PROMINENT VARIATIONS IN THE SONGS OF GAMBEL'S WHITE-CROWNED SPARROWS

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This paper describes prominent variations in songs of adult Gambel's White-crowned Sparrows (*Zonotrichia leucophrys gambelii*) tape-recorded on breeding grounds in Alaska, in the southwestern part of the wintering range, and on a migration route at Watson Lake in southern Yukon Territory. Analysis of these variations is prerequisite to answering the question of whether dialects and/or geographic variation in song exist in this migratory race. The question is important, for if localization of song patterns can be documented, songs of wintering birds may provide clues to the location of their breeding areas. In spite of the many Gambel's Sparrows banded every year, almost nothing is known of the specific wintering and breeding localities of individual birds. We are aware of only one case of a Gambel's Sparrow which was banded in winter and later recaptured on its breeding grounds (L. R. Mewaldt, pers. comm.).

Dialects and/or geographic variation in song have been shown in the genus *Zonotrichia* by several authors. Marler and Tamura (1962) and Baptista (1972) describe local dialects in populations of the permanently resident race of White-crowned Sparrow (*Z. l. nuttalli*) in central California. Baptista (1973, in press and in prep.) has also studied dialects of the Puget Sound White-crowned Sparrow (*Z. l. pugetensis*). Borror and Gunn (1965) describe variations and review the literature on song of the White-throated Sparrow (*Z. albicollis*). Nottebohm (1969) defines dialect and sub-dialect areas for the Rufous-collared Sparrow (*Z. capensis*) in central Argentina, and King (1972) describes song variations for populations of this species in northwestern Argentina.

In this paper we identify elements common to all songs of Gambel's Sparrows we have recorded to date, describe several categories of variation, illustrate the prominent variations in each song element, and describe their distribution among the populations sampled.

METHOD AND PROCEDURES

Sources of data

Over 1,800 songs representing about 360 birds were tape recorded in 11 breeding and 4 wintering areas, and on a migration route in the Watson Lake area of southern Yukon Territory. Table 1 lists specific recording sites grouped according to geographic area. Fifteen of the recording sites include one or more pairs of neighbors which we noted as singing within earshot of each other. Most members of these pairs were singing alternately when we were recording. In the last column of Table 1, the total number of possible combinations of singing neighbors are given for each of these recording sites.

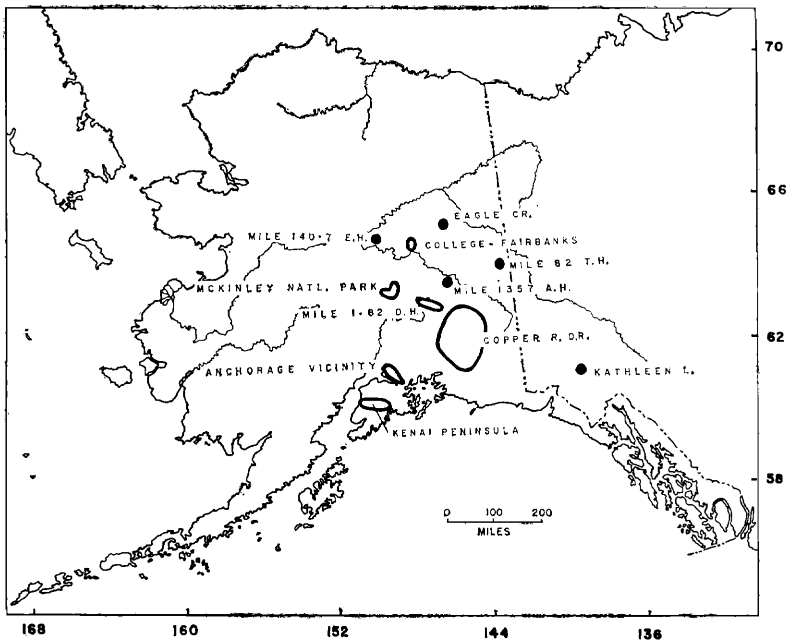

FIGURE 1. Map of Alaska showing locations of breeding areas where songs were recorded.

Figure 1 shows the locations of the breeding areas sampled. These lie between latitudes 60° 25′ N and 65° 27′ N and between longitudes 137° 14′ W and 151° 16′ W, and hence represent only a small fraction of the breeding range of this race.

Identification of race

Songs of the Puget Sound White-crowned Sparrow (*Z. l. pugetensis*), which winters in California with the Gambel's Sparrow, are readily distinguishable by ear and are excluded from this paper. The singers we could see clearly had pale gray lores, which distinguish *Z. l. gambelii* from the black-lored Eastern and Sierran White-crowned Sparrows (*Z. l. leucophrys* and *Z. l. oriantha.*) In 22 years of banding White-crowned Sparrows at Goleta, California, where most of the winter songs were recorded, we have never trapped or seen a black-lored bird. In the Watson Lake area, DeWolfe, West and Peyton (1973) handled more than 500 White-crowned Sparrows. With one exception, all had the pale gray lores of *Z. l. gambelii.*

Recording and graphing

At each breeding locality we recorded at random whichever singers were accessible including, when possible, the songs of birds on adjacent territories. At Goleta we recorded all song variations

TABLE 1.
Localities, dates, and number of birds recorded, 1967-1972.

Locality	Lat. range (°N.)	Long. range (°W.)	Recording dates	Recording sites[1] (south to north)	No. birds recorded	No. pairs singing neighbors[2]
I. Breeding (south to north)						
Kenai Peninsula	60°25′-	149°28′-	31 May 67;	Kenai Lake	1	
(n = 20)	60°33′	151°16′	22-23 May 68	Skilak Lake	4	
				Hidden Lake	7	5
				Scout Lake Loop	5	2
				Kenai Town	3	
Haines Junction, Y. T. (n = 1)	60°35′	137°14′	11 May 68	Kathleen Lake	1	
Anchorage &	61°03′-	149°06′-	30 May 67;	Potter Marsh	2	
vicinity (n = 8)	61°46′	149°55′	14-22 June 68	Anchorage	1	
				Palmer	5	6
Copper River Drainage	61°31′	143°57′	27 May - 5 June 67;	Chitina	1	
(n = 15)	62°43′	146°26′	9-14 May 69;	Mile 71, Richardson H.	2	
			18 June 71	Kenny Lake	1	
				Mile 93, Richardson H.	1	
				Taslina River Bridge	2	
				Glennallen	1	
				Gulkana airfield	5	4
				Mile 24 Tok cut-off	1	
				Slana	1	
Mile 1 - 82.5	63°03′-	146°01′-	23-24 June 71;	Tangle Lakes	3	2
Denali Highway	63°09′	147°32′	2 July 71	Mile 39 Denali H.	1	
(n = 7)				Mile 63.8 " "	1	
				Mile 82.5 " "	2	
McKinley Nat'l Park	63°20′-	148°15′-	11 June - 1 July 71	Mile 110, 112, 126		
(n = 12) (mile 83	63°51′	149°02′		Denali H.	3	

Denali H. -north side McKinley Nat'l Park)				McKinley Village	2	1
				Wonder Lake	5	
				Otto Lake, Healy	2	1
Mile 1357 Alaska Highway (n = 2)	63°37′	144°58′	14 May 67	Mile 1357 Alaska H.	2	1
Mile 82 Taylor Highway (n = 1)	64°05′	141°38′	11 June 72	Walker Fork Campgrd.	1	
Fairbanks (n = 58)	64°48′-64°54′	147°44′-147°54′	11 May - 8 July 67; 20 May - 12 June 68; 22 May 69; 23-25 May 70; 4-27 June 71; 18-20 June 72	Fairbanks	5	
				Aurora Drive	4	3
				Univ. of Alaska campus & vicinity	32	23
				Smith Lake & "	8	1
				Musk Ox Subdivision	9	7
Mile 140.7 Elliott Highway (n = 1)	65°10′	150°09′	4 July 70	22 mi. E. of Manley	1	
Mile 104.5 Steese Highway (n = 1)	65°27′	145°27′	6 June 71	Eagle Creek	1	
II. Migration Route						
Watson Lake area, Y. T.	60°01′-60°07′	128°48′-129°05′	2-10 June 67; 1-17 June 68	Watson Lake town; mile 651-653, 657, 660, 679 Alaska Highway	113	
III. Wintering (south to north)						
Tucson, Ariz.	32°15′	110°57′	26 Nov 70	City	3	
San Diego, Calif.	32°45′	117°10′	24 Nov 67	Imperial Beach	5	
Blythe, Calif.	33°38′	114°35′	28 Nov. 70	Edge of Colorado River	5	
Goleta, Calif.	34°20′	119°50′	15 Oct. 66 - 9 Apr. 67; 10 Oct. 67 - 10 Apr. 68; 3 Nov. 68 - 14 Apr. 69; 18 Nov. 70	Univer. of California campus	90	

[1]sites in italics include 5 or more singers on adjacent territories
[2]neighbors = birds singing within earshot of one another

distinguishable by ear. At Watson Lake we recorded each migrant singing near a daily patrol route on or adjacent to the Alaska Highway.

Peyton used a MKH 104 microphone with a 39-inch parabolic reflector and a Nagra III tape recorder operated at 15 in./sec. DeWolfe used an Electrovoice microphone, model 655C, in a 24-inch parabolic reflector, and a portable Uher 4000 Report L tape recorder fitted with a preamplifier matching the microphone impedance. She recorded songs at 7 1/2 in./sec. The two methods yield comparable spectrograms.

After Peyton recorded a few songs of each bird, in some cases he played back the song of the same or another singer to bring the bird closer to the microphone. DeWolfe never used artificial inducement. Peyton never heard a singer change its song after playback, nor did DeWolfe detect any change when she audited Peyton's recordings. However, Baptista (1974) induced, by playback, change of song type and theme matching in both *Z. l. nuttalli* and *Z. l. pugetensis*.

All tape-recordings were audited and the variations detectable by ear were noted. The songs of 250 adults, including all breeding birds recorded, were chosen for sound spectrographic analysis with a Model 6061B Kay Electric Sound Spectrograph.

Artifacts of recording and graphing

Whether or not the singer faced the microphone continuously affected the loudness of the recording and the frequency range of the spectrogram trace. Also, neither the first nor second syllables in the slow trill register if the trace intensity is weak. Differences in strength of recording may also account for gradations between segmented and broken forms of whistle.

Margins of measuring error

Margins of error in measuring the spectrograms were determined to be 0.02 second for the time axis and 0.3 kHz for the frequency axis. The number of syllables uttered in a fast trill could be measured within $\pm$ 4 syllables per second.

Terminology

Because we found that the number of times a given song element is uttered may vary, we abandoned the numerical designations for successive song elements used in our previous paper (Peyton and DeWolfe, 1968) and use, instead, descriptive terms to designate the four elements common to all songs so far recorded: "whistle", "warble", "buzz" and "trill". We describe variations in these elements according to the terminology of Rice and Thompson (1968), paraphrased as follows:

Syllable: a sound represented by a continuous trace on a spectogram.

Figure: a sound which produces a single, complete and distinct impression on the ear. It may be simple, i.e. composed of one syllable, or compound, comprising several syllables forming a unit. "Figure" is synonymous with our term "song element" and with "natural song unit".

Phrase: any group of figures generally sung together.

Frequency envelope: the frequencies (in kHz) of points outlining the periphery of the sonagram of a *figure*.

Our terms "simple figure" and "syllable" are synonymous with "note" as used by Nottebohm (1969) and King (1972). Our "compound figure" is the same as "note complex" as used by Heckenlively (1970).

RESULTS

General features of the song

The song of Gambel's Sparrow lasts about two seconds. Duration of 115 songs recorded on the breeding grounds varied from 1.63 to 2.45 seconds (mean + SD = 2.06 + 0.177 sec.). In rhythm and note pattern the song is relatively simple. Each complete song we have recorded includes four kinds of elements or figures: whistle, warble, buzz and a terminal section which, with rare exceptions, is a trill. The four elements are always sung in the order given, but the number of times an element is uttered may vary. The warble may be doubled or, very rarely, tripled, and the buzz is usually sung twice. Figure 2 shows a typical song with its four kinds of elements. These were briefly characterized in a previous report (Peyton and DeWolfe, 1968). With three exceptions, discussed below, no other type of song element has been recorded at any of the 16 areas sampled.

The whistle, buzz, and trill correspond to elements in the song of Nuttall's Sparrow (cf. our Fig. 2 with Fig. 1 of Marler and Tamura, 1962). The warble is not present in songs of *Z. l. nuttalli* described by these authors, nor does it appear to have an exact counterpart in the songs of *Z. capensis* shown by Nottebohm (1969) or King (1972).

Nature of the variations

Songs of Gambel's Sparrows vary in all characteristics readily displayed in spectrograms. Each element varies as to duration, relative loudness, and median frequency of its trace. Warble, buzzes, and trill vary as to overall range of frequency envelope. The magnitude of pitch changes between song elements also varies. There are prominent differences in the form of each element, as a result of variations in structure, arrangement, and/or number of syllables. The rate at which the repeated syllable in the trill is uttered also varies.

Variations detectable by ear include the shortening, or complete omission, of song elements, and/or changes in the number of times a given element is uttered.

Extremes of duration and frequency of each song element

Table 2 shows the extremes of duration and frequency within which the variations mentioned above occur. The number of

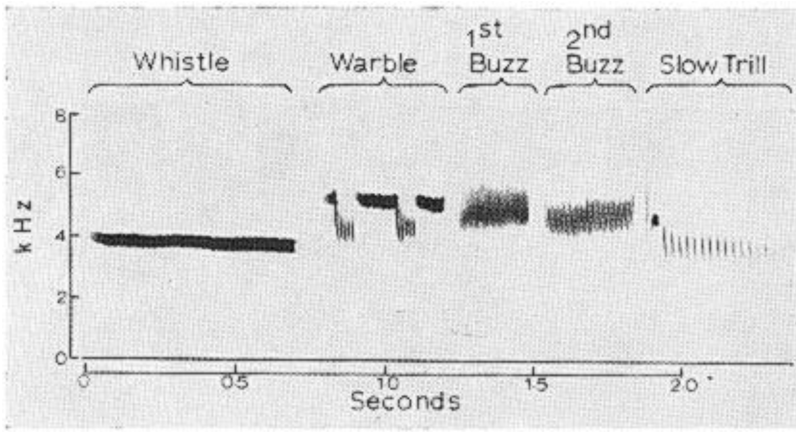

FIGURE 2. A typical song of *Z. l. gambelii,* showing the four kinds of song elements common to all complete songs.

examples of the four song elements is not identical, because some songs were either incomplete or failed to yield a clear trace of every song element.

TABLE 2.

Extremes of duration and frequency in spectrograms of common song elements, in all songs recorded to date.

Song element	n	Duration (seconds) Shortest	Duration (seconds) Longest	n	Frequencies, center of trace (kHz) Lowest	Frequencies, center of trace (kHz) Highest
1. Whistle	245	0.22	0.76	250	2.7	5.5
					Ranges, bottom and top of frequency envelop (kHz)	
				n	Bottom	Top
2. Warble	248	0.24	1.05[1]	248	2.0–4.5	3.5–6.7
3. Buzz						
First buzz	218	0.17	0.32	230	3.5–4.7	4.8–6.7
Second buzz	177	0.16	0.40	177	3.7–4.7	4.8–6.0
4. Trill						
Fast trill	114	0.18	0.60	114	2.5–3.5	3.8–4.5
Slow trill	116	0.22	0.62			
1st syllable				97	2.7–4.4	4.6–7.5
3rd syllable				107	2.5–3.9	4.0–6.0

[1]duration of a triplet of warble form #10; see text.

Prominent variations in form of the song elements

Figures 3 through 7 show spectrograms of the prominent variations in form of the four kinds of song elements.

A. *Whistle.* The spectrogram of the whistle consists of a sustained syllable or syllables, of nearly the same frequency throughout. Figure 3 shows three forms of whistle: continuous, segmented, and broken. The dark and light bands of the segmented form correspond to variations in amplitude in an oscillogram of a White-crowned Sparrow whistle in Greenewalt (1968, Fig. 39). We find gradations between the segmented and broken forms, and we have one example in which the same singer uttered both these forms of whistle during one bout of singing. The whistle corresponds to "Phrase A" of the song of Nuttall's Sparrow (Marler and Tamura, 1962).

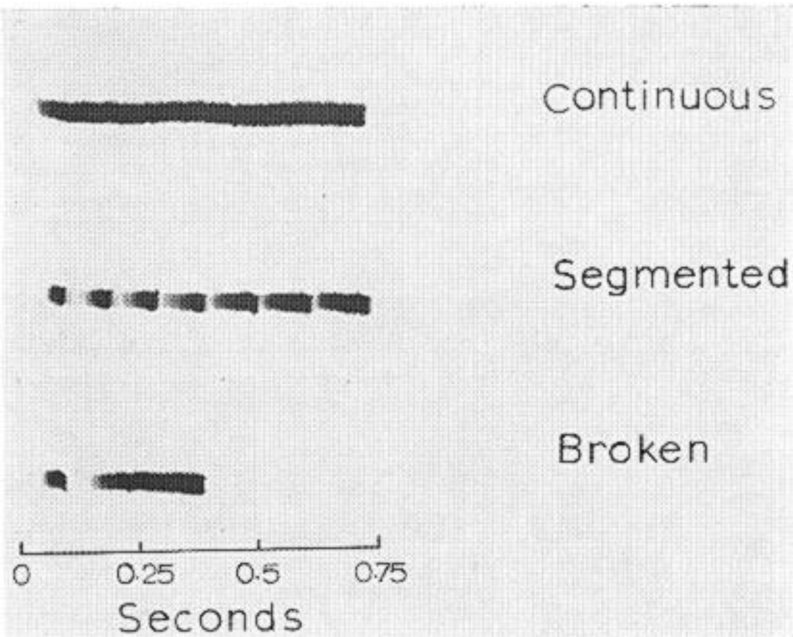

FIGURE 3. Spectrograms of three forms of whistle.

B. *Warble.* This is either a simple or a compound figure of widely variable frequency. Figure 4 shows spectrograms of 10 different forms of warble with characteristic modulation patterns. They are numbered arbitrarily. In all except form #1, doubling of the frequency modulation pattern is complete. Forms #6 through 9 include a short syllable of relatively narrow frequency range preceding the doubled part of the figure. Form #10 is usually sung twice in one song. It is readily distinguishable by ear from all other forms of warble. As we extend our recording to other areas of the

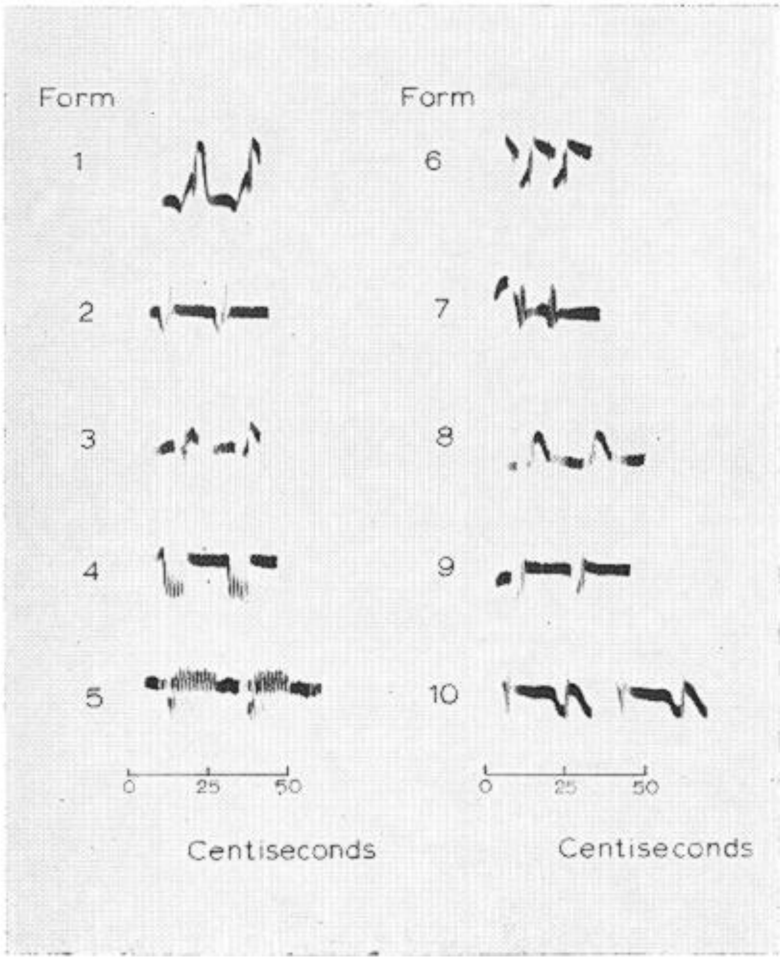

FIGURE 4. Spectrograms of ten forms of warble.

breeding and wintering ranges we expect to find additional forms of this markedly variable song element. Each of the 10 forms of warble shows minor individual variations in structure of its component syllables.

The forms of warble vary in duration, from a mean ± standard deviation of 0.27 ± 0.028 second for 17 examples of the shortest warble form, #6, to a mean of 0.60 ± 0.039 second for 12 examples of the doubled warble form, #10. The latter is significantly longer than is the next longest form, #5, which averages 0.52 ± 0.032 second in duration for 9 examples ($P < .001$). Yet duration of the songs containing warble forms #10 and 5 (means = 2.15 ± 0.178 and 2.27 ± 0.129 seconds, respectively) do not differ significantly in length ($P > 0.1$). This is because birds singing the double warble form #10 usually omitted the second buzz, whereas those using form #5 included two buzzes per song.

C. *Buzz.* This is the least obviously variable of the song elements. It is usually sung twice, with the center of the frequency envelope of the second buzz slightly lower than that of the first. Figure 5 shows two minor variations in spectrograms of this element: one is nearly uniform in trace intensity over the wide frequency range, whereas the other shows horizontal variations in trace intensity which result in a layered appearance. In songs of some individuals the two buzzes are almost identical in general form. In others, as in the bottom of Figure 5, the second buzz resembles a fast trill. The buzz section of the song of Gambel's Sparrow probably corresponds to "Phrase B" of the Nuttall's Sparrow as shown in Figure 1C of Marler and Tamura (op. cit.)

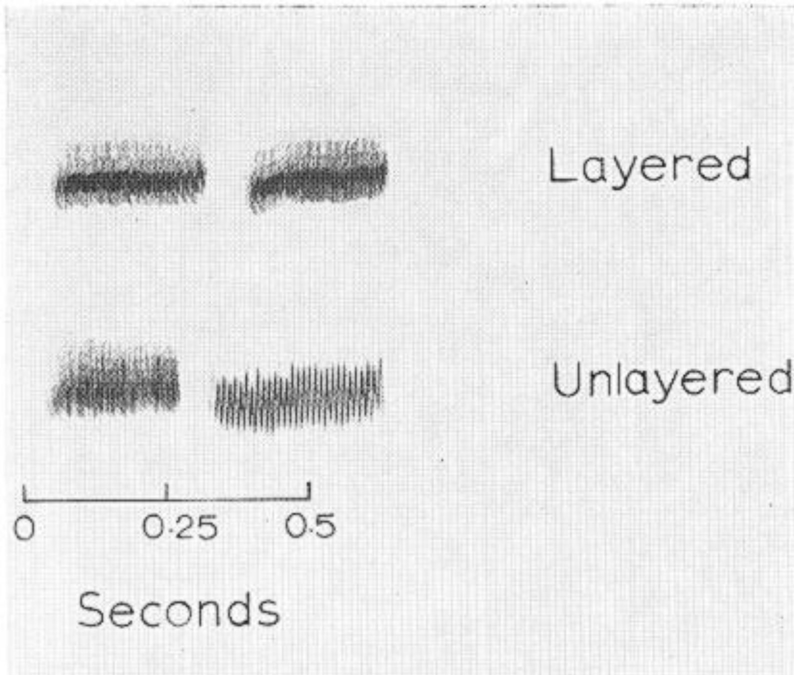

FIGURE 5. Spectrograms of two forms of first and second buzz.

D. *Trill.* Figure 6 illustrates two forms of this compound figure, the fast and the slow trill. They are distinguishable by ear. In both forms, the repeated syllables are uttered at a rate faster than are syllables in the trill portion of the song of Nuttall's Sparrow (cf. our Fig. 6 with Fig. 1C of Marler and Tamura, 1962). The fast trill usually consists of only one kind of syllable, repeated from about 72 to 96 times per second. Exceptions to this are trills recorded from three birds in which the syllable repetition rate was much faster:

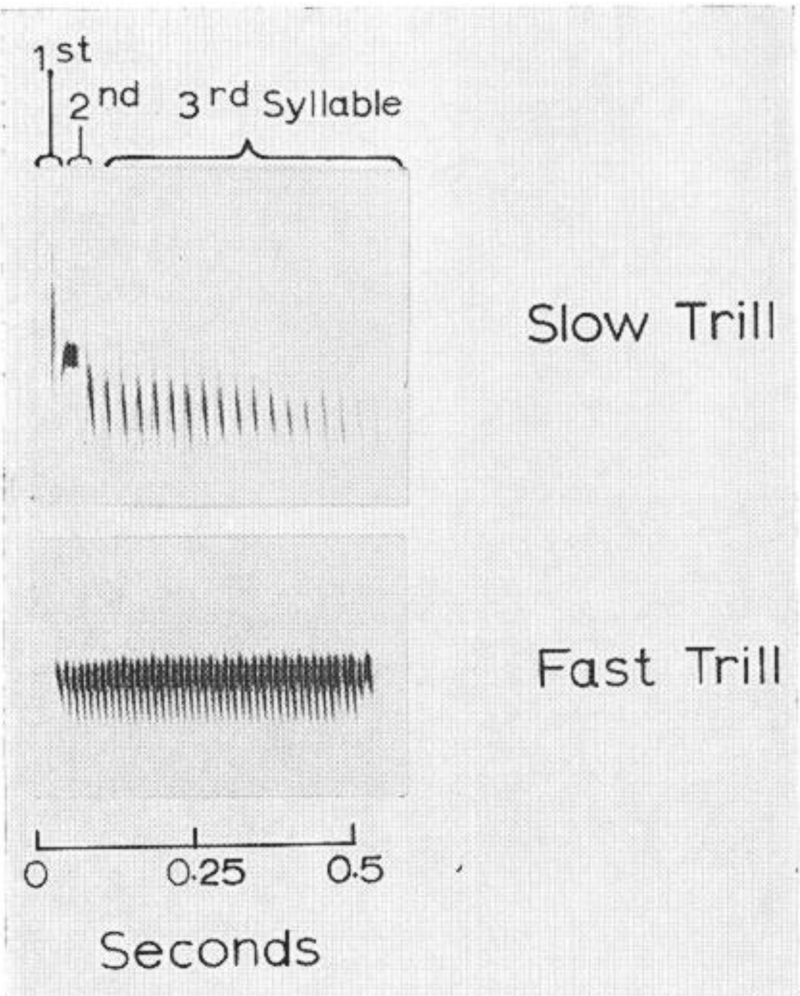

FIGURE 6. Spectrograms of two forms of terminal song element.

156 times per second. The slow trill comprises three kinds of syllables. The first, sung once, has a wide frequency range. The second, also sung once, has a narrow frequency range. The third, intermediate in frequency range, is delivered about 28 to 56 times per second.

To date, we have not found any prominent variations in syllable form in either the fast or slow trill. The form of syllables in the fast trill sung by Gambel's Sparrows on the Kenai Peninsula is approximately the same as that of birds recorded over 200 miles north in McKinley Park. Likewise, the general form of syllables in the slow trill recorded in one bird's song on the Kenai Peninsula, and in songs of two individuals from McKinley Park, is almost identical with that in slow trills recorded from singers in the Fairbanks area some 300 and 100 miles north, respectively.

As we record additional songs, we may find trills intermediate between the fast and slow forms as described here. One such example has already been found by Luis Baptista (pers. comm.).

With only two exceptions, all birds whose songs we have recorded used only one form of trill during a bout of singing. One exception, discussed in the next section, concerns a song that ended in a 3-figure phrase. The other exception was a bird recorded in Fairbanks which alternately sang songs with slow trills (repeated syllables uttered 40 times per sec.) and with very fast trills (syllables delivered at rate of 156/sec.).

Kessel and Schaller (1960) heard Gambel's Sparrows consistently singing both forms of trill in the Upper Sheenjek Valley in northeastern Alaska.

E. *An exceptional song ending*. Figure 7 illustrates a song with a terminal phrase of three figures, the first and third of which are down-slurred notes and the middle one of which resembles a buzz. This exceptional ending was recorded by Peyton in 1967 at Skilak

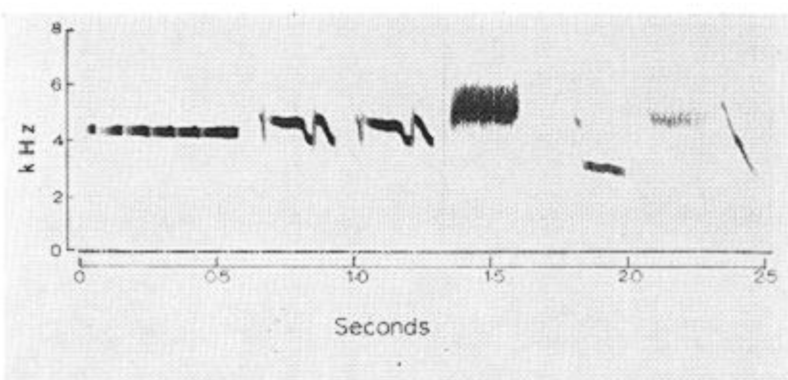

FIGURE 7. Spectrogram of a song with a terminal element comprising a 3-figure phrase. Note also that the warble form #10 is sung twice, and that only one buzz is uttered.

Lake, Alaska, and again in 1968 at the same site by DeWolfe, when she recorded a bird which ended one song with the three-figure phrase, and another with a typical fast trill. DeWolfe had recorded a similar terminal phrase at Goleta, California, on 31 March 1968. Because it had not been recorded there in previous months, it may have been sung by a spring migrant which had wintered farther south. This song ending is readily distinguishable by ear, but we have not detected it in the Gambel's Sparrow except at the two sites mentioned. The last two figures of this terminal phrase are, however, typical of *Z. l. pugetensis* in parts of Oregon and Washington (Baptista, 1974).

Variations in individual repertoires

Wintering adults frequently omit one or more elements from their songs, shorten the whistle or the trill, or vary the number of times a given song element is uttered. Such variations are detectable by ear. We also heard them, but very rarely, in songs of breeding individuals. In addition, as already stated, we found two breeding birds each of which uttered two forms of the terminal song element during single bouts of singing.

Table 3 shows the means ± SD for some variable characteristics in repertoires of five breeding individuals, as revealed by spectrograms. The songs of birds #1, 2, 3 and 5 were recorded during single bouts of singing. Bird #4 sang daily from the same perch and was presumed to be the same individual. Its songs were recorded over a nine-day period. Not shown in Table 3 are slight variations which occurred in the duration of buzzes and trill of the same bird. In most cases these fell within, or were only slightly greater than, the margin of error of measurement. The repertoires of these five individuals were stable as to the forms of warble, buzzes and trill, and as to rate of utterance of the repeated trill syllable. The forms of whistle were also stable in four of the five repertoires. One bird sang both segmented and broken forms of whistle.

Inspection of all available spectrograms, impressions from many hours of listening to songs both in the field and on tape, and the analysis of individual repertoires just described all suggest that the form of each song element is relatively stable in the repertoire of a given adult Gambel's Sparrow. Before we can demonstrate conclusively the stability of individual repertoires, however, we must record and analyze songs of the same color-banded birds throughout one or more breeding seasons.

Summary of categories of variation

Categories of variation in song identified to date include (1) those due to spectrogram artifacts, discussed in the method section; (2) omission of part of the song, commonly by shy, wintering birds; (3) in individual repertoires, minor variations in duration and in frequency of the spectrogram trace centers of the song elements; and (4) subtle variations between individuals, in structure of warble syllables and in the buzz, which would require statistical treatment to express them quantitatively.

In a search for dialects the first three categories mentioned above are not applicable and the fourth is of minor importance. Therefore in the remainder of this paper we shall focus on a fifth category, that is, prominent variations which our study indicates are likely to be relatively stable within individual repertoires. These include (1) variations in form of whistle, warble and terminal song element; (2) variations in pitch relations between whistle and warble; (3) variation in the ratio of warbles to buzzes uttered per song (if two warbles occur, then usually only one buzz is uttered, and vice versa.)

Song Patterns

A. *Combinations of prominent variations.* The variations in song

TABLE 3.
Variable characteristics in songs of 5 individuals (mean ± SD)

Bird no.[1]	No. Songs	Form of Warble (code no.)	Form(s) of Whistle	Duration (Sec.) Complete Song	Duration (Sec.) Warble	Frequency of trace center (kHz) Whistle	Frequency of trace center (kHz) Warble	Frequency of trace center (kHz) Buzz I	Frequency of trace center (kHz) Buzz II	Frequency of trace center (kHz) Trill
1	6[2]	4	Seg.	2.29 ±0.054	0.39 ±0.014	3.87 ±0.053	4.55 ±0.028	5.06 ±0.085	4.81 ±0.063	3.92 ±0.117
2	6[2]	1	Seg.	2.02 ±0.032	0.29 ±0.017	3.50 ±0	4.23 ±0.069	4.91 ±0.067	4.73 ±0.085	3.93 ±0.110
3	6[2]	4	Seg. & Br.	2.18 ±0.044	0.36 ±0.008	3.37 ±0.048	3.97 ±0.075	4.86 ±0.079	4.64 ±0.046	4.02 ±0.160
4	6[2]	9	Br.	1.91 ±0.016	0.40 ±0	4.82 ±0.038	3.67 ±0.038	5.19 ±0.075	5.04 ±0.089	3.68 ±0.047
5	4[2]	6	Br.	2.09 ±0.027	0.29 ±0.027	5.00 ±0	5.04 ±0.021	4.96 ±0.108	4.54 ±0.041	3.85 ±0.359

[1]Birds # 1, 2, 3 and 5 recorded at College, Alaska; Bird # 4, at Taslina River
[2]Songs recorded in one bout of singing
[3]Songs recorded during 9-day interval

elements described above are not combined randomly. Certain warble forms in our collection occur exclusively either with the fast or the slow trill, and or with a whistle either higher cr lower in pitch than the median of the warble trace. Also, as stated above, the doubled warble form #10 is usually sung with only one buzz.

Table 4 gives the percentages of each warble form we have found combined with a given form of trill, for 208 complete songs from breeding, wintering and migration localities. Although almost half (49%) the total number of songs end in fast trills, the proportion of fast trills combined with a given type of warble does not approach 50%, even for warble forms such as #2, 6 and 10, of which we have a large number of examples.

Figure 8 presents statistical data on median frequency of whistle trace for spectrograms of breeding birds, grouped according to form of warble and arranged from top to bottom of the graph according to decreasing frequency of whistle trace center. The mean of whistle frequencies sung with warble form #9 is significantly higher than

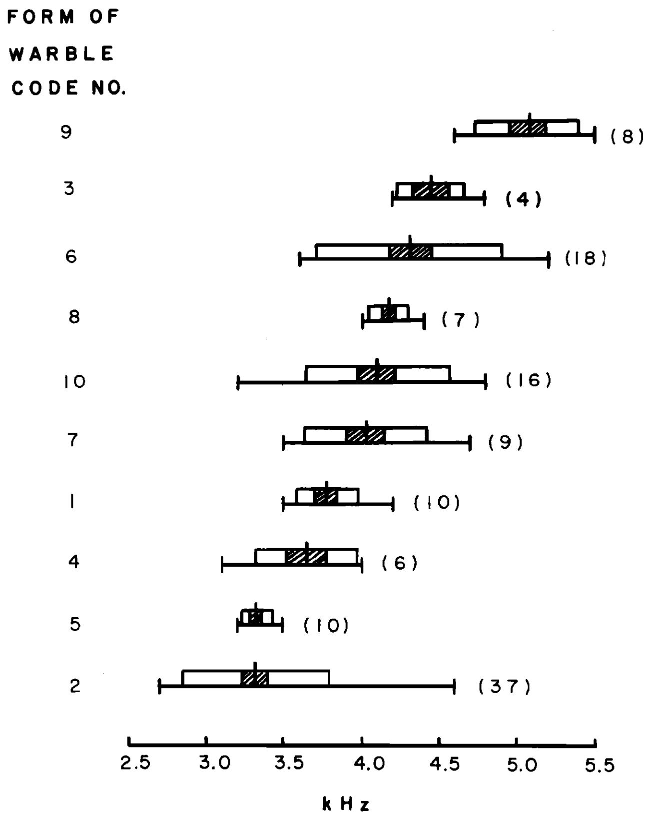

FIGURE 8. Frequencies of whistles which are combined with each form of warble. Abscissae = whistle frequency (mean, SE, SD and total range).

TABLE 4.
Percent of each warble form combined with a given form of trill (for birds recorded at all sites).

	FORM OF WARBLE (code number)										
	1	2	3	4	5	6	7	8	9	10	Total
No. examples of warble form	13	53	9	18	15	33	17	5	14	31	208
Percent of each form combined with a fast trill	15.4	66.0	33.3	0	0	3.0	88.2	100	100	87.1	
Percent of each form combined with a slow trill	84.6	34.0	66.7	100	100	97.0	11.8	0	0	3.2	
Percent of each form combined with 3-figure phrase	0	0	0	0	0	0	0	0	0	9.7	

that sung with any other form of warble (t-values range from $P <$ 0.02 to $P < 0.001$, depending on the form of warble with which #9 is compared). The mean of whistle frequencies combined with warble forms #1 through 8 and #10 each differs significantly ($P < 0.05$) from the mean whistle frequency of at least three other warble forms. For example, the mean of whistle frequencies sung with form #8 is 4.185 kHz. This differs significantly from the means of whistle frequencies sung with warble forms #9, 1, 4, 5 and 2, but not from means of those sung with warble forms #6, 3 and 10.

Although the range of whistle frequencies with which warble form #2 is combined is wide, the pitch relationship between whistle and ensuing warble is the same, for all examples of this form, whether recorded from breeding, wintering or migrating birds. In 49 songs containing warble form #2, the whistle is pitched lower than is the center of the warble sonagram trace. In contrast, the 14 songs containing warble form #9 all have whistles pitched higher than the center of the warble's frequency envelope. No such consistent pitch relationship exists between warble forms #6 and 10 and their respective whistles.

B. *A code for song patterns.* We devised a code for the combinations of five types of song variables: form of whistle, relative pitch of whistle and warble, form of warble, the number of buzzes uttered, and form of the terminal element. WH stands for whistle, WA for warble, B for Buzz, and T for terminal song element. The subscript abbreviations "cont.", "seg.", "br.", or "inter." are placed in front of WH to indicate whether the whistle trace is continuous, segmented, broken, or intermediate in form between the latter two types. WH is followed by the subscript "lower", "same" or "higher" to indicate the pitch relation between whistle the warble. WA is followed by the code number (1 - 10) of the form of warble, and B or BB indicate whether one or two buzzes are uttered. T is followed by "f", "s", or "phr." to indicate whether the terminal element is a fast trill, a slow trill, or a phrase. The code for the song in Figure 2 is: $_{\text{cont.}}\text{WH}_{\text{lower}}\text{WA}_4\text{BB T}^{\text{s}}$. That for the song in Figure 7 is: $_{\text{seg.}}\text{WH}_{\text{lower}}\text{WA}_{10}\text{WA}_{10}\text{B T}_{\text{phr.}}$

C. *Number of song patterns.* The number of theoretically possible song patterns, using all combinations of the five variables mentioned in the preceding paragraph, is 720 (4 forms of whistle x 3 possible pitch relations between whistle and warble x 10 forms of warble x 2 possible numbers of buzzes uttered x 3 forms of terminal song element = 720). We have found 48 of these patterns among the 126 complete songs of breeding birds recorded to date. If we find ultimately that the "intermediate" form of whistle is merely an artifact of recording, thus reducing the number of whistle forms to three, then the possible combinations of these five variables would be 540. Because the combination of warble forms with forms of trill appears to be non-random (Table 4) and the pitch relation between whistle and some forms of warble is non-random (Fig. 8) we should not expect to find all of the theoretically possible combinations, even if in the future we greatly extend the range of our recordings.

Distribution of prominent variations in form of song elements

Because designation of song patterns is highly subjective, we have not plotted distribution of entire song patterns. Instead, we show the occurrence of each prominent variation in form of a song element among the 16 localities where we recorded (Table 5) and within 8 small groups of breeding birds (Table 6). In Table 7 we compare members of pairs of singing neighbors as to the forms of song elements they uttered.

A. *Forms of whistle.* Tables 5 and 6 indicate that the broken form of whistle is the most widespread, and the continuous form, the most restricted in occurrence among the localities and breeding groups sampled. The data do not show any marked localization for form of whistle: at least two forms were present in each area with a sample size > 5, and within each local breeding group. Table 7 shows that members of more than half of 52 pairs of singing neighbors (57.7%) sang different forms of whistle.

B. *Forms of warble.* Table 5 shows marked differences in occurrence of the 10 forms of warble. There is some suggestion of geographic restriction of forms #9 and 10, which to date have not been found at any of our recording localities north of mile 1-82.5 Denali Highway or of the Cooper River Drainage area, respectively. The absence of form #10 in the Fairbanks-College area is noteworthy, because a deliberate effort was made there, in 1968 and 1971, to find birds using this form of warble. Even within small breeding groups the variety of warble forms is striking.

The variety of forms of warble sung by neighbors within earshot of each other is especially impressive. Table 7 shows that, of 55 pairs of singing neighbors, members of 41 pairs, or 74.5%, sang different forms of warble. Even in the songs of a given pair singing the same form of warble, minor differences in fine structure of the warble are present in the spectrograms. It is highly probable that such differences can be detected by the birds. Konishi (1969) found that auditory neurons in *Z. leucophrys* exhibit 1 impulse per experimentally applied click ("100 per cent time-locking") when the interclick interval = only 1.6 milliseconds.

There is evidence of temporal variation in the relative abundance of birds at Fairbanks singing a given form of warble. In 1967, 5 out of 12 birds recorded (about 42%) sang warble form #2. In 1971, 2 out of 29 (about 7%) of singers recorded at the same locality used warble form #2. In contrast, in 1967 warble form #6 was uttered by only 1 of 12 singers (8%), whereas in 1971, 34% (10 out of 29) of the singers recorded used warble form #6.

C. *Forms of trill.* A simple presence-absence tabulation of the forms of trill does not show the uneven distribution of fast and slow trills among the birds in each locality sampled. Therefore, at each location where both fast and slow trills were recorded, the total number of each is given in parentheses in Tables 5 and 6. Table 5 shows that most of the fast trills recorded on breeding grounds (60 out of 64 or 94%) were recorded south of lat. 63°40′N, whereas most

TABLE 5.
Occurrence of forms of whistle, warble and trill at all localities sampled

	No. songs and birds	Form of whistle			Code no. of form of warble										Form of trill		
		Cont.	Seg.	Br.	1	2	3	4	5	6	7	8	9	10	f	s	phr.
Breeding locality																	
[1]Kenai Peninsula	20-21		+	+		+		+			+	+	+	+	+ (18)	+ (1)	+ (2)
Haines Junc.	1			+									+		+		
Anchorage & vicinity	8	+	+	+		+					+	+	+	+	+		
Copper R. Drainage	15		+	+		+					+		+	+	+		
Mile 1-82.5 D. H.	7	+		+		+					+	+	+		+		
[1]McKinley Nat'l Park	11-12	+		+		+				+	+	+			+ (9)	+ (2)	
Mile 1357 A. H.	2		+			+									+		
Mile 82 T. H.	1			+						+						+	
[1]Fairbanks	56-58	+	+	+	+	+	+	+	+	+	+				+ (4)	+ (52)	
Mile 140 E. H.	1			+		+										+	
Mile 104 S. H.	1			+		+										+	
Migration Route																	
Watson Lake & vicinity	47-51	+	+	+	+	+	+	+	+	+	+			+	+ (32)	+ (19)	
Wintering locality																	
Tucson, Ariz.	1		+							+							
San Diego, Calif.	5		+											+			
Blythe, Calif.	4		+	+		+				+	+			+			
[1]Goleta, Calif.	34-40	+	+	+	+	+		+	+	+	+		+	+	+ (21)	+ (12)	+ (1)

[1] localities where not every song was complete, hence a variable n is given.
numbers in parentheses = no. of trills

TABLE 6.
Occurrence of forms of whistle, warble and trill in small groups of breeding birds. Symbols as in Table 5.

	No. songs and birds	Form of whistle			Code no. of form of warble										Form of trill		
		Cont.	Seg.	Br.	1	2	3	4	5	6	7	8	9	10	f	s	phr.
Breeding group																	
Hidden Lake	7		+	+		+						+	+	+	+		
Scout Lake Loop	5		+	+							+	+	+	+	+		
Palmer	5	+	+	+		+					+		+	+	+		
Gulkana Airfield	5		+	+		+								+	+		
[1]Wonder Lake	4-5	+		+		+				+	+				+	+	
															(3)	(1)	
[1]Univ. of	23-25	+	+	+	+	+	+	+	+	+	+				+	+	
Alaska Campus															(2)	(21)	
[1]Smith Lake	6-8	+	+	+	+	+	+	+		+						+	
Musk Ox	9	+		+		+			+	+						+	

TABLE 7.
Comparison of song characteristics between members of pairs of singing neighbors (breeding birds)

	Song characteristic	No. pairs of singers	Percent of pairs, members of which used: Same form	Different form
Introductory part	1. Form of whistle	52	42.3	57.7
	2. Form of warble	55	25.5	74.5
Trill	3. Form	54	90.7	9.3
			Percent of pairs, members of which repeated syllable at	
			Same rate, ± 4/sec.	Different rate
	4. Rate of utterance of repeated trill syllable	53	60.4	39.6

of the slow trills recorded on breeding grounds (55 out of 58, or 95%) were found north of this latitude. Thus some north-south segregation of the forms of trill appears to exist among the breeding localities sampled to date. Within a given breeding population, all or most birds sang the same form of trill. Table 6 shows that, in 6 of the 8 small breeding groups sampled, all individuals used the same type of trill, and that even where both fast and slow trills occurred, most members of each population used the same form.

Table 7 substantiates the data in Tables 5 and 6 as to similarity of the form of trill in singers of the same population. Of 54 pairs of singing neighbors, members of 49 pairs (90.7%), sang the same form of trill. Sixty per cent of neighbor pairs sharing the same form of trill uttered the repeated syllable at the same rate ± 4/sec.

D. *Warble and trill forms in songs of migrants.* Table 5 shows that migrants recorded at Watson Lake included singers using eight of the ten forms of warble so far identified, and both fast and slow forms of trill. DeWolfe, West and Peyton (1973) documented influxes of Gambel's Sparrows into Watson Lake region in 1968 on 2, 5 and 9 May. Each of these influxes included birds uttering at least five different forms of warble, and both fast and slow trills. Birds using warble forms #1, 3 and 10 were recorded during the same influx. As stated above, warble forms #1 and 3 have to date been found among singers on breeding grounds only in the Fairbanks area, whereas warble form #10 has been recorded in breeding birds only from the latitude of Gulkana south (Table 6).

E. *Pitch relations of whistle and accompanying warble.* A tabulation of occurrence of whistles lower than, higher than, or of the same pitch as the median frequency of the ensuing warble revealed neither any geographic localization, nor any consistent pattern within breeding groups, of a specific pitch relation between whistle and warble.

F. *Rate of utterance of trill syllable.* Tabulation of ranges and means of rate of syllable utterance in the fast trill showed no consistent north-south variation among breeding localities sampled. Rates of utterance for all breeding localities ranged from 72 to 96 syllables per second, except for the three fast trills recorded at Fairbanks-College, in which the syllables were sung at the rate of 156/sec. This is the only locality where we recorded trills with so high a rate of syllable delivery.

The maximum difference in rate of utterance of syllables in the fast trill between members of a local breeding group (20/sec. at Scout Lake Loop) is almost as great as the range in rate of utterance for all breeding localities (24/sec.). Rates of syllable delivery varied between 76 and 96/sec. at Scout Lake Loop, between 80 and 88/sec. at Hidden Lake and between 84 and 92/sec. at Palmer.

The two breeding groups in which slow trills occurred showed variations in rate of syllable delivery between 28 and 48/sec. at Musk Ox Subdivision, and between 36 and 44/sec. at Smith Lake. Table 7 shows that out of 53 pairs of singing neighbors, members of 21 pairs (39.6%), differed by more than 4 syllables per second as to the rate of utterance of the repeated syllable of the trill.

Comparison of total song length between members of singing pairs

We have stated that when birds sing a long warble section, such as when they use two warbles of type #10, they usually sing only one buzz. Thus the long warble section does not necessarily increase the total duration of the song. We tested whether there was any correlation between the song lengths of singing neighbors. We found none. The pair-wise correlation coefficient of 46 randomly ordered pairs was very close to zero.

Statistical analysis of song characteristics from three breeding areas

Thorough statistical treatment of variation in Gambel's Sparrow songs must await collection of more data. Table 8, prepared using a format comparable to that of Table 2 in King (1972), shows the mean $\pm$ SD of several variable characteristics of song recorded at three locations with adequate sample size: Kenai Peninsula, McKinley Park area and Fairbanks. It suggests that, when sufficient data become available, statistical analysis of song characteristics may reveal facts pertinent to geographic variation. For example, songs from the Kenai Peninsula differed significantly from those recorded at McKinley Park as to duration of warble, median frequency of whistle, and the rate the syllables in fast trills were uttered. Kenai Peninsula songs differed significantly from those recorded at Fairbanks as to duration of warble, and median frequency

TABLE 8.
Statistical characteristics (mean ± SD) of songs from 3 breeding areas of *Z. l. gambelii*[1]

Variable[5]	Breeding area Kenai Peninsula[2]	McKinley Park area[3]	Fairbanks[4]
Duration, complete song (seconds)	(18) 2.07 ±0.201 *ab*	(11) 2.01 ±0.181 *a*	(55) 2.13 ±0.151 *b*
Duration, warble (seconds)	(20) 0.50 ±0.122 *a*	(12) 0.36 ±0.053 *b*	(58) 0.37 ±0.093 *b*
Frequency (kHz) of trace center of			
whistle	(20) 4.04 ±0.516 *a*	(12) 3.47 ±0.579 *b*	(58) 3.80 ±0.628 *ab*
warble	(20) 3.96 ±0.351 *a*	(12) 3.76 ±0.418 *a*	(58) 4.32 ±0.467 *b*
buzz I	(19) 4.95 ±0.159 *a*	(12) 5.01 ±0.187 *a*	(58) 4.96 ±0.195 *a*
buzz II	(7) 4.89 ±0.164 *a*	(10) 4.84 ±0.161 *a*	(58) 4.72 ±0.158 *b*
fast trill	(18) 3.55 ±0.094 *a*	(9) 3.62 ±0.106 *a*	
slow trill			(52) 3.87 ±0.246
No. syllables/0.25 sec			
fast trill	(16) 20.69 ±1.309 *a*	(9) 22.44 ±1.065 *b*	
slow trill			(53) 10.34 ±1.466

[1]numbers of birds and songs appear in parentheses
[2] = 1967, 1968; [3] = 1971; [4] = 1967, 1968, 1970, 1971 and 1972
[5]values followed by same letter (compare across) do not differ significantly (i. e. $P > 0.05$ that means are the same).

of warble and of second buzz. Songs from McKinley Park differed significantly from those recorded at Fairbanks as to duration of complete song, and median frequency of warble and of second buzz.

Since all recordings in McKinley Park were made in one season (1971) we also calculated means, for 1971 only, for the Fairbanks birds. Comparison of means for 1971 alone yield different results. The difference in mean duration of the complete song between the two areas is not statistically significant ($P > 0.1$). On the other hand, the differences between the two areas as to the means of median frequency of whistle and of buzz I are significant ($P < 0.01$ and $P < 0.05$, respectively) when data for 1971 alone are compared. This is further evidence of temporal variation in song.

DISCUSSION

This section includes speculations to stimulate further work on problems related to song variation in the Gambel's Sparrow suggested by this study.

Relation of song structure to acoustic properties of habitat.

Morton (1970 and pers. comm.) correlated characteristics of bird song and of sound propagation in forest, edge and grassland habitats in Panama. He hypothesizes that in open country, selection would favor songs carrying temporal information, which is not distorted in temperature and wind stratified environments. White-crowned Sparrows occupy windy country, and a typical breeding territory includes considerable lengths of edge between shrubbery and open ground or grass. The Gambel's Sparrow's song, which includes warbles and trills carrying much temporal information, would seem well suited for propagation under the acoustic conditions Morton describes for habitats combining edge and grassland.

Evidence for individuality of migrant flight schedules

The fact that warble forms #1, 3 and 5 were recorded from migrants passing through Watson Lake indicates the possibility that some Gambel's Sparrows using this migration route may have been destined to breed at least as far north as Fairbanks, because these forms of warble have to date not been recorded in Alaska south of this locality. The fact that warble forms #8 and 10 were also recorded at Watson Lake suggests that some birds passing this point may have been destined to breed at or south or the latitude of Gulkana, (62°16′N) because these forms of warble have not yet been recorded north of this locality. The facts that birds singing warble forms #1 and 10 were recorded on the same date in Watson Lake, and that singers uttering both fast and slow trills were recorded during each of three influxes of Gambel's Sparrows into Watson Lake in 1968, suggest that migrants arriving there on the same day may have been destined for different breeding localities. Thus analysis of song patterns of migrants passing through the Watson Lake area supports the hypothesis of DeWolfe, West and Peyton (1973) that "flocks" of Gambel's Sparrows arriving at Watson Lake were actually aggregates of individuals, each following its own flight schedule, rather than cohesive units destined for the same breeding grounds.

Comparisons with songs of other Zonotrichia

A. *Testosterone-injected female Gambel's Sparrows.* Kern and King (1972) compared songs of testosterone-injected female Gambel's Sparrows with the advertising song of a normal captive male. Although caution must be exercised in interpreting reproductions of spectrograms, we think that songs designated as "abortive" may not be so abnormal as these authors suggest. Their Figure 4, for example, shows a song element, uttered three times, which in its general form resembles warble form #4 in our recordings. It would be interesting to know which forms of warble were used in the breeding population where the experimental females hatched. Baptista (in press) recorded the song of a testosterone-injected female Sparrow mated to a male whose repertoire consisted solely of song themes of *Z. l. pugetensis.* Her song most closely resembled that of Nuttall's Sparrow males in the area in which she was nesting (and presumably also in which she had hatched). The female appeared to have tried to learn the song typical of her home and not of her mate.

B. *Nuttall's Sparrows of the San Francisco Bay Region.* The many forms of warble confer greater individual variability on the first half of the Gambel's Sparrow's song than is present in the comparable section of the Nuttall's Sparrow's song as shown in Figures 2-4 of Marler and Tamura (1962) and in Figure 1 of Marler (1966). In contrast, the stereotyped syllable structure in the terminal element of *gambelii* songs provides no evidence for local dialects such as Marler and Tamura found in the trills of Nuttall's Sparows in the San Francisco Bay Region.

C. *White-throated Sparrow.* Like the songs of *Z. albicollis* analyzed by Borror and Gunn (1965) Gambel's Sparrows exhibit a large number of song patterns, the song varies greatly in structure of the second song element, and the occurrence of the various forms of some elements indicates the existence of geographic variation but not of local dialects.

In their 12-year study of songs of *Z. albicollis,* Borror and Gunn document temporal variation in the song patterns used at a given locality. Our data on songs of Gambel's Sparrows at Fairbanks suggest temporal variation in relative abundance of warble forms #2 and 6. We should also mention DeWolfe's impression that the number of birds wintering on the University of California campus at Goleta which use warble form #10 may be increasing. None used it in winter of 1967. When migrants passed through Goleta in late March 1968, DeWolfe listened specifically for birds uttering warble form #10, but heard only one. Now, 5 years later, birds sing this form there throughout the winter, and during fall and spring migration as well. As Borror and Gunn state, "song pattern distribution and incidence should be treated as dynamic rather than static phenomena."

D. *Rufous-collared Sparrow.* Nottebohm (1969) designates variations in the introductory part of *Z. capensis* songs as "themes." His Table 1 shows from 2 to 16 themes in each of the 13 localities sampled. Similarly, we found several different warble forms in songs of each small breeding group of Gambel's Sparrows (Table 6). On the basis of pitch, structure and rate of delivery of the trill notes, Nottebohm (op. cit.) has defined five dialect areas for *Z. capensis* in central Argentina, over a north-south distance of about 400 miles. Four of these areas are (Chapman, 1940) inhabited by the subspecies *Z. c. hypoleuca.* We distinguish two common forms of trill in Gambel's Sparrows, also over a north-south distance of about 400 miles, in southern and central Alaska. Our data suggest that most birds singing the fast trill breed south of most individuals using the slow trill (Table 5).

In contrast, we have to date found no trill variations in *Z. l. gambelii* suggestive of local dialects comparable to the "sub-dialects" Nottebohm shows in his Figure 12 for songs of *Z. capensis* from Sierra Grande at different altitudes. Another difference between the two taxa relates to degree of similarity between songs of neighbors. Nottebohn's Figures 3, 4 and 8 indicate a closer similarity between the introductory part of songs of *Z. capensis* neighbors than we found in the whistle-warble part of songs of *Z. l. gambelii* neighbors.

King (1972) states that within three trill-rate "zones" associated with different habitats, the themes of the opening phrase of the song of *Z. capensis* in northwestern Argentina are distributed nonrandomly. The ten forms of warble we have identified in the Gambel's Sparrow song are likewise combined non-randomly with the two common trill forms (Table 4).

Similarities with other genera

Our study of *Z. l. gambelii* indicates that, in the matter of presence or absence of song dialects, *Z. leucophrys* may be similar to *Pipilo erythophthalmus.* Borror (1959) found no evidence of dialects in this species, but Kroodsma (1971) did. Also, variation in Gambel's Sparrow songs appears to resemble that in *Certhia brachydactyla* (Thielke, 1965) in that some syllables in songs of both species may be distributed in mosaic fashion.

Repertoire size

Several authors report that White-crowned Sparrows are predisposed to sing only one song (facts summarized in Marler, 1970). However, Banks (1964), Baptista (1973, 1974), and we have found that occasionally individuals may sing 2, 3 or even 4 patterns. In this respect *Z. leucophrys* resembles other taxa of *Zonotrichia,* as discussed by King (1972).

Survival value of high individual variability in song

Although we were disappointed that our analysis of Gambel's Sparrow songs did not furnish clues to the location of breeding areas of individuals, our data suggest interesting possibilities with respect to survival value of high individual variability in song in a migratory bird. Goldman (1973) found that in the Field Sparrow (*Spizella pusilla*) a given individual generally sang only one type of song, and that neighboring males very rarely sang identical songs. Our data suggest that a comparable situation may obtain in Gambel's Sparrows. Falls (1969) presents evidence suggesting that male White-throated Sparrows recognize one another individually by song alone. If we assume that this is true for Gambel's Sparrows, we can hypothesize that a high degree of individual difference in songs of neighboring males is of survival value. The Gambel's Sparrow is absent from its breeding grounds 8 or 9 months of each year. When the birds return to the nesting grounds mates must be reunited or new mates found, and territorial boundaries must be relearned or new ones established. Any mechanism facilitating quick recognition of individuals in a local breeding population should be of value.

If individual variation in song facilitates recognition of mates and neighbors, less time and energy would be needed to establish, or re-establish, pair bonds and territories. As Goldman (op. cit.) points out, the time and energy saved can be devoted to reproduction. Such considerations should be of far greater importance to the migratory Gambel's Sparrow than to permanently resident Nuttall's Sparrows. Selective pressures fostering individual differences in songs of breeding neighbors may therefore be stronger in Gambel's than in Nuttall's Sparrows.

SUMMARY

Songs of 360 adult Gambel's White-crowned Sparrows, tape-recorded during a five-year period in Alaska, California, and at Watson Lake, Y. T., have four song elements in common: whistle, warble, buzz, and a terminal element which is usually a trill. Spectrogram traces of each element vary as to duration, median frequency, and form. We have identified 4 prominent forms of whistle, 10 of warble, 2 of buzz, and 3 of terminal element.

In songs of neighbors on adjacent territories, and in small breeding populations, the form of warble varies between one individual and another, whereas the form of trill is usually the same. The 10 forms of warble and 3 forms of terminal song element differ geographically and in relative abundance at the localities sampled.

The stereotyped structure of syllables in the trill of Gambel's Sparrow songs provides no evidence for local dialects as found in songs of Nuttall's Sparrows in the San Francisco Bay Region and in *Zonotrichia capensis* from Sierra Grande in central Argentina. Similarities and differences occur between song characteristics of *Z. l. gambelii* and those of *Z. capensis* in northwestern Argentina.

Songs recorded from the Kenai Peninsula and the McKinley Park and Fairbanks areas show statistically significant differences in duration of warble, median frequency of whistle and/or of warble and buzz, and rate of utterance of syllables in the trill. Songs recorded at Fairbanks in different years suggest temporal variation in relative abundance of birds singing a given form of warble.

We speculate that the high degree of individual variation in the introductory part of the song of Gambel's Sparrow may be of survival value to a bird absent from its mate and nesting grounds for the greater part of each year.

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