

## SHARING OF VOCAL SIGNALS AMONG SONG SPARROWS

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**ABSTRACT.**—In the scrub habitat along the central California coast, Song Sparrows (*Melospiza melodia*) are sympatric with White-crowned Sparrows (*Zonotrichia leucophrys*). Songs of male White-crowned Sparrows exhibit dialects and it was previously thought that these might be initiated by a founder effect. This hypothesis could be tested weakly by looking for concordant dialect systems among several songbird species in the same region. Given the known pattern of song variation in White-crowned Sparrows, I asked if vocal variation in Song Sparrows matched that of White-crowned Sparrows. Seven Song Sparrows were recorded at each of four sites located within the boundaries of three dialect areas of White-crowned Sparrows. Repertoire size of the Song Sparrows ranged from 6–18 songs (median 10). The 22 kinds of trills and 50 kinds of notes most commonly sung by Song Sparrows were examined for similarities among individuals and samples. Vocal sharing was not concordant with the dialects of White-crowned Sparrows. Only one or two types of notes or trills varied geographically in accordance with dialect variation in White-crowned Sparrows. Nor was there strong evidence for dialects in Song Sparrows that were discordant with those of White-crowned Sparrows. The results did not support the colonization hypothesis for the origin of dialects.

Dialectal variation in the vocal repertoire of male songbirds has been thoroughly documented for a variety of species, progress has been made in understanding its origins in the learning process, and advances have been made in discovering the behavioral and ecological significance of dialects (Thorpe 1958, Marler 1970, Milligan and Verner 1971, Lemon 1975, Baptista 1975, Baker 1982, Payne 1982). How a geographic mosaic of dialect populations becomes established in historical time is less well known.

It has been hypothesized that dialects originate allopatrically, perhaps as a consequence of drift in song features during isolation or perhaps as a result of a founder effect (Thielcke 1973, 1976; Baker 1975; Baptista 1975). Some suggestive evidence for this general view can be found in the results of Mundinger (1975) and Jenkins (1978). Dialects in the resident White-crowned Sparrow (*Zonotrichia leucophrys nuttalli*) populations of central coastal California could represent colonization events that occurred following major burns of the habitat (Baker 1975). Both Song Sparrows (*Melospiza melodia*) and White-crowned Sparrows occupy the coastal scrub habitat of the Point Reyes National Seashore, Marin Co., California. The vegetation is a fire climax community characterized by the woody shrub *Baccharis pilularis* and a variety of forbs (Munz and Keck 1959). Following a fire, which is typically fast and "cool," *Baccharis* regrows from the root and forbs gradually fill in over subsequent years (unpubl. data from observations

on a 5–10 ha burn in the Seashore in 1980). Young birds of the year may colonize a regenerating area after a large-scale burn occurs and thus initiate a new dialect. For this to happen, the founders may be either birds who have not completed song learning, or few in number to allow vocal drift to occur in subsequent seasons. As the population grows, and young birds learn from resident males in subsequent generations, a new dialect would be established.

The rationale for the present report on Song Sparrows is derived from this general model of dialect formation. Song Sparrows resemble White-crowned Sparrows in many aspects of their general biology. In the Point Reyes area, they occupy the same scrub habitat, they are territorial and monogamous, and learning plays a significant role in the acquisition of song (Nice 1937, Johnston 1956, Mulligan 1966, Halliburton and Mewaldt 1976, Kroodsma 1977, Mewaldt and King 1977). These similarities led me to hypothesize that dialects of Song Sparrows might match those of White-crowned Sparrows. I reasoned that the empty habitat created by a fire would be colonized by a variety of bird species, resulting in the development of dialects among those species that are capable of doing so. Moreover, if dialects represent populations of individuals adapted to local environmental conditions (Nottebohm 1969) then one might expect similar local adaptations in other closely related bird species. Ecological geneticists view it as strong evidence for natural selection when two or more species have concordant patterns of gene fre-

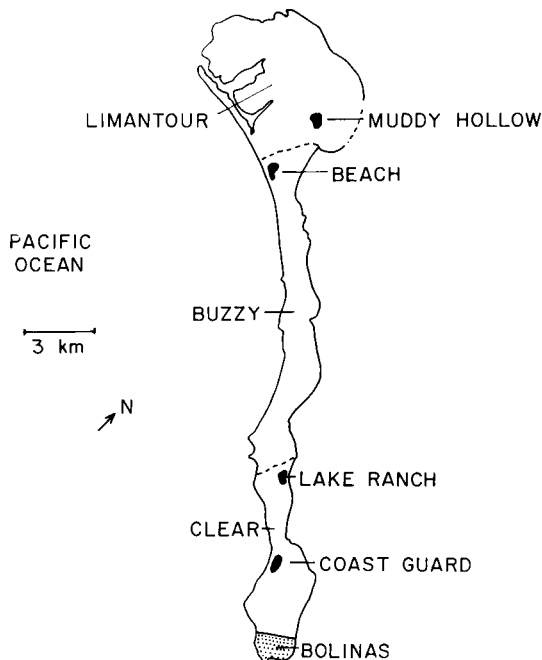


FIGURE 1. Map of the study area showing the four recording sites for Song Sparrows within the dialects of White-crowned Sparrows.

quency change through space (Koehn and Mitton 1972, Clarke 1975, Johnson 1975). My study did not evaluate genetic variation in the two species and therefore cannot test directly the local adaptation hypothesis. Finding concordant dialect variation in two or more species would constitute evidence for both the founder and local adaptation hypotheses. To look for concordant spatial variation in song dialects of Song Sparrows and White-crowned Sparrows, I recorded Song Sparrows at four sites within three dialect areas of White-crowned Sparrows.

## MATERIALS AND METHODS

I recorded songs of seven male Song Sparrows at each of four locations in the Point Reyes National Seashore, Marin Co., California. Each bird was recorded through several cycles of its repertoire to ensure thorough sampling of song types. Song Sparrows may add one or more new songs with successive cycles through the repertoire and it is only with exhaustive recording that one can obtain the definitive repertoire size (Mulligan 1966). My experience was that 30–60 min of recording obtained virtually all the song types in the repertoire of an individual. This period was then used for recording all the birds in this study.

The first recording site was on the Coast Guard/RCA property immediately south of the southern end of the National Seashore. The second site was near Lake Ranch, approxi-

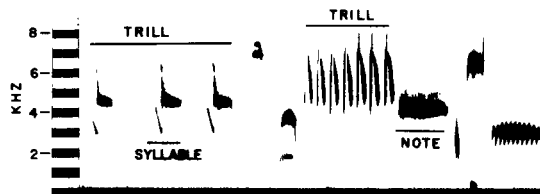


FIGURE 2. Sonogram of Song Sparrow song with marked parts to show the terminology used in the paper (note, syllable, phrase, etc.). The example shown is 2.4 s in total duration.

mately 4 km northwest of the first site and well into the National Seashore. Both of these sites were within the Clear dialect region of White-crowned Sparrows (Baker 1975). The third site was about 14 km farther up the coast from Lake Ranch, south of Limantour Beach and within the Buzzy dialect of White-crowned Sparrows. The fourth site was in Muddy Hollow, near the trailhead, approximately 3 km north of the Limantour Beach recording site. Muddy Hollow was within the Limantour dialect of White-crowned Sparrows (Fig. 1). The four sample sites will be referred to as Coast Guard, Lake Ranch, Beach, and Muddy Hollow.

Recording was accomplished with a Uher 4200 Report Stereo IC recorder and a Uher microphone mounted in a 60-cm parabolic reflector. Tape speed was 9.5 cm/s. Songs were transformed to audiospectrograms on a Kay Elemetrics 7029A sonagraph set on the 80–8,000 Hz range and wide band (300 Hz) filter selections. One representative sonogram of each song type in the repertoire of each bird was selected for analysis.

Singing behavior of this species is organized to produce a repertoire of songs. Each particular song type lasts approximately 2–3 s and is composed of a sequence of separate notes. A “note” is a continuous trace on the sonogram, a “syllable” is a note or combination of notes that is sequentially repeated in a song, and this entire unit of repeated syllables constitutes a “trill” (Mulligan 1966, Harris and Lemon 1972). A typical song begins with trill syllables, often with an accelerating tempo, and contains several unrepeated notes and one or more additional trills through the remainder of the song. Most notes are brief but some whistles and frequency-modulated buzzes are considerably longer. Figure 2 shows a typical song and the terminology used in this report.

Previous work showed that on the basis of whole song patterns, dialects were absent in the Song Sparrow populations of San Francisco Bay, but that on the basis of individual syllables and notes, dialects were present in

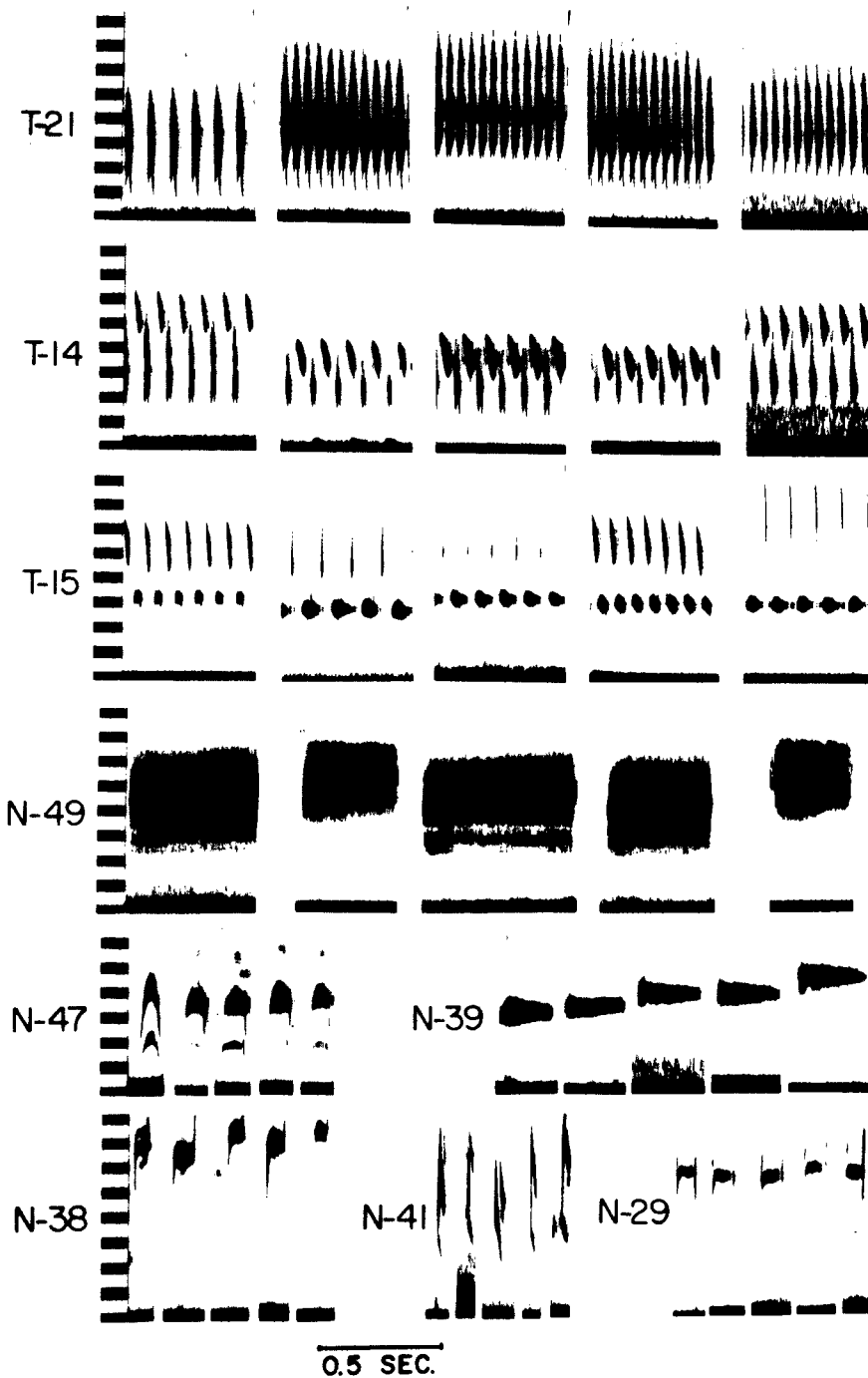


FIGURE 3. Variation within categories of trill syllables and notes among five different birds for each of three different types of trill syllables and six different types of notes.

Song Sparrows in Maine and Quebec (Borror 1965, Mulligan 1966, Harris and Lemon 1972). Furthermore, studies of song learning in the Swamp Sparrow (*Melospiza georgiana*) indicate that syllables and notes are probably the units of cultural inheritance enabled by song learning during the early sensitive phase (Marler and Peters 1977). For these reasons, I de-

cid to examine individual notes and syllables as the units of comparison among individuals and between samples. All notes and syllables were classified blindly, without knowledge of the geographic location of the birds. Some examples of the range of variation within categories of trill syllables and note types are illustrated in Figure 3.

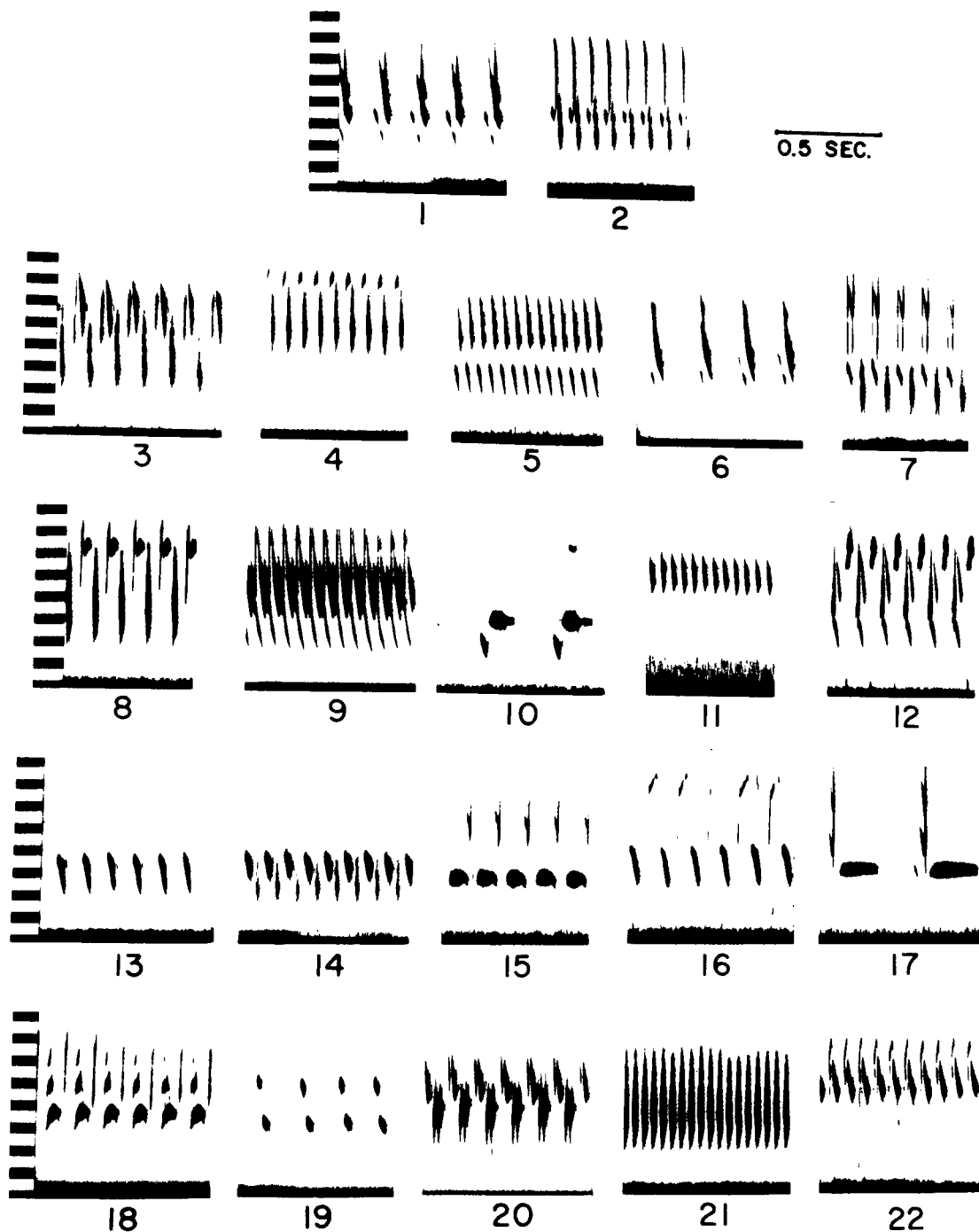


FIGURE 4. Trill syllable types. The 22 most common are shown.

## RESULTS

I adopted the strict meaning of "dialect" for this study of Song Sparrows, following closely the definition stated by Mulligan (1966:58) "In the present context the term dialect means, or ought to mean, that all or most of the members of a local population have some peculiarity in their songs which is distinctive." Thus, for a

population in my study to have a different dialect nearly all the individuals should sing a shared character in at least one of the songs in their repertoires. Other populations should sing this character rarely or not at all. In my samples of seven birds, I considered a population to have a dialect if six of seven birds had a particular song feature that was sung by no

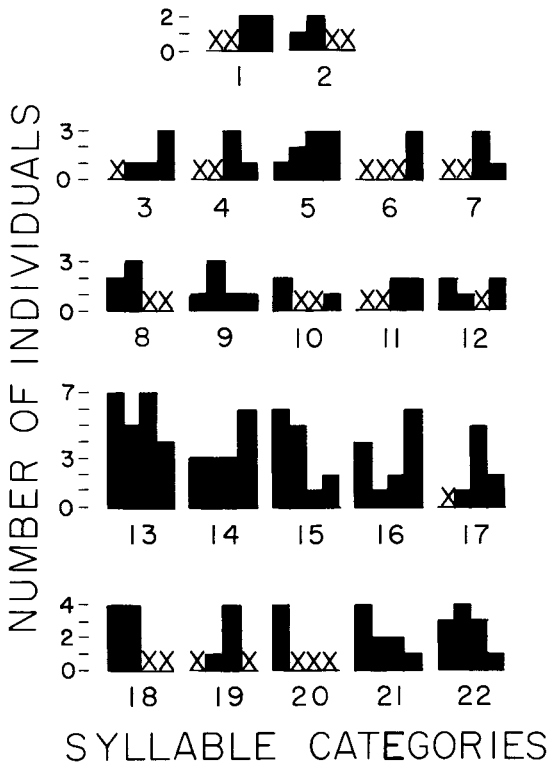


FIGURE 5. Frequency histograms of trill syllable types. For each type of trill, the sample locations are arranged in sequence along the abscissa from left to right Coast Guard, Lake Ranch, Beach, Muddy Hollow. An X indicates that no individual in the sample sang that type of trill.

more than one individual in one or more other samples. These definitional considerations and the consequences of relaxing them will be discussed later.

The repertoire size of the 28 birds recorded ranged from 6 to 18 with a median of 10 songs per male. As Mulligan (1966) found, males virtually never shared whole songs, whether from the same or different samples. Two neighboring males in the Lake Ranch sample shared a song and two neighbors in the Coast Guard sample shared a song. Some birds sang trill syllables similar to those of other individuals. I selected for analysis the 22 types of trill syllables most frequently sung by the total sample of 28 birds. To be included, a trill syllable had to be sung by at least three birds (Fig. 4). In contrast to whole songs for which there was virtually no similarity among individuals, trill syllables of various types were often common to several individuals (Fig. 5). The most common trill syllable, #13, was found in the repertoire of 23 of the 28 birds. Of the four trill syllables that met the criterion of being common, (13, 14, 15, 16), none followed a pattern in which one or more of the samples

could be called a dialect. Trill syllable #15 came close to meeting the criterion since the Coast Guard and Lake Ranch samples had six and five birds, respectively, who sang it but only one and two birds from Beach and Muddy Hollow, respectively, who sang the syllable. Similarly, trill syllable #18 had a suggestive geographic pattern that conformed with White-crowned Sparrow dialects, but only four of seven birds in each of the Coast Guard and Lake Ranch samples possessed the syllable.

Examining individual notes (Fig. 6) also provided no compelling evidence for dialect patterns over the four samples. To be included in this analysis, a particular note had to be sung by at least three individuals of the total sample of 28 birds. The common notes were widely shared among the four samples (Fig. 7). For example, notes 36, 45, 47, and 49 were found in 27 of 28 birds. Of the 50 notes depicted in Figures 6 and 7, none met the criteria of being common in one or more samples and rare or absent in the rest. As with trill syllables, certain patterns of presence and absence suggested concordance between Song Sparrow song variation and that of White-crowned Sparrows (e.g., notes 1, 11, 12, 16, 22, 27, 28, 31) but none met the strict definition of dialect.

To obtain a simple summary index of the amount of sharing of trill syllables among the seven individuals within any sample, I determined the number of trill syllable types sung by three or more individuals in the sample (from Fig. 5). Dividing this value by 22, the total number of trill syllable types, gave the index of sharing. The value of the sharing index averaged 33% (range 27–36) for the birds within the four samples. Treating note types in the same way (from Fig. 7), the index of sharing averaged 64% (range 58–68). To obtain a summary index of the amount of sharing of trill syllable and note types among the four geographic samples, I determined the number of trill or note types sung by at least one individual in all four samples. This index of sharing was 36% for trill syllables and 58% for note types.

## DISCUSSION

From the data presented here, I conclude that Song Sparrows in the Point Reyes populations do not have song dialects that vary concordantly with those of White-crowned Sparrows. Nor is there any strong evidence for calling any of the four samples of Song Sparrows distinct from any other, and therefore these populations do not exhibit dialectal variation. On the basis of entire song repertoires, each male Song Sparrow was unique. On the basis of comparisons of whole songs, sharing between

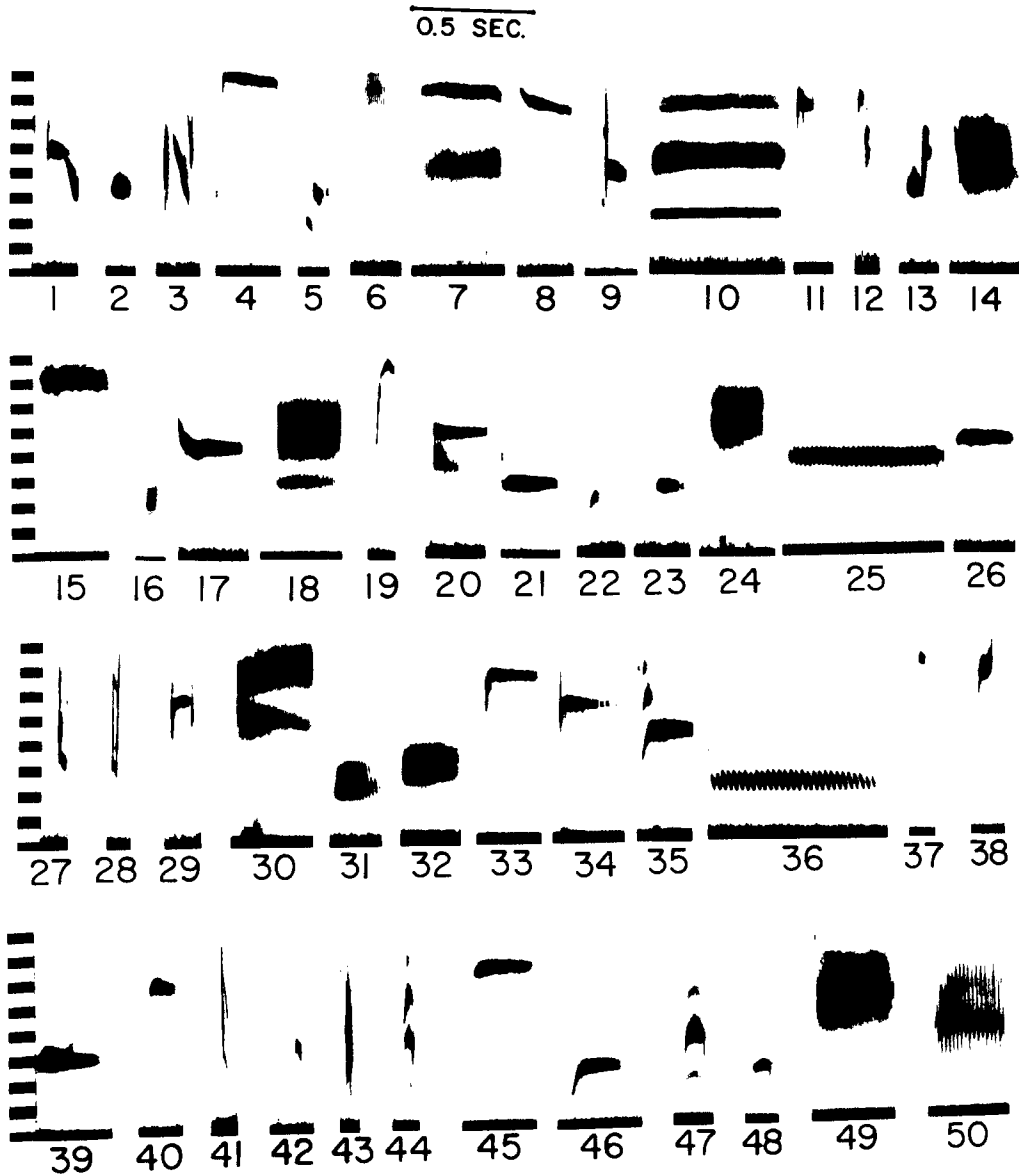


FIGURE 6. Note types. The 50 most common are shown.

individuals was rare. On the basis of trill syllables, there was considerable sharing among individuals within samples (33% sharing) and between samples (36% sharing) but none of this corresponded to the strict definition of dialect. Finally, on the basis of individual notes, the most fundamental component of song, there was again much similarity between individuals within samples (64% sharing) and among samples (58% sharing); none of the sharing patterns produced dialects.

From his emphasis on songs and trill syllables, Mulligan (1966) concluded that the three geographic races of Song Sparrows he studied around the San Francisco Bay also did not

have dialects. He did not, however, present a note-by-note data base against which careful comparisons could be made. Different investigators, of course, may differ in the degree of "splitting" and "lumping" when grouping notes or trill syllables into categories. Only the birds can tell us the final answer about categorical perception.

Harris and Lemon (1972, 1974) demonstrated the existence of dialects in Song Sparrows, but they differed with Mulligan (1966) and the present study in the meaning of "dialect." Harris and Lemon (1972) studied at two major locations, Parc Cote Ste. Catherine and Mont St. Hilaire, Quebec, separated by

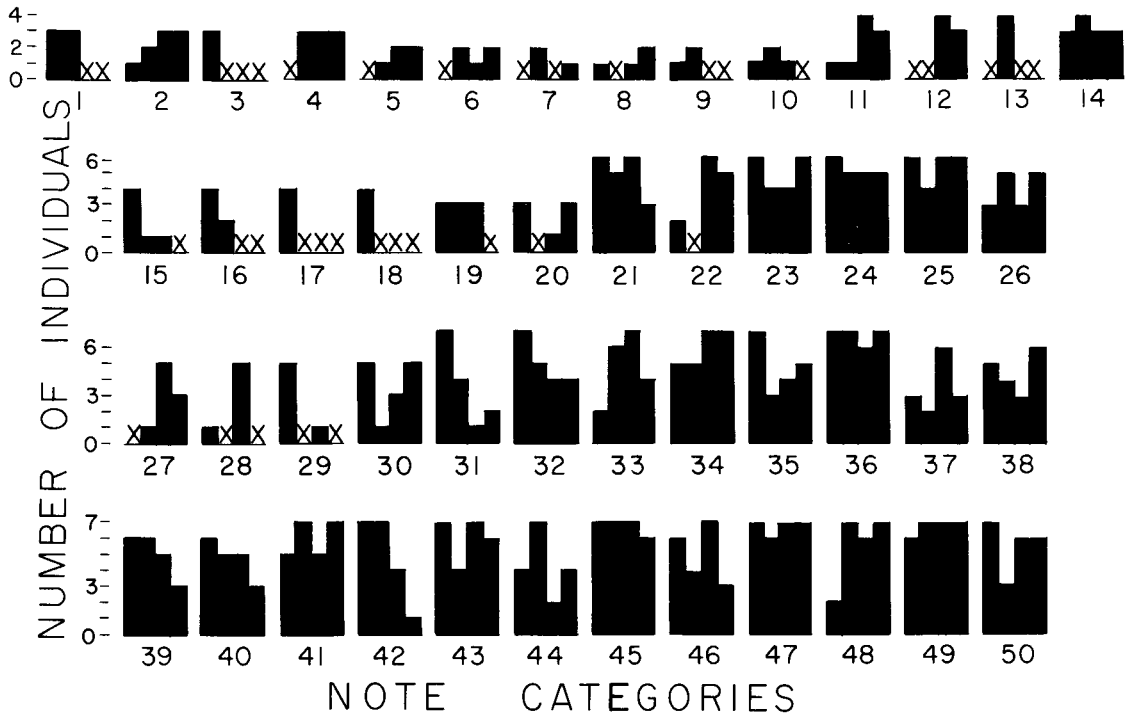


FIGURE 7. Frequency histograms of note types. For each type of note, the sample locations are as in Figure 5. An X indicates that no individual in the sample sang that type of note.

about 37 km. They found the average sharing of syllables among birds within each location to be 20–40%, but between locations sharing was practically zero. The minor sharing between locations fits Mulligan's definition of dialect but the relatively low sharing within a population does not.

Harris and Lemon (1974) tested for dialect discrimination between Song Sparrow populations by experimenting with playbacks to territorial males at the Parc Cote Ste. Catherine site. Despite the low amount of sharing within dialects, responses to the local and foreign dialects differed significantly (they used one-tailed statistical tests, however). Most interestingly, Harris and Lemon found considerable variation in the response of individuals to the playback stimulus (e.g., number of songs by each bird as listed in top of their Table 2). This could imply that the lack of a dialect marker common to all individuals caused some confusion for certain subjects of the playback experiments.

Alternatively, the Harris and Lemon (1974) playback results imply that a particular syllable type, while sung by only 20–40% of the birds, is nevertheless common enough to be familiar to most or all the males in a population. This could occur if the 20–40% of the birds who sang the syllable were scattered evenly over the population. Similarly, since

virtually no sharing occurred between dialects, almost any song from an alien dialect would be unfamiliar. Taken together, these postulates suggest it is possible that to any particular male the auditory environments of the local and alien dialect populations are perceived to be discretely different. This might occur even though an observer would have only about a 20–40% chance of assigning unambiguously a particular male in the correct dialect, unless of course the observer memorized the repertoire of every individual in the population.

Adopting the less restrictive view of dialects used by Harris and Lemon, and applying it to my data, still does not show strongly convincing dialect patterns. Using the criterion that three of seven birds in a sample (43%) have a particular trill syllable that is absent in other samples, there are three such cases (Fig. 5): syllable #6 distinguishes Muddy Hollow from the other samples, #18 distinguishes both Coast Guard and Lake Ranch from the others, and #20 distinguishes Coast Guard from the rest. Suggestive patterns are also seen in trill syllables #4, 7, and 19. Applying the same criterion to the distribution of note types also provides few clear cases (Fig. 7): three in Coast Guard (#3, 17, 18), one in Lake Ranch (#13), and none in Beach or Muddy Hollow. Applying the criterion to the grouped samples of Coast Guard (CG) + Lake Ranch (LR) in

comparison to Beach (B) and Muddy Hollow (MH), which groupings are then concordant with the three White-crowned Sparrow dialects, there is one note (#1) present in 6 of 14 of the combined CG-LR birds that is absent in both B and MH. There is also one note (#12) present in both the B and MH samples that is absent in CG-LR. Notes #16 and 28 also have suggestive patterns corresponding to dialects concordant with those of White-crowned Sparrows. Other possible groupings of notes in Song Sparrow samples that do not correspond to dialects of White-crowned Sparrows can also be found, for example notes #4 and 19 (Fig. 7). These results do not make a strong case for the existence of dialects in these Song Sparrows as only one or two notes in 50, or one or two trill syllables in 22 distinguish the two dialects. It is nonetheless conceivable that this degree of difference is sufficient for the birds to make a discrimination.

I also calculated patterns of sharing as did Harris and Lemon (1972) by making all possible paired comparisons of note sharing within and between samples. This was accomplished according to the Harris and Lemon formulation in which twice the number of notes shared between two birds is divided by their total notes and this value converted to percent. For example, if bird #1 in sample #1 sings 29 different notes and bird #2 in sample #1 sings 28 different notes, of which 24 are shared, then the percent shared is  $(24 + 24)/(28 + 29) \times 100 = 84\%$ . The standard error on this proportion is 5%. Applying this approach to my data gave no convincing patterns corresponding to dialects. For example, there was an average of  $71 \pm 6\%$  note sharing among birds in the Coast Guard sample,  $65 \pm 7\%$  among birds in the Muddy Hollow sample (the two samples most distant from one another), and  $59 \pm 7\%$  sharing between the two samples. These values are group averages and the attendant standard errors of the proportions; therefore, the overlap among the three values suggests that they are not significantly different. Thus, the amount of note sharing within a sample is not different from the sharing between samples. Syllable and note sharing among Song Sparrows studied by Eberhardt and Baptista (1977) was  $56 \pm 8\%$ .

Both methods of examining similarity of song between samples suggest an absence of dialects in my four samples of Song Sparrows. The significant difference between Harris and Lemon's (1972) results and mine may be due to differences in population structure and distance between samples. The populations that Harris and Lemon found to differ in song components were 37 km apart whereas the two most distant samples in my study were 20 km

apart. Probably more important than distance, however, is that in the Point Reyes National Seashore habitat was continuous, posing no ecological barriers to dispersal. Although Harris and Lemon did not discuss this point, maps of their study region indicate that their two populations were isolated by intervening habitat unsuitable for Song Sparrows, probably a significant barrier to dispersal.

My study yielded no strong evidence that Song Sparrows have dialects over the same geographic region where White-crowned Sparrows have dialects. The minor evidence that suggests concordance between the two species in song variation requires playback experimental evidence to refute it. I tentatively accept the view that song variation of the two species is not concordant, which does not support the colonization hypothesis of dialect formation. This conclusion cannot be considered a strong refutation of the colonization hypothesis of dialect formation because it rests on some fairly weak assumptions. First, it assumes that the two species would respond to the availability of the new habitat in the same way. This could be erroneous if the two sparrows differ in their minimal habitat requirements for colonization. Second, it assumes that both species would generate song variants in the same way. The experiments of Kroodsmas (1977) on Song Sparrows and of Marler (1970) on White-crowned Sparrows strongly indicate that the Kaspar Hauser innate songs of the two species are qualitatively different. The innate song of the White-crowned Sparrow is considerably unrefined in comparison to the natural adult song whereas that of the Song Sparrow is much closer to the normal adult song structure. Therefore, even if young Song Sparrows colonize a new area they may carry along a suite of song components that is not depauperate. Important evidence to test the colonization hypothesis would be obtained by observing the process through time. Such an opportunity would arise following a large-scale fire in the coastal scrub environment.

#### ACKNOWLEDGMENTS

Thanks go to D. B. Thompson for field assistance, M. A. Cunningham for discussions of ideas, S. C. Golian for making sonograms, and L. Martini and L. Ryan for help with data reduction. D. E. Kroodsmas, L. F. Baptista, and H. G. Kramer provided helpful advice on the manuscript. Financial support was provided by the National Science Foundation (DEB-78-22657, BNS-82-14008).

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*Condor* 85:490

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## RECENT PUBLICATIONS

**The Emergence of Ornithology as a Scientific Discipline: 1760-1850.**—Paul Lawrence Farber. 1982. D. Reidel Publishing Co., Dordrecht, Holland. 191 p. \$39.50. Source: Kluwer Boston, Inc., 190 Old Derby St., Hingham, MA 02043. During the late 18th and early 19th centuries natural history was transformed from a general and highly literary activity into a set of specialized scientific disciplines. This monograph uses ornithology as a case study for examining that process, it being one of the first zoological disciplines to emerge and one that attracted considerable attention and support. Farber is a historian of science, not an ornithologist, and he takes a broader approach than previous histories of ornithology. He relates the evolution of this discipline to changes in its social, economic, philosophical, religious, and scientific context. The rise of ornithology is shown to be linked with colonialism, the growth of museums, and the 19th century vogue of natural history. While this well-written book is aimed at scholars of Western intellectual history, it deserves to be read by ornithologists who want to learn about their roots. Notes (including references), index.

**Flight of the Storm Petrel.**—Ronald M. Lockley. 1983. Paul S. Eriksson, Middlebury, Vermont. 192 p. \$16.95. Storm-petrels are unfamiliar to many birders although they inhabit all the oceans except the Arctic and one species is reputed to be the most numerous sea bird, if not the most numerous of all birds in the world. It is amazing that such small birds (one species weighs no more than a Song Sparrow) manage to survive tempestuous conditions and migrate tens of thousands of kilometers annually. Lockley has enjoyed a life-long fascination with storm-petrels and in this book he has synthesized and distilled all that he and others have learned about them. The first half is devoted to *Hydrobates pelagicus*, by far the best-known of the 21 species, and the second half deals with the remainder. A wealth of information is presented in a clear and non-technical style, interwoven with Lockley's own experiences. A good read in natural history, this book conveys not only a lot of facts but also the author's pleasure in acquiring them. The text is illustrated with many nice pen-and-ink drawings by Noel W. Cusa. Maps, references, index.