SONG IN A POPULATION OF BLACK-THROATED SPARROWS

DONALD B. HECKENLIVELY[1]

Department of Biology
New Mexico State University
Las Cruces, New Mexico 88001

Among the aspects of behavior associated with breeding biology, song production of the territorial male passerine is one of the most readily quantified. The study of song variation in bird populations may give information on functions of song in communication, and also indicate the nature and extent of selective pressures to which the birds are subjected (Marler 1960). The Black-throated Sparrow, *Amphispiza bilineata*, is a suitable species for the study of song variation. Bailey (1917, 1923) mentions the variability in its song; and likewise, Peterson (1961:296) alludes indirectly to possible variability. Nonetheless, detailed spectrographic analysis of its song has not previously been made. Study of the Black-throated Sparrow is also of interest because of the lack of attention given this species in the literature (Smyth and Bartholomew 1966).

TERMINOLOGY

Current terminology in bird song literature has been adopted, wherever applicable, to avoid excessive introduction of new terms (cf. Marler and Isaac 1961; Konishi 1964; Wildenthal 1965). The terminology used by Mulligan (1963) has been used here as far as possible; the distinction made by Borror (1960) between trills and buzzes was found to be applicable and also has been adopted. By "song" I refer at least to vocal patterns rendered by territorial male birds during the breeding season (Heckenlively 1967). "Song" is purposely not defined more tightly because all functional contexts are not fully explored. The terminology is illustrated in figure 1 and defined as follows.

Song-type. A grouping of song sub-components of a characteristic morphology and in a characteristic temporal sequence.

Note. Any sound that produces a continuous mark on the spectrogram.

Syllable. The basic unit repeated in a trill or buzz; either a single note or a group of notes.

Phrase. A natural section of the song, distinguishable from other phrases either temporally or by a change in form (e.g., a buzz followed by a trill); usually consisting of a croak, note-complex, trill, or buzz, but occasionally a single note.

[1] Present Address: Museum of Zoology, University of Michigan, Ann Arbor, Michigan 48104.

Croak (CR). A phrase-type consisting of a series of low-pitched, fuzzy notes.

Note-complex (NC). A natural note group, distinguishable temporally, but containing dissimilar notes, unlike trills or buzzes.

Buzz (BZ). A series of one-note syllables, repeated at a rate exceeding 30 per sec and usually having a broad frequency range (i.e., unmusical).

Trill (TR). A series of similar syllables, repeated at a rate slower than 30 per sec and usually consisting of notes with distinct, limited frequency spread (i.e., musical).

METHODS AND MATERIALS

The study was carried out with a population of Black-throated Sparrows resident in the Rio Grande Valley near Las Cruces, New Mexico (Dona Ana County, 106°41' W, 32°18'30" N). Creosotebush (*Larrea divaricata*) was the dominant plant on the 46.4 ha study plot (Gardner 1951). The site used for this study was contained within the study area used by Raitt and Maze (1968), who report the conditions of the area in more detail. The population was studied from June to September 1964 and from February to June 1965. Although banding was attempted during 1965, identification of the individuals in the population ultimately depended on simultaneous sight records of individuals, recognition of distinctive individual songs, and the strong territoriality exhibited by the birds.

A Nagra IIIBH tape recorder was used for recording and playback in the field and a Viking 85 recorder was used for laboratory playback. Recordings were made at 15 ips, using a University 401 Omnidirectional microphone mounted in a parabolic reflector. Audiospectrograms were made on a Kay Electric Company Sonagraph, using the High Shape circuit and Wide Band filter setting.

During the spring of 1965 most of the recordings were obtained by playing recorded Black-throated Sparrow songs to territorial males and recording their responses. Songs obtained with this induction technique do not appear to differ in their morphology from spontaneously offered songs, and spontaneous and induced songs have not been differentiated in the analysis.

Unless otherwise indicated, all estimates of song parameters are given as the mean $\pm$ one standard deviation. Statistical notation follows Simpson et al. (1960).

RESULTS

About 800 songs were tape-recorded from 22 singing males on the study site during 1964 and 1965, averaging 33 songs (range 6–176) from each bird in 1965. For analysis, "song variation" was defined as the number of song-types from each individual and in the population. Accordingly, each recognizably
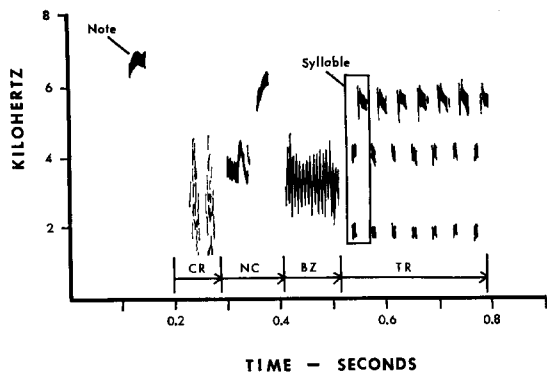
FIGURE 1. Audiospectrogram of a song from individual C4, illustrating terminology used.

TABLE 2. Analysis of two-act sequences in phrase ordering in Black-throated Sparrow songs.

Sequence	χ^2	P
Facilitative:		
INT-NC	22.56	<0.001
INT-CR	17.50	<0.001
CR-NC	46.63	<0.001
NC-BZ	37.50	<0.001
BZ-TR	37.34	<0.001
TR-INT	108.91	<0.001
Inhibitive:		
NC-NC	5.48	<0.02
NC-INT	19.91	<0.001
BZ-NC	9.00	<0.005
INT-BZ	6.89	<0.01

different song of each bird was subjected to audiospectrography; this procedure yielded 67 song-types from the population. One bird, F41, was recorded on two occasions, and a total of nine song-types was found in his recordings, the highest number from any given bird. Two other birds, C6 and E5, each had seven song-types, the next highest number. A statement of the mean number of song-types per individual is not meaningful because of small samples from some of the birds. The values for the three birds give some indication of the potential number of song-types in an individual repertoire. Assuming that these birds are representative, approximately half of the total number of song-types in the population have been sampled in this study.

GENERAL DESCRIPTION OF THE SONG

A quantitative statement is highly desirable for the sequence in which the various phrase-types are used, since songs of the Black-throated Sparrow are somewhat complex (figs. 4–6). A modification of the statistical technique of Hazlett and Bossert (1965) was used. First, a matrix of two-act sequences

TABLE 1. Frequency distribution of two-act sequences in phrase ordering in Black-throated Sparrow songs.

Preceding act	Event following act[b]				
	NC	CR	BZ	TR	INT
NC[a]	23 (38)	18 (13)	41 (16)	28 (21)	1 (23)
CR	38 (13)	0 (4)	0 (5)	0 (7)	0 (8)
BZ	4 (16)	0 (5)	0 (7)	28 (9)	15 (10)
TR	0 (21)	0 (7)	5 (9)	7 (12)	51 (13)
INT	46 (23)	20 (8)	1 (10)	0 (13)	

[a] NC = note-complex, CR = croak, BZ = buzz, TR = trill, INT = interval between songs.
[b] The expected value, based on random ordering of phrases, is placed parenthetically beside each observed value.

was tabulated (table 1), recording the number of occurrences of each kind of phrase after a given phrase-type. Inter-song intervals were included in the matrix as a test of phrases characteristically starting and finishing a song. Using a chi-square test, the number of occurrences recorded in each box of the matrix was then compared to a value expected by random sequencing of phrase-types within the song. This expected value was obtained by multiplying the frequency among all phrases of a given following phrase by the total number of phrases following each phrase-type. In table 2, which summarizes the results of this analysis, a two-act sequence was considered "facilitative" if it occurred significantly more often than expected from random sequencing; a sequence was considered "inhibitive" if occurrence was significantly less than expected.

The song of the Black-throated Sparrow appears to be divided into two general sections: (a) an introduction, containing a croak and note-complexes, and (b) a repetitive section made up of trills, buzzes, or both. Table 3 presents the frequencies of the sequences of phrases found. A croak is not always present, but when it occurs it tends to be placed early in the introduction, with a note-complex following, and is never directly followed by a trill or buzz. No case of more than one croak per song was recorded. Generally, two repetitive phrases occur in a song, usually a buzz followed by a trill. The sequence of a trill followed by another trill is less frequent than the buzz-trill sequence. Only one instance of more than one buzz per song was recorded in the population. On the basis of the two-act sequences, the "most probable" song would appear to be either CROAK/NOTE-COMPLEX/BUZZ/TRILL or NOTE-COMPLEX/BUZZ/

TABLE 3. Phrase sequences in 67 song-types of Black-throated Sparrows.

Sequence	No. song-types	Sequence	No. song-types
a. NC-BZ	4	o. CR-NC-BZ-TR	7
b. NC-TR	4	p. CR-NC-NC-TR	2
c. NC-NC-BZ	2	q. CR-NC-NC-TR-TR	1
d. NC-NC-TR	1	r. CR-NC-NC-BZ-TR	1
e. BZ-NC	1	s. CR-NC-NC-TR-BZ	1
f. NC-TR-TR	1	t. NC-CR-NC-TR	3
g. NC-TR-BZ	1	u. NC-CR-NC-BZ	3
h. NC-BZ-TR	3	v. NC-NC-CR-NC-TR	1
i. NC-NC-BZ-TR	8	w. NC-CR-NC-NC-TR	2
j. NC-NC-TR-BZ	2	x. NC-CR-NC-TR-TR	1
k. NC-BZ-TR-TR	1	y. NC-CR-NC-NC-TR-TR	1
l. NC-BZ-TR-BZ-TR	1	z. NC-CR-NC-BZ-TR	7
m. CR-NC-BZ	2	aa. NC-BZ-NC-NC-TR	1
n. CR-NC-TR	4	bb. CR-NC-BZ-NC-TR-TR	2

TRILL. These two sequences, or some simple elaboration of them, represent 44.8 per cent of the phrase sequences found in the population. The former (o + r + z + bb of table 3) constituted 25.4 per cent of the total, the latter (h + i + k + l of table 3), 19.4 per cent.

COMPONENT CHARACTERISTICS

Note-complex morphology. A total of 43 different note-complexes were distinguishable in the song-types. Of these, 13 were to some extent shared among individuals in the population (fig. 2; table 4), the remainder being found in the repertoire of a single individual. However, the shared note-complexes represented the majority (72.5 per cent) of the total note-complexes appearing in the song-types. Even with the sharing, there was some individual variation in the expression of a given note-complex (compare note-complex b in figure 7 or note-complex d in figure 4d and figure 6a).

Croaks might be regarded functionally as note-complexes by their placement in the introductory section of the song. Yet croaks were sufficiently distinctive to warrant naming as a separate phrase-type, since no other note-complex had a rigidly repetitive pattern. Croaks in the population had a mean duration of 0.118 ± 0.062 sec and a repetition rate of 19.64 ± 7.34 syllables/second ($N = 38$). Maximum frequency of croaks was 4.66 ± 0.83 kHz and minimum frequency was 1.32 ± 0.62 kHz. Comparing variability in mini-
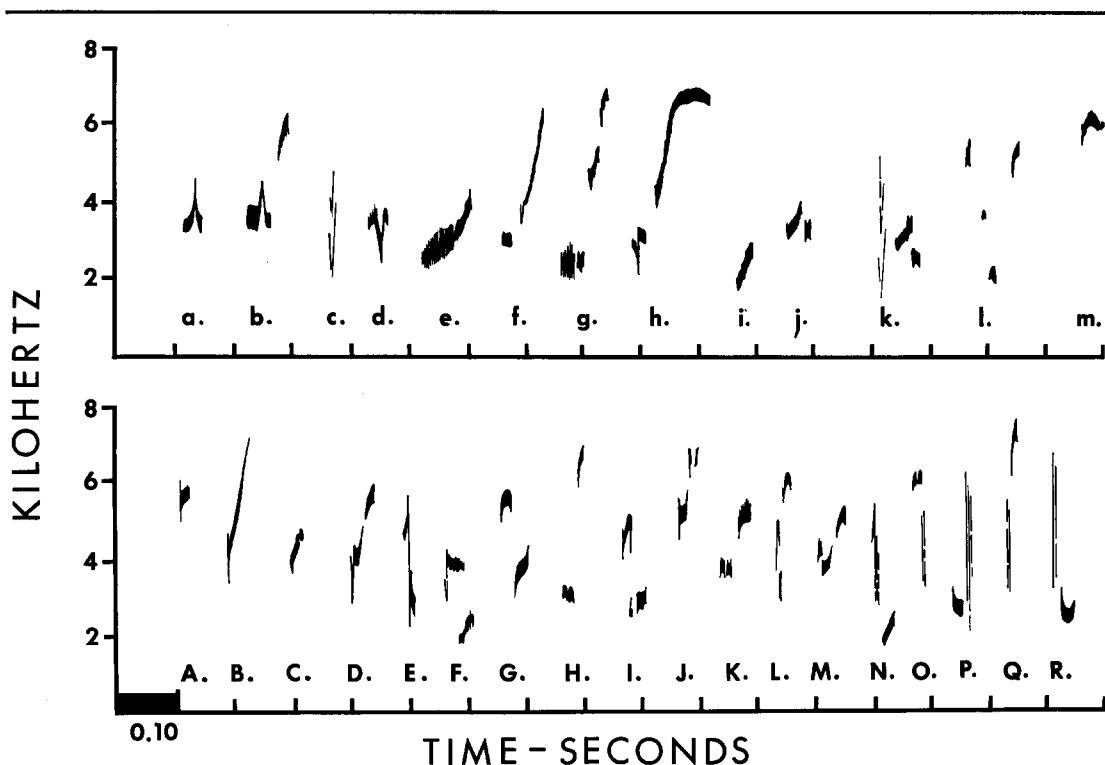

FIGURE 2. a through m: Note-complexes appearing in the repertoires of more than one individual in the study population; designation of note-complexes by letters the same as in table 4. A through R: Representative trill syllables (A–C, single-trill syllables; D–H, double-trill syllables; I–M, triple-trill syllables; and N–R, buzz-trill syllables).

TABLE 4. Note-complexes appearing in the repertoires of more than one individual in the study population.

Source	No. song-types	Note-complexes[b]													No. others
		a	b	c	d	e	f	g	h	i	j	k	l	m	
Individual[a]															
C6	7	+	+		+	+		+						+	2
E4	5	+		+	+				+	+				+	1
E5	7				+			+		+				+	3
F41	9	+	+			+			+			+		+	4
F42	6						+				+	+		+	1
H6	5		+		+	+		+		+			+		2
Population															
67 song-types[c]		5	6	4	6	5	6	4	3	8	3	4	2	7	38
22 individual repertoires[c]		5	4	3	5	5	3	4	3	8	3	4	2	7	

[a] Table compares only the six individuals with a sample repertoire of five or more song-types.
[b] Designation of letters to note-complexes is the same as in fig. 2.
[c] Number of song-types or individual repertoires in which the note-complex appeared.

mum frequency of the song-types without croaks with variability in minimum frequency of all song-types one finds that the low minimum frequency of the croak phrases significantly increased variability of this parameter ($F = 2.31$, $P < 0.05$). Mean minimum frequency of song-types without croaks was significantly higher than that of song-types with croaks ($t = 7.70$, $P < 0.001$).

Buzzes and trills. The song-types included two distinctly different kinds of buzzes. One exhibited a high, narrow frequency spectrum and fast repetition rate ("high buzzes"), and the other had a broader frequency range and slightly slower rate ("low buzzes"). These two kinds of buzzes were statistically different in all parameters except the mean number of syllables in a phrase (table 5). Indeed, the only rationale for regarding them as the same kind of phrase is that their use in song-types was mutually exclusive; i.e., in no case was one kind of buzz used in a song-type containing the other.

Trills could be differentiated by the number of notes in a syllable. Trills with single-note syllables ("single-trills") comprised 18 per cent of all trills; trills with two-note syllables ("double-trills") were the commonest, making up 53 per cent of the total, and 10 per cent of the trills had three-note syllables ("triple-trills"). The remainder of the trills were a unique form of the double-trill, in which one note of the syllable was a single note of narrow frequency range and the other note had a broad, buzz-like frequency range ("buzz-trills").

Buzzes, buzz-trills, and single-trills tended to be somewhat stereotyped throughout the population, but double-trills and triple-trills were more specific to the individual in syllable structure. Of the 35 syllable-types encountered, 23 (65.7 per cent) were found in only one individual, and none was found in more than four birds (fig. 2).

Complexity of syllable structure was reflected in overall characteristics of the kinds of trill phrases (table 6). Double-trills and triple-trills were both significantly longer in duration than single-trills ($t = 3.41$, $P < 0.01$; $t = 2.37$, $P < 0.05$, respectively), but double-trills and triple-trills were very similar in their durations ($t = 0.10$, $P > 0.50$). Duration of buzz-trills did not differ materially from either single-trills or double-trills ($P > 0.50$ for both). The number of syllables in a trill was essentially the same for all kinds of trill phrases ($P > 0.50$ for all comparisons). Repetition rate of single-trills was significantly faster than that of double-trills ($t = 4.02$, $P < 0.01$), triple-trills ($t = 3.41$, $P < 0.01$), or buzz-trills

TABLE 5. Characteristics of buzzes.

Parameter	High buzz	Low buzz	P of similarity	F[a] (P)
Duration (sec)	0.194 ± 0.016	0.246 ± 0.012	$P < 0.001$	1.80 ($P > 0.20$)
Maximum frequency (kHz)	6.34 ± 1.27	4.85 ± 0.97	$P < 0.001$	1.70 ($P > 0.20$)
Minimum frequency (kHz)	5.69 ± 1.23	2.44 ± 0.70	$P < 0.001$	3.10 ($P < 0.05$)
No. of syllables	20.76 ± 7.12	18.32 ± 5.62	$P > 0.20$	1.61 ($P > 0.20$)
Repetition rate (syllables/sec)	110.2 ± 41.1	75.6 ± 21.6	$P < 0.001$	3.61 ($P < 0.02$)
Sample size	17	28		

[a] Test of differences in variance, $F = s_1^2 / s_2^2$.

TABLE 6. Characteristics of trill phrases.

	Single-trill	Double-trill	Triple-trill	Buzz-trill	All trills
Duration (sec)[a]	0.343 ± 0.13 (11)	0.493 ± 0.13 (33)	0.500 ± 0.13 (6)	0.421 ± 0.11 (12)	0.453 ± 0.14 (62)
No. syllables	5.36 ± 1.43 (11)	5.58 ± 1.84 (33)	5.39 ± 1.28 (6)	5.46 ± 1.30 (12)	5.50 ± 1.60 (62)
Repetition rate (syll./sec)	16.40 ± 3.61 (11)	11.63 ± 3.34 (33)	10.93 ± 1.97 (6)	13.37 ± 2.88 (12)	12.74 ± 3.64 (62)
Maximum frequency (kHz)	5.68 ± 0.88 (12)	5.76 ± 1.09 (32)	5.42 ± 0.72 (6)	6.15 ± 0.51 (13)	5.79 ± 0.93 (63)
Minimum frequency (kHz)	4.34 ± 1.09 (12)	2.90 ± 1.14 (32)	2.03 ± 0.41 (6)	2.07 ± 0.70 (13)	2.92 ± 1.26 (63)

[a] Sample size in parentheses.

($t = 2.24$, $P < 0.05$). Double-trills and triple-trills did not differ in repetition rate ($t = 0.49$, $P > 0.50$). Repetition rate of buzz-trills did not differ significantly from double-trills ($t = 1.60$, $P > 0.10$) or triple-trills ($t = 1.86$, $P > 0.05$). The rate of repetition among repetitive phrases (tables 5, 6) shows a clear separation between trills and buzzes. The differences in the rate illustrate the separation of these phrases in the terminology section and confirm the distinction made by Borror (1960: 27) between trills and buzzes on the basis of the subjective impression of the listener.

Frequency maxima and minima of trill phrases also reflect structural complexity. Minimum frequency of double-trills was significantly lower than that of single-trills ($t = 3.78$, $P < 0.001$), and triple-trills were significantly lower than double-trills ($t = 1.84$, $P < 0.05$). Buzz-trills were significantly higher than triple-trills in frequency maximum ($t = 2.56$, $P < 0.05$) and lower than double-trills in frequency minimum ($t = 2.45$, $P < 0.05$).

Temporal analysis. Figure 3 compares time intervals within note-complexes, within trills, and between phrases. Intervals within buzzes were too fine to measure with accuracy. Mean duration of intervals within note-complexes was 0.028 ± 0.024 sec, while mean duration of intervals within trills was 0.019 ± 0.012 sec. These values were significantly different ($t = 6.42$, $P < 0.001$). Both mean intra-phrase intervals were significantly shorter than the mean inter-phrase interval of 0.064 ± 0.048 sec ($t = 2.04$, $P < 0.05$ for intra-trill intervals; $t = 4.44$, $P < 0.001$ for intra-note-complex intervals).

Borror suggested (pers. comm.) that playback of songs to territorial males can increase rate of singing. This was tested by comparing cadences (Reynard 1963) of birds recorded in July 1964, when no playback was used, with cadences of birds recorded in March 1965, when playback was used to induce singing. The mean cadence of 1964 birds was 3.009 ± 1.861 sec ($N = 109$), while the mean of 1965 birds was 3.088 ± 2.163 sec ($N = 194$). These cadence values did not differ significantly ($t = 0.455$, $P > 0.50$) and the average value from both years, 3.059 ± 1.432 ($N = 303$) was used to calculate singing rate, 19.61 songs/min. Mean duration of the song was 1.02 sec (table 7). Thus performance time, that part of the song bout actually spent singing (Hartshorne 1956), was about 33.3 per cent. Several times, however, song bouts were witnessed in which the singing appeared to be almost continuous, so the calculated performance time may be only approximate.

The pattern in which the song-types were ordered within a song bout is of interest. There was a definite tendency in the population toward alternation, presenting the songs in an ABABABAB order. Alternation was tape-
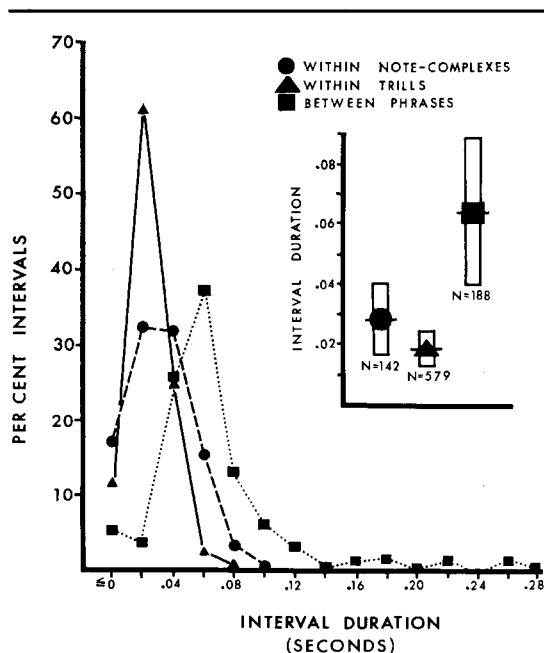

FIGURE 3. Comparison of intervals within note-complexes, within trills, and between phrases.

TABLE 7.   Interspecific comparison of population song parameters.

	Mexican Junco[a]	Oregon Junco[b]	Brown Towhee[c]	Black-throated Sparrow
General form	NC + TR, in variable order	TR	introduction (1 note) + TR	introduction (complex) + TR or BZ
Song duration (sec) $\bar{x} \pm \text{SD}(V)$[d]	1.63 ± 0.29 (17.8)	1.49 ± 0.20 (13.6)	1.52 ± 0.31 (20.4)	1.02 ± 0.31 (30.4)
No. phrases/song $\bar{x} \pm \text{SD}(V)$	3.7 ± 1.4[e] (37.8)	1 (occasionally 2)	2	3.85 ± 1.06 (27.5)
No. syllables/trill $\bar{x} \pm \text{SD}(V)$	10.1 ± 2.9 (28.7)	14.1 ± 4.4 (31.1)	10.4 ± 4.5[b] (43.3)	5.50 ± 1.60[f] (29.1)
Max. frequency (kHz) $\bar{x} \pm \text{SD}(V)$	6.39 ± 0.51 (8.0)	6.53 ± 0.65 (9.9)	5.86 ± 0.86 (14.6)	6.86 ± 0.91 (13.2)
Min. frequency (kHz) $\bar{x} \pm \text{SD}(V)$	2.09 ± 0.25 (11.9)	2.98 ± 0.12 (4.0)	1.86 ± 0.35 (19.0)	1.62 ± 0.60 (37.0)
Sample size	67	77	61	67

[a] From Marler and Isaac 1961.
[b] From Konishi 1964.
[c] From Marler and Isaac 1960.
[d] Coefficient of variation $(V) = $ (standard deviation/mean) (100).
[e] Phrases per song not available; value is syllable types per song.
[f] $N = 62$.

recorded in 17 of the 22 birds, and witnessed in the field numerous times. This singing pattern is unusual among passerines. Borror (1959, 1961) notes that alternation is common in Eastern Phoebes (*Sayornis phoebe*) and that it occasionally occurs in Wood Pewees (*Contopus virens*), Traill's Flycatchers (*Empidonax traillii*), and Rufous-sided Towhees (*Pipilo erythrophthalmus*). However, it contrasts sharply with the Oregon Junco, *Junco oregonus* (Konishi 1964) and the Brown Towhee, *Pipilo fuscus* (Marler and Isaac 1960), both of which sing the same pattern a number of times before going to another (AAAABBBB).

OVERALL CHARACTERISTICS AND INTERSPECIES COMPARISON

Table 7 summarizes overall characteristics of Black-throated Sparrow song and compares them with those of some other emberizines (Marler and Isaac 1960, 1961; Konishi 1964). It is not particularly fruitful to compare mean values for the various song parameters; not surprisingly, all parameter means differ significantly. Variability of the parameter estimates is of greater interest, since Black-throated Sparrows vary uniquely. They are more variable in song duration than the other emberizines in table 7, but the comparison is statistically significant only in the case of Oregon Juncos ($F = 2.39, P < 0.01$). Maximum frequency is not particularly variable in any of the four species, yet Black-throated Sparrows are more variable than Mexican Juncos, *Junco phaeonotus* ($F = 3.16, P < 0.01$), and Oregon Juncos ($F = 1.95, P < 0.01$). Black-throated Sparrows are significantly more variable than

the other three species in minimum frequency (least $F = 2.82; P < 0.01$ for all comparisons).

Thorpe and Lade (1961) characterize most emberizines' songs as short, repetitive, stereotyped, and rather simple, while acknowledging some highly variable species, such as Song Sparrows (*Melospiza melodia*) and Lark Sparrows (*Chondestes grammacus*). This is perhaps somewhat oversimplified. As a check, the emberizines listed in Robbins et al. (1966) were examined, since both verbal and pictorial representations of their songs are available in this book. Categorizing the songs as (1) trill only, (2) introduction plus trill, or (3) more complex, one finds that 70 per cent (33 of 47 species) fit in the first two categories. More complex singers include Vesper Sparrows (*Pooecetes gramineus*), Lark Sparrows, Mexican Juncos, Rufous-crowned Sparrows (*Aimophila ruficeps*), Tree Sparrows (*Spizella arborea*), Lincoln's Sparrows (*Melospiza lincolnii*), Song Sparrows, and possibly others. The Black-throated Sparrow is also marginal to a strict "introduction plus trill" format, since the introduction is complex and variable and replacement is variable between trills and buzzes.

Detailed syllable structure is highly variable in most emberizine populations (Marler and Isaac 1961). Here, the Black-throated Sparrow is typical, since the majority of its syllable types are unique to individual birds (fig. 2). Yet the number of syllables per trill is a conservative character in Black-throated Sparrows. Significantly more variable are Mexican Juncos ($F = 3.28, P < 0.01$), Oregon Juncos ($F = 7.50, P < 0.01$), and Brown Towhees ($F = 7.91, P < 0.01$).

TABLE 8. Comparison between the song-types of four Black-throated Sparrows and the rest of the population.

	Song duration (sec) $\bar{x} \pm$ SD (V)	No. phrases/song $\bar{x} \pm$ SD (V)	Max. frequency (kHz) $\bar{x} \pm$ SD (V)	Min. frequency (kHz) $\bar{x} \pm$ SD (V)	Sample size
C6	1.08 ± 0.33 (30.6)	4.14 ± 0.90 (21.7)	7.43 ± 0.65 (8.78)	1.27 ± 0.62 (49.1)	7
E5	1.04 ± 0.30 (29.0)	3.57 ± 0.53 (14.9)	6.44 ± 0.60 (9.27)	1.30 ± 0.51 (39.4)	7
F41	0.93 ± 0.13 (13.6)	3.44 ± 1.1 (33.8)	7.36 ± 0.65 (8.82)	1.69 ± 0.31 (18.1)	9
F42	1.10 ± 0.34 (31.1)	4.50 ± 0.83 (18.6)	7.08 ± 0.88 (12.37)	1.00 ± 0.51 (50.6)	6
Rest of population	1.02 ± 0.34 (33.1)	3.84 ± 1.15 (29.9)	6.69 ± 1.29 (19.3)	1.83 ± 0.64 (34.9)	38

INDIVIDUAL VARIATION

One meaningful approach to describing the variation in songs of a given individual is to compare that bird with the rest of the population, establishing a perspective from which to examine the individual. Three significant parameters of the song are song duration, the number of phrases per song, and the frequency range. Comparison of C6, E5, F41, and F42 individually with the rest of the population in these three parameters (table 8) shows that the individuals do not differ greatly from the rest of the population. There is about as much variation among individuals

as between any individual and the rest of the population in song duration and frequency minimum. Yet mean minimum frequencies of C6, E5, and F42 all differ significantly from the rest of the population (least $t = 2.08$, $P < 0.05$). Conversely, none of the birds differs significantly from the rest of the population in mean frequency maximum, but the rest of the population is collectively more variable than C6 ($F = 3.92$), E5 ($F = 4.69$), and F41 ($F = 3.97$, $P < 0.05$ for all). Although population variability in number of phrases per song is generally greater than the individual variabilities, none of the
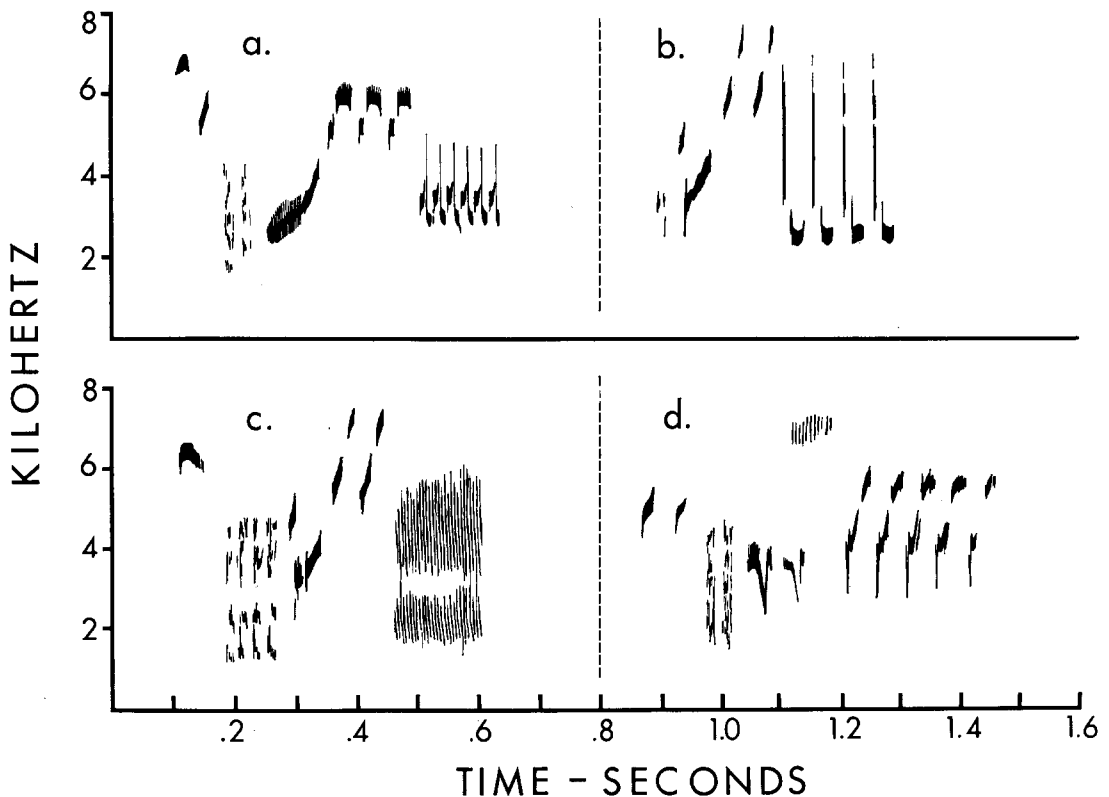
FIGURE 4. Four song-types from the repertoire of individual F41.
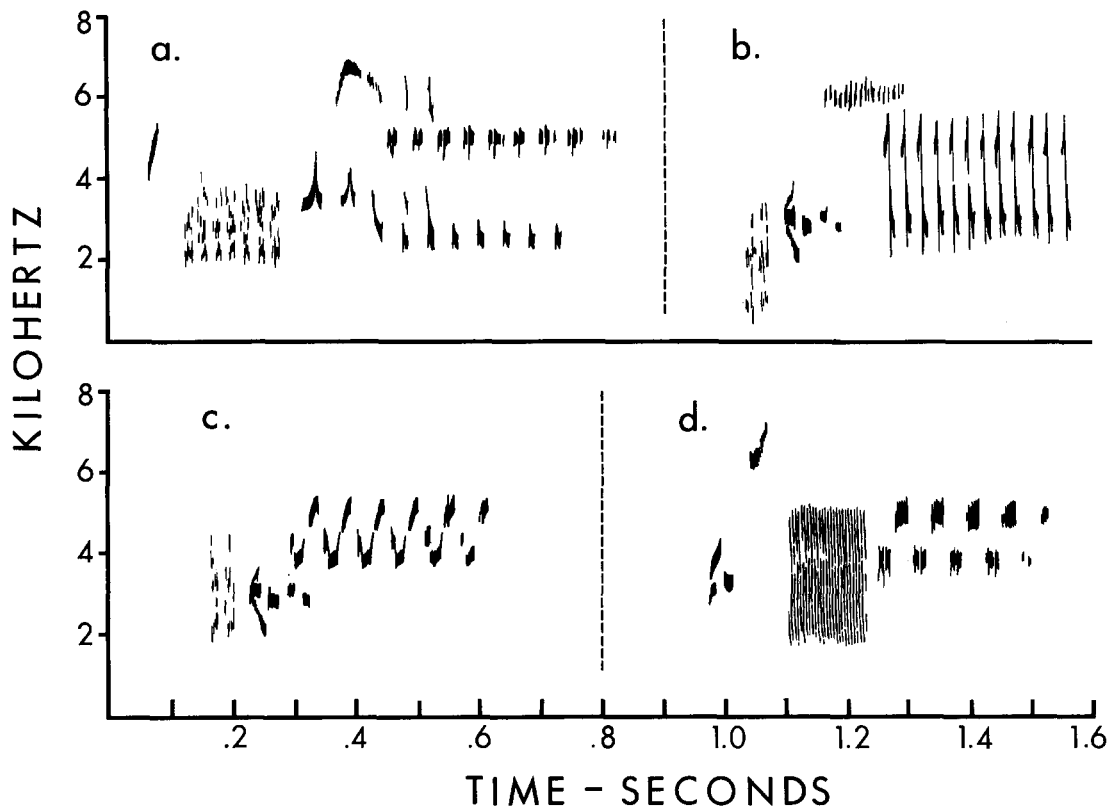
FIGURE 5. Four song-types from the repertoire of individual E5.

birds is significantly different from the population in mean number of phrases.

Black-throated Sparrows achieve variability in individual repertoires by combining basic groups of note-complexes, trills, and buzzes in various arrangements. Thus, a given note-complex may appear with either a trill or a buzz (fig. 4b, c), or with different kinds of trills (fig. 5b, c). Inclusion of one or two introductory notes before a note-complex, or the inclusion of a croak in the introduction, would be sufficient change in the song pattern to constitute a new song-type by the definition used in this study. Within an individual's repertoire of syllable-types, some recurrent note morphs can be found, such as the "flag-like" note included as the upper note in several syllable types of C6 (fig. 6a, b, d).

One song pattern, note-complex b (fig. 2) plus a buzz, appeared in several contexts in the repertoires of six individuals. This pattern was used alone by three individuals as a song-type (fig. 7c, d). It also appeared with simple modification, such as an introductory croak (fig. 7a, b, e). Three song-types were found in which this motif had been incorporated as part of a longer song-type (e.g., fig. 1).

Black-throated Sparrows exhibited another complex vocal pattern that was both mixed into singing bouts and rendered by itself. This pattern consisted of a rapidly warbled series of notes that dropped progressively in frequency (fig. 8), called a "descending series" in this paper. Several examples from three individuals (F41, F42, and C6) have been examined, and the morphology of the descending series appears to be relatively stereotyped and specific to the individual (cf. figs. 7b and 8c). The descending series appears to have some function as a signal in high-intensity agonistic contexts. Descending series were first heard in late summer, 1964, during fighting observed between two birds. Excerpting from field notes of 21 August 1964:

"07:45. Two Black-throats in (assumed) agonistic behavior—flying at each other, exchanging complex calls, maybe rapid antiphony. One chased the other about 200 ft N through the brush; both landed on the same bush about 10 ft apart. No further action at each other. Third bird seen within 10 ft of where the two started. . . ."

Later that same morning two other birds were observed fighting, again rendering a "complex exchange of calls." Territorial bound-
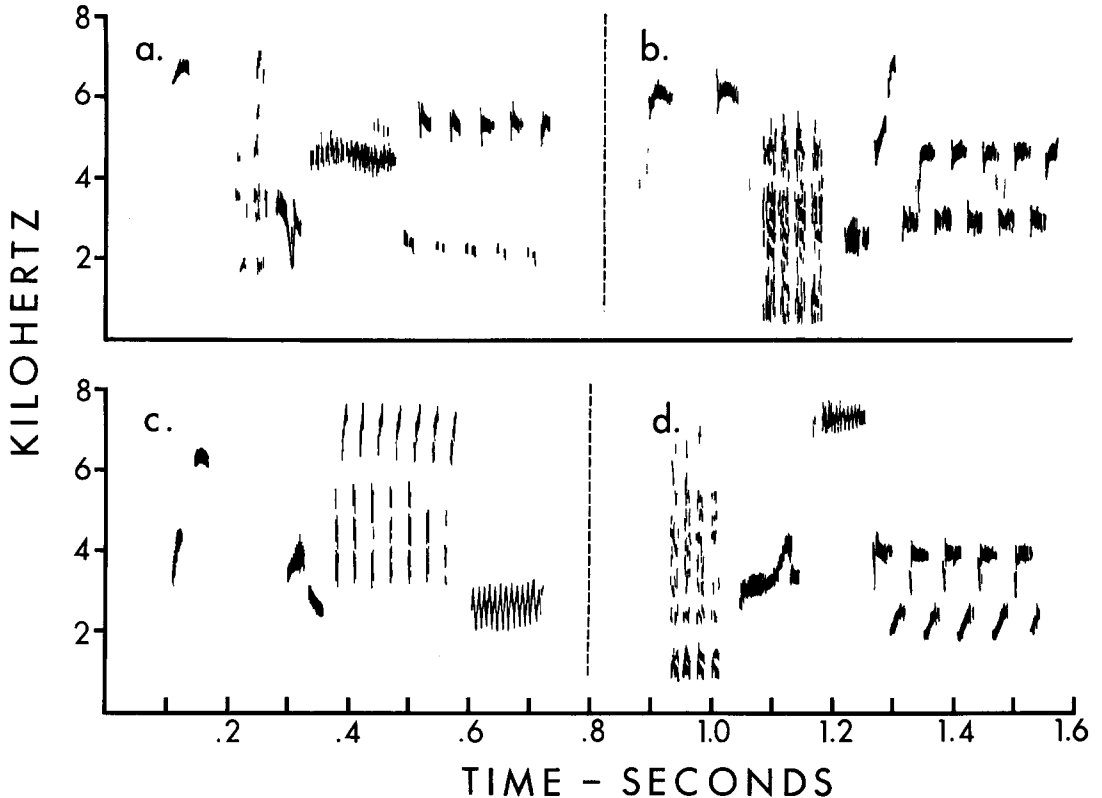
FIGURE 6. Four song-types from the repertoire of individual C6.

aries were observed to be breaking down at that time, although some of these displays may have been directed at wandering fledgling sparrows. During the spring, 1965, descending series were occasionally mixed with singing of birds in response to taped playback, in general correlating with intense response to the playback. On the basis of later spectrography of recordings, the vocalizations described as a "complex exchange" of calls in earlier field notes appear to have been the descending series of one bird rather than an exchange between two.

DISCUSSION

VERSATILITY AND CONTINUITY

Hartshorne (1956) has postulated that continuity of singing (i.e., performance time) and versatility in singing show a positive correlation. Hartshorne's explanation of the correlation involves a monotony threshold which inhibits the repetition of the same song at too fast a rate, allowing time for the memory of the previous utterance of the song to dispel so that the rendition of the song may retain "freshness." Assuming, as did Hartshorne, that song functions are "social and psychological," selection for such a correlation

could be postulated if it enhanced song's effectiveness by maintaining the attentiveness of the singer. The remaining question is whether or not such a satiety threshold for repetition exists.

In fact, satiation to repetition of a particular act is well known and has received attention in psychological studies. Postulate Number One of Thompson's (1960:201) Two-factor Theory of Inhibition appears to be a close correlate of Hartshorne's suggestions:

"Whenever an organism makes a response, there is developed an increment of inhibition which decreases the probability of recurrence of that same response. This condition is called response inhibition (I_R). The amount of I_R developed by a series of response evocations is a negative growth function of the number of evocations and dissipates as a simple negative growth function of time."

The Black-throated Sparrow is a semi-versatile, semi-continuous singer by Hartshorne's hierarchy. With the typical pattern of alternation between two song-types in a song bout, *Amphispiza bilineata* cannot be considered highly versatile, regardless of the total number of songs in the repertoire, because the short term pattern of singing is the determining factor in continuity by Hartshorne's definition. On the other hand, a pattern of alter-
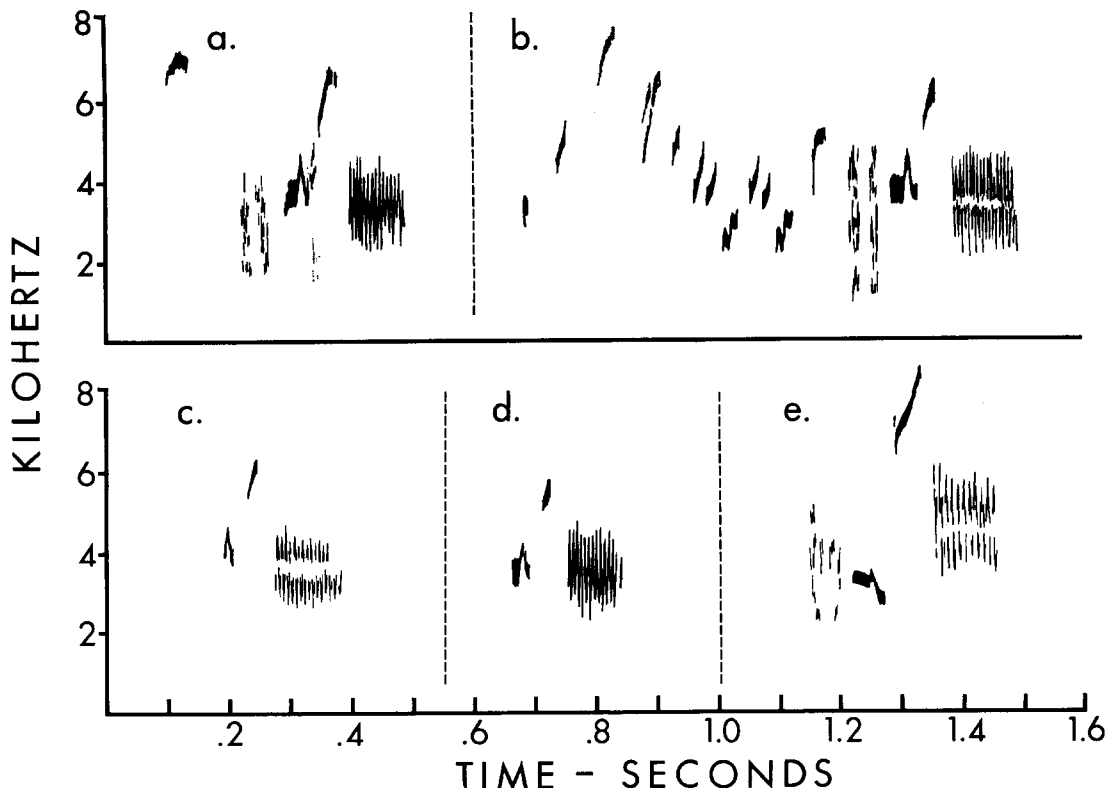
FIGURE 7. Examples of the shared song pattern including note-complex b and a buzz. Sources: (a) individual C4, (b) C6, (c) H6, (d) H7, and (e) C6.

nation logically would seem to permit higher continuity than that observed from the calculations based on the population means of duration and singing rate, since the inhibition to one song-type would have sufficient time to dissipate partially during the rendition of its alternative. The data on singing rates seem to bear out this idea. If the maximum observed rate of singing an alternating pattern (30.0 songs/min) is multiplied by the average song duration of the population (1.02 sec), a performance time of 52 per cent is derived. The Black-throated Sparrow, then, has a potential for high continuity by Hartshorne's definition.

VARIABILITY AND SPECIES SPECIFICITY

Variability in song may be viewed from two standpoints: that of variation in the population, and that of the variation in any given individual. Borror (1961) considers a species population to be highly variable if there are more than 12 different songs in the population, with little or no overlap between individuals. Similarly, he considers an individual to be variable if there are more than six songs in its repertoire. By both criteria

the Black-throated Sparrow qualifies as a variable singer. Only four overlaps between individuals were found among 22 birds studied, and the most variable individual encountered in the population had at least seven to nine song-types. This does not approach the variability in the Song Sparrow (Mulligan 1963), in which individuals have been recorded with as many as 23 song-types, but it compares quite well with the Cardinal (*Richmondena cardinalis*), with 11 song-types per individual (Borror 1961). Rufous-sided Towhees have been recorded with as few as seven song-types per individual, but individuals have exhibited as many as 19–22 song-types (Borror, pers. comm.). Before definite conclusions may be made about song in the Black-throated Sparrow the variation should be studied in other geographical locations as well.

Marler (1959, 1960) has postulated that bird song is under conflicting selective pressures. If song is to serve as a reproductive isolating mechanism, then it must be specifically distinct. Thus, the song would be subject to selective pressure for stereotypy. Conversely, if the song is to function in intraspecific com-

and Ficken 1966), possibly implicating the relatively higher variability in minimum frequency (table 8) as a factor in individual recognition.

Definition of species-specific characteristics in the song of the Black-throated Sparrow is problematical, since highly variable characters are difficult to visualize in a role requiring stereotypy. Marler (1960) has suggested that individual and species recognition functions are relegated to different parameters of the song. The fine details most logically would function in individual recognition in the Black-throated Sparrow because of the uniqueness to individuals. Thus parameters that probably function in individual recognition include the syllable structure of the trills, the arrangement within the note-complexes, and the arrangement and ordering of the phrases. Also, the relatively high variability in minimum frequency suggests that notes of lower frequency might be involved in individual recognition. Conservative characters in Black-throated Sparrow song that probably function in species recognition include the general format of introduction and repetitive sections, the number of syllables per trill, song duration, and buzz and trill combinations. Perhaps a buzz-trill sequence is required as part of the repertoire, although this could be dialectal.

Several approaches might be tried which would clarify the role of song and the relationships between the components of the song. Experiments on vocal versus visual communication (Heckenlively 1967) could be expanded to include the Sage Sparrow, preferably in geographical locations where the congeneric birds are breeding sympatrically. Also, the song of the Sage Sparrow needs to be studied. A third approach, possibly yielding the greatest amount of information, would be experiments on the reaction of territorial males and unmated females to altered or electronic song (Falls 1963; Marler 1967). The minimum requirements for a song identifiable by the birds as their own—that is, the minimum species-specific song—might thus be determined.

SUMMARY

Song structure and variation were studied in a population of 22 Black-throated Sparrows, using audiospectrography. Typically, song format includes a complex introduction followed by a buzz, trill, or both. Black-throated Sparrows are highly variable singers, both as individuals and as a population. In comparison with several other emberizines studied at the population level, Black-throated Sparrows are more variable in song duration and frequency range, and less variable in number of syllables per trill. Factors apparently important in the song variation are the lack of closely related sympatric species and reduced numbers of bird species in desert scrub habitat. Large territories appear to encourage selection for variation in overall pattern and for acoustical territorial defense.

ACKNOWLEDGMENTS

LITERATURE CITED

BAILEY, A. M., AND R. J. NIEDRACH. 1965. Birds of Colorado. Denver Museum of Natural History, Denver, Colo.

BAILEY, F. M. 1917. Handbook of birds of the western United States. Houghton Mifflin Co., Boston.

BAILEY, F. M. 1923. Birds recorded from the Santa Rita Mountains in southern Arizona. Pacific Coast Avifauna no. 15.

BEHLE, W. H. 1960. The birds of southeastern Utah. Univ. Utah Biol. Ser. 12(1):1–56.

BORROR, D. J. 1959. Variation in the songs of the Rufous-sided Towhee. Wilson Bull. 71:54–72.

BORROR, D. J. 1960. The analysis of animal sounds. p. 26–37. In W. E. Lanyon and W. N. Tavolga [eds.] Animal sounds and communication. AIBS Publ. no. 7. Washington, D. C.

BORROR, D. J. 1961. Intraspecific variation in passerine bird songs. Wilson Bull. 73:57–78.

DIXON, K. L. 1959. Ecological and distributional relations of desert scrub birds of western Texas. Condor 61:397–409.

FALLS, J. B. 1963. Properties of bird song eliciting responses from territorial males. Proc. XIII Intern. Ornithol. Congr., Ithaca, p. 259–271.

FICKEN, R. W., AND M. S. FICKEN. 1966. A review of some aspects of avian field ethology. Auk 83:637–661.

GARDNER, J. L. 1951. Vegetation of the creosote-bush area of the Rio Grande Valley in New Mexico. Ecol. Monogr. 21:379–403.

GRINNELL, J., AND A. H. MILLER. 1944. The distribution of the birds of California. Pacific Coast Avifauna no. 27.

HARTSHORNE, C. 1956. The monotony-threshold in singing birds. Auk 73:176–192.

HAZLETT, B. A., AND W. H. BOSSERT. 1965. A statistical analysis of the aggressive communications systems of some hermit crabs. Anim. Behav. 13: 357–373.

HECKENLIVELY, D. B. 1967. Role of song in territoriality of Black-throated Sparrows. Condor 69:739–740.

KONISHI, M. 1964. Song variation in a population of Oregon Juncos. Condor 66:423–436.

LIGON, J. S. 1961. New Mexico birds. Univ. New Mexico Press, Albuquerque.

MARLER, P. 1959. Developments in the study of animal communication. p. 150–206. In P. R. Bell [ed.] Darwin's biological work, some aspects reconsidered. John Wiley and Sons, Inc., New York.

MARLER, P. 1960. Bird songs and mate selection. p. 348–367. In W. E. Lanyon and W. N. Tavolga [eds.] Animal sounds and communication. AIBS Publ. no. 7. Washington, D. C.

MARLER, P. 1967. Animal communication signals. Science 157:769–774.

MARLER, P., AND D. ISAAC. 1960. Song variation in a population of Brown Towhees. Condor 62:272–283.

MARLER, P., AND D. ISAAC. 1961. Song variation in a population of Mexican Juncos. Wilson Bull. 73:193–206.

MULLIGAN, J. A. 1963. A description of Song Sparrow song based on instrumental analysis. Proc. XIII Intern. Ornithol. Congr., Ithaca, p. 272–284.

PETERSON, R. T. 1961. A field guide to western birds. Houghton Mifflin Co., Boston.

RAITT, R. J., AND R. L. MAZE. 1968. Densities and species composition of breeding birds of a creosotebush community in southern New Mexico. Condor 70:193–205.

REYNARD, G. B. 1963. The cadence of bird song. Living Bird 2:139–148.

ROBBINS, C. S., B. BRUUN, AND H. ZIM. 1966. Birds of North America. Golden Press, New York.

SIMPSON, G. G., A. ROE, AND R. C. LEWONTIN. 1960. Quantitative zoology. Harcourt, Brace, and Co., New York.

SMYTH, M., AND G. A. BARTHOLOMEW. 1966. The water economy of the Black-throated Sparrow and the Rock Wren. Condor 68:447–458.

THOMPSON, M. E. 1960. A two-factor theory of inhibition. Psychol. Rev. 67:200–206.

THORPE, W. H., AND B. I. LADE. 1961. The songs of some families of the passeriformes. II. The songs of the buntings (Emberizidae). Ibis 103a:246–259.

WILDENTHAL, J. L. 1965. Structure in primary song of the Mockingbird (Mimus polyglottos). Auk 82:161–189.