

INTER-POPULATIONAL SONG DIALECT DISCRIMINATION IN THE WHITE-CROWNED SPARROW

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The fact that song types vary among coastal California populations of the White-crowned Sparrow (*Zonotrichia leucophrys nuttalli*) has been known for some time (Blanchard 1941). It was not until the advent of the sound spectrograph, however, that an unambiguous analysis of these inter-population variations could be performed. Using this technique, Marler and Tamura (1962) found that each male's song type remains constant from year to year and that there are constant and distinctive differences among populations with respect to song type. They therefore refer to the songs of different populations as "dialects." Of fundamental importance in determining the functional significance of these dialects is the question of whether or not the birds themselves discriminate among them. One approach to this question is to observe the behavioral responses of the individuals of one population to the recorded songs of their own and of other populations.

Earlier work suggests that at least one function of song in the White-crowned Sparrow is territorial defense. A territorial male will respond with song (sometimes accompanied by chase and attack) to visual and/or auditory stimuli from another male intruding within his territory (Blanchard 1939, 1941). A study of vocal responses of captive male White-crowned Sparrows to recorded songs of their own and another species revealed a higher probability of response to the songs of their own species (Milligan 1966). Thus it seems reasonable to expect that male White-crowns can also discriminate among different dialects of their own species and that they would respond more strongly to playback of their own dialect. The central purpose of the present study was to test this hypothesis. In addition, data were accumulated on the seasonal changes in the response of male and

female White-crowns to playback of recorded song; these results are presented elsewhere (Verner and Milligan 1971).

STUDY AREAS

Field work was conducted in three separate locations along the California coast: (1) Berkeley, Alameda County, within the city; (2) Sunset Beach State Park, 5 mi. N of Watsonville, Santa Cruz County; and (3) Point Reyes (designated as Inverness), 5 mi. W of Inverness, Marin County. White-crown songs recorded in these three localities have been analyzed on a sound spectrograph by Marler and Tamura (1962, 1964) and sonagrams are depicted in figure 1.

METHODS AND MATERIALS

Songs to be utilized for playback were recorded in each of the three study areas on a Uher 4000S portable tape recorder at 7½ ips. Later, a single song was selected from each of the tapes and copied onto a loop taking exactly 15 sec to complete one revolution at 7½ ips. Playback tapes were then copied from the loop at 3¾ ips. Sonagrams of the songs recorded at the two speeds revealed no differences.

Each playback session lasted 35 min and always included playback of the local dialect and one of the non-local dialects. A session began with 5 min of silence (period S-1), followed by 5 min of one dialect consisting of one song each 15 sec until 20 songs had been played (period C-1), 5 min of silence (S-2), 5 min of a second dialect (C-2), 5 min of silence (S-3), 5 min of the dialect beginning the session (C-3), and a final 5-min silent period (S-4). The local dialect always occurred either as C-1 and C-3 or as C-2 only. For example, at Inverness a session might begin with a cut of Inverness song, be followed by Berkeley song, and conclude with Inverness. This session would be designated Inverness-Berkeley-Inverness, abbreviated IBI. Thus, the following combinations were used in each of the three areas: Berkeley—BIB, IBI, BSB, SBS; Inverness—IBI, BIB, ISI, SIS; and Sunset Beach—SBS, BSB, SIS, ISI. Unfortunately, human interference restricted the number of sessions we were able to complete at Berkeley and no SBS or BSB sessions were obtained there.

In the field we attempted to place the speaker within the territory of a male that was or had recently been singing. We found it advisable to observe the bird selected for playback for several minutes before proceeding since some males had excessively large territories or were feeding young with food gathered off their territory at distances beyond the range of the speaker. The Uher 4000S tape recorder was used for playback at 3¾ ips. A speaker designed and built by W. R. Fish was used at the end of a 50-ft lead.

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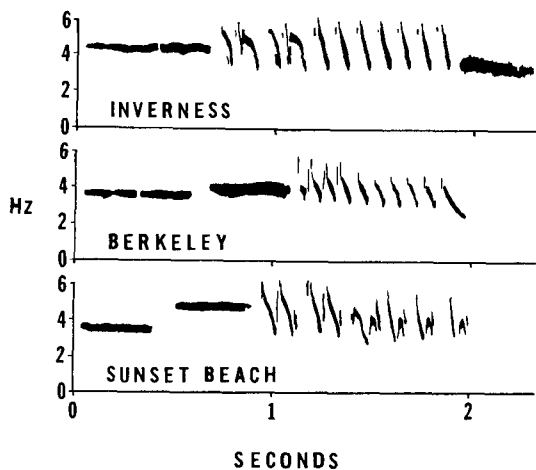


FIGURE 1. Tracings of sonagrams of songs similar to those used in reciprocal playbacks reported here.

Field work began on 21 July 1964 and continued during every month until 26 July 1965. Since White-crowned Sparrows are more likely to sing and be dispersed onto territories during the breeding season than at other times of the year, the present analysis will treat only those sessions carried out during the breeding season. On the basis of mating and nesting behavior, the breeding season has been approximately delimited as 1 April–31 August. The same male was never used as a subject twice on the same day, although sessions were sometimes carried out in the same territory on two successive weeks. Many males were individually color-banded after a session by luring them into a mist net by placing the speaker at the base of the net and playing their native dialect.

During the playback session the bird's behavior was recorded in as much detail as possible, with one observer describing the behavior while the other recorded it on standardized sheets in a shorthand system devised to fit the behavioral repertoire of the White-crowned Sparrow. The following five behavioral responses have proved most useful in characterizing the relative intensity of the subject's response to playback.

Songs. Song rate normally increased when the playback cut began. Although the birds typically delivered complete songs, occasionally just the initial phrase or the first two phrases were sung. Partial songs of this type were weighted equally with full song.

Flights. The number of flights per unit time usually increased with playback. Hopping has not been included in this category since hopping birds were sometimes hidden from view and their behavior not recorded.

Approach time. This is a measure of the time taken to approach within given distances of the speaker after the first song of a cut has played. Each 5-min period of the playback session was divided into 20 segments of 15 sec each, and these were assigned numbers from 20 to 1 with the interval following the first song being number 20. Three distance categories were estimated (0–10 ft, 10–20 ft, and 20–30 ft) and the time interval during which a bird approached to within any of the three distance categories was recorded. If the bird was already within 25 ft of the speaker when playback began, it could not score for that distance range (20–30 ft). If it approached from 50 to 25 ft after the second song had played, it scored 19. Other distance

categories were similarly scored and the mean of the scores for the three categories was used as an index of the bird's approach time. For example, if the bird above came no closer than 21 ft from the speaker, his score for that cut would be $(19 + 0 + 0)/3 = 6.3$. Note that by numbering the 15-sec time segments in reverse chronological order, low approach time scores indicate a slow response, while a score of 20 is indicative of an immediate response.

Nearest distance. Birds typically responded by approaching the speaker, some even using it as a song perch during a session. The nearest distance to which a bird approached the speaker was estimated in feet.

Trill. A call note quite distinct from song, the trill is used by males and females, but more commonly by females. The total number of trills delivered by the female during a cut was used as the only index of her response intensity.

For each bird the value of a given response during the initial 5-min silent period (S-1) has been subtracted from the value obtained during each of the other 5-min periods. For example, if a bird sang twice during S-1 and 15 times during the first playback cut (C-1), his song score for C-1 was 13. In this way the initial silent period serves as an index to the level of increase of any particular behavior, presumably in response to playback. Transformed values of this sort are used throughout the remainder of this paper, except in figures 3 and 4.

Data were first subjected to the Kruskal-Wallis test (Siegel 1956) to determine whether or not all three distributions (responses to the three dialects) were taken from the same population. Mann-Whitney *U* tests were then applied to determine whether or not there were significant differences ($P < 0.05$) between responses to the native and each of the non-native dialects.

Where the Kruskal-Wallis test yields a significant difference, the Mann-Whitney *U* results may be taken at face value. However, where only a Mann-Whitney *U* test shows a significant difference, the difference between the two distributions is slightly less significant than indicated by the alpha level. These statistics are not capable of handling the overall trend of primary interest here (greater responsiveness to native dialects). Rather, each sub-section of the data has been analyzed separately. The lack of significant results in cases where the average response values nevertheless follow the overall trend should not prevent us from drawing conclusions from those data. We feel that the statistics should be used to suggest where the greatest reliability lies.

RESULTS

MALE RESPONSES

A major implication of the statistical results is that *song* and *flight* are more reliable measures than are *approach time* and *nearest distance*. This is to be expected from the nature of the data, since it is more difficult to estimate distance than to determine whether or not a song or flight occurred.

Figure 2 depicts means of transformed scores for all C-1 periods in each of the three study areas for each dialect. To obtain sufficiently large samples for adequate statistical analysis, many C-1 period results from males

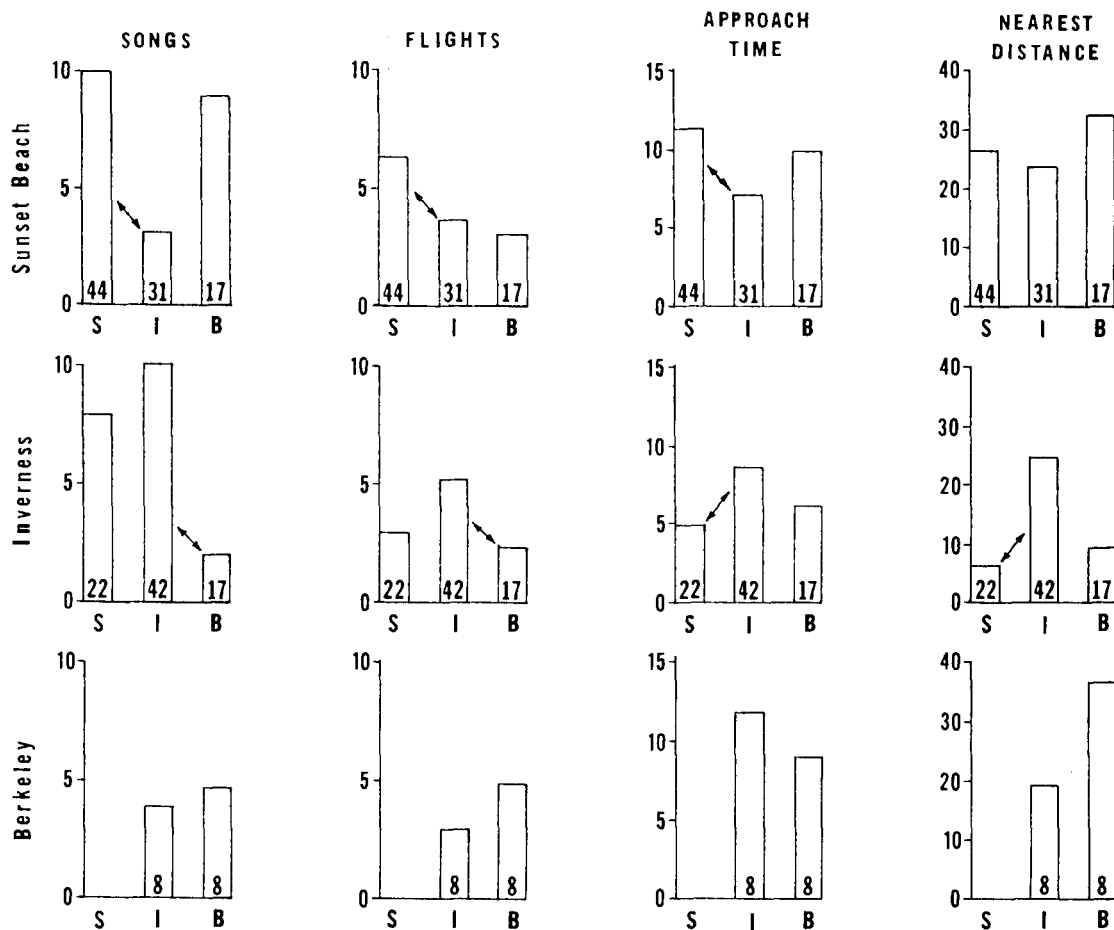


FIGURE 2. Means of all C-1 period scores of four responses by males in each of three populations to playback of their respective dialects (S = Sunset Beach, I = Inverness, B = Berkeley). Means for S-I periods for *songs* and *flights* have been subtracted from mean C-1 scores. Ordinates represent numbers per 5 min for *songs* and *flights*, *approach time* intervals (see text), and *nearest distance* to the speaker in feet. Arrows connecting columns indicate a difference significant at the 0.05 level. Sample sizes are indicated at the bottom of each histogram column.

exposed to playback more than once have been included in the calculations reported here. Even though it was determined that male White-crowned Sparrows habituated to the playback situation (Verner and Milligan 1971), each dialect in each population was approximately equally represented by males exposed to playback more than once. Thus habituation should have affected all samples nearly equally and should not invalidate conclusions drawn here. It would, however, result in smaller apparent changes in behavior than would result if only males exposed to playback just once were treated.

Figures 3 and 4 are based only on males exposed to playback for the first time. Figure 5 shows trill responses of females during all C-1 periods.

While these data clearly indicate the ability of White-crowned Sparrows of both sexes to

discriminate between native and non-native dialects, it is also nonetheless clear that the birds manifested marked behavioral changes in response to non-native dialects. The most surprising result of this study is the uniform failure of males in all three populations to come nearest the speaker in response to their native dialect (see *nearest distance* column in fig. 2).

If males discriminate between native and non-native dialects, we would predict that a male's response to a complete 35-min session would present an unambiguous up-down-up or down-up-down graphic pattern, depending upon whether the native or a non-native dialect initiated the session. This situation was approximated by Inverness males during sessions employing Song Sparrow (*Melospiza melodia*) songs in place of a non-native dialect (fig. 3). Figure 4 depicts the summed results of ISI

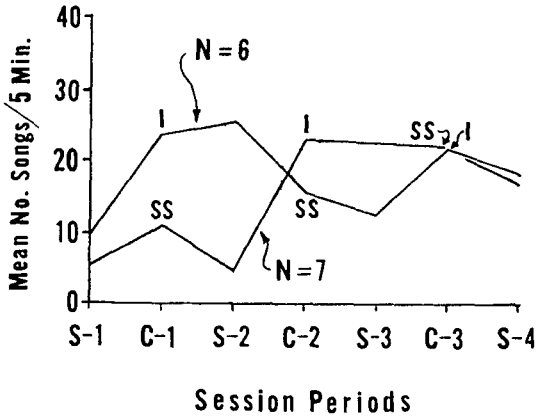


FIGURE 3. Means of full-session *song* responses of Inverness males to their native dialect (I) and Song Sparrow (SS) songs. Both I-SS-I and SS-I-SS sessions are shown.

and IBI sessions and of SIS and BIB sessions at Inverness. Clearly the predicted shapes of these curves are not found and this evidently results from a prolonged residual effect of a playback cut that carries over the intervening 5-min silent period into the next playback cut. Essentially the same results were obtained in all three populations. In general, the native dialect elicited a lower response when it followed a cut of non-native dialect than it did when presented first. Conversely, the non-native dialect elicited a better response when it followed the native dialect than when it was presented first. Although only the curves for *song* response are shown, *flight*, *approach time*, and *nearest distance* were treated in the above manner and show basically the same trend.

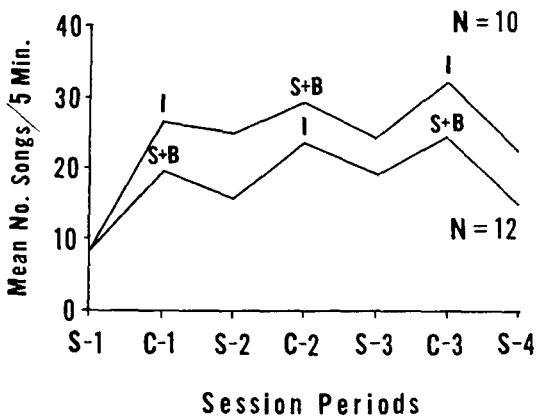


FIGURE 4. Means of full-session *song* responses of Inverness males to native (I) and non-native (S + B) dialects. The upper curve represents a summation of ISI and IBI sessions; the lower curve represents a summation of SIS and BIB sessions.

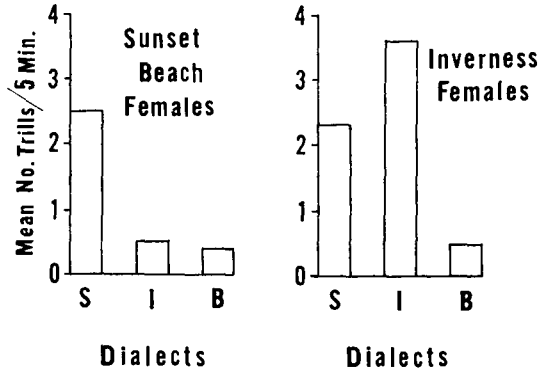


FIGURE 5. Mean numbers of *trills* given by Sunset Beach and Inverness females in response to playbacks of three dialects (S = Sunset Beach, I = Inverness, B = Berkeley).

FEMALE RESPONSES

Only occasionally did female White-crowned Sparrows respond to playback during the breeding season. Figure 5 shows the average *trill* rates of females at Sunset Beach and Inverness to the different dialects. In both areas there was a greater response to the native dialect, although females, like the males, manifested a response even to the non-native dialects.

DISCUSSION

A distinction should be made between the playback technique employed here and the traditional methods employed by psychologists to investigate discriminative behavior of animals. The advantage of using the playback technique in the field is that it tells us something about the functional significance of the stimuli presented, since we observe the natural behavior of the birds. However, this technique does not delimit the bird's discriminative capabilities. We do not know whether the imperfect discrimination of dialects by White-crowned Sparrows reported here reflects limitations of their sensory apparatus or whether it is of purely functional significance. One way to explore these limits is to use the stimulus as a cue for a reward or punishment. If, for example, food were used as a reward and a hungry bird failed to show good discrimination, we could feel more confident that he was incapable of making such a discrimination. It would be fruitful to use these two approaches together in an effort to separate the functional significance of a given behavior from the limits placed upon that behavior by the animal's sensory capacity. Even without these data, however, it is feasible to examine the possible significance of the observations reported here.

NEAREST DISTANCE

The unexpected finding that male White-crowns come nearer to a speaker broadcasting a non-native dialect than to one broadcasting a native dialect is of singular importance to any study employing approach distance as an index to responsiveness. For example, from the fact that males approached the speaker during this study we drew the unwarranted conclusion that the nearer the approach the more effective was the stimulus. Behaviorally, the playback may induce a motivational impasse in the birds, with a tendency to approach countered by one to flee. The native dialect could elicit a stronger flight tendency than a non-native one, so that male White-crowns would not come as near the source of the native dialect.

SPECIATION IN THE
WHITE-CROWNED SPARROW

Marler and Tamura (1962) suggested that differences in dialect may be indicative of incipient speciation in the various resident populations of the White-crowned Sparrow. As these authors suggest, genetic differences must be separated from environmental ones in evaluating the question of speciation. They have shown (1962, 1964) that dialect differences in the White-crowned Sparrow are not genotypic; a hand-reared young from one population will not selectively learn his population's dialect when exposed equally to it and to a non-native dialect. The present study does not exclude the possibility that greater responsiveness to native dialects is learned also.

There is a large body of literature documenting the phenomenon of stimulus generalization (see Mednick and Freedman 1960; Evans 1967). When an animal is trained in a discrimination paradigm with one stimulus and is then exposed to others on the same continuum, he will respond most strongly to the training stimulus and in varying degrees to other stimuli along the continuum, depending upon their degree of similarity to the original stimulus. White-crowned Sparrows in their natural habitats hear primarily their local dialects from the time they are hatched. Further, they are more likely to engage in territorial combat with a bird singing the native dialect, partly because such birds are the only ones likely to establish territories in the area, and partly because the native dialect elicits a stronger response from a male. Although migrants may be present in the three study areas, they are usually gone by the time the breeding season is well under way. Moreover, we heard migrants singing in only one of our three study

areas on only one day in the fall. Thus, the "training stimulus" in this case would be the native dialect, and we may simply have seen a "generalization gradient" resulting from the bird's experience with the local dialect and lack of experience with other dialects. A logical next step is to study discrimination in birds which have been exposed equally to all three dialects.

Whatever the mechanism, the fact that females responded more strongly to the native dialect suggests that males singing the local dialect are more likely to attract mates. Consequently, selection would favor those males and also tend to favor uniformity in the structure of the songs of all males in a given population. Moreover, since Marler and Tamura (1964) have shown that young birds can effectively learn song by the time they are 28 days old but that they cannot effectively change a learned song pattern after they are about 100 days old, it would be dysgenic for birds older than 100 days to move from one population to another and probably so even for birds older than 28 days. Since young White-crowned Sparrows are essentially dependent upon their parents up to the age of 28 days, it appears unlikely that any would emigrate to other populations. The net effect would be to isolate each resident population of White-crowned Sparrows. This could certainly provide the stage for speciation, if the isolation were complete enough for a sufficient period of time. However, neither our data nor those of Marler and Tamura provide evidence of genotypic differences between populations, and to date there is no significant evidence of morphological differences among the various California populations of the White-crowned Sparrow (Banks 1964). We must conclude that while these various resident populations may represent incipient species, there is certainly no evidence to support such a view.

SPECIES-SPECIFICITY OF SONGS

Recently there have been attempts to determine which parameters of avian song might serve to identify the species and which might serve to identify the individual singer (Abs 1963; Falls 1963). As Marler (1960) pointed out, selection for both capacities would be in conflict, and the only way to achieve both is to have some parameters of the song convey species-specific information while others convey information unique to the individual. The facts that White-crowned Sparrows responded well to non-native dialects which humans can clearly distinguish from the native dialects, but that they responded barely, if at all, to

Song Sparrow song when it was presented first in a session suggests that there are species-specific parameters of the various White-crown dialects that transcend population barriers. Just what these might be is unknown, but these populations provide an ideal situation for field investigation of this phenomenon.

THE RESIDUAL EFFECT

The fact that there is a residual effect shows how flexible discriminative behavior is, in that the level of discrimination can change depending upon what an animal has been exposed to within the very recent past (in this case 5–15 min previously). There are at least two possible mechanisms involved here. (1) Previous work, especially in the area of psychophysics, has shown that when an animal is exposed a number of times to a certain stimulus, it becomes "sensitized" (see Kimble 1961) and will respond to the next stimulus in the way it did to the previous series, even though the next stimulus may be different. The fact that male White-crowned Sparrows did not respond to Song Sparrow song when it was presented first in a session but did respond when the Song Sparrow cut followed the White-crown cut appears to be a good example of such a phenomenon. (2) It is known that increases in testosterone level will increase the responsiveness of the White-crowned Sparrow to playback (Milligan 1966). It is possible that playback itself produces immediate increases in hormone level which last a short time beyond the actual stimulus and cause an increase in response to the next series of stimuli. This hypothesis would predict the observed increase in response to a non-native dialect when it follows playback of the native one. It would not, however, predict our observation that the response to the native dialect is less when it follows than when it precedes a non-native dialect.

SUMMARY

Reciprocal playback of native and non-native dialects of White-crowned Sparrow songs from three populations in northern, coastal California were undertaken in an effort to determine whether or not the birds could discriminate among dialects. While both males and females responded well to native and non-native dialects, both sexes consistently demonstrated a stronger response to the native dialect. There is, further, a residual effect of playback. Exposure to the native dialect enhances responsiveness to later playback of a non-native

dialect if such a playback occurs within the time period of the residual effect (not determined in this study, since a standard period of 5 min of silence separated each playback cut). Conversely, initial exposure to a non-native dialect depresses responsiveness to later playback of the native dialect.

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