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INTRASPECIFIC AND INTERSPECIFIC SONG MIMESIS IN CALIFORNIA SONG SPARROWS

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INTRODUCTION

Geographical variation in song and song dialects have been popular research topics in the last two decades (reviews in Thielcke, 1969; Lemon, 1975). Song dialects in White-crowned Sparrows (*Zonotrichia leucophrys*) are well known. It has been found, however, that although dialects exist for the subspecies *Z. l. nuttalli*, *pugetensis*, and *oriantha* (Marler and Tamura, 1962; Baptista, 1974, 1975, 1977; Orejuela and Morton, 1974; Baker, 1975), Alaskan White-crowned Sparrows (*gambelii*) show no dialect variation (DeWolfe et al., 1974). Kroodsma (1971) and Borror (1959, 1975) found similar results for the Rufous-sided Towhee (*Pipilo erythrophthalmus*)—although dialects are absent in eastern subspecies, birds in Oregon share similar themes. More recently, Munding (1975) reported distinct dialects for eastern House Finches (*Carpodacus mexicanus*). However, Bitterbaum and Baptista (in prep.) found sharing of syllables and groups of syllables in California House Finches but no sharing of entire songs.

The Song Sparrow (*Melospiza melodia*) is a highly variable singer with a large repertoire of songs and syllables (Mulligan, 1963, 1966). Wheeler and Nichols (1924) concluded that there was regional variation in pitch, pronunciation, or both that would enable one to separate birds of one locality from those of another. Borror (1961) and Harris and Lemon (1972) concur with Wheeler and Nichols, reporting dialects in the Song Sparrow. However, Mulligan (1966) studying California populations reported variability so great within a single individual, that no similarity could exist between individuals.

During the 1973 breeding season, we noticed what was apparently a high incidence of theme sharing in a population of Song Sparrows in southern California. We also recorded what appeared to be Song Sparrow imitations of local Wrentit (*Chamaea fasciata*) syllables. These data, plus the conflicting reports on the presence or absence of song dialects in the Song Sparrow, and intraspecific geographical variation as to presence or absence of dialects in the species listed above, prompted us to conduct a detailed study of Song Sparrow songs in our region during the 1974 breeding season.

METHODS AND MATERIALS

The Study Area

The study was conducted at Scholl Canyon Park, Glendale, California. It consists of seven man-made terraces against a hillside in a regional park covered with trees, bushes, and grass. Circum-annual watering keeps this area green, permitting the occupancy of Song Sparrows and making this a mesic ecological island surrounded by xeric chaparral. Eight Song Sparrows were recorded from this area. One additional individual, whose territory was separated from the canyon by a street and was approximately 0.25 miles from the other birds, was also recorded.

Identification of Individuals

Birds were not banded but were recognized by individually unique song patterns and singing locations as in Harris and Lemon (1972). Birds were recorded as living on one of the seven levels, either on the left side (#1), the middle (#2), or the right side (#3). For example, the Song Sparrow on the right side of Level I was recorded as LI-3. The bird from the other canyon was labelled as O-1.

Analysis of Songs

Recordings of songs were made from March to June 1974, using a Uher 4000 Report 1C Tape Recorder with an Electro-Voice 635A Dynamic Omnidirectional Microphone mounted on a 24-inch parabolic reflector. Tape speed was 3.75 in/sec, and recordings were analyzed on a Kay Electric Sonograph, Model 7029A, using the wide band setting.

Three spectrograms of each song type per individual were made. Thereafter, only variants of those song types detected by audition were graphed. A catalogue of syllables and notes was then made as in Thompson (1970), permitting comparisons between individuals. Terms used in the description of songs are those of Mulligan (1966).

SYLLABLE AND SONG SHARING BETWEEN BIRDS

The Individual Song

Songs of Song Sparrows are highly variable, but may be characterized by short introductory phrases, a central trill, and a terminal flourish of notes (Borror, 1965; Mulligan, 1966). The male uses an extensive repertoire of songs that consist of: (1) distinct song types, each composed of unique sequences of syllables, notes, and note complexes (Fig. 1), and (2) variations of the former arising from the addition or omission of various notes in each theme.

Repertoire size for this population ranged from five to 12 themes per bird (excluding two birds for which less than 20 songs were recorded), with the mean being 7.33 (Table 1).

Syllable Sharing

Comparison of all the syllables and notes found in the population (Figs. 2 and 3) with each individual's repertoire revealed extensive

TABLE 1.
Descriptive statistics of the song repertoires of individual birds.

Bird	No. of songs recorded	No. of songs graphed	No. of song patterns	Total no. of syllable & note types	No. of shared syls & notes	No. of unshared syls & notes	% of syls and notes shared	% of syls and notes unshared
0-1	109	45	12	39	25	14	64.1	35.9
L1-1	67	29	9	24	24	0	100.0	0.0
L1-3	89	46	9	27	24	3	88.9	11.1
L2-1	14	14	3	7	7	0	100.0	0.0
L2-2	14	13	1	4	4	0	100.0	0.0
L2-3	72	39	9	27	23	4	85.2	14.8
L4-2	41	22	9	28	27	1	96.4	3.6
L4-3	74	35	9	29	26	3	89.7	10.3
L5-1	31	14	5	19	19	0	100.0	00.0
Mean	56.78	28.56	7.33	22.67	19.69	2.78	91.59	8.41
SD	±33.49	±13.39	±3.54	±11.08	± 8.49	±4.49	±11.80	±11.80

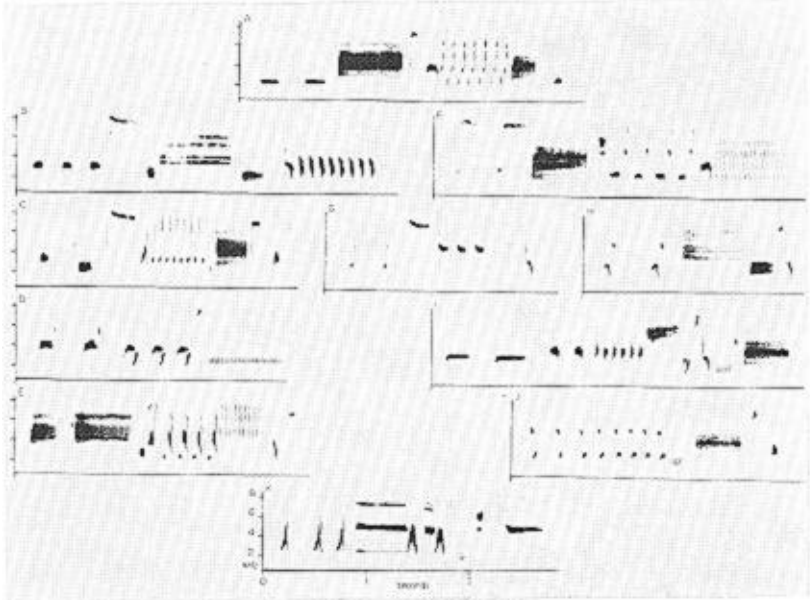


FIGURE 1. Eleven of the 12 song patterns sung by Song Sparrow 0-1.

sharing between birds. No syllable was shared by every bird, and some syllables were unique to an individual's repertoire. Birds on the terraced slopes shared from 85.2% to 100% of the syllables in their individual repertoires. Bird O-1, from the neighboring canyon, shared only 64.1% of his syllables (Table 1). All syllables used by birds L1-1, L2-1, L2-2, and L5-1 were shared with other individuals in the population, although not all syllables were shared with each other. However, only one to nine song types were recorded for these individuals. It is conceivable that other song types containing unshared syllables were not used and were thus missed by the investigators.

Degree of syllable sharing between pairs of Song Sparrows was determined using the method of Harris and Lemon (1972). For example, of the 27 notes and syllables used by L1-3 and the 24 used by L1-1, 14 were found in both repertoires, giving a value of $(14 + 14)/(27 + 24) \times 100 = 54.9\%$. All birds were compared in this manner, yielding an average of $42.19 \pm 18.53\%$ (Table 2). Exclusion of L2-1 and L2-2, for which less than five song types were recorded, gives a mean value of $56.2 \pm 7.89\%$.

Theme Sharing

Identical sequencing of like syllables was found in the repertoires of four birds (Fig. 4). Additionally, five birds shared themes that were almost identical, each theme differing slightly in one or two syllable types in the introductory or terminal portions. When these data are pooled, five birds shared from one to three themes with

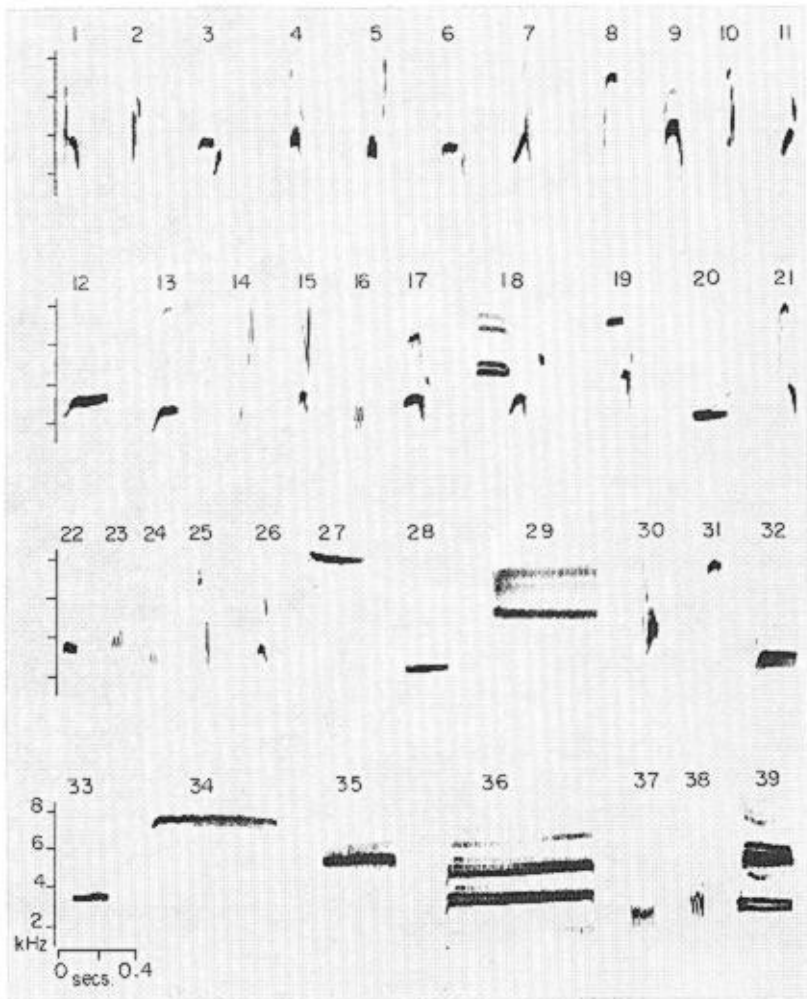


FIGURE 2. Catalogue of shared syllables and notes from Song Sparrow songs.

from one to three other individuals (Table 3; Fig. 4). Song pairs A1-A2 and D1-D2 (Fig. 4) are identical in sequencing and number of syllables. Pairs B1-B2 and C1-C2 are not exactly identical, variations being in syllable morphology rather than sequencing. Songs A1, B1, and C1 are from bird L4-3; A2, B2, and C2 are from bird L1-1, illustrating two birds sharing three themes.

INTERSPECIFIC MIMICRY

Armstrong (1963) points out that some avian species, such as the Mockingbird (*Mimus polyglottos*) and Gray Catbird (*Dumetella carolinensis*), mimic regularly whereas others, such as Meadowlarks (*Sturnella* spp.), mimic only closely related species. Still

TABLE 2
Degree of syllable sharing between pairs of Song Sparrows (%)

Bird	0-1	L1-1	L1-3	L2-1	L2-2	L2-3	L4-2	L4-3	L5-1
0-1	—	47.6	45.4	17.4	18.6	51.5	50.8	47.1	49.3
L1-1	—	—	54.9	32.3	14.3	54.9	69.2	67.9	60.5
L1-3	—	—	—	41.2	25.8	63.0	65.5	50.0	52.5
L2-1	—	—	—	—	18.2	23.5	28.6	33.3	15.4
L2-2	—	—	—	—	—	25.8	18.8	18.2	8.7
L2-3	—	—	—	—	—	—	61.8	50.0	56.5
L4-2	—	—	—	—	—	—	—	63.2	68.1
L4-3	—	—	—	—	—	—	—	—	50.5

other species, such as the White-crowned Sparrow, have demonstrated no interspecific mimicry (Marler and Tamura, 1964; Marler, 1970).

Mulligan (1966) cross-fostered Song Sparrows under Canaries and found no mimicry of the foster-parents' vocalizations. However,

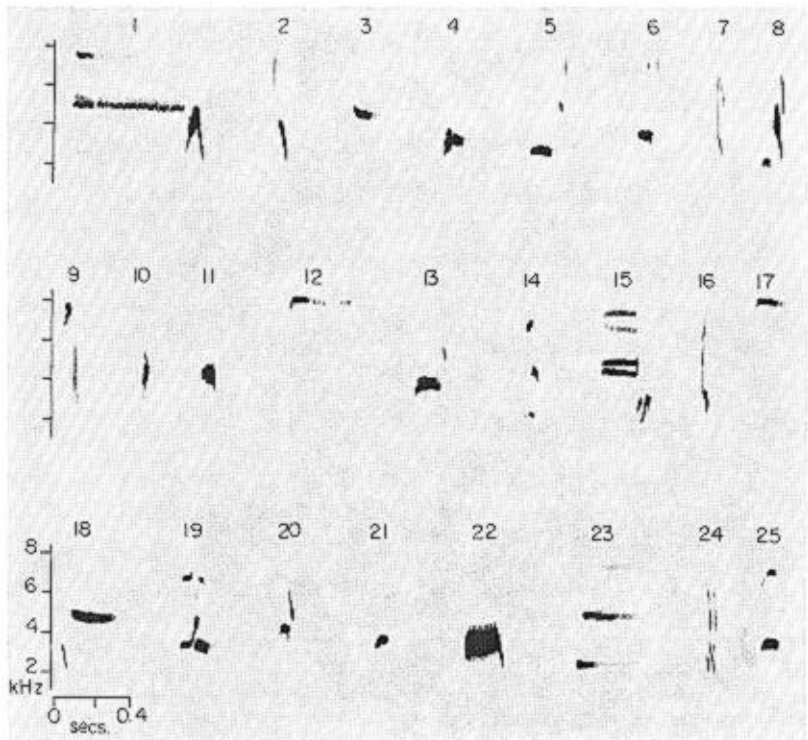


FIGURE 3. Catalogue of unshared syllables and notes from Song Sparrow songs.

Kroodsma (1976) repeated Mulligan's experiment and found that Song Sparrows may copy some song elements from Canaries. Except for our Song Sparrow L2-2, for which only one song type was recorded, all the other birds in our study used what were apparently Wren tit syllables in their repertoires. Seven of these eight birds used mimetic syllables in one theme and one bird used them in two themes. Three of the eight individuals used mimetic syllables in the introductory phrases, whereas five birds used them later in the song (Fig. 5).

Yeoman (1975) studied Wren tit songs in the San Francisco Bay region of California and described them as beginning with an introductory portion consisting of a series of notes followed by a trill. Wren tit songs in our study area conform to this description (Fig. 5, A to D). Yeoman (1975) distinguished 10 types of territorial songs used by Wren tits; her classification was based on the number, kind, and arrangement of notes comprising each song. She recognized five basic note types, one of which (note type 4) was shaped like a cane or inverted "J." There are several variations of this note: one of these was rounded or dome-shaped (see introductory notes in song type 7 of Yeoman, 1975), a second type was pointed at the apex and shaped like a Gothic arch (as in trill of song type 5 of Yeoman, 1975), and a third type was shaped like an inverted "u" with two squared-off corners (song type 5 of Yeoman, 1975). All three of these notes occurred in our study area (songs A, B, and C

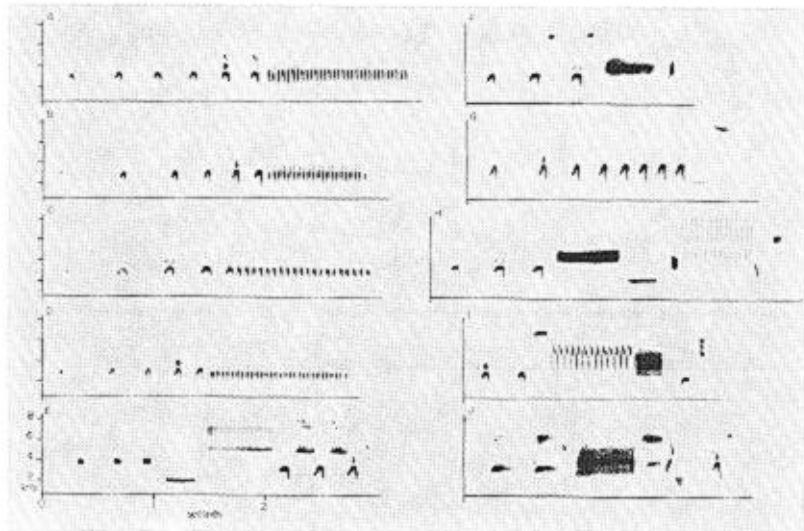


FIGURE 5. Songs A to D are Wren tit themes from Scholl Canyon. Songs E to J are Song Sparrow songs containing Wren tit syllables. Different types of arrows in Songs A to D indicate three different introductory syllable types used by Wren tits. The same arrows in Songs E to J illustrate the same Wren tit syllables in Song Sparrow songs. Song G was recorded during our pilot study in 1973. The rest of the Song Sparrow songs were recorded in 1974.

respectively in Fig. 5), and all three of these notes appeared in the local Song Sparrow songs (compare songs A and I, B and G, C and H, Fig. 5).

Armstrong (1963:73) cautioned that calls of one species may fortuitously resemble those of other species. Could the similarities in the Wrentit and Song Sparrow syllables be a result of chance? This might indeed be the case if matching was found in only one syllable type. However, since resemblances were found in three syllable types, we would favor interspecific mimesis as an explanation for the similarities rather than convergence. Baptista spent many hours in the marshes of the San Francisco Bay of California (where Wrentits are absent) listening to Song Sparrow songs and did not hear these distinct introductory syllables.

DISCUSSION

Mulligan (1966) and Borror (1965) found a few cases of Song Sparrows sharing whole themes. However, Harris and Lemon (1972) found no instances of identical songs sung by two birds. Five Song Sparrows in our study shared themes with others in the population. Syllables and notes that comprise songs in our California population are also shared with other birds in the population. Syllable sharing is apparently more extensive for this community than in the one studied by Mulligan (1966) and somewhat more than in that studied by Harris and Lemon (1972). Song Sparrows from Quebec react more strongly to playback of songs from their home population than to songs from alien populations (Harris and Lemon, 1974). Harris and Lemon (1974) proposed that songs containing syllables frequently heard by the individuals elicited stronger responses than songs containing syllables with few or no familiar syllables.

Harris and Lemon (1972) have suggested that the apparent disparity between Mulligan's (1966) and Borror's (1965) and their own data might not be real because the authors emphasized different parameters of song in their respective studies. Mulligan studied primarily patterns of timing, whereas Borror and Harris and Lemon treated variation in notes and combinations thereof. However, Mulligan (1966:15; and pers. comm.) actually looked for similar syllables in the repertoires of different birds and found very few. There is, therefore, geographical variation in the amount of intraspecific song or syllable mimesis in Song Sparrows as has been reported in White-crowned Sparrows, Rufous-sided Towhees, and House Finches (see Introduction).

There is, moreover, geographical variation in repertoire size. Borror's (1961) Maine population averaged 8.25 themes and birds from Quebec averaged nine themes (Harris and Lemon, 1972). In the San Francisco Bay area, Mulligan (1966:15) noted that no bird sang fewer than 10 themes. Thirteen birds that he studied in detail had repertoires ranging from 10-23 themes and averaged 15.8. Our southern California population averaged 7.33 themes (Table 1).

The development of dialects requires isolation of the population, a means of transmitting the dialect between generations, and some source of variation that causes divergence between localities (Harris and Lemon, 1972; Nottebohm, 1972; Baptista, 1975; Lemon, 1975). Additionally, in order to perpetuate dialects, males must continue to breed in the same area, and juveniles must not disperse over great distances. Marshall (1948) and Johnston (1961) found that California races of Song Sparrows are more sedentary and hold smaller territories than do races in other parts of the country. Moreover, Mulligan (1966) and Kroodsma (1976) have demonstrated song learning in the Song Sparrow. Why the higher incidences of theme sharing reduced repertoire size and the higher percentage of syllable sharing in the Southern California birds versus the northern Californian, Maine and Quebec birds studied by Mulligan, Borror, and Harris and Lemon?

Tompa (*in* Mulligan, 1966:59) and Mulligan (*in* litt.) studied populations of Song Sparrows on Mandarte Island, British Columbia. They noted reduced repertoire size and high incidence of sharing in this small and dense insular population. Song Sparrows in our study area live in a small ecological island (see Methods and Materials). We propose that perhaps the original colonizers brought with them a small repertoire of syllables and themes. Their descendants were, therefore, born into a relatively poor acoustical environment as compared with Song Sparrows raised in optimum Song Sparrow habitat supporting large numbers of males singing a large repertoire of syllables and themes. The increased amount of syllable and theme sharing in our birds is perhaps partially a reflection of a small pool of syllables and themes from which to mimic. Harris and Lemon (1972) also noted a high incidence of syllable sharing in birds holding adjacent territories versus birds that were more widely dispersed. Birds in our study area were packed into an isolated patch of habitat, probably increasing interactions between individuals during song development and thus increasing syllable and theme mimesis. Our data, may, therefore, be an artifact of isolation in marginal habitat.

Nice's (1943) observations on song development in hand-reared captives lend some support to our hypothesis. Two birds were captured at about five or six days of age and hand-reared. They vied with each other for dominance status and eventually sang six themes each, exact duplicates of each other, a phenomenon never otherwise observed.

Interspecific Mimicry in the Fringillidae

Imitation of conspecifics plays a large role in song learning in many species of birds (Marler and Mundinger, 1971; Nottebohm, 1972; Lemon, 1975). Interspecific mimicry has been less often documented. In laboratory studies, juveniles insufficiently exposed to songs of conspecifics may sometimes mimic interspecifically (Lanyon, 1960; Baptista, 1973). Species that naturally mimic in the wild are apparently not as prevalent. Among fringillids, European Greenfinches (*Chloris chloris*) have been found to freely

mimic other sympatric passerines (Güttinger, 1974). Some fringilids such as the House Finch (Baptista, 1972), Vesper Sparrow (*Poocetes gramineus*) (Kroodsma, 1972), Oregon Junco (*Junco oreganus*) (Laidlaw Williams, in press), Chaffinch (*Fringilla coelebs*) (Thieleke, 1962; Knecht and Scheer, 1968), Chipping Sparrow (*Spizella passerina*), Bachman's Sparrows (*Aimophila aestivalis*) and Rufous-sided Towhee (Borror, 1968) are facultative mimics. Kroodsma (1973) and Baptista (1972) suggested that insufficient exposure to songs of adult conspecifics in nature might stimulate interspecific learning of songs.

Since mimicry in Song Sparrows is apparently rare, mimesis in this population of these emberizines merits an explanation. Perhaps because few conspecifics were present and few conspecific songs were heard, the founders and their progeny mimicked interspecifically. Introductory phrases in Wrentit songs bear some resemblance to those in "pure" Song Sparrow songs in pitch, syllable duration and rhythm. These similarities may have prompted Song Sparrows to select Wrentit phrases as models for mimesis. Robinson (1975) recently studied Lyrebirds (*Menura* spp.) that regularly mimic a variety of species and found, similarly, that songs selected for mimesis were similar in frequency to conspecific songs.

SUMMARY

Variation in the songs of Song Sparrows in a California population were studied. Most of the syllables and notes in a male's song repertoire were shared with the other birds in the community. Some birds also shared from one to three whole themes with other individuals. Mimicked Wrentit syllables were found in the introductory or later phrases of the repertoires of eight of the nine birds. Song Sparrows are geographically variable in their tendency to mimic intraspecifically, southern California populations sharing more syllables than do northern Californian, eastern and Canadian populations. It is proposed that increased syllable and theme sharing might be a reflection of a small population in marginal habitat exposed to a small pool of syllables from which to mimic.

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