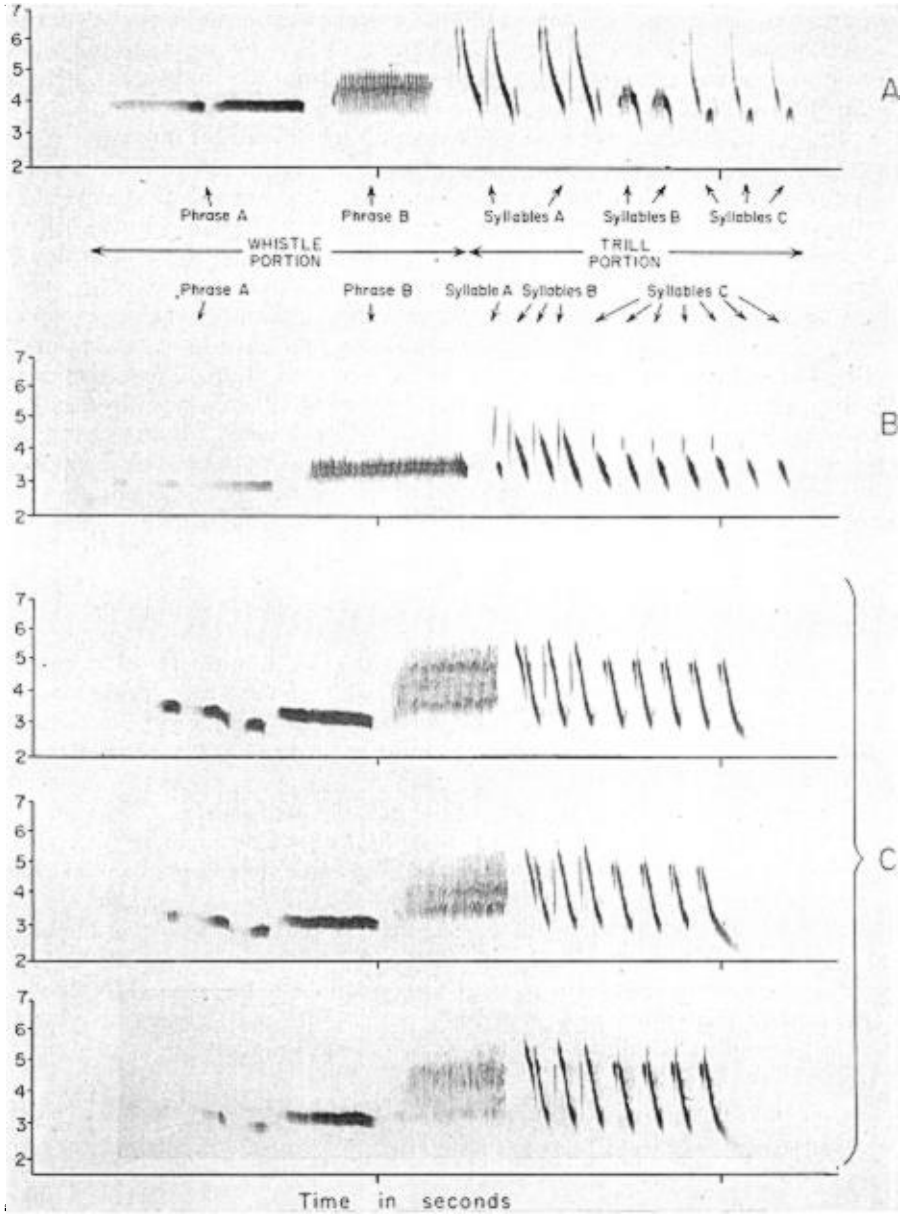

Fig. 1. A and B, sonagrams of two song types, illustrating the terminology used in describing different parts of the song. C, three songs from one bird illustrating the two main types of variation found in songs of the same individual. The top song is complete, the middle song lacks one C-syllable, and the bottom one has a curtailed A-phrase in the whistle portion of the song. The sonagrams in this and other figures are photographs of sonagrams which were retouched with white paint to mask inscriptions and some background noise.

indicates, there are many variations within this pattern. We have made no attempt to describe those occurring outside our study areas. It is known that different character-

istics prevail not far away. Thus birds in Marin County, California, may have a whistle at the end of the song as well as at the beginning, and Peterson mentions other deviations from the general pattern. Two typical examples from the study areas are shown in figures 1A and 1B.

To describe the parts of the song we have arbitrarily divided it into two parts, the whistle portion and the trill portion. As in previous studies the term note is used for any continuous trace on the sonagram, a phrase is a note or group of notes in the whistle portion, which is not immediately repeated, and a syllable is a note or group of notes which is usually repeated one or more times, making up the trill portion (see Marler and Isaac, 1961). Although trill syllables are occasionally only given once we use the same term for them since in other respects they appear identical to those which are repeated. The two main parts of the whistle portion have been labeled phrases A and B. The syllables in the trill portion are labeled syllables A to C in the order in which they appear. In no case were there more than four syllable types in a trill.

Songs are often delivered in long sessions from the same perch. During such sessions of singing behavior there is a rather regular pattern of delivery. For example the Berkeley birds, with an average song duration of 1.9 seconds, paused about 11 seconds between songs, thus spending about 17 per cent of singing time in actual song.

VARIATIONS IN INDIVIDUAL BIRDS

Many hours of listening to White-crowned Sparrow singing have left us with the impression that, after a period of plasticity in early spring, each bird sings essentially the same song pattern from about March to June. In a series of 35 consecutive songs from one bird which was analyzed, the duration of the songs varied somewhat (1.75 ± 0.61 seconds), but inspection of the sonagrams revealed the same basic pattern throughout (fig. 1C). Variation in over-all duration occurred either because the long notes in the whistle portion varied in duration in successive renderings, or because syllables were omitted from the last part of the trill, the number of C syllables varying between four and five. We may note that regardless of whether four or five syllables were given, the last one always terminated with a lower frequency than the others. Thus the variation does not arise simply from omission of the last syllable (fig. 1C). Variation in the whistle portion of the song seems to be largely a result of fluctuations in the amplitude of the notes, although this is difficult to distinguish from actual omission of some of the parts. In spite of these variations, the general impression is one of consistent conformity to a single song pattern, at least through one year and, on the basis of studies of captive birds, probably throughout adult life.

TABLE 1

STATISTICS ON SONGS IN DIFFERENT POPULATIONS OF WHITE-CROWNED SPARROW

Population	Sample size Birds	Songs	Duration in sec.	No. notes	No. syllables and phrases	Maximum frequency	Minimum frequency
Sunset Beach, 1959	26	26	[1]2.1±0.2	31.1±6.4	10.2±1.08	6.78±0.54	2.36±0.20
			[2](1.7—2.6)	(18—45)	(8—15)	(5.3—7.8)	(1.9—2.6)
Sunset Beach, 1960	20	20	2.0±0.2	27.5±4.0	9.6±1.6	6.14±3.1	2.24±0.12
			(1.7—2.5)	(20—37)	(7—13)	(5.5—6.4)	(2.0—2.5)
Berkeley, 1959 and 1960	13	13	2.0±0.2	23.6±4.0	15.2±2.0	6.53±0.69	2.28±0.22
			(1.7—2.2)	(15—32)	(12—19)	(5.6—7.8)	(2.0—2.6)
Inspiration Point, 1960	10	10	1.9±0.1	25.1±4.8	13.4±1.0	5.92±0.31	2.11±0.33
			(1.7—2.1)	(17—33)	(11—15)	(5.4—6.6)	(1.3—2.5)

[1] Mean and standard deviation. [2] Range.

VARIATION OF POPULATIONS

The Sunset Beach population in 1959.—Statistics on the songs of 26 birds recorded at Sunset Beach in April, 1959, reveal a relatively homogeneous sample (table 1). The data are derived from one representative sonagram from the recordings of each bird. The over-all duration ranges from 1.7 to 2.6 seconds with a mean value of 2.1 ± 0.2 seconds. Evidently song duration varies relatively little within this population, and the same may be said of the number of notes and syllables plus phrases (31.1 ± 6.4 notes, 10.2 ± 1.8 syllables and phrases). Similarly the maximum and minimum frequencies are relatively consistent. As has been found in studies of other species, the minimum frequencies represented on the sonagrams vary less than the maximum frequencies (Marler and Isaac, 1960*a*, 1960*b*, 1961).

If the over-all quantitative properties of the songs give an impression of homogeneity, this is further reinforced by a survey of their qualitative characteristics. Figure 2 shows the songs of eighteen of these birds from 1959 selected for illustration because of the lack of background noise. Consider first the trill portions, where there is a

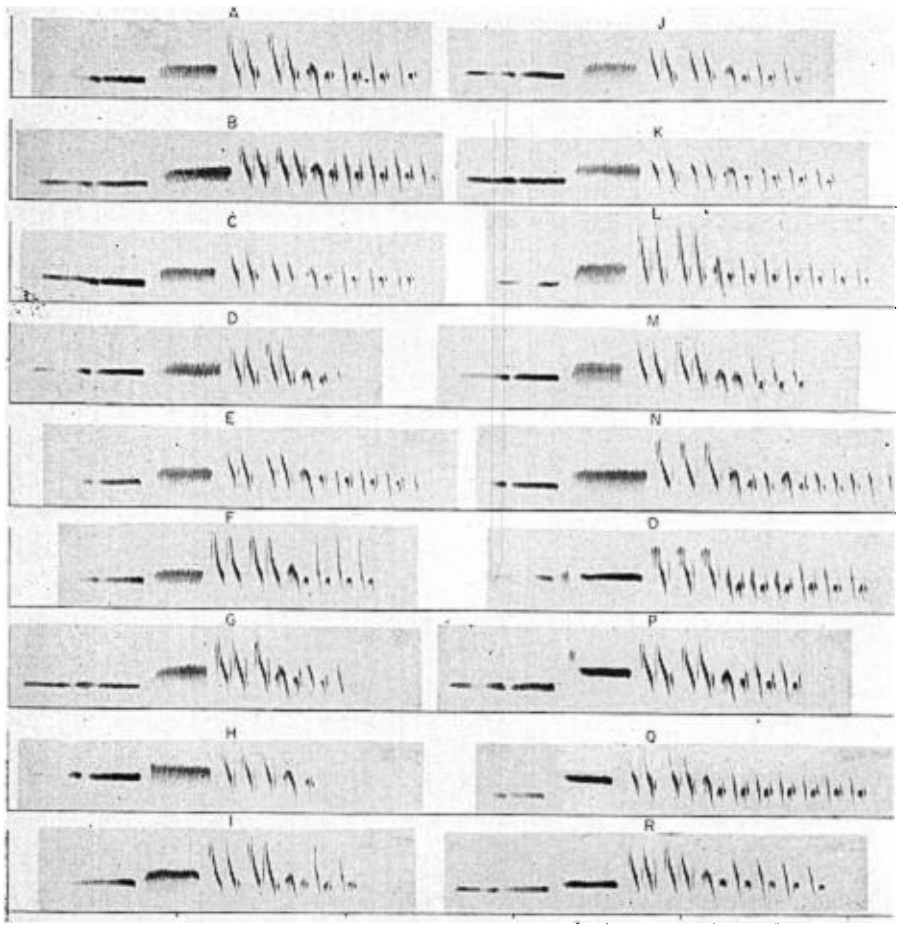

Fig. 2. Songs of eighteen birds recorded at Sunset Beach, Santa Cruz County, in April, 1959. In this and the two following figures the horizontal time scale is marked at one second intervals. The vertical frequency scale ranges from two to seven kilocycles per second.

remarkable degree of correspondence in the structure of the individual syllables. Syllable A has a similar structure in all of the songs, with minor variations in the shape and number of notes (see Song O). There are usually two groups of notes in each syllable (for example, A-F, I-M, P-R) but occasionally the groups constitute individual syllables (H, N, O). In one case only half of the second syllable A is given (Song G). Syllable B which is usually given once, and occasionally two or three times (Songs M, N and O), has an almost identical structure in all of the birds, although the number of notes may vary between two and four. Syllable C also varies little from bird to bird (compare A, B, J, L, M, O, P and Q, for example).

In the whistle portion of the song, phrases A and B are present in every case. Phrase A consists of one long tone of almost constant frequency, sometimes divided into two or more notes, either by complete breaks or by more moderate reductions of intensity. Phrase B is more variable. Sometimes it is a pure tone (O-R). Usually it is a vibrato note (A-N), the rate of which varies from about 50 to about 200 oscillations per second in different birds. In some individuals in which phrase B is not a vibrato there is a note or group of notes between phrases A and B (O and P), adding to the impression of greater qualitative variability in the whistle portion of the song, as compared with the trill portion.

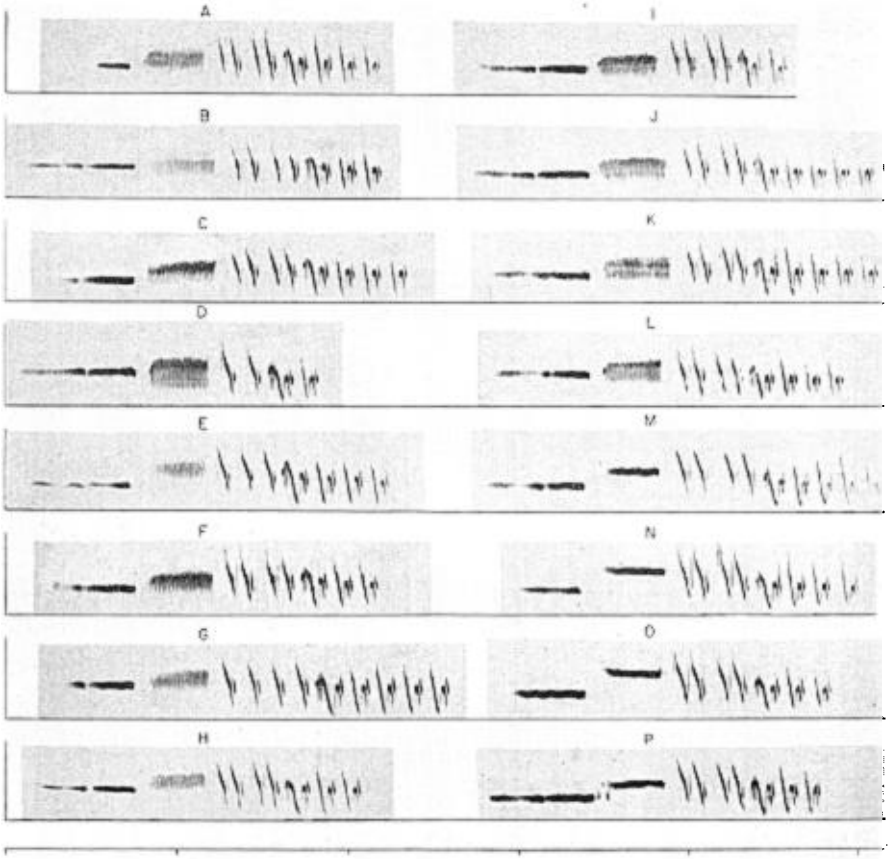

Fig. 3. Songs of sixteen birds recorded at Sunset Beach in May, 1960.

The Sunset Beach birds in 1960.—In order to gain some impression of the stability of the song types from year to year, we returned to exactly the same area in May, 1960, and recorded songs of 20 birds, 16 of which are shown in figure 3. The birds were not banded so that we have no idea how many individuals are represented in both samples. The correspondence in song types between the two years is striking. There is a similar proportion of vibrati in phrase B of the whistle portion. The structure of syllables A, B and C in the trill portion of the songs is closely similar. The over-all statistics for song duration, numbers of notes and syllables, and maximum and minimum frequencies vary little from the previous year (table 1). A few birds in which phrase B is a pure tone also have short notes interposed between phrases A and B, as in the 1959 sample (fig. 2, O, P; fig. 3, P). Our conclusion is that the song characteristics are stable within this population over a period of two years. On the basis of what is known of the longevity of passerines (Lack, 1954), it seems reasonable to assume that some newcomers were represented in the 1960 population, and we may infer that young birds develop a song type which resembles that of the population within which they are living.

Songs of the Berkeley population.—In view of the lack of variability between the Sunset Beach samples of 1959 and 1960, the Berkeley records for the two years have been merged, giving a total of 13 birds. The over-all statistics are similar to those for the Sunset Beach birds (table 1), except for the somewhat larger number of syllables in the trill portion of the song. Once more the sample is relatively homogeneous. The pattern of the songs is similar in the two areas, with the whistle portion preceding the trill. Once more the B phrase may be either a whistle or a vibrato note. However it is clear from qualitative inspection that there are striking differences between the two populations in the structure of the syllables which make up the trill (fig. 4, I-P).

Of the three basic syllable types in each trill, syllable C is most clearly and consistently different. Each syllable consists of only one or two notes, instead of the three notes in the Sunset Beach songs, and the notes have a different shape. In addition the last C syllable in the trill of the Berkeley birds often descends to a lower frequency than those which precede it, a phenomenon never encountered in the Sunset Beach songs. The Berkeley songs have no equivalent of the elaborate B-syllable of the Sunset Beach sample. However the Berkeley A and B syllables, which are generally fairly similar to each other, do bear some resemblance to the A syllables of the Sunset Beach songs. In this and other respects the songs of the two populations have characteristics in common. Nevertheless those differences which exist are unambiguous and consistent, so that the home locality of a single bird chosen at random could be accurately assigned on the basis of its song pattern.

Songs of the Inspiration Point population.—The ten birds recorded in May of 1960 at Inspiration Point were living in a restricted area about two miles from the center of Berkeley. Measurements of the sonagrams once more reveal a very homogeneous sample, similar in most respects to those from the other populations (table 1). There were more syllables and phrases per song than in Sunset Beach songs. In this they resembled the Berkeley songs, and the resemblance is still more evident in the qualitative properties of the songs (fig. 4, A-H). Syllables A and B in the trill are very similar in the two samples. Only the C syllables of the trill show any consistent difference, with a slightly more elaborate structure than those in the Berkeley songs, and with a maximum frequency which is closer to that in the earlier parts of the trill. The last C syllable often descends to a lower frequency than the preceding ones, as in the Berkeley songs. The trill portion of the song is remarkably consistent throughout the sample. Both phrases A and B had a very similar structure in all birds, all of the B phrases being

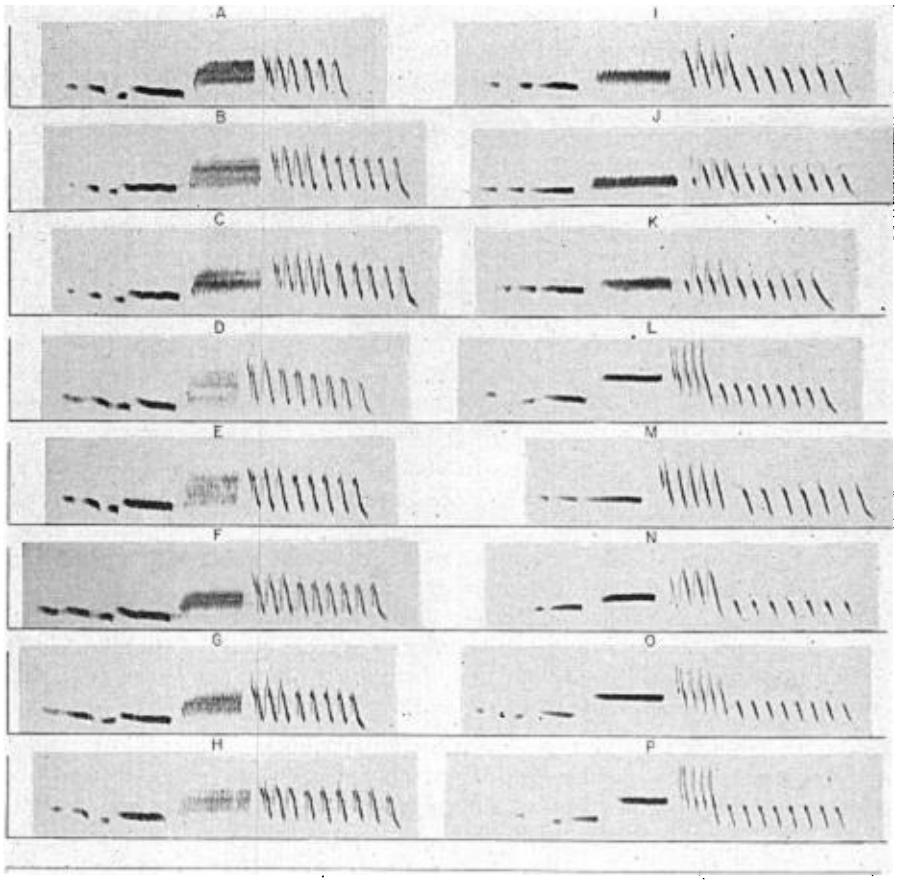

Fig. 4. A-H, songs of eight birds recorded at Inspiration Point, Contra Costa County, in May, 1960. I-P, songs of eight birds recorded in Berkeley, Alameda County, in April, 1959, and May, 1960.

vibrati. The B phrases of the Berkeley songs, which may be either vibrato or non-vibrato, are so variable in this respect that it is difficult to be sure whether the difference is consistent. All of the vibrati in our sample of Berkeley songs had a narrower frequency span than those in the Inspiration Point songs.

Conclusions from a comparison of songs in the three populations.—There is a high degree of stereotypy in the songs of adult male White-crowned Sparrows within each of the three populations under study. This consistency is most striking in the Inspiration Point sample, where it involves all parts of the songs, so that sonagrams of the songs of different birds are almost identical. In the other two samples there is more variation, particularly in the whistle portion of the song, and also to a lesser degree in the early parts of the trill portion. Even here, in the last sequence in the trill the syllables are often almost identical in form from bird to bird. The differences between songs of the three populations are equally consistent. The syllables in the latter part of the trill are the most reliable index and permit a complete separation of all three samples. The syllables in the earlier part of the trill showed more resemblances from sample to sample,

particularly in the songs of birds from Berkeley and Inspiration Point, which were only about two miles apart.

The whistle portion of the song varies sufficiently within a population that the significance of differences between populations is difficult to assess. In any one sample the second note may be either a whistle or a vibrato. The rate of the vibrato may vary from bird to bird. In the Sunset Beach songs there were more vibrati, and in the Berkeley songs more pure tones in this part of the song. In the Inspiration Point songs they were all vibrati.

DISCUSSION

Geographical variation has been demonstrated in the songs of many species (see Benson, 1948; Borror, 1961) and in a few cases there is evidence that the variation is manifest as a series of local song "dialects." In the European Chaffinch (*Fringilla coelebs*) one of the best studied examples (Promptoff, 1930; Poulsen, 1951; Marler, 1952; Thorpe, 1958), the situation is complicated by an appreciable degree of intrapopulation variability in song, as in a number of other species. In such cases the distinction between song patterns in different areas must be made on a statistical basis. The remarkable characteristic of White-crowned Sparrow song is the occurrence of local "dialect" variation together with a high degree of stereotyping of song patterns within a population. This combination of properties would make possible something which in other species with local song dialects would be difficult, namely determination of the locality in which a single bird is living on the basis of its song pattern.

There is thus a complete differentiation between the song patterns in separate populations of the same species which might be construed as a possible sign of incipient speciation as pointed out by Thorpe (1940), Huxley (1942), and Mayr (1942). However, as all of these authors have pointed out it is necessary to determine the extent to which differences in local song "dialects" can be attributed to genetic differences before their significance in the process of speciation can be assessed. The nature of the variation in White-crowned Sparrow song makes it an ideal subject for genetic and ontogenetic studies, unlike species with a high degree of intrapopulation song variability. The process of song development under artificial conditions is much easier to understand if it can be associated with an accurate prediction about the song patterns which the same individual birds would have developed had they been left in the natural state.

Studies now in progress on the development of White-crowned Sparrow song under artificial conditions suggest that differences in local song dialects are not genotypic but phenotypic, as has proven to be the case with the Chaffinch (Thorpe, 1958). However, in the Chaffinch, most of the learning of song patterns from adults takes place at the age of about nine months, after any dispersal and exchange of young birds between populations has been completed. In the White-crowned Sparrow most of the learning seems to take place in the first few weeks of life while they are still in the locality of their birth. The stereotypy and stability of the song "dialects" suggest that little exchange of individuals between populations occurs after the song patterns have been learned. Thus in this case there may be a potential relationship between song "dialects" and the genetic constitution of populations, either indirect, if young birds simply do not wander far, or direct, if they wander but are attracted to breed in areas where they hear the song type which they learned in their youth. Furthermore, it is also necessary to explore the possibility that a female's choice of a mate may be affected by song types heard in youth, since this would have repercussions upon the genetic constitution of the population. We hope to answer some of these questions in future studies. Meanwhile

it seems advisable to leave open the possibility that the study of local song dialects may have a significant bearing upon problems of speciation in certain kinds of birds.

This investigation also raises the broader issue of the direct functional significance of variation in bird song, if any. It has been argued that the value of the facilitation of individual recognition by song may help to explain the high degree of intrapopulation variability in some bird songs, and there is experimental evidence that such recognition does occur (Hinde, 1958; Weeden and Falls, 1959). How then can we understand the striking lack of individuality in most parts of the song of White-crowned Sparrows? Have they dispensed with the need for individual recognition, or do the variations in the whistle portion of the song suffice for this purpose? It is even possible that some other requirement overrides a need for individuality, perhaps related to the particular mode of song development in this species. Further work is required before the validity or relevance of these speculations can be determined.

SUMMARY

Analysis of song patterns in three populations of White-crowned Sparrows, two close together and one distant, revealed an unusual degree of homogeneity in certain characteristics within each population. In one case the patterns remained similar over two consecutive breeding seasons. There were also distinctive and consistent differences between song patterns of the three populations, the divergence being greatest between those separated by the greatest distance. This constitutes one of the clearest examples of "dialects" in bird song. The possibility is discussed that such song variations may be signs of incipient speciation.

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