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THE SHORT SONG OF BREWER'S SPARROW: INDIVIDUAL AND GEOGRAPHIC VARIATION IN SOUTHERN IDAHO

Terrell D. Rich¹

ABSTRACT.—Brewer's Sparrows (*Spizella breweri*) have two song types—a “short” song that has 1 to 3 trill types and a “long” song that has 5 to 10 or more trill types. I describe the short song and examine patterns of individual and geographic song variation from 15 sites on the Snake River Plain in southern Idaho. Territorial males sang the short song regularly during the breeding season. Two-trill song types comprised 72.9% of all song types, with 3-trill types (18.8%) and 1-trill types (8.2%) less frequent. Over 90% of the males sang their song type(s) essentially without variation. Many trill types appeared most often in only 1 of 3 possible song positions, i.e., 1st, 2nd, or 3rd trill. Trill types that occurred in different song positions differed in syllables per second, trill and syllable duration, and frequency variables. First trill types were more variable than 2nd or 3rd trill types. There was no evidence that birds at sites closer together shared more trill types or pairs of trill types than those farther apart. There was no tendency for territorial neighbors to sing similar song types. Brewer's Sparrows' small territories, dense populations, and apparently high rate of annual turnover may mediate against the evolution of song sharing or vocal dialects.

Key words: Brewer's Sparrow, *Spizella breweri*, song dialects, geographic variation, Idaho, individual variation, sagebrush, Snake River Plain.

Brewer's Sparrow (*Spizella breweri* Cassin) is a migratory species that is abundant during the breeding season over large expanses of sagebrush (*Artemisia* L. spp.) steppe in the western U.S. (Wiens and Rotenberry 1981, Rotenberry et al. 1999). Despite this abundance, Brewer's Sparrow song has not been described previously except in general terms (Bent 1968, Rising 1996, Doyle 1997, Rotenberry et al. 1999). Brewer's Sparrows have 2 song types—a “short” song that has 1 to 3 trill types and a “long” or “extended” (Doyle 1997) song that has 5 to 10 trill types, sometimes more. The long song is most often described, albeit inadequately, in field guides and other references.

My main purpose is to provide the first description of the “short” song of Brewer's Sparrow across a portion of the Snake River Plain in southern Idaho. The nature of song variation is of interest because Brewer's Sparrow is currently undergoing significant rangewide population declines (Saab and Rich 1997, Sauer et al. 1997) and is commonly detected and monitored by song during the breeding season. Changes in detectability over the breeding season have been described (Best and Petersen 1985). A more complete understanding of

its vocal behavior will help to ensure accurate monitoring.

I also examined patterns of geographic song variation, specifically testing the null hypotheses that there is no relationship between the geographic distance between males and the number of trill types or pairs of trill types shared. Geographic variation in song across multiple spatial scales provides insights into the behavior, social organization (Payne 1981, 1983), and ontogeny of song development (Kroodsma 1996). As I will show, there is no evidence for song sharing, song matching, or vocal dialects in this species within the study area. Small territory size, dense populations, and high turnover are consistent with the idea that Brewer's Sparrow is an r-selected species where simple songs emphasizing species identity prevail over a more complex social structure that might be enhanced by song sharing among neighbors (Payne 1981, 1983). This situation is contrasted with that of the broadly sympatric Sage Sparrow (*Amphispiza belli*), which exhibits vocal dialects in the same geographic area and habitats (Rich 1981) and in other parts of western North America (Wiens 1982).

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STUDY SITES

In May and June 1977, 1978, and 1979, I recorded songs of 284 Brewer's Sparrows from 15 sites on the Snake River Plain in southern Idaho (Fig. 1): BB, Bingham-Bonneville county line; BT, Kettle Butte; C, E, and SA, along U.S. Highway 26; CM, near Craters of the Moon along the road to Blizzard Mountain; DF, Deadman Flat; GR, Great Rift National Monument; HH, Huddles's Hole; JF, Juniper Flat; MB, 2 km north of Menan Buttes; MLF, Medicine Lodge Flats; PB, Pillar Butte; T, 1 km north of Atomic City; and VC, east slope of a prominent volcanic cone 2 km south of Atomic City. Songs of individual males are labeled by site name and a number, e.g., PB-2, BT-7. Site SA (Fig. 1) was sampled in all 3 years, and site CM was sampled in both 1978 and 1979. These resampled sites are treated separately and labeled SA7, SA8, SA9, CM8, and CM9, respectively, with numbers representing the year recorded.

METHODS

Songs were recorded between sunrise and about 1100 hours from 2 May to 19 June each year. At each site all males were recorded in one morning in an area of about 2 km² or less. I recorded as many neighboring birds as possible. Once I chose the next bird to record, I began counting the number of songs he sang as I approached him. I noted how many songs were sung with variation and the type of variation, e.g., truncation, extra trill, or 2nd song type. Due to Brewer's Sparrows' small territories, most males recorded at each site were within hearing distance of at least one, and usually several, neighbors. I noted all cases where territorial neighbors were recorded.

Most vocalizations were recorded with a Dan Gibson Electronic Parabolic Microphone and Audiotronics model 147A cassette recorder. Some songs were recorded on a Uher 4000 Report L recorder. I noted in the field which song was most typical for a given male and analyzed that song. Sound spectrograms were prepared on a Voice Identification, Inc. Series 700 sound spectrograph using the 300 kHz wide band and 80–20,000 frequency scale.

Spectrograms of short songs were randomized so their identities were not known. I then defined and cataloged syllable types. A syllable type was the largest unit of song that was

repeated to form a trill type. Each syllable type was identified by a letter and a number, e.g., A1, E12. Letters identify generally similar syllable types but are arbitrary and do not play a role in analysis. In defining syllable types, I considered their sound-spectrographic shapes but not their frequency. This approach emphasizes subtle similarities in shape in preference to time and frequency variables.

Although individual birds were not marked, inspection of the sonograms from SA7, SA8, and SA9 did not reveal any short songs that were the same between years. The same situation existed for sonograms from CM8 and CM9. Thus, I assumed that no individual male was re-recorded in successive years and that males do not change songs between years, and I treated these as independent samples. This clearly is a major assumption, but there is some evidence from the congeneric Clay-colored Sparrow, *S. pallida* (Knapton 1982, 1994), that this assumption is justified.

I analyzed similarities within and among sites in 3 ways. First, similarity values between pairs of sites were derived from Jaccard's coefficient (Southwood 1978) for trill types shared. Values range from 0.0 (no similarity) to 1.0 (perfect similarity) for each comparison. Second, the same analysis was conducted for pairs of trill types shared. For the latter, I compared how many consecutive pairs of trill types were shared between individuals. For example, song A1 B1 C1 has 3 trill types and 2 pairs of trill types (A1 B1 and B1 C1). Third, time and frequency variables were measured on the spectrograms: trill duration; syllable duration; syllables per second; minimum, maximum, and dominant frequency; and frequency range. Amplitude sections were used to determine dominant frequency. Durations were measured to the nearest 0.05 second, frequencies to the nearest 0.3 kHz, and syllables per second to the nearest 0.1. Syllables per second was chosen as a means of incorporating information on inter-syllable interval because the latter were often very brief and difficult to measure accurately. For all variables, the position of the trill in the song (1st, 2nd, 3rd) was also identified so that in a 3-trill song type there were 21 variables.

Univariate statistical analysis follows Zar (1974). Stepwise discriminant function analysis was performed with computer programs in the BMDP series (Dixon 1981). The null

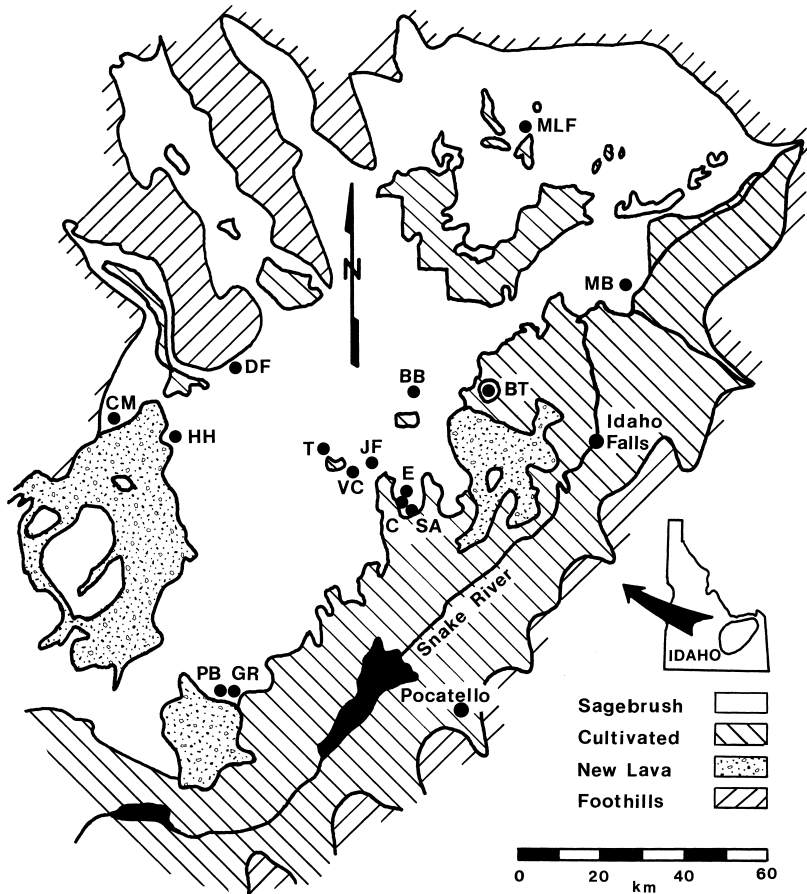


Fig. 1. Map of the upper Snake River Plain in Idaho composed from 1980 LANDSAT images. Lettered points are sites where Brewer's Sparrow songs were recorded.

hypotheses that there were no relationships between the matrix of distances among sites and the matrix of similarity values based on trill types shared or pairs of trill types shared were tested with Mantel's test (Schnell et al. 1985).

RESULTS

General Vocal Behavior

The Long Song

Brewer's Sparrows sang 2 types of songs—a "long" song (Doyle 1997) and a "short" song (Fig. 2). The long song (see sonograms in Kicka et al. 1999, Rotenberry et al. 1999) was sung much less frequently than the short song and appeared to be a vocalization stimulated by other males and/or females during the peak

of breeding activities (personal observation, Bent 1968, Willing 1970). Typically, a male began singing short songs and moved among perches while several of his neighbors were doing the same. Then as one male began singing the long song, many of his neighbors switched to their long songs. Often, some of the neighboring males, and possibly females, were rather close together, e.g., within 10 m, at the onset of the long-song singing. There was often considerable chasing involved as well. I also have elicited long songs from males by playing back recordings of their own short songs. A truncated long song could usually be distinguished from a short song because it began with a distinctive sequence. In particular, the long song is not simply the short song with additional trills appended.

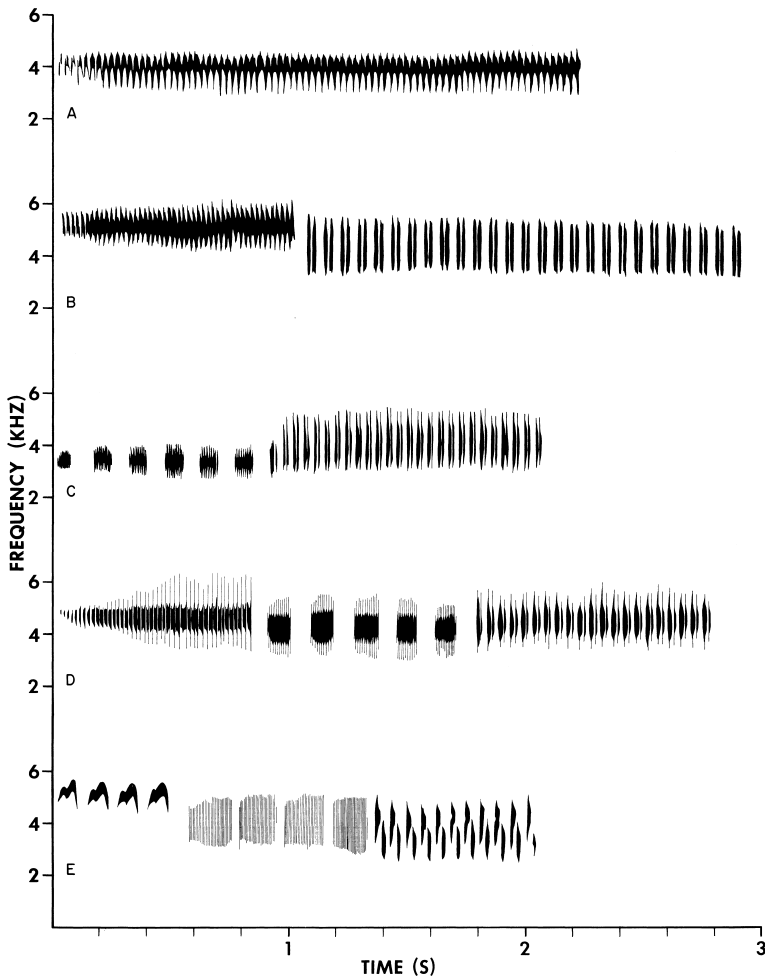


Fig. 2. Brewer's Sparrow short songs: A, a 1-trill song type composed of a single syllable type A6; B, a relatively typical song type composed of a higher-frequency, faster syllable type (A3) followed by a lower-frequency, slower syllable type (C8); C, another 2-trill song type E3 C6; D, a 3-trill song type A12 E3 C6; E, an uncommon 3-trill type, G E3 C5, showing a 1st trill type unique to 1 male.

The Short Song

NUMBER OF TRILLS PER SONG.—Territorial males sang the short song regularly during the breeding season. It consisted of 1 to 3 trills, depending on the bird (1 male sang 4 trills), and was sung with only minor variation (see below). Males sang in bouts that ranged from 4 to 143 songs, depending on the individual. Two-trill song types (Figs. 2B, C) comprised 72.9% of all song types, with 3-trill types (18.8%, Figs. 2D, E) and 1-trill types (8.2%, Fig. 2A) less frequent. In other parts of the Snake River Plain, in southern Oregon, northern Nevada, and southwestern North Dakota,

2-trill song types also were by far the most common type (personal observation).

VARIATION WITHIN INDIVIDUALS.—Of the 284 males recorded, I have data on song variation for 255 (Table 1). Of these, 190 (74.5%) sang song bouts with no variation aside from minor differences in trill duration. Another 33 males sang songs with substantial truncations, i.e., trills that had been sung completely were abruptly stopped before completion. In this group 18.8% of all songs heard were truncated. Six males (among the 33) truncated some songs after I recorded and then played back their own songs, and 3 others truncated songs after a neighboring male flew to a nearby perch and

TABLE 1. Nature and degree of song type variation within the short songs of individual Brewer's Sparrows on the Snake River Plain in southern Idaho.

No. males	% males	No. songs heard	Type of variation	Variable songs	
				No.	% ^a
190	74.5	3628	None	0	0.0
33	12.9	685	Truncated	129	18.8
10	3.9	170	Added 1 trill	48	28.2
8	3.1	174	Deleted 1 trill	31	17.8
6	2.4	232	2 song types	47	20.3
2	0.8	49	Punctuated 1st trill	20	40.8
2	0.8	35	Alternate 2nd trill	10	28.6
1	0.4	24	Replaced 2nd and 3rd trill type with 4th	6	25.0
1	0.4	33	3 song types	12	36.4
1	0.4	16	Combined 1st and 2nd trill types	2	12.5
1	0.4	35	Other	15	42.9

^aPercent of number of songs heard.

sang. Several other cases were undoubtedly caused by my presence, as males sang invariable songs at a steady rate while I approached them and then truncated some songs as I neared for recording. Therefore, I believe the truncated songs were caused by disturbances and were not meaningful variations. The 8 males who deleted 1 terminal trill should be considered similarly.

The remaining 24 males (9.5%) had song variations of consequence (Table 1). Ten males added a trill to an average of 28.2% of their songs. Six males had 2 different song types, and 1 had 3 types. Two males occasionally punctuated their 1st trill with a brief pause, and 2 others substituted a different 2nd trill in some songs. Three males with other variations were noted.

If the males who sang truncated songs and those who occasionally deleted a terminal trill are considered to have had invariable songs in the absence of disturbance, then 231 (90.6%) males sang without variation. Variation in the remaining 24 males affected 26.9% of their songs.

SYLLABLE TYPES AND TRILL TYPES.—Fifty-two syllable types were defined and cataloged from a total of 292 songs recorded from all males sampled (Fig. 3). The most common syllable type was A3, which occurred in 95 males (33.5%) and was the only type appearing at all 15 sites and in all years. The next most frequent type, B3, was sung by 59 males (20.8%). At the other extreme, 14 syllable types were unique to individual males. Unique types G

and H (Fig. 3) were particularly unusual for Brewer's Sparrows (personal observation).

PAIRS OF TRILL TYPES.—There were 323 pairs of trill types, i.e., combinations of consecutive trill types (excluding 24 one-trill songs) among all birds, and I classified 152 different pairs of types. Among those pairs, 105 (69%) were sung by only 1 male. The most common pair of trill types, A3 B3, was sung by 23 different males. The next most common, A3 C2, was sung by 11 different males.

The 24 one-trill song types were composed from only 10 different trill types, and 8 one-trill song types were unique. The most common syllable type, B3, was sung by 6 males. Thus, B3 appeared in the most common 1-trill and 2-trill song types. Among the 55 three-trill song types, only 5 were shared by 2 males.

POSITION OF TRILL TYPES.—Many trill types appeared mostly in only 1 of 3 possible song positions (Table 2, Fig. 3). The most striking example was syllable type A3, the most common type, that appeared 90 times as a 1st trill, 4 times as a 2nd trill, and only once as a 3rd trill. Types A6 and A9 occurred only in the 1st position. Other syllable types were most common in the 2nd position, e.g., B3, C2, C11, and E2. Only uncommon syllable types A5 and D5 occurred most often in the 3rd position. All other types that appeared in the 3rd position more than 2 times occurred most frequently in the 2nd position, e.g., B1, B3, C8, and C9.

DISCRIMINANT ANALYSIS OF SYLLABLE TYPES.—The syllable types that occurred in different positions within a song type had obvious

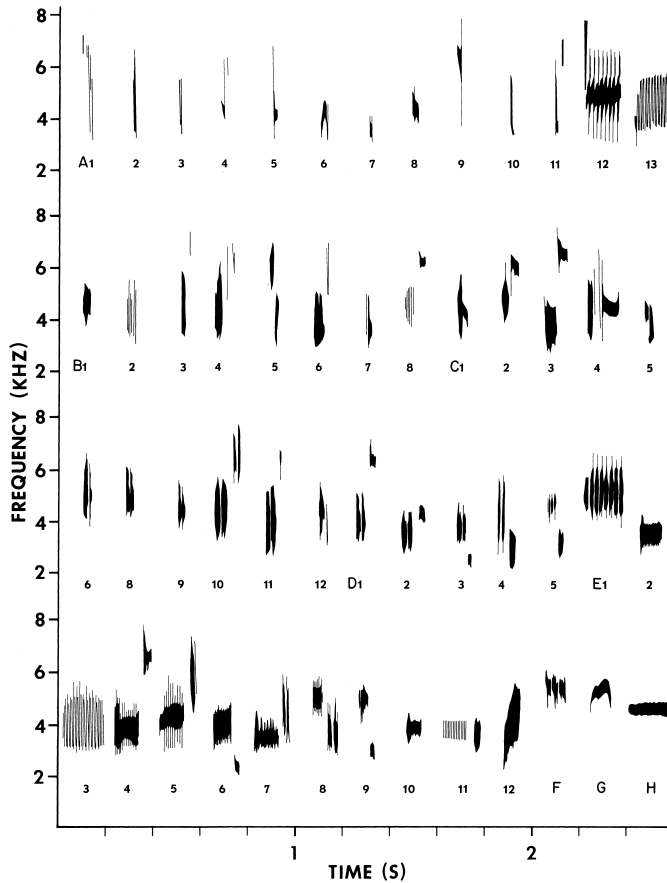


Fig. 3. Syllable type catalog for Brewer's Sparrow. For types A12 and A13, several repetitions of the type are shown.

differences, in many cases, in duration, trill rate, and frequency (Fig. 3). To further define these differences, I examined trill types by song position: the only trill in a 1-trill song (1-of-1), the 1st trill in a 2-trill song (1-of-2), and so on up to the 3rd trill in a 3-trill song (3-of-3).

Summary statistics for these data revealed several differences by position (Table 3). Song types with more trills had shorter trills. Syllable duration was more constant, except for the 2-of-3 position, which was longest. Syllables per second showed the greatest variation among positions and is one of the most obvious features differentiating syllable types (Fig. 3). In 2- and 3-trill song types, 1st trills were faster than later trills, whereas trill rate of 1-trill song types was slower. Maximum frequency also showed substantial differences, with 1st trills being higher than later trills. Minimum frequency and dominant frequency varied in proportion to maximum frequency. Frequency

range was greatest in trill types of 1-trill songs, with other positions only slightly less.

Discriminant analysis of the 6 trill-position groups revealed that syllables per second was the most important discriminating variable (Table 4). Trill duration was next, while syllable duration and minimum frequency, although also significant discriminators, did not greatly improve the *U*-statistic.

The classification matrix (Table 5) showed that most trill types were correctly classified by song position. One-of-one trill types were the most distinctive, with 91.7% correctly classified. In the 1-of-2 category, 55.9% were correctly placed, but 24.4% were classified in the 1-of-3 position. One-of-three category trills were also confused somewhat with the 1-of-2 category. The 2-of-2 category was distinguishable 60.6% of the time, but 21.1% were incorrectly classified into category 3-of-3. Similarly, 27.3% of the 3-of-3 trills were placed as 2-of-2

TABLE 2. Frequency of occurrence by song position, i.e., 1st, 2nd, or 3rd trill of song, for 52 syllable types in the short songs of 284 Brewer's Sparrows on the Snake River Plain in southern Idaho.

Syllable type	Frequency in position			Syllable type	Frequency in position		
	1	2	3		1	2	3
A1	4	2	0	C8	0	18	5
A2	2	0	0	C9	3	12	6
A3	90	4	1	C10	0	4	0
A4	2	0	0	C11	1	12	1
A5	1	1	2	C12	0	3	2
A6	48	0	0	D1	1	11	2
A7	19	2	0	D2	0	1	0
A8	14	0	0	D3	0	1	0
A9	28	0	0	D4	0	3	0
A10	1	0	0	D5	0	0	1
A11	2	0	0	E1	1	0	0
A12	0	1	0	E2	8	26	2
A13	1	0	0	E3	2	3	1
B1	2	12	5	E4	0	10	1
B2	5	5	2	E5	1	0	0
B3	12	42	4	E6	2	0	1
B4	1	7	2	E7	0	2	0
B5	0	15	1	E8	2	6	1
B6	0	5	0	E9	0	1	0
B7	14	4	2	E10	0	1	0
B8	0	2	0	E11	0	1	1
C1	0	2	1	E12	0	1	0
C2	9	24	1	F	1	0	0
C3	0	4	0	G	1	0	0
C4	1	2	0	H	1	0	0
C5	9	7	1				
C6	3	11	9				

trills. In short, there was similarity mainly between 1-of-2 and 1-of-3 categories, i.e., 1st trill types, and between 2-of-2 and 3-of-3 categories, i.e., last trill types.

Geographic Song Variation

SHARING OF TRILL TYPES AND PAIRS OF TRILL TYPES.—There was a weak inverse relationship between trill type sharing and geographic distance between pairs of sites (Fig. 4). A similar pattern resulted from plotting scores for the sharing of pairs of trill types (not shown). As these points are not independent, the "regression" lines have no statistical meaning. However, one can test the null hypotheses that there was no relationship between the matrix of distances among sites and the matrices of similarity values based on trill types shared and pairs of trill types shared. Neither null hypothesis was rejected: for trill types shared, $t = -0.06$, $P > 0.50$ and for pairs of trill types shared, $t = -0.69$, $P > 0.50$ (Mantel's Test; Schnell et al. 1985).

NEIGHBORS ON TERRITORIES.—There were 136 pairs of males that were neighbors on ter-

ritories. Among these pairs, 29% of trill types and 2% of pairs of trill types were shared (Table 6). The observed sharing of trill types was not different from the sharing exhibited by randomly selected pairs of males (Table 6). Thus, there was no tendency for neighbors to sing similar songs.

DISCUSSION

Evidence presented here suggests that there is 1 stereotyped short song for most male Brewer's Sparrows (Willing 1970). For those few males with more than 1 song type, the alternate types were sung in a regular manner, suggesting that one could expect to hear the entire repertoire in a few minutes. Three other *Spizella* sparrows also have 1 song type per male: Field Sparrow, *S. pusilla* (Heckenlively 1976); American Tree Sparrow, *S. arborea* (Weeden 1965); and Chipping Sparrow, *S. passerina* (Borror 1959, Marler and Isaac 1960, Albrecht and Oring 1995). The Clay-colored Sparrow (Knapton 1982, 1994), has 1–3 (usually 2) song types per male, and these are stable for at least

TABLE 3. Mean and standard deviation for 7 variables for 615 Brewer's Sparrow trill types by position in the short song. For example, "1 of 1" means that the trill is the only trill in a 1-trill song type and "2 of 3" means that the trill is the 2nd trill in a 3-trill song type.

Variable	Trill position					
	1 of 1	1 of 2	1 of 3	2 of 2	2 of 3	3 of 3
Trill duration (s)	2.21 (0.38)	1.04 (0.31)	0.82 (0.19)	1.37 (0.32)	0.94 (0.26)	1.17 (0.37)
Syllable duration (s)	0.03 (0.02)	0.02 (0.02)	0.02 (0.01)	0.03 (0.02)	0.06 (0.04)	0.03 (0.02)
Syllables/second	20.7 (10.8)	49.0 (19.9)	46.3 (13.6)	15.1 (6.1)	15.8 (17.9)	17.5 (8.3)
Maximum frequency (kHz)	6.4 (1.1)	6.3 (0.8)	6.2 (0.9)	5.8 (0.8)	5.6 (0.9)	5.9 (0.7)
Minimum frequency (kHz)	3.2 (0.7)	3.5 (0.7)	3.5 (0.7)	3.1 (0.5)	3.1 (0.5)	3.1 (0.4)
Dominant frequency (kHz)	4.6 (0.8)	4.9 (0.8)	4.9 (0.9)	4.2 (0.6)	4.2 (0.7)	4.3 (0.6)
Frequency range (kHz)	2.9 (1.0)	2.7 (0.9)	2.6 (0.9)	2.6 (0.6)	2.4 (0.7)	2.7 (0.6)

TABLE 4. Variables selected in discriminant analysis of Brewer's Sparrow short song trill types in 6 song positions.

Order	Variable entered	<i>U</i> -statistic	<i>F</i>	<i>P</i>
1	Syllables/second	0.438	157.16	0.001
2	Trill duration	0.252	121.3	0.001
3	Syllable duration	0.216	83.33	0.001
4	Minimum frequency	0.202	62.64	0.001

1 year. Thus, I assume that the short songs of Brewer's Sparrow are stable over time.

In addition to individual stereotypy is what might be called species stereotypy. Although 41.8% of all songs were unique by syllable type composition, results of the tabulation of syllable types by position and discriminant analysis of trill types by position revealed a considerable uniformity among individuals and sites in general song structure. The typical 2-trill song may be represented by a higher-frequency, faster trill followed by a lower-frequency, slower trill. This is exactly what Dawson (in Bent 1968) portrayed when he characterized Brewer's Sparrow song as "weeeezzz, tubitubitubitubitub." The discriminant analyses revealed that 1st trills were more variable than either 2nd or last trills, consistent with the prediction that the greatest complexity in broadcast song should occur near the beginning as an aid to individual recognition (Craig and Jenkins 1982).

Notable parallels in short song structure exist between Brewer's Sparrow and the Clay-colored Sparrow (Borror 1961, Willing 1970, Knapton 1982, 1994). Clay-colored Sparrows breed in brush habitat (*Symphoricarpos occidentalis*) that appears structurally similar (Knapton 1979) to the sagebrush of Brewer's Sparrow, and occasionally even hybridize with Brewer's (Rising 1996, N. Mahoney personal

communication). Syllable type A3 of Brewer's Sparrow, the most common type, is virtually identical to that shown in Knapton (1982:191) for the Clay-colored Sparrow. Maximum frequency in Clay-colored Sparrows is nearly the same (about 6.3 kHz) as that in 1st trills of Brewer's Sparrow, whereas minimum frequency in the Clay-colored Sparrow is lower (about 2.2 kHz vs. about 3.5 kHz in 1st trills of Brewer's Sparrow). Clay-colored Sparrows also sing more syllables per second (70) than Brewer's Sparrow (about 48 in 1st trills), although some syllable types, e.g., A3, sound much like the buzz of clay-colored (personal observation).

Knapton (1982) also made a distinction between long and short songs in the Clay-colored Sparrow, the former being sung near the incubating female/nest site and the latter being sung away from the nest site (Knapton personal communication). At least 4 other species—Five-striped Sparrow (*Aimophila quinquestriata*; Groschupf 1985), Cassin's Sparrow (*Aimophila cassinii*; Groschupf 1983), Great Reed Warbler (*Acrocephalus arundinaceus*; Catchpole 1983), and Redwing (*Turdus iliacus*; Lampe and Espmark 1987)—exhibit a similar use of simple and complex songs. This phenomenon also may occur in Brewer's Sparrow. In all these species, song behavior is consistent with the argument that long complex

TABLE 5. Classification matrix from discriminant analysis of Brewer's Sparrow short song trill types by position in song. For example, "1 of 1" means that the trill is the only trill in a 1-trill song type and "2 of 3" means that the trill is the 2nd trill in a 3-trill song type.

Group	Percent correct	Number of cases classified into group					
		1 of 1	1 of 2	1 of 3	2 of 2	2 of 3	3 of 3
1 of 1	91.7	22	0	0	2	0	0
1 of 2	55.9	5	119	52	14	13	10
1 of 3	52.7	0	15	29	0	2	9
2 of 2	60.6	19	2	1	129	17	45
2 of 3	54.5	0	3	3	4	30	15
3 of 3	63.6	1	0	1	15	3	35
TOTAL	59.2	47	139	86	164	65	114

TABLE 6. Sharing of trill types and pairs of trill types by Brewer's Sparrow neighbors on territories and by randomly selected pairs of males.

Types of pairs of males	Number of Pairs	Trill types shared	Pairs of trill types shared
Observed pairs of neighbors	136	39 (29%)	2 (2%)
Random pairs from within sites			
Sample 1	136	42 (31%)	10 (7%)
Sample 2	136	37 (27%)	8 (6%)
Sample 3	136	35 (26%)	4 (3%)
Random pairs from all sites	136	48 (35%)	0 (0%)

songs have evolved through intersexual selection, whereas short stereotyped songs repeated in bouts have evolved through intrasexual selection and are used mainly in territorial defense (Catchpole 1980, Catchpole and Slater 1995).

There also are similarities between Brewer's Sparrow and Chipping Sparrow song (Borror 1959, Marler and Isaac 1960, Willing 1970, personal observation). Whereas the Chipping Sparrow normally sings a single long trill (Borror 1959), Marler and Isaac (1960) and Bent (1968) report birds with 2-trill songs and 1 individual with a 6-trill song (B. Walker personal communication). Borror (1959) classified Chipping Sparrow song into 28 different patterns. Those I judged to be most like Brewer's Sparrow song, patterns 1-4 (Borror 1959:352), were classified by Borror as having a buzzy quality and either 1- or 2-part syllables.

I have 2 suggestions for those monitoring Brewer's Sparrow populations by song. First, the monitor should listen to a singing bird through several song renditions and listen for repeated song types in order to be certain (s)he is hearing a single bird. Because of the assumed stereotypy of the short song in most individuals, males can be readily identified and tallied.

If an individual has a 2nd or 3rd song type, it is likely that he will sing those much less often than his primary type. Even with more than 1 type, individual males can be readily identified and mentally tracked.

Second, a monitor must be able to distinguish long songs from short songs. One also must avoid tallying 2 birds when a single male switches from the long to the short song, or vice versa. The long song has a sequence of trills and a quality that I believe also is stereotyped among males. Although the syllable types may vary, the long song can be quickly recognized.

Analysis of geographic variation in Brewer's Sparrow song in this study revealed no patterns. The general nature of geographic variation is summarized by the scattergrams that show a weak inverse, nonsignificant relationship between sharing of trill types, or pairs of trill types, and geographic distance. Neighbors on territories shared no more trill types or pairs of trill types than did randomly paired males. Knapton (1982) also found that neighboring Clay-colored Sparrows did not tend to share song types. This was especially important for 12 pairs of males composed of returning adults and "new" males occupying adjacent territo-

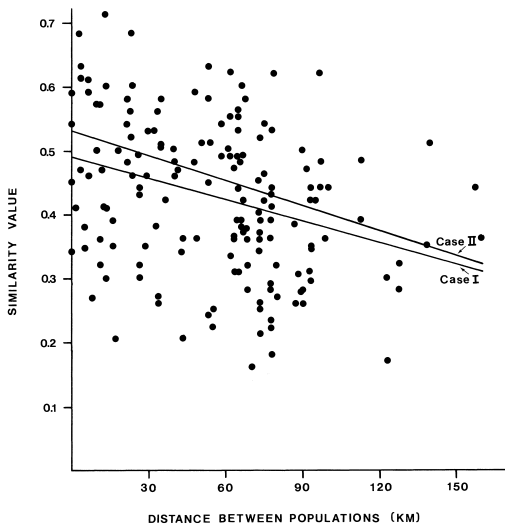


Fig. 4. Scattergram of song similarity values, based on trill types shared, and geographic distance between all pairs of Brewer's Sparrow populations. For the "regression" lines, Case I includes all points and Case II excludes the 4 self \times self points for populations sampled in the same site in different years. The relationships between song similarity and distance were not significant.

ries for the first time. He also concluded that young male Clay-colored Sparrows probably do not copy the songs of adults. The lack of song sharing between members of these pairs suggests that the social adaptation model of Payne (1981, 1982, 1983) may not apply to Clay-colored Sparrows or Brewer's Sparrows.

Among Clay-colored Sparrows, 63% of the adult males returned to the breeding area—many to the same territories—whereas only 18% of adult females and none of 146 nestlings returned (Knapton 1982). Although I did not have marked birds and I did not specifically attempt to evaluate this phenomenon, the fact that no sonograms from the same geographic site in subsequent years (SA7, SA8, SA9 and CM8, CM9) were the same suggests that there was considerable annual turnover in this species or that the same bird sang a different song each spring. Such turnover obviously would confound the establishment of dialects. Turnover was considered as a possible explanation for the lack of dialects in the White-throated Sparrow, *Zonotrichia albicollis* (Lemon and Harris 1974), and the Rock Wren, *Salpinctes obsoletus* (Kroodsma 1975).

Another factor that may indirectly work against song sharing in Brewer's Sparrow is the small territory size (0.65 ha per pair; Rich

unpublished) and high densities (Wiens and Rotenberry 1981). Even if a young male does learn his song from other males through social interaction (Payne 1981), he is presented with a large number of songs from which to learn. Not only the short songs but also the more complex long songs offer a variety of trill types to copy. This is further complicated by the great amount of social interaction, especially chasing, that occurs early in the breeding season. It seems possible that an individual's short song could be composed of trill types from more than 1 model and perhaps from long, as well as short, songs. On the other hand, Indigo Buntings (*Passerina cyanea*) also have closely packed territories with many neighbors, but a young male focuses on only a single model when it learns and copies a song (Payne 1996).

Because signals "must coevolve with other life history parameters" (Kroodsma 1996), several other potentially important factors affecting geographic song variation are suggested by contrasting Sage Sparrows (*Amphispiza belli*) and Brewer's Sparrows, a "key comparative situation" (Kroodsma 1996). Rich (1981) and Wiens (1982) both found a high degree of song sharing among neighboring Sage Sparrows, and Rich (1981) studied birds on some of the same sites as covered in this paper. This suggests that there were no habitat or landscape features that similarly affected dispersal and habitat selection by these broadly sympatric species, at least on the sites covered in this study. Baker (1983) came to a similar conclusion after finding no concordance between the spatial variation in songs of White-crowned Sparrows (*Zonotrichia leucophrys*) and Song Sparrows (*Melospiza melodia*) on the same sites.

Brewer's Sparrows are smaller (8.9–11.8 g) than Sage Sparrows (17.4–20.4g; Wiens and Rotenberry 1980) and have much wider niches (14.58 and 5.52, respectively; Rotenberry and Wiens 1980), based on habitat variables. The breeding density of Brewer's Sparrow also varies over a wider range (29–533 km⁻²) than that of the Sage Sparrow (16–172 km⁻²; Wiens and Rotenberry 1981).

Greater yearly variation in populations of Brewer's Sparrow also is strongly suggested by Breeding Bird Survey (BBS) data (Sauer et al. 1997). I calculated BBS count coefficients of variation (CV) over the period 1966 to 1996 for all routes that had been run for more than 9 years and for which Brewer's Sparrows,

Sage Sparrows, and Sage Thrashers (*Oreoscoptes montanus*) all were present. This screen helped ensure that I examined variation in core habitat for these sagebrush obligates. Among the 48 routes that met these criteria, Brewer's Sparrow count CVs exceeded Sage Sparrow count CVs on 40 routes.

This information suggests that Brewer's Sparrows are a relatively r-selected species, whereas Sage Sparrows are relatively K-selected. One might predict that Brewer's Sparrow life spans will be shorter, productivity will be more variable, and dispersal will be greater (Pianka 1983) than for Sage Sparrows. Under these conditions it may be more adaptive for breeding individuals to emphasize species identity over individual identity. The selective advantage of breeding within a short life span following greater dispersal might take precedence over the advantages of a more complex social structure mediated by vocal communication (Kroodsma 1974, 1979, Baker and Mewaldt 1978, Jenkins 1978, Baptista and Morton 1982, Payne 1982, 1983, 1996). Groschupf (1983) makes a similar argument for the lack of song sharing among Cassin's Sparrows. This species depends on spatially and temporally unpredictable rainfall and "must be ready to locate, advertise, and defend a territory, and successfully attract a female in a very short time."

Kroodsma (1996) urged the further study, specifically, of *Spizella* sparrows, including genetics, signal variation, and ontogeny. The study of Brewer's Sparrow offers several other research avenues. We do not fully understand the taxonomic status of *S. b. taverneri* (Swarth and Brooks 1925, American Ornithologists' Union 1957, Sibley and Monroe 1990, Rising 1996, Doyle 1997, Klicka et al. 1999), the functions of the long or the short song (Catchpole and Slater 1995), the individual and geographic variation in the long song, the ontogeny of any vocalization (Kroodsma 1996), or how the functions of these signals compare to those of Sage Sparrows (Rich 1981, Wiens 1982) and Sage Thrashers (Reynolds et al. 1999) sharing the same habitats and territories.

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LITERATURE CITED

- ALBRECHT, D.J., AND L.W. ORING. 1995. Song in Chipping Sparrows, *Spizella passerina*, structure and function. *Animal Behavior* 50:1233-1241.
- AMERICAN ORNITHOLOGISTS' UNION. 1957. Check-list of North American Birds. 5th edition. Lord Baltimore Press, Baltimore, MD.
- BAKER, M.C. 1983. Sharing of vocal signals among Song Sparrows. *Condor* 85:482-490.
- BAKER, M.C., AND L.R. MEWALDT. 1978. Song dialects as barriers to dispersal in White-crowned Sparrows, *Zonotrichia leucophrys nuttalli*. *Evolution* 32:712-722.
- BAPTISTA, L.F., AND M.L. MORTON. 1982. Song dialects and mate selection in montane White-crowned Sparrows. *Auk* 99:537-547.
- BENT, A.C. 1968. Life histories of North American cardinals, grosbeaks, buntings, towhees, finches, sparrows, and allies. U.S. National Museum Bulletin, Washington, DC. Reprinted by Dover Press, New York.
- BEST, L.B., AND K.L. PETERSEN. 1985. Seasonal change in detectability of Sage and Brewer's Sparrows. *Condor* 87:556-558.
- BORROR, D.J. 1959. Songs of the Chipping Sparrow. *Ohio Journal of Science* 59:347-356.
- _____. 1961. Songs of finches (Fringillidae) of eastern North America. *Ohio Journal of Science* 61:161-174.
- CATCHPOLE, C.K. 1980. Sexual selection and the evolution of complex songs among European warblers of the genus *Acrocephalus*. *Behaviour* 74:149-166.
- _____. 1983. Variation in the song of the Great Reed Warbler *Acrocephalus arundinaceus* in relation to mate attraction and territorial defence. *Animal Behavior* 31:1217-1225.
- CATCHPOLE, C.K., AND P.J.B. SLATER. 1995. Bird song-biological themes and variations. Cambridge University Press, Cambridge, U.K.
- CRAIG, J.L., AND P.F. JENKINS. 1982. The evolution of complexity in broadcast song of passerines. *Journal of Theoretical Biology* 95:415-422.
- DIXON, W.J., EDITOR. 1981. BMDP statistical software. University of California Press, Berkeley.
- DOYLE, T.J. 1997. The Timberline Sparrow, *Spizella (breweri) taverneri*, in Alaska, with notes on breeding habitat and vocalizations. *Western Birds* 28:1-12.
- GROSCHUPF, K. 1983. Comparative study of the vocalizations and singing behavior of four *Aimophila* sparrows. Doctoral dissertation, Virginia Polytechnic Institute and State University, Blacksburg, VA.
- _____. 1985. Changes in Five-striped Sparrow song in intra- and intersexual contexts. *Wilson Bulletin* 97:102-105.
- HECKENLIVELY, D.B. 1976. Variation in cadence of Field Sparrow songs. *Wilson Bulletin* 88: 588-602.
- JENKINS, P.F. 1978. Cultural transmission of song patterns and dialect development in a free-living bird population. *Animal Behavior* 25:50-78.

- KLICKA, J., R.M. ZINK, J.C. BARLOW, W.B. MCGILLIVRAY, AND T.J. DOYLE. 1999. Evidence supporting the recent origin and species status of the Timberline Sparrow. *Condor* 101:577–588.
- KNAPTON, R.W. 1979. Optimal size of territory in the Clay-colored Sparrow, *Spizella pallida*. *Canadian Journal of Zoology* 57:1358–1370.
- _____. 1982. Geographic similarity and year-to-year retention of song in the Clay-colored Sparrow (*Spizella pallida*). *Behaviour* 79:189–200.
- _____. 1994. Clay-colored Sparrow (*Spizella pallida*). In: A. Poole and F. Gill, editors, *The Birds of North America*, No. 120. Academy of Natural Sciences, Philadelphia, and American Ornithologists' Union, Washington, DC.
- KROODSMA, D.E. 1974. Song learning, dialects, and dispersal in the Bewick's Wren. *Zeitschrift für Tierpsychologie* 35:352–380.
- _____. 1975. Song patterning in the Rock Wren. *Condor* 77:294–303.
- _____. 1979. Vocal dueling among male Marsh Wrens: evidence for ritualized expressions of dominance/subordination. *Auk* 96:506–515.
- _____. 1996. Ecology of passerine song development. Pages 3–19 in D.E. Kroodsma and E.H. Miller, editors, *Ecology and evolution of acoustic communication in birds*. Cornell University Press, Ithaca, NY.
- LAMPE, H.M., AND Y.O. ESPMARK. 1987. Singing activity and song pattern of the Redwing *Turdus iliacus* during the breeding season. *Ornis Scandinavica* 18: 179–185.
- LEMON, R.E., AND M. HARRIS. 1974. The question of song dialects in the songs of White-throated Sparrows. *Canadian Journal of Zoology* 52: 83–98.
- MARLER, P., AND D. ISAAC. 1960. Physical analysis of a simple bird song as exemplified by the Chipping Sparrow. *Condor* 62: 124–135.
- PAYNE, R.B. 1981. Population structure and social behavior: models for testing the ecological significance of song dialects in birds. Pages 108–120 in R.D. Alexander and D.W. Tinkle, editors, *Natural selection and social behavior: recent research and new theory*. Chiron Press, New York.
- _____. 1982. Ecological consequences of song matching: breeding success and intraspecific song mimicry in Indigo Buntings. *Ecology* 63:401–411.
- _____. 1983. The social context of song mimicry: song-matching dialects in Indigo Buntings (*Passerina cyanea*). *Animal Behavior* 31:788–805.
- _____. 1996. Song traditions in Indigo Buntings: origin, improvisation, dispersal, and extinction in cultural evolution. Pages 198–220 in D.E. Kroodsma and E.H. Miller, editors, *Ecology and evolution of acoustic communication in birds*. Cornell University Press, Ithaca, NY.
- PIANKA, E.R. 1983. *Evolutionary ecology*. Harper and Row, New York.
- REYNOLDS, T.D., T.D. RICH, AND D.A. STEPHENS. 1999. Sage Thrasher (*Oreoscoptes montanus*). In: A. Poole and F. Gill, editors, *The Birds of North America*, No. 463. The Birds of North America, Inc., Philadelphia, PA.
- RICH, T.D. 1981. Microgeographic variation in the song of the Sage Sparrow. *Condor* 83:113–119.
- RISING, J.D. 1996. A guide to the identification and natural history of the sparrows of the United States and Canada. Academic Press, San Diego, CA.
- ROTENBERRY, J.T., M.A. PATTEN, AND K.L. PRESTON. 1999. Brewer's Sparrow (*Spizella breweri*). In: A. Poole and F. Gill, editors, *The Birds of North America*, No. 390. The Birds of North America, Inc., Philadelphia, PA.
- ROTENBERRY, J.T., AND J.A. WIENS. 1980. Habitat structure, patchiness, and avian communities in North American steppe vegetation: a multivariate analysis. *Ecology* 61:1228–1250.
- SAAB, V.A., AND T.D. RICH. 1997. Large-scale conservation assessment for neotropical migratory landbirds in the Interior Columbia River Basin. General Technical Report PNW-GTR-399, USDA Forest Service, Pacific Northwest Research Station, Portland, OR.
- SAUER, J.R., J.E. HINES, G. GOUGH, I. THOMAS, AND B.G. PETERJOHN. 1997. The North American Breeding Bird Survey results and analysis. Version 96.4. Patuxent Wildlife Research Center, Laurel, MD.
- SCHNELL, G.D., D.J. WATT, AND M.E. DOUGLAS. 1985. Statistical comparison of proximity matrices: applications in animal behaviour. *Animal Behavior* 33:239–253.
- SIBLEY, C.G., AND B.L. MONROE, JR. 1990. *Distribution and taxonomy of birds of the world*. Yale University Press, New Haven, CT.
- SOUTHWOOD, T.R.E. 1978. *Ecological methods*. 2nd edition. Chapman and Hall, New York.
- SWARTH, H.S., AND A. BROOKS. 1925. The Timberline Sparrow, a new species from northwestern Canada. *Condor* 27:67–69.
- WEEDEN, J.S. 1965. Territorial behavior of the Tree Sparrow. *Condor* 67: 193–209.
- WIENS, J.A. 1982. Song pattern variation in the Sage Sparrow (*Amphispiza belli*): dialects or epiphenomena? *Auk* 99:208–229.
- WIENS, J.A., AND J.T. ROTENBERRY. 1980. Patterns of morphology and ecology in grassland and shrubsteppe bird populations. *Ecological Monographs* 50:287–308.
- _____. 1981. Habitat associations and community structure of birds in shrubsteppe environments. *Ecological Monographs* 51:21–41.
- WILLING, R.M. 1970. The role of song in the behaviour and evolution of three species of spizellid sparrow: sonograph and field play-back studies. Masters thesis, Simon Fraser University, Vancouver, British Columbia.
- ZAR, J.H. 1974. *Biostatistical analysis*. Prentice-Hall, Inc, Englewood Cliffs, NJ.

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