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GEOGRAPHIC VARIATION IN THE SONG OF BELDING'S SAVANNAH SPARROW (*PASSERCULUS SANDWICHENSIS BELDINGI*)

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GEOGRAPHIC VARIATION IN THE SONG OF BELDING'S SAVANNAH SPARROW (*PASSERCULUS SANDWICHENSIS BELDINGI*)

Richard Alan Bradley[1]

Synopsis: The song of Belding's Savannah Sparrow, resident from Santa Barbara, California, south to El Rosario, Baja California del Norte, was studied during the spring of 1973. Songs were recorded from individuals at 14 of the 15 remaining breeding localities of this subspecies and analyzed with an audiospectrograph. Recordings of color-banded birds indicated that each male sang a single highly stereotyped song pattern. Detailed analysis of intrapopulational and interpopulational variation was made. The study of interpopulational variation yielded a mosaic pattern of song "dialects." The occurrence of such song dialects has been substantiated elsewhere for a variety of species. The present study involves very small adjacent, but isolated populations.

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INTRODUCTION

Geographic variation in bird song has been the subject of recent studies and has taken several forms. The early emphasis was on documentation of variation within species having wide distributions. More recently comprehensive studies have been conducted using recordings from many localities or analyzing variation between local contiguous or isolated populations. Perhaps the best summary of the work on geographic variation in bird song is by Thielcke (1969).

Early work on the Chaffinch (*Fringilla coelebs*) and other species revealed a distinctive mosaic pattern of variation (Thielcke 1969). Song patterns used by most of the birds in one place are similar to their neighbors' songs, while individuals from other populations have different themes. Often an entire system of such variants is found when several different populations are studied. The term "song dialect" refers to this type of variation. Many authors discussed the evolutionary significance of song dialects. Mayr (1963) stated that geographic variation of song is a widespread isolating mechanism in birds. Other workers expressed similar ideas about song as an isolating mechanism (Thorpe 1961, Marler and Tamura 1964, Lanyon 1969, Nottebohm 1969, Thielcke 1969, Armstrong 1973).

Nottebohm (1972) summarized the proposed mechanisms of such isolation:

> "It is necessary to assume that female birds develop a preference for the song dialect of the area where they are born, and that this preference is revealed in their choice of partner. Males in turn must learn to sing the dialect of their birth area. If birds of both sexes migrate or wander between fledgling age and their first breeding season, they must return to breed in the same general area where they were raised. In this fashion an assortative mating system based on song preferences reinforces a more or less loose philopatry."

The Savannah Sparrow (*Passerculus sandwichensis*) is one of the most widely distributed of North American sparrows. The species breeds from 71°N (Barrow, Alaska) south to 16°N (Hacienda Chancol, Guatemala) and is divided into 18 subspecies that vary considerably in size, proportions, and coloration (American Ornithologists' Union Check-list 1957, supplement 1973). Of the 18 subspecies 8 are restricted to the coastal marshes of California and northwestern Mexico. Van Rossem (1947) presented an excellent review of the seven races that breed in western Mexico.

The Savannah Sparrow form that breeds along the coast from Santa Barbara south to El Rosario was originally named as a full species, *Passerculus beldingi*, by Ridgway (1885). This race, now known as *Passerculus sand-*

wichensis beldingi (American Ornithologists' Union Check-list 1957) is referred to here as Belding's Sparrow. The name Savannah Sparrow is used when referring to the species in general.

Belding's Sparrow is restricted to the tidal salt marshes of southern California and northwestern Baja California. In a preliminary census conducted in conjunction with this study, I estimated a population of fewer than 3,000 singing males (Bradley 1973). The restriction of this subspecies to local patches of salt marsh has produced small isolated populations ideal for the study of geographic variation. The pattern of song variation within the species, as outlined by Borror (1961a) is well suited to the development of song dialects: (1) each bird sings only one song pattern, (2) variation occurs between different individuals, and (3) song patterns used in any particular location show considerable overlap.

Because of restrictions of distance and time, recordings could be made of only a limited number of populations. As a result, a somewhat arbitrary decision was made to restrict the study to the coastal populations now assigned to *P. s. beldingi.* Recordings from another coastal subspecies (*P. s. alaudinus*) in central and northern California indicate a continuum of similar patterns of variation in that subspecies, and perhaps throughout the species. This study was conducted primarily in the spring of 1973, although some additional observations and recordings were made later in 1973 and early in 1974. Tape recordings were made of 280 different individuals at 14 of the 15 known remaining breeding sites of Belding's Sparrow. No recordings were made at Ensenada Bay, Baja California del Norte, because of time limitations and the small, widely-scattered nature of that population.

ACKNOWLEDGEMENTS

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METHODS

RECORDINGS

Most of the recordings in this study were made with a Uher 4000 Report S tape recorder and a Uher M 512 microphone mounted on either a 61 cm or a 76 cm fiberglass parabolic reflector. Some additional recordings were made with a Sony TC 800 recorder and a Sony ECM 19 B microphone mounted on the 61 cm reflector. All recordings were made at a tape speed of 19 cm/s. Recordings were made in the field with a hand-held reflector during the peak period of song activity in the morning. Copies of the recordings are on file in the Bioacoustic Archive of the Florida State Museum, Gainesville.

Belding's Sparrow is a bird of the coastal salt marshes of southern California and is largely restricted to *Salicornia*-covered tidal flats. Each singing individual, presumed to be a male, defends an exclusive territory in this habitat and regularly sings from one or more exposed perches within his territory.

When I surveyed a particular location, I made recordings beginning with an individual at one edge of the marsh and continued in a regular pattern from territory to territory until the entire nesting area had been traversed. Usually I recorded 5 to 10 songs from each individual. As males of this subspecies defend very small territories (Bradley 1973), each singing bird could be identified by its song perch location.

Great care was taken to record songs from distinct individuals. In those cases where a large number of birds were singing from a relatively small area, only a few individuals were recorded if any probability of confusion existed. With this method only small samples could be obtained from some sites, but these samples are free from duplication. At some locations the samples were recorded on two or more dates. In each case additional recordings for the sample were made in parts of the marsh where birds had not been previously recorded. A list of locations visited and sample sizes obtained is presented in Table 1. Information on the approximate population size at each location is presented elsewhere (Bradley 1973).

TABLE 1.—LOCATION DATA.

Number	Location and City	Sample Size	Letter Code
01	Goleta Slough, Santa Barbara	7	GS
02	El Estero, Carpinteria	28	EE
03	Mugu Lagoon, Point Mugu	28	PM
04	Playa del Rey, Los Angeles	4	PR
05	Anaheim Bay, Seal Beach	61	AB
06	Huntington Harbour	5	HH
07	Bolsa Chica Lagoon, Orange County	0	BC
08	Upper Newport Bay, Newport Beach	30	NB
09	Santa Margarita Lagoon, Oceanside	29	SM
10	Agua Hedionda Lagoon, Carlsbad	10	AH
11	San Elijo Lagoon, Cardiff	4	SE
12	Los Penasquitos Estuary, Del Mar	21	LP
13	Imperial Beach, Imperial Beach	8	IB
14	Ensenada Bay, Ensenada	0	EB
15	San Quintin Bay, San Quintin	34	SQ
16	Laguna El Rosario, El Rosario	11	ER

Playback of recorded song was successful in eliciting close approach and song in several individuals tested at Anaheim Bay. Although the song of each individual proved to be constant, no playback was used during the sampling portion of this study to avoid any possible influence on the songs to be recorded.

To determine the amount of individual variation in song, and to verify information about the territoriality of males of this form, a number of individuals were color-banded. Birds were captured in mist nets set across the surface of the marsh in the evening. In addition to a Fish and Wildlife Service numbered aluminum band, three colored plastic bands were used on each bird to produce individually recognizable combinations. Songs of some additional known, but not color-banded individuals were recorded in the study period. These unbanded individuals were chosen because they occupied solitary or readily identifiable territories where they could be found repeatedly. All work on individual variation was carried out at the main study location at Anaheim Bay. This site was relatively free from outside interference.

ANALYSIS

One or more songs of each individual recorded were analyzed on a Kay Elemetrics Corp. Sona-Graph, model 7029 A, employing the 160-16, 000 Hz scale, HS (high-shape) equalization, and narrow band filter. Each audiospectrogram was then analyzed in detail. Each song was transcribed into an alphabetic sequence and every distinguishable note given a paired code of two letters. A total of 86 distinct note types were named from recordings made during this study (Figs. 1 and 2). The first letter of the paired code (upper case) designates the general note type (e.g. B notes are usually high-pitched introductory notes). The second letter (lower case) indicates the specific variant of that particular note type. When one note is repeated two to several times in sequence, a number follows the two-letter code indicating the number of repetitions (e.g. the note Ca repeated three times would be coded as Ca3). A complex string of letters and numbers is then constructed as a representation of the specific song pattern of an individual. For example, the song pictured in Figure 3 would be coded as AaBb4PaDaDbDcKaFdFeJa. In a few cases a phrase (composed of many similar notes or syllables) was named with only one pair of letters. Sequences so named are rapidly modulated buzzes or buzz phrases. It would be difficult to count each modulation in a buzz, and I believe that enumerating each as a separate note would be meaningless. Differences in the rate of modulation and tonal quality of the buzz phrases are indicated by the different lettered codes assigned to them.

Recordings of the songs from several known individuals were analyzed for diurnal and seasonal variation. Finally, comparisons were made of inter- and intrapopulational variation in the songs.

TERMINOLOGY

The nomenclature of bird song is nearly as variable as the number of studies conducted. In this paper I have tried to use universally recognizable terminology, although in some cases it may differ considerably from some other published works.

SONG.—The term song is here applied to the basic species-specific or "primary" song as distinguished from the other call notes of a species.

SONG BOUT.—A series of songs given in sequence at a more or less regular rate, ending with a much longer pause or with the cessation of song.

NOTE.—A note has been almost universally defined as the smallest unit of bird song. It is represented on an audiospectrogram as a continuous trace. Schwartz (1972) gave a similar definition for the term "figure."

PHRASE.—A group of notes that combine to form a recognizable unit is termed a phrase (the "note complex" of some authors). The individual notes that combine to form a phrase were termed syllables by Marler and Tamura (1962).

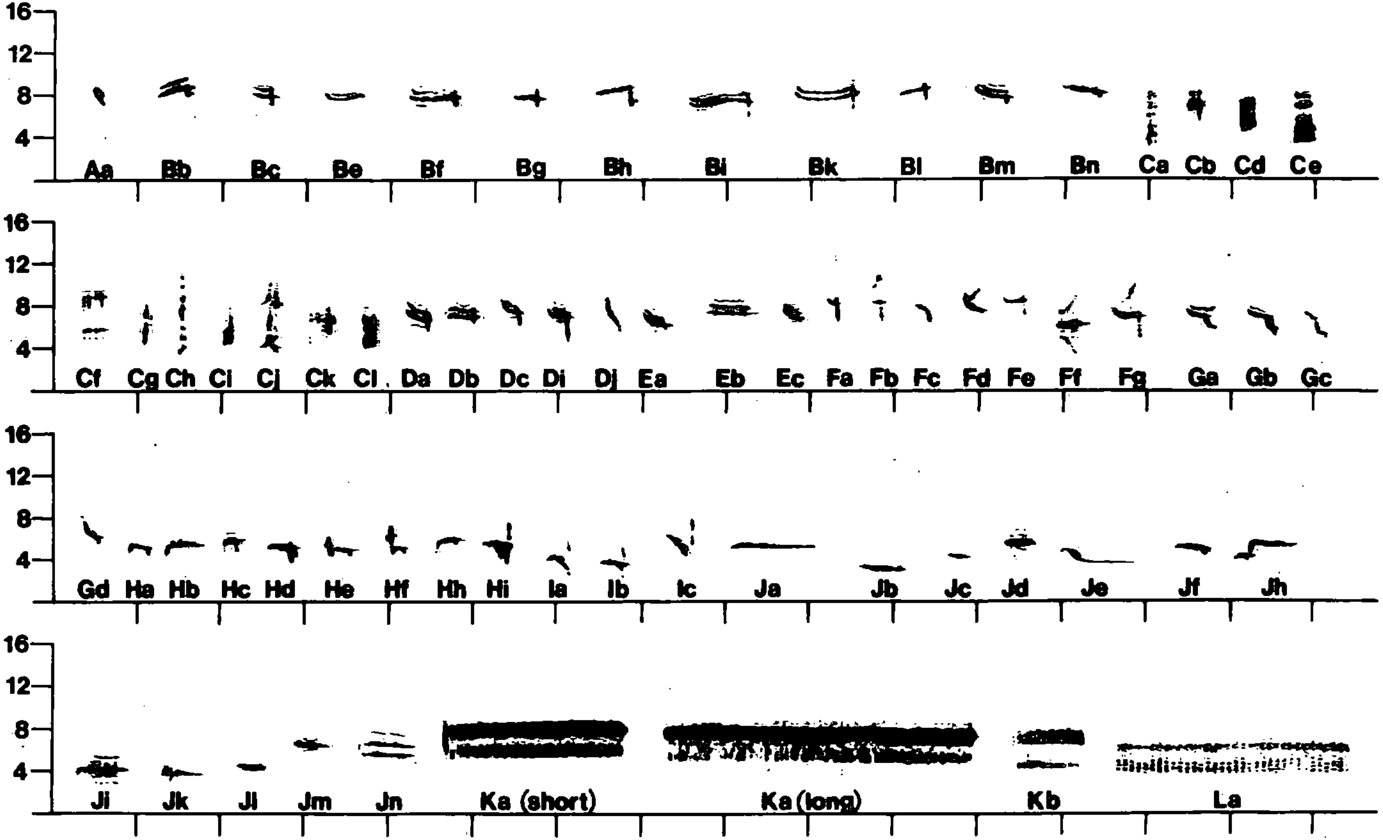
BUZZ.—A phrase made up of many similar notes uttered in rapid succession is a buzz. Borror (1965) used the term buzz for sounds consisting of notes repeated at a rate greater than 40 per second, or a single note that fluctuates at this rate. It should be noted that audiospectrograph analysis yields little information about the nature of the modulation in a buzz. It is nearly impossible to tell if a sound is frequency or amplitude modulated (Greenewalt 1968). For an accurate determination of the nature of the modulation within a buzz or other complex note, one should use an oscilloscope as Greenewalt (1968) demonstrated.

SONG PATTERN.—The particular sequence of notes and phrases that comprise the song of an individual is considered as one song pattern (equals "song type" or "theme" of other authors). In some cases several individuals may sing songs of the same song pattern.

RESULTS

CALL REPERTOIRE

In addition to the primary song of the species, the chief subject of this study, the Savannah Sparrow has a number of other typical vocalizations. Gobiel (1970) described the various calls in this species' repertoire. I heard


16
12
8
4
Aa
Bb
Bc
Be
Bf
Bg
Bh
Bi
Bk
Bl
Bm
Bn
Ca
Cb
Cd
Ce
16
12
8
4
Cf
Cg
Ch
Ci
Cj
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Ea
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Fg
Ga
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16
12
8
4
Gd
Ha
Hb
Hc
Hd
He
Hf
Hh
Hi
Ia
Ib
Ic
Ja
Jb
Jc
Jd
Je
Jf
Jh
16
12
8
4
Ji
Jk
Jl
Jm
Jn
Ka (short)
Ka (long)
Kb
La

and recorded many of the same call notes he described, as well as a few additional ones.

Dwight (in Chapman 1896) described the typical call note of the species as a vigorous "chipping." Gobiel referred to this note as a softer version of the "tsip" alarm note. Spectrograms of the typical call note recorded in the present study are presented in Figure 2. This note ranges in frequency from 8.5 to 10 kHz and is rather weak with a duration of less than 0.05 seconds. Both sexes uttered this "chip" note in a variety of contexts.

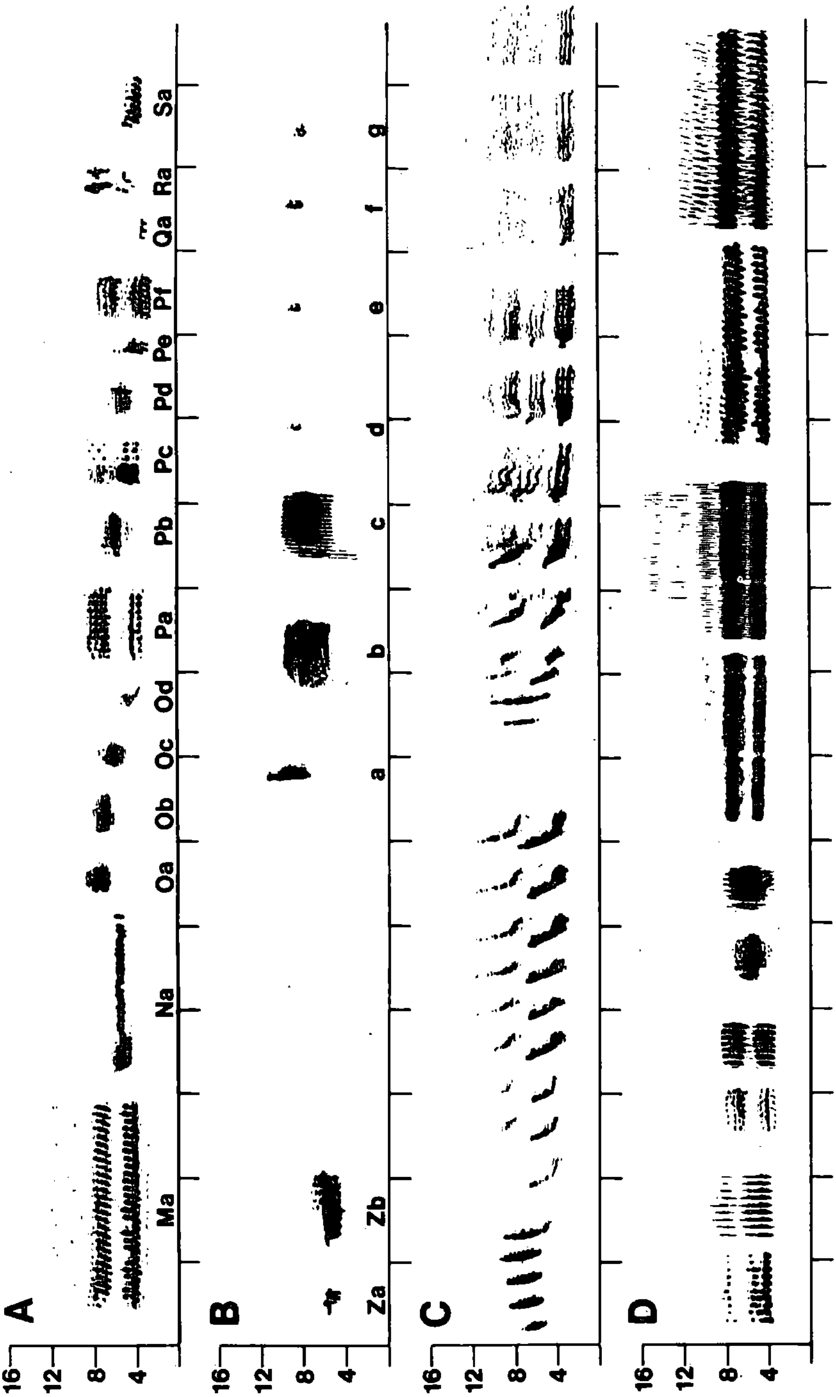
A slight variant of the typical call note described above was also recorded. This variant was associated with copulation. Although I have heard both sexes using this copulatory note, it is more frequently uttered by the female. The structure of the copulatory note is illustrated in Figure 2. The frequency and temporal characteristics of this note are quite similar to those of the typical call note. The copulatory note is given just prior to copulation and is repeated in rapid succession with intervals of less than 0.5 seconds.

The alarm note of the species is much louder and harsher than the typical call note. Gobiel described the alarm note as "tsup" or "tsip." A spectrogram of this note is included in Figure 2. The frequency range of the alarm note (7 to 11 kHz) is much greater than that of the typical call note and is considerably louder. The time interval between successive alarm notes depends upon the emotional state of the calling bird. In general the rendition increases in rate, intensity, and volume as an intruder moves deeper into the nesting territory. The functions of the alarm note are to warn other sparrows of impending danger and probably to distract a potential predator from the nest or young.

The intraspecific agonistic note is actually a loud buzz, which Gobiel termed the hostile note. Both wide and narrow band spectrograms of this buzz are presented in Figure 2. The hostile buzz is usually uttered twice in close succession. Gobiel described the resultant sound as "psst-psst" or "buzt-buzt." When delivered on the ground this buzz is usually accompanied by stereotyped posturing. The calling bird crouches down with its tail slightly cocked and the wings lowered and fluttering out to the sides. On a few occasions I saw actual attacks made by two adjacent territorial males that were displaying and buzzing to each other. In addition this buzz is frequently given during an aerial chase.

The last and most complex call is presented in Figure 2. I have termed this vocalization the flight slur; it is actually a complex sequence of notes lasting

FIGURE 1.—Spectrograms of the different note types. Each of the note types from Aa to La are illustrated here in alphabetical order. A few of the combinations that might be expected (Bd, Bj, Cc, etc.) were not present and have either been superseded by new naming schemes or proved indistinguishable from existing note types. Two examples of the Ka buzz are included to demonstrate the continuous variability in the length of this phrase. In all figures frequency is plotted on the ordinate in kHz. In Figures 1 and 2 time is plotted on the abscissa in 0.2 seconds, in Figures 3 through 15 in seconds.


A
B
C
D
16
12
8
4
Ma
Na
Oa
Ob
Oc
Od
Pa
Pb
Pc
Pd
Pe
Pf
Qa
Ra
Sa
Za
Zb
a
b
c
d
e
f
g

about 3.2 seconds. Although I noted this sound given most frequently at the end of an airborne chase sequence, occasionally it is given from within the vegetation (Barbara Massey, pers. comm.). The flight slur may be analagous to the "flight song" described by Gobiel, who stated that the flight song was used in communication between two members of a mated pair. I am not certain of the function of the flight slur, but I believe it is associated with aggression.

FEATURES OF SONG DELIVERY

To me, the delivery of the Savannah Sparrow's primary song is perfunctory, almost seeming mechanical at times. The singer usually perches in an upright stance with the head held slightly back and utters the song with the bill wide open. The song of Belding's Sparrow is usually given while the bird is perched atop a sprig of *Salicornia.* I have also seen birds singing from higher perches, such as the tip of small mounds of soil, fence posts, and other wooden structures, as well as an occasional utility line. In addition to these typical singing perches I have several times seen birds singing from open mudflats. During intense territorial disputes males even uttered the primary song in flight.

Although several authors have written of the male's song there is little direct evidence that only the male is capable of song. I made observations on 10 individuals that I caught and color-banded. Of these 10 birds, 6 were known to be males (cloacal protuberances present), 1 was a known female (brood patch present), and 4 were not sexable. In the term of this study, I saw the known female only twice after banding. She did not sing, but she did utter the typical call note of the species. Of the six color-banded males only four were seen subsequently, and all four sang regularly.

In addition to these observations of color-banded individuals, twice I saw mating. Both times the male engaged in song bouts before and after the copulatory act. The female was silent except for the copulatory note.

Additional studies of more color-banded individuals need to be undertaken, but considering closely related species (Bent 1968) and the observations made in this study, song is most probably limited to the male. Herein singing birds are assumed to be males.

The singing rate (number of songs per minute) varies with the time of day, season, and the emotional state of the singing bird. This rate usually ranges

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FIGURE 2.—Spectrograms of the different note types and calls. Line A and the first portion of B represent a continuation of the list of note types from Ma through Zb. The last part of B illustrates the typical call notes of the species: a—alarm note, b—agonistic buzz (narrow band), c—agonistic buzz (wide band), d through f—typical call notes (three repetitions), and g—precopulatory note. Line C is the flight slur. Line D shows different buzz phrases, first a narrow band, then a wide band spectrogram of the same buzz. The phrase pairs in sequence are Pa, Pf, Pb, Ka, and Ma buzzes.

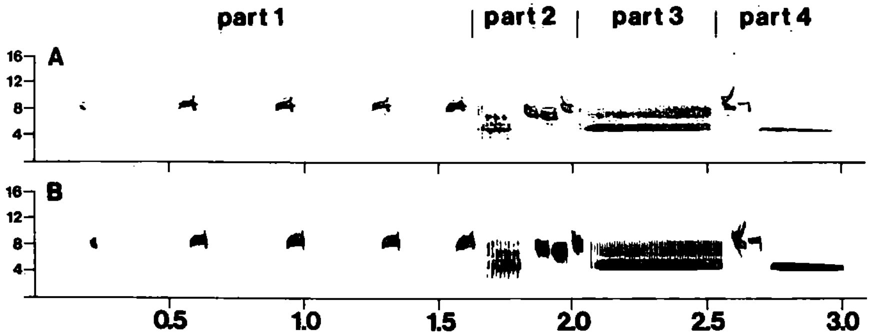

FIGURE 3.—The four parts of a song. A is a narrow band spectrogram of bird song number 05-50, B a wide band spectrogram of the same song.

from six to eight songs per minute. Singing may begin just before sunrise, but the peak of song occurs most often between 30 and 90 minutes after sunrise. In general, song activity decreases throughout the day with a lull during the midday hours. Song activity makes a secondary peak in the evening and may continue until well after dark. For example, on 27 March 1973 the evening song peak was at 1830 (about 20 minutes after sunset) and singing continued until about 1900. I heard sporadic songs as late as 2200. King (1972) also reported hearing night song from the Rufous-collared Sparrow (*Zonotrichia capensis*).

In addition to diurnal variation, the rate of singing changes with the season. I first heard song at the main study area (Anaheim Bay) on 26 January, when a few males were singing sporadically. On 2 February there was considerably more song activity, and I saw several territorial chases. The height of singing in 1973 lasted from mid-February through mid-May. Song activity was noticeably lower in late May and dropped off rather quickly in June. By the end of July adult song activity was very low, but I began to hear subsong from birds of the year. In late August subsong activity was high, and only occasional adult songs were heard. The following winter (1973-1974) song activity began earlier in the year. By 24 December adult song was heard occasionally, and it was noticeably more regular on 9 January (Barbara Massey, pers. comm.).

The rate of singing can be increased artificially by recording an individual's song and then playing it back through a loudspeaker. With this technique I could increase the rate of song to approximately 12 songs per minute. That one individual rarely sings alone is interesting to note. The song of one bird tends to stimulate all of his territorial neighbors, which frequently transforms relative silence into a peak of song activity by a chain reaction of singing and countersinging.

THE STRUCTURE OF THE PRIMARY SONG

The primary song of the Savannah Sparrow is a rather unmusical series of thin high-pitched chips and buzzes. One of the most accurate general descriptions of the song of the Savannah Sparrow is given by Borror (1961b). Although the Belding's Sparrow songs recorded in this study have qualities similar to those Borror described, several differences are apparent.

The high pitched and rather weak nature of the primary song of the Savannah Sparrow may be related to the territory size and habitat preferences of the species. As I have already mentioned, males of this species command very small territories. Pairs nest primarily in open grassland or marshland habitats. As distances between neighbors are quite small with little or sparse intervening vegetation, no necessity exists for a louder or lower pitched song that would carry farther. In fact, the weak nature of the song may well render the singing males less conspicuous to predators. The characteristics of Savannah Sparrow song conform well to the theory, discussed by Emlen (1971a), Jilka and Leisler (1974), and Morton (1975), relating the quality of a species' song to its habitat.

The songs of individuals recorded in this study ranged in length from 1.7 to 3.1 seconds, and most songs were between 2.0 and 2.5 seconds long. The notes range in frequency from 2 to 12 or 13 kHz (certain harmonics may reach 16 kHz or higher). Most of the sound energy is concentrated between 4 and 11 kHz.

The structure of the primary song is best described by treating it in four sections (Fig. 3). The first section (Part I) is composed of three to eight similar notes. These introductory notes average higher in pitch than the remainder of the song. Most are named as variants of note B (Fig. 1 and 2). As the spectrograms of notes Bb through Bn show, the structure of the note includes a horizontal portion and a vertical portion. The horizontal portion represents a continuous tone of one frequency and the vertical portion a sharp staccato ending. This ending makes the sound audible as a "chip." In contrast, a note that lacks this sharp ending has a more melodious sound (like note Ja). In addition to the introductory notes of type B, Part I often includes the very short and high-pitched note Aa, which is quite similar to the typical call note of the species. In fact a calling bird occasionally broke directly into song, incorporating the last call note or two into the introductory phrase. I heard note Aa from nearly every sparrow recorded, yet no bird included it consistently. Therefore, I have assigned very little importance to the presence or absence of note Aa.

The second part of the primary song varies in composition. Among the 50 different note types that occur in Part II many are shorter than 0.1 seconds. Individual birds include from 1 to 11 different note types. In some cases a particular note is repeated 2 to 17 times in sequence. Notes of the general types C, D, and E are frequently found in Part II. In many cases these notes are arranged in a specific pattern that may recur in songs of several other members of the same population. For example the sequence DaDbDc is common among birds recorded at Anaheim Bay. In addition to these notes, individuals often include a very short buzz in Part II. Buzzes found in Part II, unlike most of the buzzes that compose Part III, are modulated approximately 50 to 100 times per second. The buzzes that occur in Part II are classified as P, S, and Z phrases (Fig. 2).

The third part of the song is the main buzz section. It usually includes one or two K-type buzzes or an L-type buzz. Buzzes occurring in Part III are much more rapidly modulated than the type of buzz phrase found in Part II. The rate of modulation is frequently as high as 180 times per second. On the narrow band spectrograms these buzzes appear as indistinct bands, ranging in frequency from 5 to 10 kHz. With the wide band filter setting, spectrograms are produced that appear as a series of vertical streaks (Fig. 1). In addition to the buzz phrases in Part III, a few shorter notes are found occasionally between two successive buzzes. Many of the note types found between buzzes are the same as those found in Part II. Rarely a sequence of notes characteristic of Part II will also lie between the two buzzes.

The final section of the primary song is the shortest of the four parts. This "terminal flourish" is composed of one to five short high-pitched notes followed by a single low-pitched note. The high-pitched notes are occasionally complex in structure. In some cases they even appear to possess the dual-source quality described by Greenewalt (1968). Examples of such complex notes are classified as types F, I, and R. The final note is usually between 0.15 and 0.4 seconds in length and has a pure, almost whistled quality (note Ja, Fig. 1). This tonal quality is attributable in part to the narrow frequency range of the note (between 5 and 6 kHz). As will be shown later, Part IV is one of the most consistent phrases found within the songs of a particular population. In addition, most populations have one or more unique variants of this terminal flourish.

Ontogeny of the Song

To my knowledge no study on the development of song in the Savannah Sparrow has been conducted to date. A complete study, probably involving Kaspar Hauser isolates, is needed before definitive conclusions about song learning can be made, but the following observations may throw some light on the process as it may occur in the wild.

I first heard subsongs, presumably given by birds of the year, on 28 August 1973 in the marsh at Anaheim Bay. A hatching-year individual can usually be identified in the field by the grayish color of the superciliary line and loral spot, which are yellowish in an adult. The plumage of the young bird appears looser and the markings less distinct. Subsongs were delivered from the top of *Salicornia* bushes in the same general manner as the definitive songs of adult males. Young birds rarely throw back the head or open the bill and they appear to assume a more relaxed posture.

Subsong at first is a rather low volume series of buzzes and chips with little organization. Another type of subsong, which presumably represents a later stage of development, resembles the "random warbling" described for many other oscines (Lanyon 1960). Even within this phase of song development some typical call notes are still included. One of the call notes most frequently heard was a buzz similar to the hostile buzz of adult Savannah Sparrows.

I term the third type of subsong "discrete subsong." This type of song was heard more frequently late in the summer and in the fall. It consists of a shortened "warbling" song about 2.5 to 3.0 seconds long, and contains some notes reminiscent of definitive primary song..In Lanyon's (1960) scheme, this phase is probably "rehearsed song." Unfortunately I was unable to visit the study area throughout much of the fall and winter, but young birds continued to sing subsong well into December (Barbara Massey, pers. comm.). In the peak season of subsong (late summer and fall) few adults were heard, and the primary song of adult males was sporadic and irregular. Structure of adult primary song heard at this time was typical of birds recorded in the spring.

Although Mulligan (1966) found that song development in Song Sparrows (*Melospiza melodia*) was essentially innate, studies of other fringillids indicate that young birds must learn their songs from adults. Chaffinches for example produce abnormal songs when reared in isolation (Poulsen 1951, Thorpe 1958). In similar studies summarized by Marler (1967), normal song development in members of the genera *Junco* and *Zonotrichia* was also dependent upon previous auditory experience. The role of learning and other aspects of the ontogeny of the song in Savannah Sparrows remains to be worked out.

INDIVIDUAL VARIATION

The song of each Belding's Sparrow is remarkably stereotyped. A typical song bout involves 15 to 20 droning repetitions of a particular song pattern. A short pause is followed by another monotonous song bout. With occasional pauses for feeding and maintenance activities, this pattern may last an entire morning during the seasonal peak of song activity. In fact, aside from minor omissions at the beginning or ending, the song pattern of each known bird recorded remained constant throughout this study.

As an example of this constancy, I have included spectrograms of bird 05-58 in Figure 4. As shown, the song pattern (AaBb3Ce3HiDaDbDcKaFdFeJa) is the same in all this bird's songs. These recordings were made during the period 14 February-21 April. Variation seen in recordings of this individual's song includes the occasional omission of an Aa, Bb, or Ce note, as well as the length of the buzz phrase. One color-banded male (XR-RR), first recorded on 2 April 1973, was recorded singing the same song pattern 10 February 1974. Although this is the only bird I was able to record in both nesting seasons

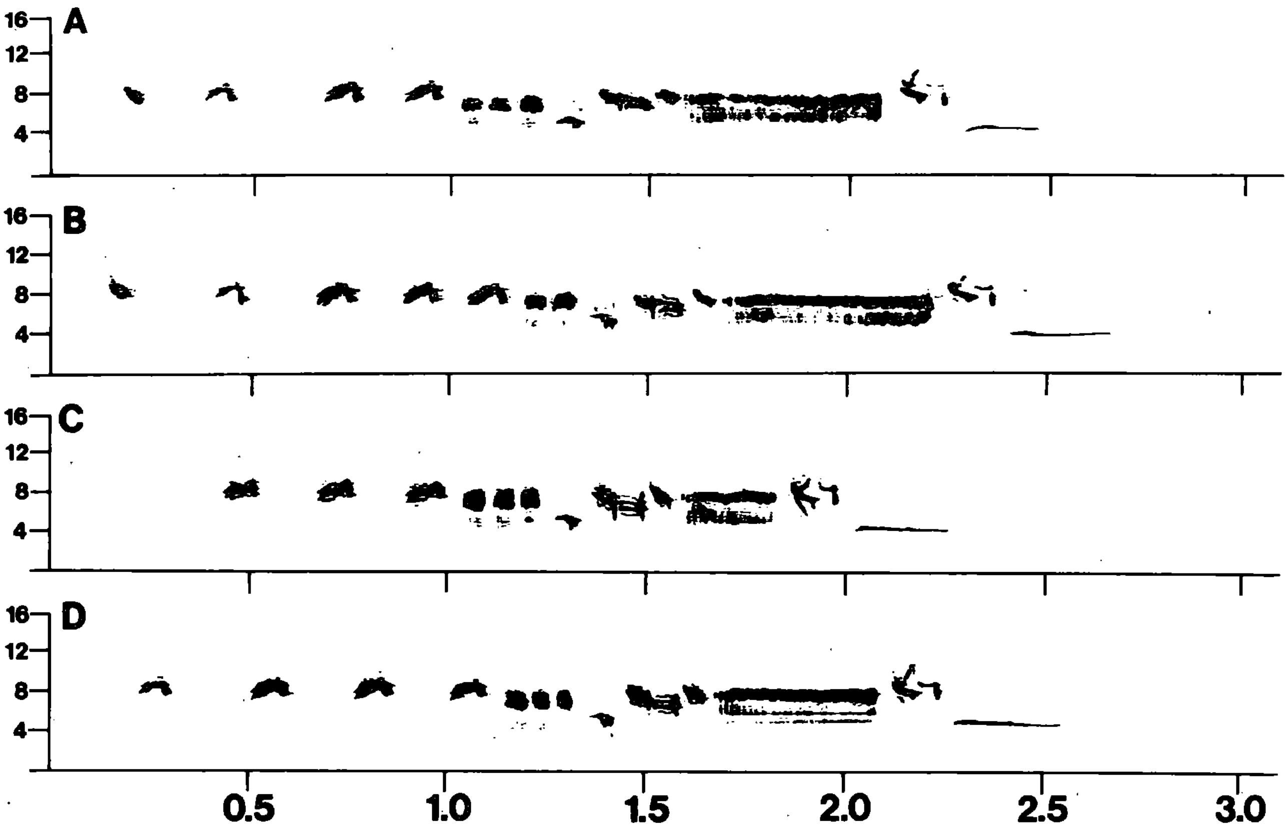

FIGURE 4.—Four spectrograms of bird 05-58. Note variation in the presence of the first introductory note Aa as well as in the number of Bb notes. This bird was one of the few that varied the number of a note in Part II (the note Ce is repeated three times in A, C, and D but only twice in B). A and B were recorded 14 February, C on 17 February, and D on 26 February 1973.

(1973 and 1974), I believe it probable that the song of most, if not all individuals is constant from year to year.

The chief variant within an individual's song is the omission of one or more A- or B-type introductory notes. A few birds varied the number of repetitions of other notes within their songs. For example, birds 05-26 and 05-58 at Anaheim Bay used either two or three C notes. In a few instances an individual cut his song short; each of these cases could be accounted for by outside disturbance. A bird that was in the middle of a song occasionally stopped to pursue an interloper in his territory. A few times I inadvertently made a sudden movement or sound that triggered an immediate cessation of song.

Although not all birds treated here as known individuals were color-banded, each was an occupant of a particular territory. Of the birds that were not color-banded, only individuals with fairly isolated territories could be followed throughout the season, such as bird 05-58 who defended a small territory along the edge of the marsh at Anaheim Bay just north of the marine laboratory trailer of California State University at Long Beach, and had no immediate territorial neighbors. This individual was easily located on each visit.

Many of the known individuals could not be located later in the season for additional recordings. One of the reasons for losing track of these birds in May and June was that a turnover in territorial males occurred after the first brood fledged. Apparently some males gave up their territories or moved to other territories after the first nesting. Others, possibly younger males, took their places and the cycle of nesting activity continued well into the summer.

In many bird species the repertoire of an individual is quite varied. Borror (1956) told of a Carolina Wren (*Thryothorus ludovicianus*) singing 22 different songs. In fact examples of species in which one individual sings a variety of song patterns can be found in many higher passerine families. Within the Fringillidae up to 24 different song patterns have been recorded from individual Song Sparrows (Nice 1943). Borror (1961a) listed 37 variants for an individual Bachman's Sparrow (*Aimophila aestivalis*) and 58 for a Lark Sparrow (*Chondestes grammacus*). In other members of the family the repertoire is not so varied. Songs of the Yellowhammer (*Emberiza citrinella*) and the Chaffinch follow a pattern, but each male has several slightly different themes (Thielcke 1969).

Belding's Sparrow is by no means unusual in having a restricted repertoire. The songs of male White-crowned Sparrows (*Zonotrichia leucophrys*), White-throated Sparrows (*Zonotrichia albicollis*), and Rufous-collared Sparrows are usually constant (Baptista 1974, DeWolfe *et al.* 1974, Marler and Tamura 1962, Nottebohm 1969), as are those of the Ortolan Bunting (*Emberiza hortulana* Conrads and Conrads 1971). Although there were a few exceptions, Thompson (1970) reported that most male Indigo Buntings (*Passerina cyanea*) sing but one song pattern. I know of no explanation for the variation in repertoire size of the various species that have been studied.

INTRAPOPULATIONAL VARIATION

Although the song of each individual Belding's Sparrow is nearly constant, the different birds in each population show considerable variation. A series of distinct song patterns were named from each recording locality. In fact the number of different patterns is usually slightly less than half of the sample size (Table 2). These song patterns do not occur with random frequency, and several song patterns are dominant. When individuals were sorted by song pattern, I found that nearly 50% of birds from a given sample sang one of the three dominant song patterns for that population (Table 2). In two marshes a single song type represented a large proportion of the sample. At Anaheim Bay 18 of the 60 individuals sampled used song pattern AB-01, and at El Estero 14 of the 28 birds recorded sang the pattern EE-02. At the other locations where relatively large samples were taken several song patterns were dominant.

TABLE 2.—FREQUENCY OF THE DOMINANT SONG PATTERNS.[1]

Location	Number of Song Patterns	Sample Size	Number Singing Dominant 3 Themes	% Singing Dominant 3 Themes
El Estero	8	30	21	70
Point Mugu	17	28	10	30
Anaheim Bay	23	61	32	52
Newport Bay	12	30	17	57
Santa Margarita	13	29	12	40
Los Penasquitos	13	21	10	48
San Quintin	15	34	14	41
Total	101	232	115	49.6

[1] This table includes only the larger populations, as analysis of populations with fewer than 20 individuals in the sample would be unproductive.

The spatial distribution of the different song patterns within a particular population was not studied in detail, but I did note that individuals with the same song patterns were somewhat clustered. In neighboring territories I frequently recorded four or five individuals with nearly identical songs. Although I was unable to plot the territories of individuals accurately, clustering can be demonstrated qualitatively by analysis of the San Quintin data recorded at two locations approximately 2 miles apart on opposite sides of this rather wide bay. Although the *Salicornia* marsh habitat is nearly continuous around the bay, there is probably little interchange between the two sites during the nesting season. When the songs of birds from these two areas were compared, I

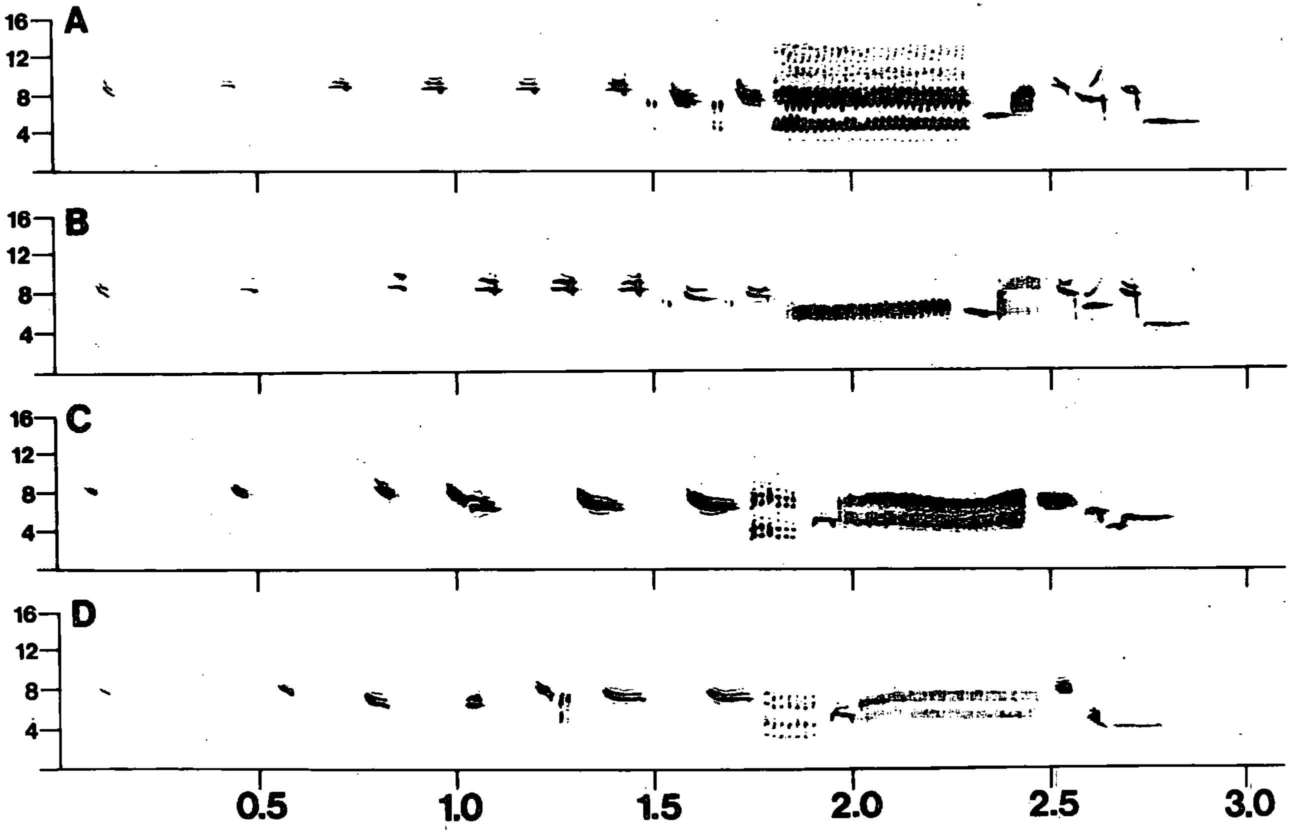

FIGURE 5.—Spectrograms recorded at Goleta Slough and Playa del Rey. A—song pattern GS-01, B—pattern GS-02, C—pattern PR-01, D—pattern PR-02.

found that only one song pattern was common to both sides of the bay. This song pattern (SQ-04) was recorded from four individuals on the east side of the bay. In addition, five song patterns were unique to the west side of the bay and nine were unique to the east side.

Clusters of similarly singing individuals were also noted in populations of Rufous-collared Sparrows (Nottebohm 1969) and Indigo Buntings (*Passerina cyanea)* (Thompson 1970). One possible explanation for the origin of clustering (supported by Thompson) is that first year birds learn their songs as they settle down on new territories in the spring. In this case they might tend to learn by imitation from their immediate neighbors. Kroodsma (1974) demonstrated that learning from neighbors occurs in Bewick's Wrens (*Thryomanes bewickii*). This theory implies that young males would undergo the transition from subsong to full song during the early spring. This is unlikely to occur in Savannah Sparrows as I noted no subsong activity during this period. In fact, on the first day songs were heard (28 January) the patterns were identical to those recorded later during the peak of song activity. Subsong was heard and recorded only in the late summer and fall.

The possibility that young birds learn their songs in the late summer from one adult, leave in winter, and then return to that specific area to form clusters seems equally remote. In contrast to other forms of the Savannah Sparrow, Belding's Sparrow is thought to be resident in the *Salicornia* marshes of coastal southern California and northern Baja California. Although Savannah Sparrows appear in flocks during the winter, it is possible that some degree of homesite tenacity restricts movement from one part of the marsh to another. Such site tenacity would explain the general tendency for birds on one side of San Quintin Bay to sing entirely different patterns from birds on the opposite side. Possibly those song patterns found in common were carried by an individual or individuals that strayed across the bay during the winter. The resolution of this question must await further study with color-banded individuals that can be followed from year to year.

A detailed analysis of intrapopulational variation was conducted at the main study area, Anaheim Bay. The sample obtained at Anaheim Bay contained 61 individuals, representing about half the estimated population of singing birds. Between 75 and 80% of the males nesting in northern and eastern portions of this marsh were recorded and yielded a total of 23 song patterns. As mentioned earlier, 18 individuals sang identical versions of the dominant song pattern AB-01. Table 1 lists the song patterns recorded at each locality and the number of individuals that sang each pattern.

Although each song pattern has a unique sequence of note types, several notes and phrases are common to most of the songs from one population. For example the introductory notes Aa and Bb were represented in each song pat-

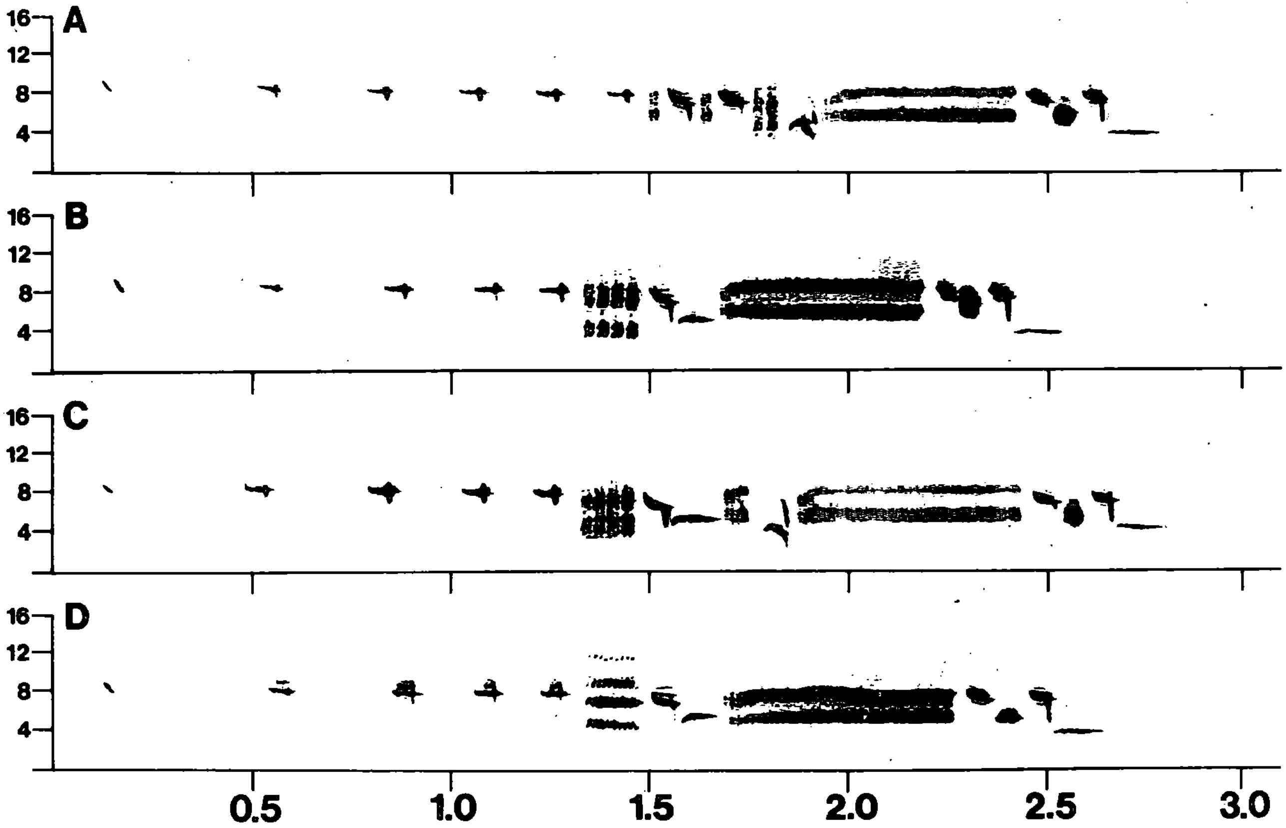

FIGURE 6.—Spectrograms recorded at El Estero. A—pattern EE-01, B—pattern EE-02, C—pattern EE-01, and D—pattern EE-06.

tern from Anaheim Bay. The phrases DaDbDc (from Part II) and FdFeJa (from the terminal flourish) were found in most of the song patterns. The occurrence of each note was tabulated for the 280 individuals recorded in this study. Of the 85 note types named herein, 35 were used at Anaheim Bay.

The only introductory notes recorded at Anaheim Bay were types Aa and Bb. The number of Bb notes varied from one to four. Even within the songs of an individual bird, the number of Bb's occasionally varied. Most variability among different song patterns occurred in Part II of the songs. This portion frequently included a short buzz of type P or a repeated series of similar notes of type C, followed by a sequence of short high-pitched notes. All but 14 individuals (six song patterns) included the phrase DaDbDc in Part II.

Part III of most songs consisted of a single K-type buzz. One individual sang an L-type buzz. None of the individuals in the Anaheim Bay sample used more than one buzz in Part III. The terminal flourish consisted of three notes in the phrase FdFeJa. Two individuals substituted a Jf for the Ja in their terminal flourishes. I recorded only one bird (number 05-18) that did not use this terminal flourish. This individual ended his song with the unusual sequence DaDcDc and was also the only representative from Anaheim Bay to use an L-type buzz.

Two other individuals sang unusual songs. Bird 05-49 sang a very long song (up to 3.1 sec) beginning with an Aa note and a series of eight short notes and two type P buzzes before using the two Bb introductory notes. These two Bb notes were followed by the typical sequence PaDaDbDcKaFdFeJa. Another odd song pattern was recorded for bird 05-20, which used four notes and a type P buzz between the first Bb and the last two Bb's of its introduction. This pattern had the same typical ending sequence as bird 05-49.

The extent of intrapopulational variation detected at the other locations is comparable to that described for Anaheim Bay. Each site had a few dominant song patterns, and the second portion of the song showed the most variability within each population. Most individuals in each sample shared similar B variants and many had a characteristic terminal flourish. Each of the larger samples included one or two individuals with unusual songs.

INTERPOPULATIONAL VARIATION

Although the songs of different individuals within one population show considerable variation, the different populations show even greater variation. Variation within a population (intrapopulational) frequently takes the form of a few different notes and phrases being substituted for the more common patterns and sequences. As I showed earlier, the basic pattern usually remains intact. Often most of the singing males share one or two dominant song patterns. Most of the intrapopulational variation occurs within the middle portion of the songs (Part II). Interpopulational variation, on the other hand, involves changes in nearly every part of the song structures. Basic patterns are

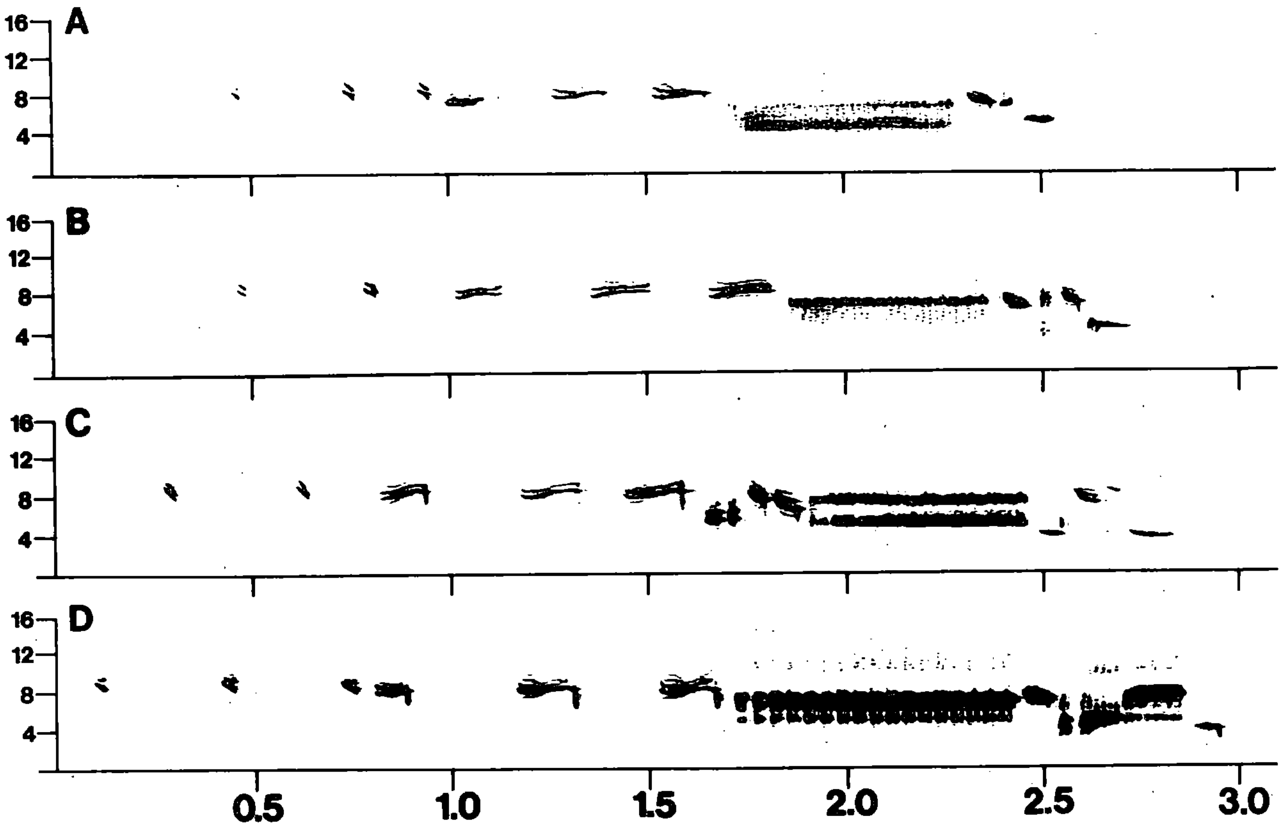

FIGURE 7.—Spectrograms recorded at Point Mugu. A—pattern PM-01, B—pattern PM-03, C—pattern PM-06, and D—pattern PM-17.

different in each population, and in many cases there are also changes in the structure of particular notes. Extensive variation between two populations does not preclude the sharing of notes and even note sequences. Such overlap is common, especially in adjacent localities, but of the 280 individuals analyzed in this study no two individuals from different populations shared the same song pattern. For illustrations of the dominant song patterns from each locality consult Figures 5-15.

VARIATION IN PART I.—Variation within the introduction involves both the number and structure of the notes. The presence of note Aa is variable even within the songs of one individual. Note Aa is the only note frequently omitted in any individual's song. As recordings of most individuals involved only one song bout on a particular date, there is no assurance that the presence or absence of note Aa from songs recorded is a constant characteristic of that individual's song. The presence or absence of an Aa note in recordings of a particular song pattern is essentially a chance event, depending on the structure of the specific songs recorded, and is thus of little if any significance.

Most introductory notes are of the general type B. All of the birds in the sample, except four individuals recorded at Playa del Ray, included at least one type B note. I named 11 different variants of type B notes (Fig. 1). All of the variants share some general time and frequency characteristics. In most cases a particular note variant is found in only one or two localities, usually close together geographically. The specific type B note variants recorded at each locality are shown in Figure 16. A listing of the approximate distances between adjacent recording localities is presented in Table 3.

VARIATION IN PART II.—The middle portion of the song of Savannah Sparrows is the most complex and varied of all four sections. In the 280-bird sample I recorded 50 different note types within Part II. As mentioned earlier, most of the types in this section are rather short and high-pitched. In addition to these notes, I found eight types of buzz phrases in Part II. In some songs a number of type C variants were used in combination to produce a loosely structured buzz or rattle. An extreme example of this is song pattern PM-17 (Table 4). In the songs of the three individuals that used this song pattern, the note C1 was repeated 14 to 17 times. The result is an audible rattle (Fig. 7). A more typical example occurred in many songs recorded at Anaheim Bay. At this location many individuals sang two, three, or four repetitions of Ca, Cb, Cd, or Ce notes. The result is a loose buzz quite similar in quality to a Pa or Pb buzz (Figs. 3 and 8). Variation within Part II took many forms. The number, structure, and arrangement of the notes change as well as the particular notes used. Any given population may also contain a number of regular patterns or sequences of notes. Variation within some localities was quite extensive, while others showed only a few different patterns. A similar situation exists in White-crowned Sparrows (Orejuela and Morton 1975).

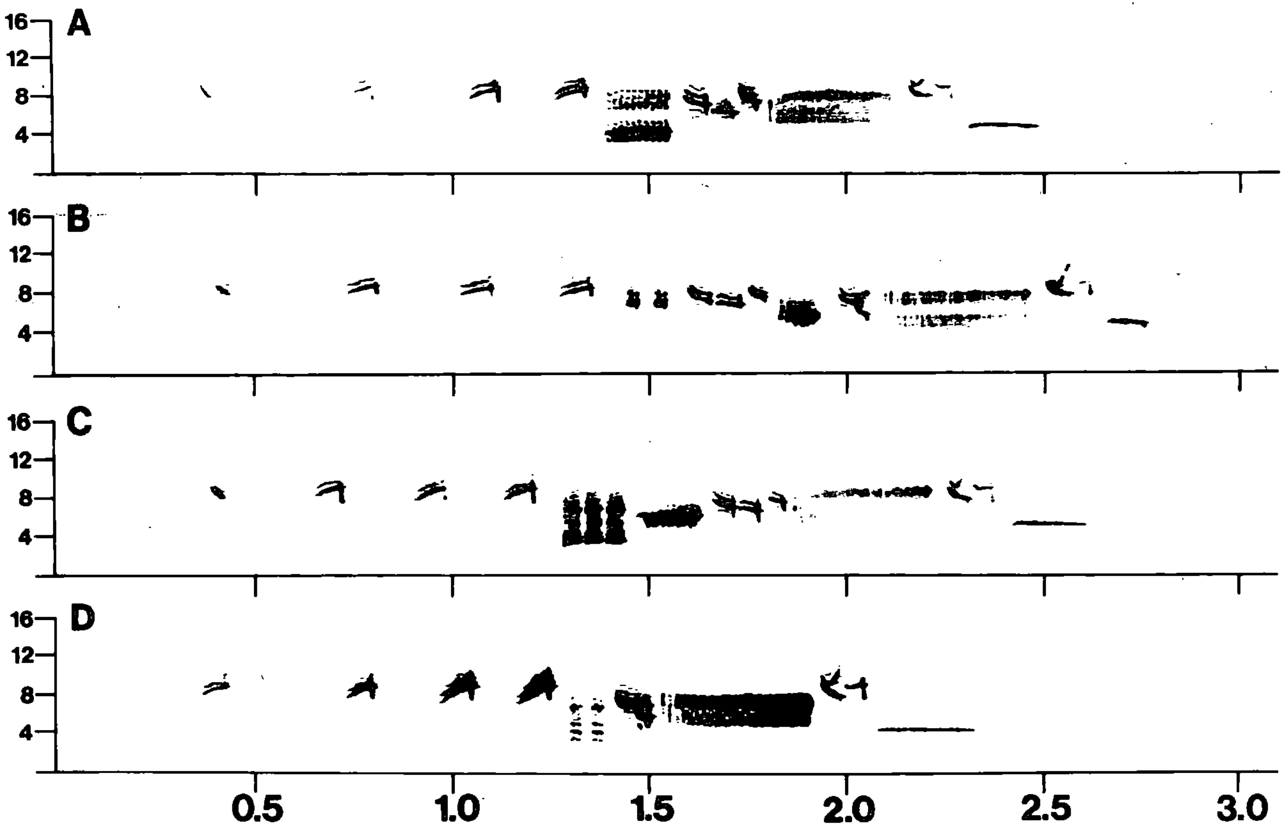

FIGURE 8.—Spectrograms recorded at Anaheim Bay. A—pattern AB-01, B—pattern AB-02, C—pattern AB-03, and D—pattern AB-15.

TABLE 3.—APPROXIMATE COASTLINE DISTANCES BETWEEN LOCALITIES (MILES).

Location	Location Number													
	01	02	03	04	05	06	08	09	10	11	12	13	15	16
Goleta Slough	X													
El Estero	20	X												
Point Mugu	59	39	X											
Playa del Rey	102	82	43	X										
Anaheim Bay	134	114	75	32	X									
Huntington H.	(136)	(116)	(77)	(34)	(2)	X								
Newport Bay	149	129	90	47	15	(14)	X							
Santa Margarita	188	168	129	86	54	(52)	39	X						
Agua Hedionda	195	175	136	93	61	(59)	46	7	X					
San Elijo Lagoon	205	185	146	103	71	(69)	56	17	10	X				
Los Penasquitos	211	191	152	109	77	(75)	62	23	16	6	X			
Imperial Beach	235	215	176	133	101	(99)	86	47	40	30	24	X		
San Quintin	415	395	356	313	281	(279)	266	227	220	210	204	180	X	
El Rosario	450	430	391	348	316	(314)	301	262	255	245	239	215	35	X

[1] Locations 07 and 14 were omitted from this table because no recordings were obtained at these sites. Distances from Huntington Harbour are placed in parentheses to emphasize the fact that this locality is part of the same marsh complex as Anaheim Bay.

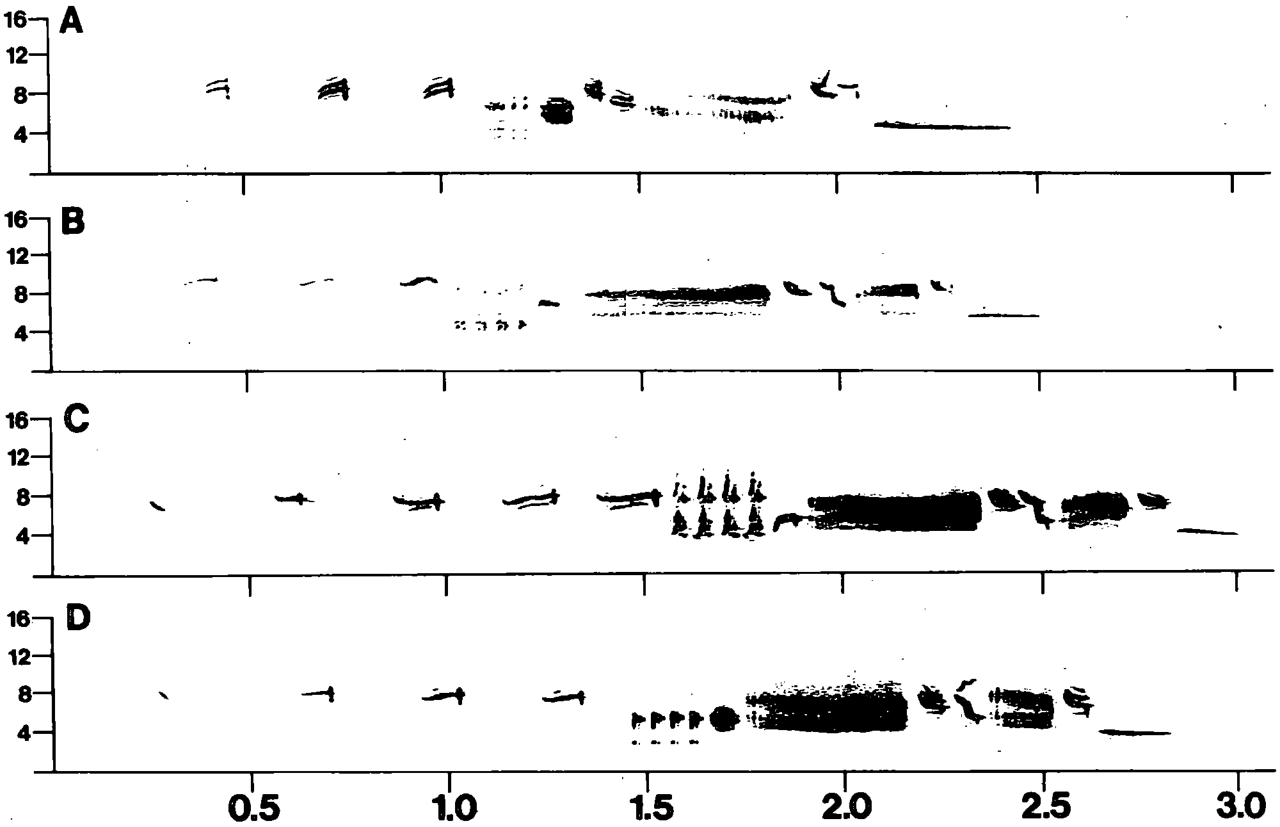

FIGURE 9.—Spectrograms recorded at Huntington Harbour and Agua Hedionda Lagoon. A—pattern HH-02, B—pattern AH-01, C—pattern AH-02, and D—pattern AH-04.

TABLE 4.—SONG PATTERNS BY LOCATION.

Pattern Number	Lettered Code	Number in Sample
	Goleta Slough (N = 7)	
GS-01	AaBg4 CaEaCaDa MaJdKb DiFgDiJb	4
GS-02	Aa2Bg4 CaEaCaDb LaJdKb DiFfDiJi	3
	El Estero (N=28)	
EE-01	Bg7 CaDiCaDaCa2Ia Ka EaOcDiJb	2
EE-02	AaBg4 Ca4DiHb Ka EcOcDiJb	14
EE-03	Bg5 Ca4EcHb Ka IaEcOcDiJb	1
EE-04	AaBg4 Ca4DiJb KbIaKa DaOcDiJb	4
EE-05	(Aa)'Bg4 CaDaCaDaCaHb Ka EaOcDiJb	1
EE-06	AaBg4 PfDiHb Ka EcOcDiJb	3
EE-07	Bg6 Ca6DiHb Ka IaDiJb	2
EE-08	Aa2Bg5 Ca4DaHb Ka IaEaOcDiJb	1
	Point Mugu (N = 28)	
PM-01	AaBhBi2 La DaCaJ1	2
PM-02	Aa2BhBi2 LaDaJcDaKb IbEaDc	1
PM-03	Aa2BhBi2 La EaCaDaJk	3
PM-04	Aa3BhBi2 CaEaOc Ka IbEaDcJb	1
PM-05	Aa2Bh4 Ca8 LaDaEaKa JcEaDc	1
PM-06	Aa2BhBi2 Cb2DcDa Ka IbEaDcJb	4
PM-07	Aa2BhBi Ca4DaCaDcJc Ka IbEaDcJb	1
PM-08	Aa2BhBi2 OcDaDb KaDaOc2Kb IbEaDc	1
PM-09	Aa2BhBi2 Ca2DaQaDcOc Ka IbEaDcJb	2
PM-10	Aa2BhBi2 OcKaDcJcEc Kb IbEaDcJb	1
PM-11	Aa2BhBi2 LaHbDaKa IbEaDcJi	1
PM-12	Aa2BhBi2 LaDcOcKb	1
PM-13	Aa2BhBi2 Oc2DcDa LaDcJcKb IbEaJb	2
PM-14	Aa2BhBi2 Ca2DaCaDcOb Ka IbEaDcJb	1
PM-15	Aa2BhBi2 Oc LaDcHeDaKa IbEaDcJb	2
PM-16	Aa2BhBi2 Ca3DaHe Ka IbEaDcJb	1
PM-17	Aa(3)BhBi2 Cl(17)EaPePb Kb Jd	3
	Playa del Rey (N = 4)	
PR-01	Aa3DcEb3 PaHa Ka ObHcJh	2
PR-02	AaEaDbOcDcCaEb2 PaHa Ka OcOdJb	2
	Anaheim Bay (N = 61)	
AB-01	Aa(2)Bb(4) PaDaDbDc Ka FdFeJa	18
AB-02	AaBb(4) Cb2DaDbDcPbGa Ka FdFeJa(orJf)	3
AB-03	AaBb(4) Cd3ZbDaDbDc Ka FdFeJa	6
AB-04	AaBb(4) Cd3ZaDa Ka (FdFeJa)	2
AB-05	AaBb(3) Ca3Gb Kb FdFeJa	1
AB-06	AaBb(3) CaDaPcDaDbDc Ka FdFeJa	1
AB-07	AaBb(3) Ca3ZbDaDbDc Kb FdFeJa	2
AB-08	(Aa)Bb(3) Oc La DaDcOc	1
AB-09	AaJmDaPdHaCaEaDcPaEcCfBb2 PaDaDbDc Ka FdFeJa	1
AB-10	(Aa)Bb3 Ca3ZaDaDbDc Ka FdFeJa	1
AB-11	(Aa)Bb3 OcPcDaDbDc Ka FdFeJa	1
AB-12	AaBb3 Ce4DbDc Ka FdFeJa	1
AB-13	(Aa)Bb4 Cd(3)DaHfDaDbDc Ka FdFeJa	2
AB-14	(Aa)Bb4 EbCaEcPcDaDbDc Ka FdFeJa	1

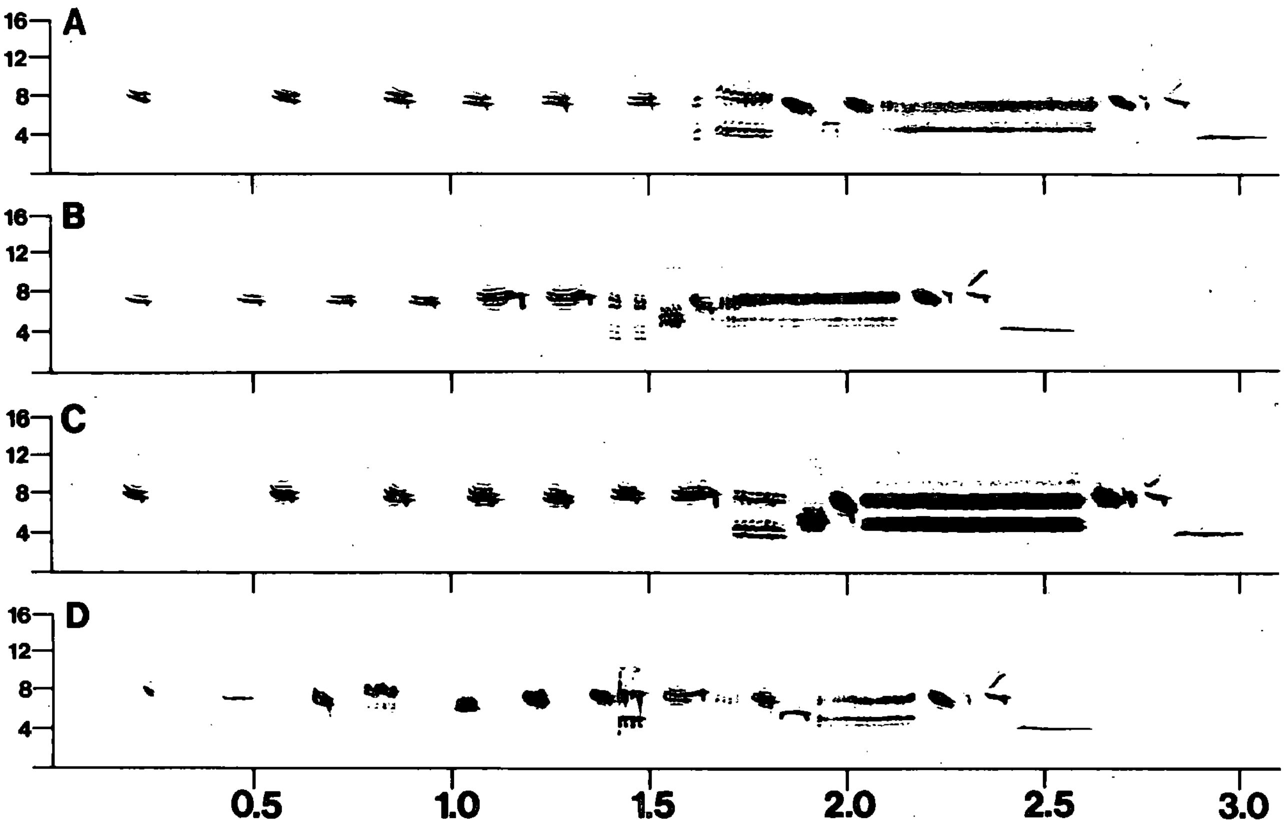

FIGURE 10.—Spectrograms recorded at Newport Bay. A—pattern NB-04, B—pattern NB-07, C—pattern NB-09, and D—pattern NB-12.

TABLE 4 (CONTINUED).

Pattern Number	Lettered Code	Number in Sample
AB-15	(Aa)Bb(4) Ca2Ga Ka FdFeJa	8
AB-16	(Aa)Bb(2) Ca2GbObDaDbDc Ka FdFeJa	2
AB-17	(Aa)Bb(4) CdPaDaDbDc Ka FdFeJa	1
AB-18	AaBb3 CbDaDbDc Ka FdFeJa	1
AB-19	AaBb(3) Ce3HiDaDbDc Ka FdFeJa	1
AB-20	AaBbEc2PcEcCfBb2 PaDaDbDc Ka FdFeJa	2
AB-21	AaBb4 PcDaHcDb Ka FdFeJa	1
AB-22	AaBb2 Ca3DaDbDc Ka FdFeJa	3
AB-23	AaBb3 Ce2DaDbDc Ka FdFeJa	1
	Huntington Harbour (N = 5)	
HH-01	AaBb3 Ca3DaDbEc Ka DcDgJa	1
HH-02	AaBb3 CeCaOaDcDb Ka FdFeJa	2
HH-03	AaBb3 Ce3ZbDbDc Ka FdFeJa	1
HH-04	AaBb4 Oc LaDcDbDcKa FdFeJa	1
	Newport Bay (N = 30)	
NB-01	Bc7 OaEa KbDaHaKa EaJb	1
NB-02	AaBc5 ChPaDaHcDa Ka FdDjJb	1
NB-04	Bc(6) ChPaDaHcEa Ka EaFaFdJa	7
NB-05	Aa2JdDcPbOcEc2CfBh CeEcHa Ka DcFaFdJa	2
NB-06	Bc4Bf2 PaDaHa Ka FaDaJa	1
NB-07	AaBc4Bf2 Ca2PdDa Ka EaFaFdJb	3
NB-08	Bc6Bf PaPdDa Ka EaFaFdJa	4
NB-09	Bc(3)Bf2 PaHd Ka EaFaFdJa	1
NB-10	Bc4Bf3 KaDbDaKbRa	1
NB-11	Bc5Bf2 Ca4HdDa Ka EaFaFdJa	1
NB-12	(Aa)Bc3 PbDiHa Ka EaFaDaJb	6
	Santa Margarita (N = 29)	
SM-01	AaBk3 Oc KaDaKb IcDaJa	5
SM-02	AaBk4 Ca20c KaDbDaKbDa Ja	2
SM-03	Aa3Bk3 Ca20c KaHfDaKb IcDaJa	4
SM-04	AaBk3 KaDa2Kb IcDaJa	1
SM-05	Aa2Bk3 Oc KbDa2Kb IcDaJa	2
SM-06	AaBk3 Oc KaDc2Kb DcJa	1
SM-07	Aa2Bk3 Ca2DcHe KaDbDcKb DcJa	2
SM-08	AaBk3 CiHd KaHfDaKb IcDaJa	2
SM-09	Aa2Bk3 Oc LaHfDcKb IbDaJa	1
SM-10	(Aa)Bk3 Cb20c KaHfDaKb DaJa	3
SM-11	Aa2Bk2 NaKbHcDaKb FcDcJa	3
SM-12	(Aa)Bk3 EcOc KaHfDaKb IcDaJa	2
SM-13	Aa2Bk2 Oc Kb IcDcJa	1
	Agua Hedionda Lagoon (N = 10)	
AH-01	Bh(3) Ca4He KaEaGcKb DaJa	2
AH-02	BhBk3 Cj4Hh KaEaGcKb EcJa	2
AH-03	AaJcBh4 Oc KaSaEaGcKb EcJa	1
AH-04	AaBh(3) Ca40c KaEcGcKb EcJa	3
AH-05	Bh(3) Ca30c KaEcGc EcJa	1
AH-06	AaBh3 PaOc KaDaGdKb DaJe	1
	San Elijo Lagoon (N = 4)	
SE-01	(Aa)Bk3 KbDcOcKbPbDaKb DaJa	2
SE-02	(Aa)Bk3 KbOcKbPdEcKb EcJa	1

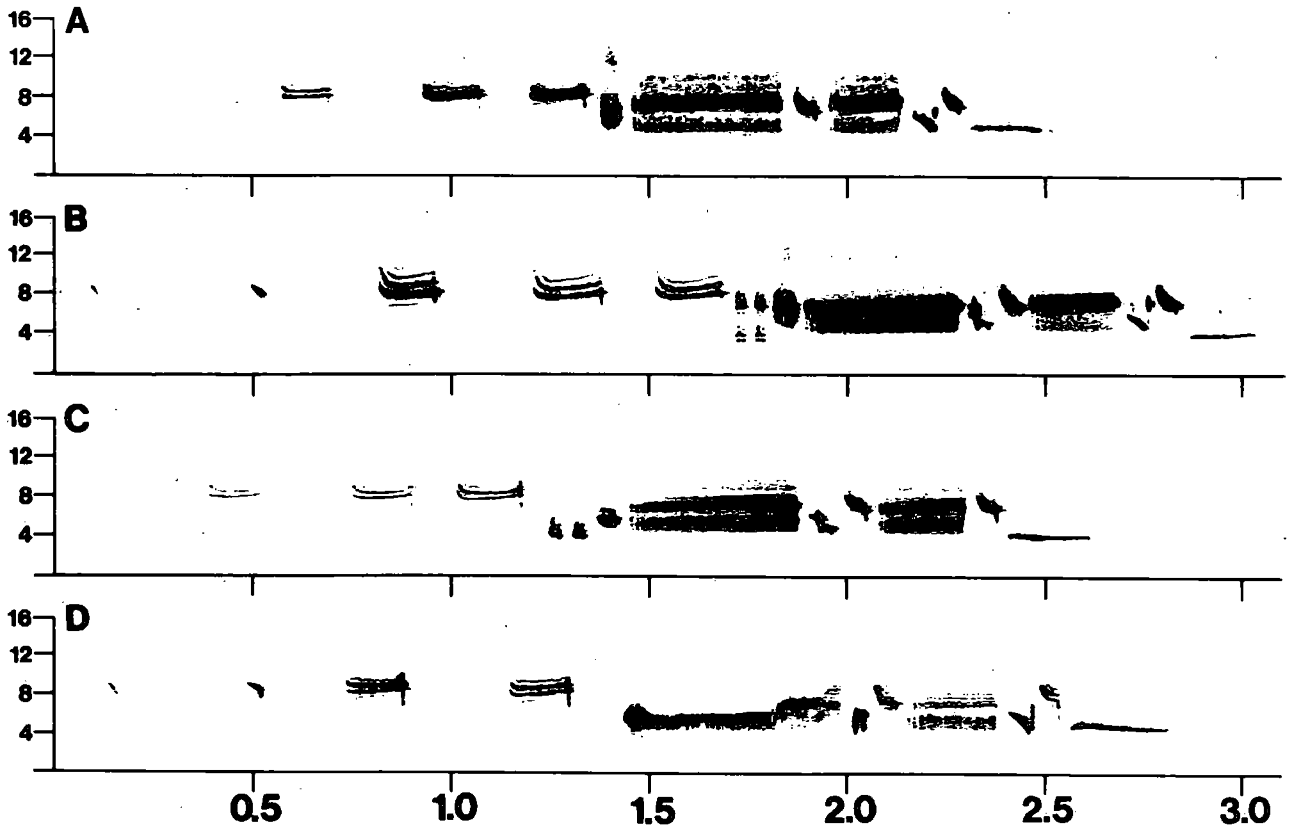

FIGURE 11.—Spectrograms recorded at Santa Margarita Lagoon. A—pattern SM-01, B—pattern SM-03, C—pattern SM-10, and D—pattern SM-11.

TABLE 4 (CONTINUED).

Pattern Number	Lettered Code	Number in Sample
SE-03	AaBk4 PaHaKb HfDbEcJa	1
	Los Penasquitos Estuary (N = 21)	
LP-01	AaBc5 PaEaJn Ka EcFaJe	4
LP-02	AaBc5 KbEcEbKa EcFaJa	1
LP-03	Bc5 PaDaEc Ka EcFaJe	1
LP-04	Bc5 Ec2EbChPaEcJc Ka EcJa	3
LP-05	Bc5 KbDcOaKa EcFaJe	1
LP-06	AaBc4 KbEc2HcDcKa EcJa	1
LP-07	Bc6 ObDcJb Ka EcJa	1
LP-08	AaBc4 Hc2EbCa2DcHc Ka EcJa	2
LP-09	AaBe5 Ca3Da KaDaHcKb DcJe	1
LP-10	AaBc3 Ec2EbCgEbCa3Ec Ka EcFaJa	1
LP-11	AaBc4 CdEaEbOcObDc Ka EcJa	1
LP-12	AaBc6 PaEaEbHc2Dc Ka EcFaJe	3
LP-13	AaBc4 Ec2EbDaCe2Dc Ka EcJe	1
	Imperial Beach (N = 8)	
IB-01	Bm3 PfHdDa Ka DaFeCaEaFgJa	1
IB-02	AaBm2 Ca2Hd Ka DaFeCaDaFgJa	2
IB-03	AaBm4 PfDaHd Ka EaFeCaEaFgJa	3
IB-04	AaBm4 Ca4HdDa Ka EaFeCaEaFgJa	2
	San Quintin Bay (N = 34)	
SQ-01	AaBh3 Eb2CgEbCaOc KaObKb EaFcJb	1
SQ-02	AaBh3 EaEbCgEbCa30c Kb EaFbJb	3
SQ-03	AaBh5 JbEaCa KaOcKb EaFbJb	1
SQ-04	AaBh3 EaEbCgEb KaOcKb EaFbJb	6
SQ-05	Aa(2)Bh3 DaEbCgEbCgJm KaOcKb DaFbJb	2
SQ-06	AaBh3 OaEbCgEbCeOc Ka EcFbJa	5
SQ-07	Aa2B14 Eb2CgEb LaOcKa EcFbJa	3
SQ-08	Aa2B12 EaEb2CgEb LaOcKa EcPa	2
SQ-09	AaB13 EcEaEbCgEb LaOcKa EcFbJb	3
SQ-10	B16 CeEaJa Ka EcFbJb	3
SQ-11	AaB13 CaDcEb2CgEb LaOcKb EcFbJb	1
SQ-12	AaB13 CeEbCeEbCgEbJb Ka EcFbJa	1
SQ-13	AaB13 Eb2CgEbCdCa20c Ka EcFbJb	1
SQ-14	B14 EaEbCiCaOc Ka EcFbJb	1
SQ-15	B14 Ea2CiCeOc Ka EcJb	1
	El Rosario (N = 11)	
ER-01	Aa2Bn5 La DaJa	1
ER-02	AaBn6 La DaJdCkDaJa	4
ER-03	AaBn5 La DiHdCkDaCkDaJa	6

[1] Notes or phrases occasionally omitted and numbers of repetitions that varied were placed in parentheses.

VARIATION IN PART III.—Variation within the main buzz section (Part III) was relatively simple. Although many individuals from the various populations included a number of notes between successive buzzes, the basic pattern of one or two K-type buzz phrases was maintained in most of the birds sampled. Within most populations the number of buzzes was constant, but

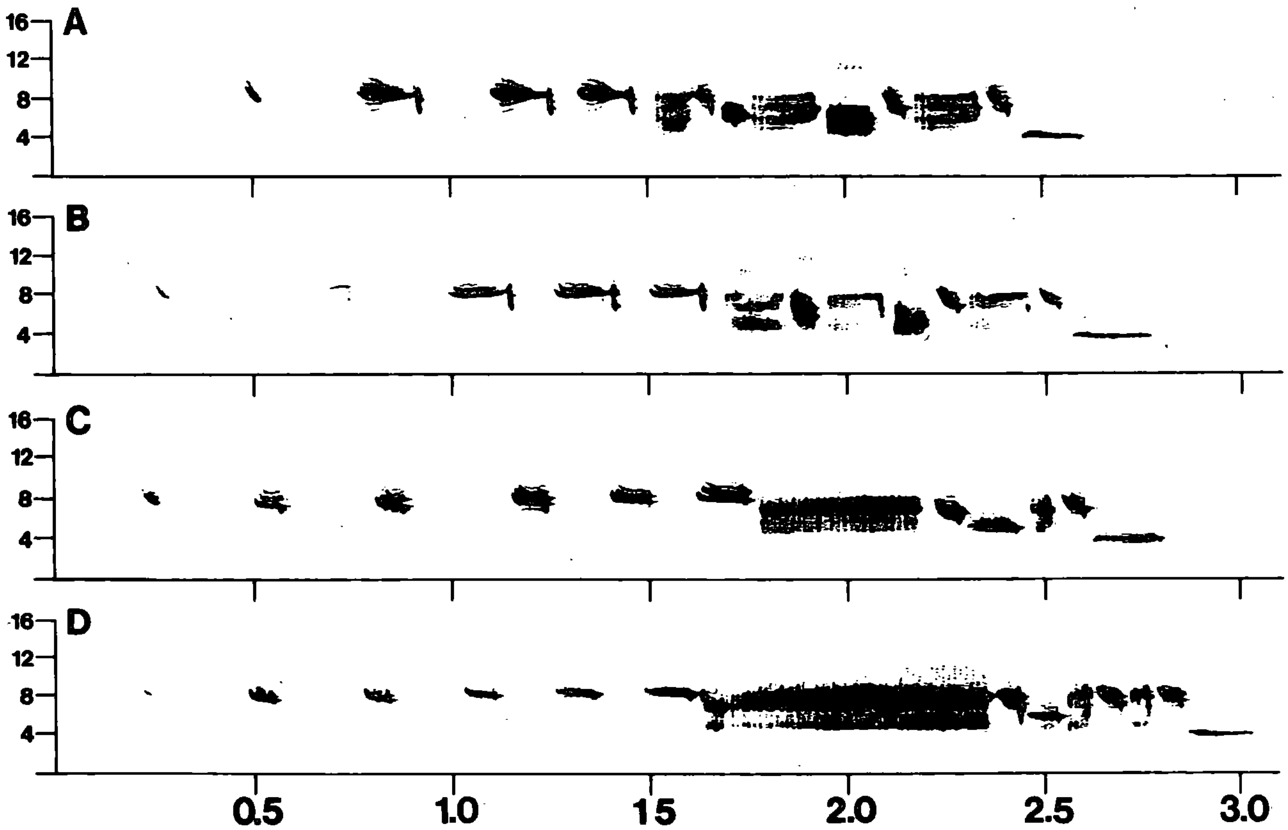

FIGURE 12.—Spectrograms recorded at San Elijo Lagoon and El Rosario. A—pattern SE-01, B—pattern SE-02, C—pattern ER-02, and D—pattern ER-03.

there were several exceptions to this general rule. In a few localities the typical Ka or Kb buzzes were replaced by La, Ma, or Na buzz phrases. In the main buzz sections of the entire sample 24 I found different note types, but most birds included only two to four notes between any two successive buzzes.

VARIATION IN PART IV.—Variation between the different populations is best demonstrated by analysis of Part IV. This terminal flourish portion of the songs was rather constant at a given location. Each population had one or a few characteristic patterns. Considerable variation existed among the several recording localities. This diversity took the form of variation in the number of notes, the general note sequence, and in some cases the structure of certain notes. The number of notes included ranged from two to eight. Most of the notes were of the general types D, E, F, I, and J. All but 7 of the 280 birds recorded in this study terminated their songs with a J-type note.

SUMMARY OF INTERPOPULATIONAL VARIATION BY LOCATION

01 GOLETA SLOUGH.—Santa Barbara, Santa Barbara County, California, close to the Santa Barbara municipal airport. The marsh is fairly large with a deep channel running down the center. The population of sparrows was probably fewer than 50 pairs. Recordings were made on 25 May of only eight individuals (Fig. 5). The songs of these birds had many short introductory notes of type Bg. The two buzzes present were separated by a single note and the terminal flourish was consistently of four notes.

02 EL ESTERO.—Less than 1 mile west of Carpinteria, Santa Barbara County, California. Although this marsh was being channelized, a large number of sparrows were still singing there. The population was estimated at 100 breeding pairs. Recordings were made on 11 May of a total of 28 individuals (Fig. 6). The introductory notes were similar to those recorded from birds at Goleta Slough, with from four to seven Bg notes followed by a series of C notes or a P-type buzz. The number of K-type buzzes varied. The terminal flourish usually consisted of three simple notes followed by a short Jb note.

03 POINT MUGU.—In the Pacific Missile Range, about 5 miles southeast of Port Hueneme, Ventura County, California. This area was visited on 4 May. Recordings were restricted to the eastern finger of the estuary, near Point Mugu State Park. Songs of 28 of the estimated 175 singing males were recorded (Fig. 7). The initial pattern BhBi2 gave their songs a recognizable opening. The main buzz was quite long (up to 0.7 seconds). Part IV consisted of three to four notes usually with an Ib note and ending with a Jb note. Three individuals used a very distinctive harsh buzz constructed of numerous Cl notes.

04 PLAYA DEL REY.—Just east of Marina del Rey, Los Angeles County, California. Recordings were made on July 21. Although only 4 of the estimated 25 males were recorded, several others that I heard were using similar

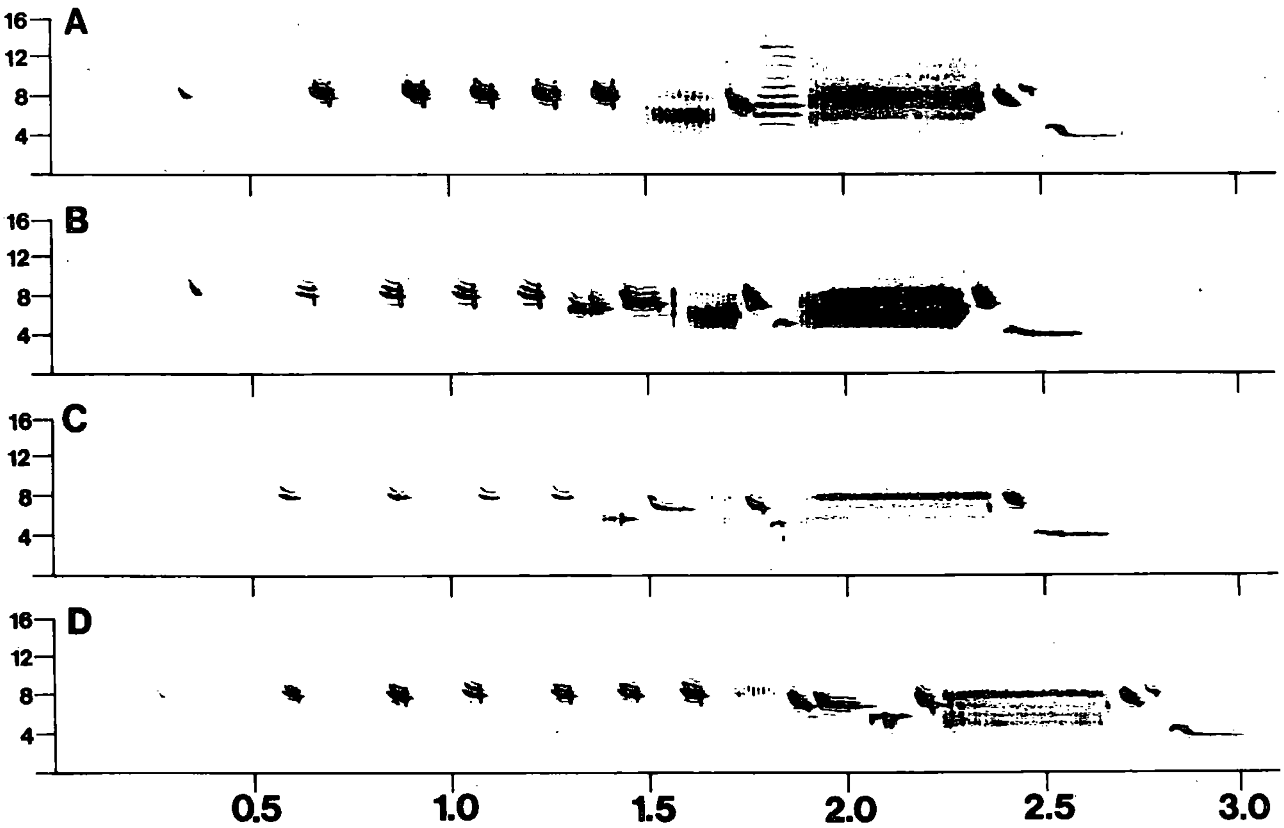

FIGURE 13.—Spectrograms recorded at Los Penasquitos Estuary. A—pattern LP-01, B—pattern LP-04, C—pattern LP-08, and D—pattern LP-12.

song patterns (Fig. 5). The songs recorded here had no B notes, and several short C, D, and E notes formed the introduction; Parts II and III consisted of a P buzz followed by a single note then a K buzz. The terminal flourish was composed of only three notes ending with a short J-type note.

05 ANAHEIM BAY.—Seal Beach National Wildlife Refuge, Seal Beach, Orange County, California. Anaheim Bay was the main study area where I made observations of individual variation and seasonal variation. In addition to recording 61 individuals, I color-banded a number of birds for individual recognition. I estimated the population here to be approximately 125 singing males. Recordings were made on the following dates: 2, 7, 14, 17, and 26 February, 3 March, 2 and 21 April, 12 and 20 May, 29 August 1973, and 10 February 1974 (Fig. 8). The songs of birds recorded at this locality began with three or four Bb notes followed by a P buzz or a series of C notes forming a buzzlike phrase. Part III had only one K-type buzz. The terminal flourish usually consisted of the pattern FdFeJa with a rather long Ja note.

06 HUNTINGTON HARBOUR.—Sunset Beach, Orange County, California. As mentioned earlier this area and Bolsa Chica Lagoon (07) to the east were both once part of the Anaheim Bay marsh complex. The combined population of Huntington Harbour and Bolsa Chica Lagoon is about 50 pairs. Five birds were recorded at Huntington Harbour on 6 June (Fig. 9). The patterns of their songs were similar to those recorded at Anaheim Bay.

08 NEWPORT BAY.—Less than 1 mile northeast of Newport Beach, Orange County, California. Although this is the largest estuary that I visited in California, the habitat was mostly *Spartina* and open mudflats. The portion of the estuary where *Salicornia* occurred supported about 130 breeding pairs of Belding's Sparrows. Recordings were made on 2 February and 16 March of a total of 30 males on the two visits (Fig. 10). The songs of these birds bore some resemblance to those recorded at Anaheim Bay. They had a variable number of introductory notes (usually four to seven), and either one or two K-type buzzes. In the song patterns containing only one K buzz it was usually preceded by a P buzz in Part II. The distinctive four-note terminal flourish EaFaFdJa was characteristic of this location.

09 SANTA MARGARITA LAGOON.—On Camp Joseph H. Pendleton just north of Oceanside, San Diego County, California, this estuary supported approximately 125 singing males. A sample of 29 birds was recorded on 28 April (Fig. 11). Most of the song patterns included three of the relatively long Bk introductory notes. Two K-type buzzes were present in the songs. The first was usually a Ka buzz about 0.4 seconds long; the second was a Kh buzz about 0.25 seconds long. The song ended with three notes usually of the pattern IcDaJa. Three individuals used the highly distinctive Na buzz in their songs.

10 AGUA HEDIONDA LAGOON.—Carlsdad, San Diego County, California. Recordings were made at this area on 24 March (Fig. 9). Although only 10 of

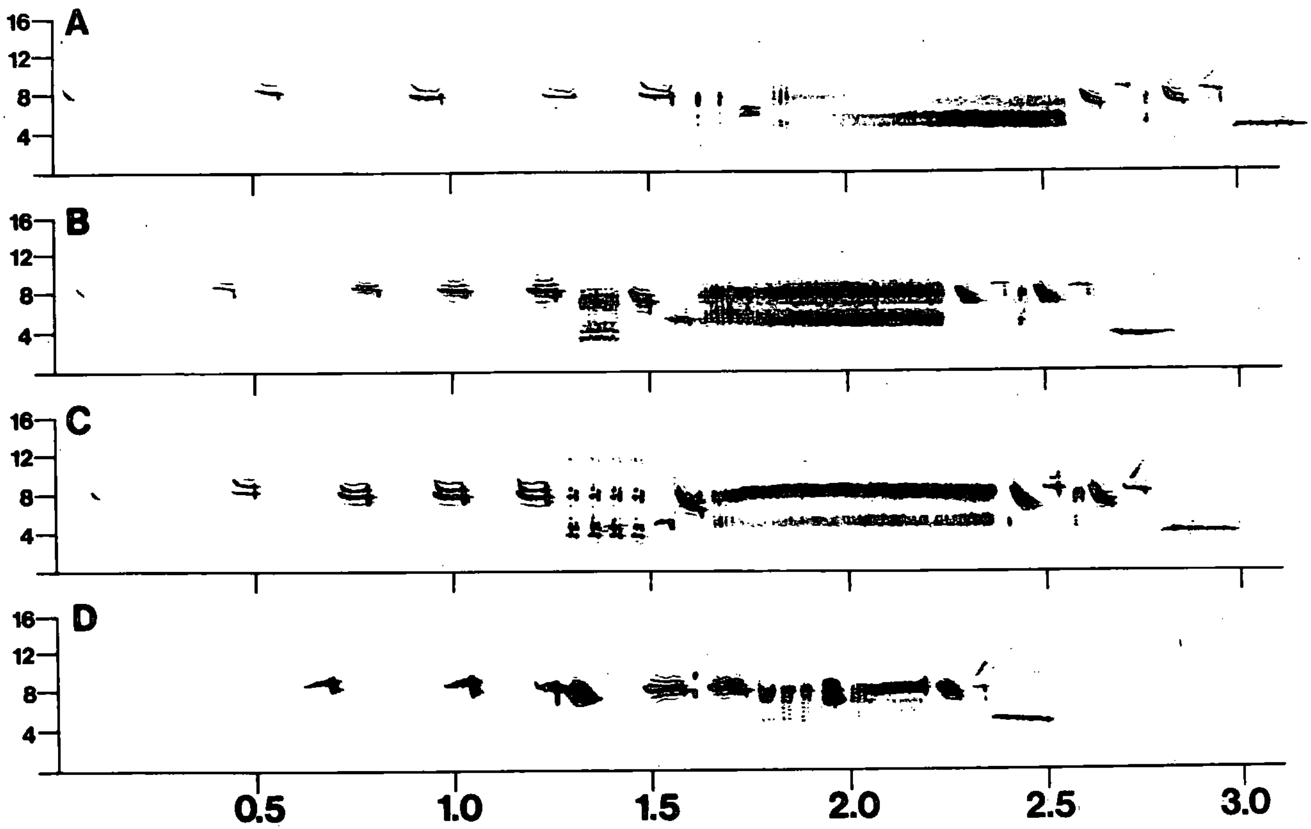

FIGURE 14.—Spectrograms recorded at Imperial Beach and San Quintin Bay. A—pattern IB-02, B—pattern IB-03, C—pattern IB-04, and D—pattern SQ-02.

the nearly 40 singing males were recorded, at least 8 more birds shared the same song patterns. The introduction included both Bh and Bk notes. Consistently two K-type buzzes were separated by two shorter notes. The terminal flourish consisted of only two notes, the last being a Ja.

11 SAN ELIJO LAGOON.—About 0.5 miles south of Cardiff-by-the-Sea, San Diego County, California. The small portion of this marsh which remained intact supported only about 17 pairs of Belding's Sparrows. On 26 March I recorded four males (Fig. 12), and their songs were similar to at least 12 other males I heard here. As far as I could determine, of 17 males defending territories here only individual 11-01 did not use three Kb buzzes. Part II of the songs was nearly absent. The song patterns were characterized by the three short buzzes. Only two terminal notes follow the second Kb buzz.

12 LOS PENASQUITOS ESTUARY.—About 2 miles south of Del Mar, San Diego County, California. This large *Salicornia* marsh is the estuary where Penasquitos Creek meets the ocean. Although some development had occurred at the southwest end of the marsh, it still maintained a population of approximately 160 breeding pairs. On 6, 8, and 29 April I recorded 21 individuals (Fig. 13). At least four to five B notes characterized the introductory phrase of songs recorded here. There were usually two K buzzes and frequently a Pa buzz. The terminal portion of the songs included two or three notes, EcJa and EcFaJa being the common patterns.

13 IMPERIAL BEACH.—About 2 miles south of Imperial Beach at the mouth of the Tijuana River, San Diego County, California. This area supported a population of approximately 100 breeding pairs, but the constant heavy winds made recording difficult. I recorded only eight individuals on 1 April (Fig. 14). Even though the sample was small, I believe that it was representative of the song patterns of the birds here. The unique Bm notes make up the introductory portion of their song. A single Pf buzz or a few C notes forming a buzz-like phrase were usually followed by a long K-type buzz (0.5 to 0.6 seconds). Part IV was long and included six notes.

14 ENSENADA BAY.—Ensenada, Baja California Norte, Mexico. Although most of the habitat at Ensenada Bay was dominated by *Spartina*, several local areas of *Salicornia* persist. These areas supported perhaps 20 pairs of Belding's Sparrows. Unfortunately none could be recorded in the time available.

15 SAN QUINTIN.—The eastern arm of San Quintin Bay, 15 miles south of Colonia Guerrero, Baja California Norte, Mexico. This huge tidal salt marsh supported a population of at least 2000 breeding pairs. I recorded birds on the east side of the inner bay on 15 April, and the west side on 16 April (Fig. 15). The sample of 34 birds recorded here was deemed representative of the different song patterns present in this population. The Aa and Bh notes combined with a pattern of E and C notes to produce a distinctive "see-saw" rhythm in the introduction. One or two closely spaced K-type buzzes were often followed by the three note terminal phrase E F J.

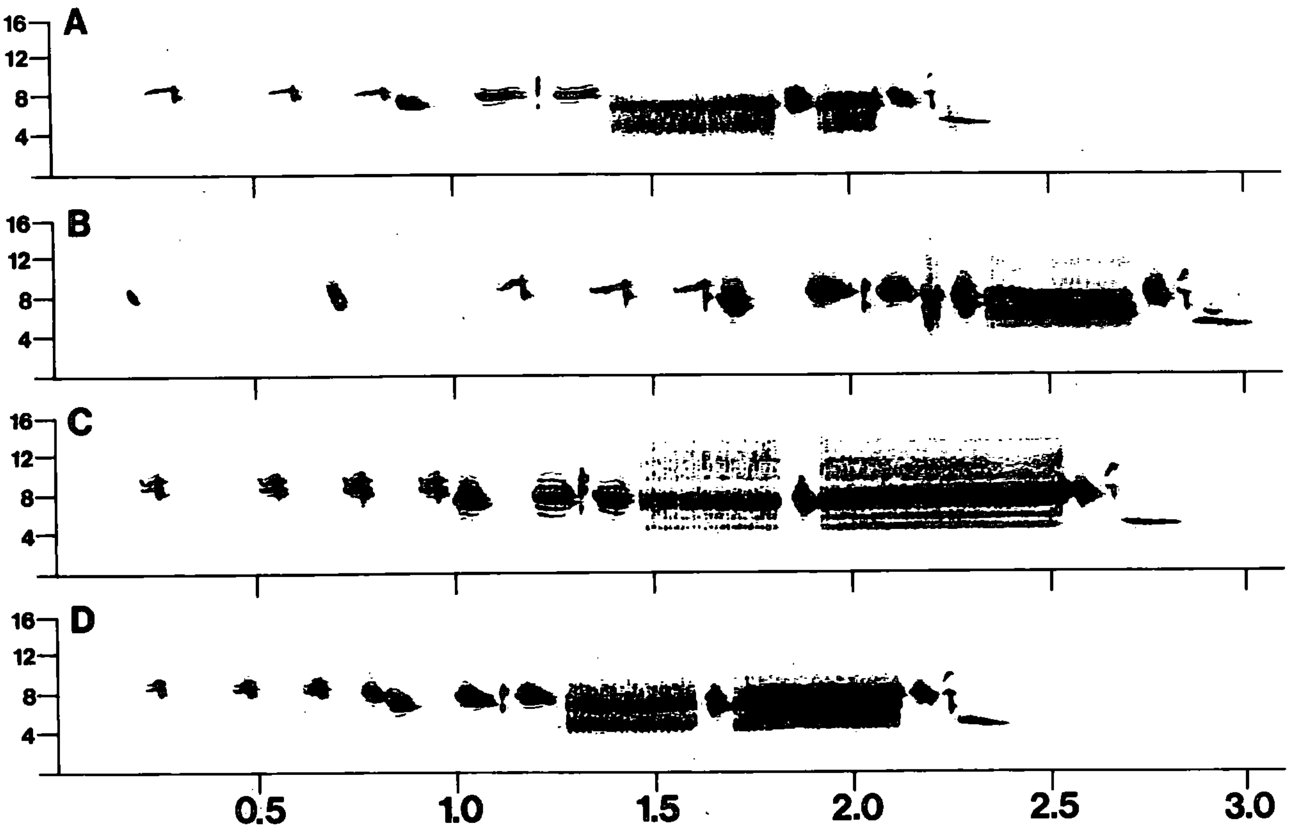

FIGURE 15.—Spectrograms recorded at San Quintin Bay. A—pattern SQ-04, B—pattern SQ-06, C—pattern SQ-07, and D—pattern SQ-09.

16 El Rosario.—Laguna El Rosario, about four miles west of El Rosario, Baja California Norte, Mexico. I made recordings of 11 of the 50 singing males at this location on 14 April (Fig. 12). The five or six introductory notes had a whistled quality. Part II of the songs was entirely absent. Rather long harsh La buzzes characterized Part III. The terminal phrase usually included between four and six short high pitched notes followed by a Ja note.

Discussion

The pattern of geographic variation in the Belding's Sparrow songs was rather complex. Each individual sang only one specific song pattern. Different individuals within a given population each sang one of a number of distinct song patterns. One or two song patterns were usually dominant at each location. Certain vocal characteristics were shared by the members of each population, and these distinguished them from birds recorded at other sites. I documented variation in the number and structure of particular notes as well as alteration of the entire song pattern. Although the songs of Belding's Sparrow are complicated, a mosaic pattern of variation was evident.

The fact that distinguishable song dialects occurred in the isolated populations of these sparrows is not surprising. Similar patterns of geographical song variation in other species have been demonstrated by many authors (Marler 1952, Marler and Tamura 1962, Ward 1966, Nottebohm 1969, Thielcke 1969, Harris and Lemon 1972, and Grimes 1974). The presence of well-defined dialects over such short distances is more interesting. The current study involved recordings from a single subspecies (*P. s. beldingi*). Other studies have sometimes involved more than one subspecies over much greater distances (Nottebohm 1969). Evidently the sedentary nature of Belding's Savannah Sparrow and its specific habitat requirements have produced effective isolation over distances as short as 15 to 30 miles.

If geographical variation, taking the form of well defined dialects, is common in isolated populations of certain species, one may ask how such variation evolves. Perhaps even more important is the question of dialect function in speciation. A possible mechanism for the development of vocal dialects involves preferential mating of females with males having particular vocal characteristics. This mechanism has been proposed before (Nottebohm 1969, King 1972). Some evidence exists that assortative mating does not occur. Baptista (1974) found that males singing the "wrong" song dialect were successful in attracting mates, but it is important to note that assortative mating would most likely be a statistical event. A tendency for females to choose males with "correct" songs is sufficient to affect selection.

If we assume that a female sparrow is "coded" to respond to the song typical of her species, it follows that she might be so coded on a particular variant of that song. The song to which developing females (and males) are first ex-

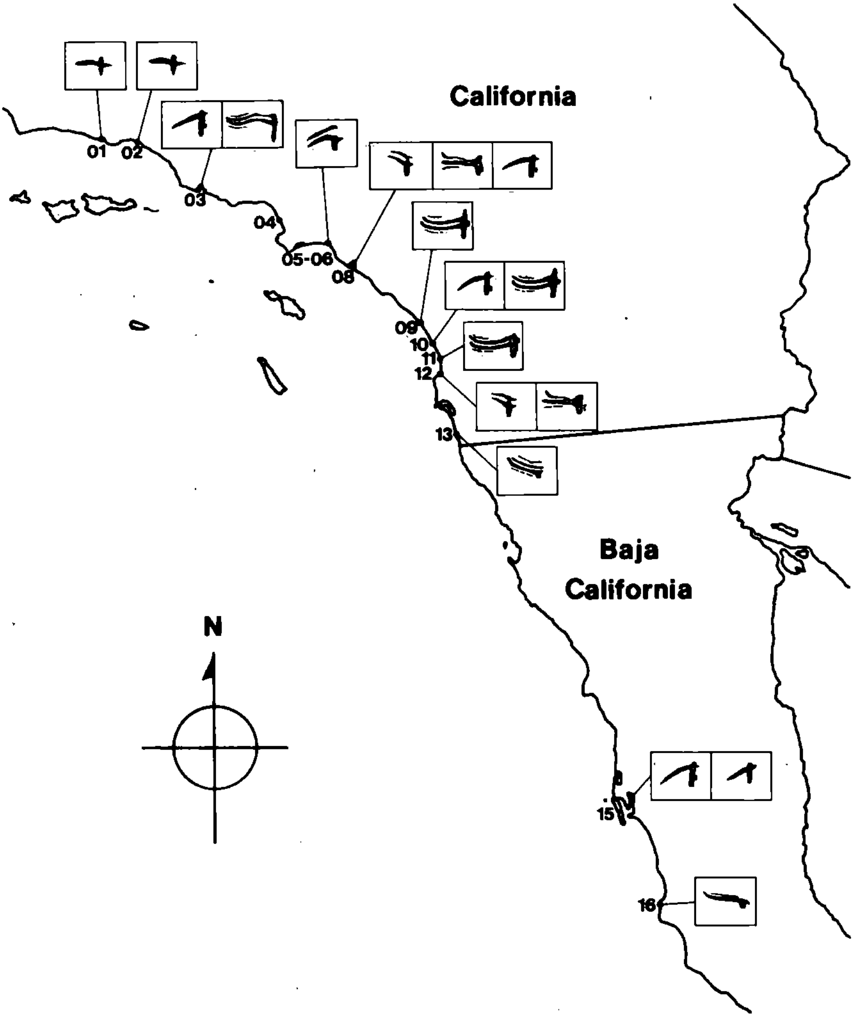

FIGURE 16.—Map localities and type B note variants. Boxes near each recording locality show basic structure of B-type note variant or variants used by members of that population. Numbers refer to the location numbers listed in Table 1. Again numbers 07 and 14 are omitted as no birds were recorded at Bolsa Chica Lagoon or Ensenada Bay. No illustration is indicated for location 04 (Playa del Rey) because B-type notes were absent from songs of birds recorded there.

posed is that of the male parent. If young females respond most strongly to this song pattern, the most prolific (fit) males would sing the most popular song patterns. The occurrence of clustering in males with similar song patterns, as observed in this study, would tend to enhance this process. Both male and female juveniles would thus be exposed predominately to one song pattern.

That higher passerines can distinguish between songs of different individuals has been shown by several authors (Marler 1956, Weeden and Falls 1959, Falls 1969, and Emlen 1971b). These studies involved responses of territorial males to recorded songs. To my knowledge, only two field studies of differential responses in adult females have been conducted. Bertram (1970) demonstrated that individual female Indian Hill Mynahs (*Gracula religiosa*) recognized their mates by vocal characteristics. Milligan and Verner (1971) mentioned that female White-crowned Sparrows responded more strongly to the local dialect. Differential responses to songs of different dialects have also been shown in territorial males (Lemon 1967, Milligan and Verner 1971, Thielcke 1973, and Harris and Lemon 1974). Again little field data are available for the responses of mature females.

The presumed function of song in attracting the female is critical to any discussion of song as an isolating mechanism. This advertising function of song has been shown for several species (Quaintance 1938, Nice 1943, Woolfenden 1956, Smith 1959, Catchpole 1973). In addition, Payne (1973a) demonstrated a high degree of assortative mating between Indigobirds imprinted upon specific mimetic songs. Positive responses have also been elicited in captive females to recordings of the advertising songs of males (Payne 1973b). Recordings of song stimulate approach in female Chaffinches (Marler 1956). Female White-throated Sparrows may even assume a soliciting posture and utter precopulatory vocalizations in response to male song (Falls 1969).

Specific functions of the song in the Savannah Sparrows are undocumented. At least part of the function includes the establishment and retention of discrete territories by the singing males. There seems little doubt that the behavior of the male during song makes him conspicuous to females seeking a mate. While these sparrows spend most of their time on or near the ground, song is nearly always given from an exposed perch, often well above the surrounding vegetation.

If song dialects are truly an important mechanism of behavioral isolation, evidence should exist of morphological or genetic variation between different dialect groups. The interaction of a dialect system with the occurrence of certain genes was shown by Nottebohm and Selander (1972) in *Zonotrichia capensis*. King (1972), in another study of *Z. capensis*, showed a correlation between song themes and the specific habitat in which the sparrows occurred. He also included some morphological data on the birds from each area. Baker (1975) found genetic differences between dialect groups in White-throated Sparrows. In the same paper he presented data showing allelic variation in another population where no dialects exist. Preliminary work that I have conducted on Orange-crowned Warblers (*Vermivora celata*) has revealed that the darker insular race (*sordida*) has a distinctly slower trill than the brightly colored mainland race (*leutescens*). In studies of very closely related species, differences in their vocalizations are often cited as possible isolating mechanisms (Lanyon 1957, Stein 1958, Schwartz 1972, Thielcke 1973).

Adaptive radiation within the coastal species of North American emberizine sparrows is extensive. Several marsh nesting species such as the Seaside Sparrow (*Ammospiza maritima*) and the Sharp-tailed Sparrow (*A. caudacuta*) have a number of different morphological variants. Along the west coast of North America, no fewer than 11 different subspecies of the Savannah Sparrow are currently recognized (American Ornithologists' Union Check-list 1957). Along the eastern coast of the continent are many marsh-inhabiting sparrows including several distinct species. Beecher (1955) believed that the Seaside Sparrows and the Sharp-tailed Sparrows were originally derived from Savannah Sparrow stock. It seems evident that speciation in coastal populations of North American sparrows is progressing at a relatively rapid rate. If song dialects are indeed an important isolating mechanism, they may play a significant role in such rapid speciation.

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