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COMPONENTS OF VARIATION IN NUPTIAL CALLS
OF THE LEAST SANDPIPER
(*CALIDRIS MINUTILLA*; AVES, SCOLOPACIDAE)

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Abstract.—Unpaired male least sandpipers (*Calidris minutilla*) emitted three main kinds of calls to attract mates and in sexual or agonistic interactions. The call types varied slightly across the nesting range (samples from British Columbia, Yukon Territory, Manitoba, and Nova Scotia). One call type, analyzed in most detail, was given in long rhythmic series during aerial displays. Tape recordings of 2,250 calls from 80 males were analyzed using four measurements on temporal characteristics and eight on frequency. Most of the variance (59–82% for the 12 characters) was attributable to variation among males, less to cells (13–41%), and least to locality (0–9%); only one variable differed significantly among geographic samples. Temporal characteristics varied more than frequency characteristics, with coefficients of variation (Vs) averaging 4 to 9% for the former and 2 to 3% for the latter. Vs were significantly heterogeneous across characters for each locality but variability profiles were very similar among localities. No Vs differed significantly among geographic samples. The extreme geographic uniformity in call structure, univariate and multivariate variation, variance components, and correlational relationships among call variables was unexpected. Comparative studies using similar quantitative techniques are needed to assess the generality of the findings. [Bioacoustics; vocalization; geographic variation; character analysis; quantitative ethology; Scolopacidae; shorebird; least sandpiper; *Calidris minutilla*.]

Documentation of phenotypic variation in natural populations is central to most areas of evolutionary biology, including development, geographic variation, natural selection, adaptation, and phylogeny (Yablokov, 1974; Soulé, 1982; Soulé and Cuzin-Roudy, 1982; Alberch, 1983; Endler, 1986). Most studies to date have been on morphological attributes, which are easy to describe or measure using museum specimens. In contrast, documenting behavioral attributes demands much time observing live animals, often under adverse field conditions, and behavior is generally difficult to describe or measure in a standardized way: it is complex both temporally and (structurally) at any point in time, can change quickly, and is highly variable among and even within individuals. Furthermore, detailed understanding of a species' natural history or social structure is often necessary even to be able to choose meaningful social classes or behavioral events for measurement (Barlow, 1977; Bond et al., 1985). Nevertheless, it is clear that our understanding of evolutionary pattern and process will remain incomplete until behavioral variation and plasticity are better documented, so there has been an increased emphasis on studying ecologically relevant variation and linking morphological to behavioral variation (Curio, 1977; Schoonhoven, 1977; von Brockhusen, 1977; Łomnicki, 1978; Arnold, 1981a, b; Grant and Grant, 1983; Fitzpatrick, 1985).

For several reasons, the field of bioacoustics has much to offer the study of behavioral variation: sound attributes can be related fairly directly to the morphology of sound-producing structures; behavioral functions of sounds (e.g., bird songs) are fairly well understood; methodology and instrumentation for sound recording and analysis are standardized; a vast amount of descriptive literature is available; and many interesting ecological, systematic, and evolutionary questions apply. For example, animal sounds that are transmitted over long distances can be viewed

within an ecological-adaptive framework, leading to predictions that sounds are structurally adapted to withstand alteration by the physical environment (Wiley and Richards, 1982) or are structurally distinctive to enhance species recognition in complex communities (Becker, 1982; Miller, 1982; Kroodsma, 1985). Ecological concepts of niche shift, expansion, and compression are useful in exploring the latter possibility: species in sympatry with related species are predicted to occupy a smaller or more distinctive acoustic "space" (or both) relative to allopatric situations. Thus, a species could exhibit divergent character shift or reduced character variation in sympatry. Few compelling examples of character or variance shift in bird sounds exist (Becker, 1982; Miller, 1982), and one reason may be that quantitative analyses have been inappropriate or have not included all relevant levels of variation; at the very least, variation within and among individuals and among populations should be analyzed (Miller, 1982). In this study I analyze components of variation in calls of a widely distributed species of sandpiper to investigate adaptive geographic differentiation in acoustic structure.

In least sandpipers (*Calidris minutilla*) and most of the other Calidridini, unpaired males engage in conspicuous aerial displays while uttering loud simple calls in rhythmical bursts or sequences (Miller, 1983a, b). These calls (Rhythmically Repeated Calls or RRCs) advertise the presence of males over prospective nesting areas which they defend as territories until pairing. Display flights, RRCs, and defense of territory virtually cease upon pairing in most calidridine species. Two other call types (Song, Chatter) are widespread in Calidridini and seem to be associated with medium- to short-range sexual or agonistic interactions, although they are audible over long distances (Miller, 1983b). All of these call types seem likely to be physically adapted for long-distance transmission and to be species-distinctive for minimizing time and energy losses through unnecessary interactions with

heterospecifics, as well as for preventing pairing between heterospecifics.

The purposes of my study are to describe structural variation in calls within and among several populations of the least sandpiper, to relate patterns of variation to geographic distance and to coarse differences in sandpiper community structure, and to establish a quantitative framework within which comparable studies can be made. A secondary goal is to contribute to our knowledge of geographic variation in nonpasserine bird sounds; research on the Passeriformes has dominated our understanding of geographic variation and microevolution of bird sounds, and we do not know the degree to which these findings can be considered to be general (Mundinger, 1982). There have been only two previous studies of geographic variation in sounds for the approximately 200 species of shorebirds, one on nonvocal sounds (Thönen, 1968) and another on vocalizations (Miller et al., 1983; Miller, 1984).

MATERIALS AND METHODS

I recorded least sandpipers at five locations, including three in the west (W), and one each in the central (C) and eastern (E) parts of the breeding range (Fig. 1): (W1) Blackstone River Valley, Ogilvie Mountains, Yukon Territory (May and June 1979); (W2) along the Haines Highway, British Columbia (June 1982, May–July 1983); (W3) Delkatla Wildlife Sanctuary at Masset, Queen Charlotte Islands, British Columbia (May and June 1984); (C) near Churchill, Manitoba (May–July 1978); and (E) on Sable Island, Nova Scotia (May–July 1975, May–August 1976).

Recordings on Sable Island were made at 19 cm/sec using Scotch tape 176, a Uher 4200 Report Stereo IC tape recorder, and a Uher M517 dynamic microphone mounted in a Dan Gibson parabolic reflector. All other recordings were made at 19 cm/sec on Scotch tape 208, a Nagra IS tape recorder, and a Sennheiser MKH816 ultradirectional microphone. Sound spectrograms were prepared on a Kay Elemetrics Sona-Graph 7029A or Digital Sona-Graph
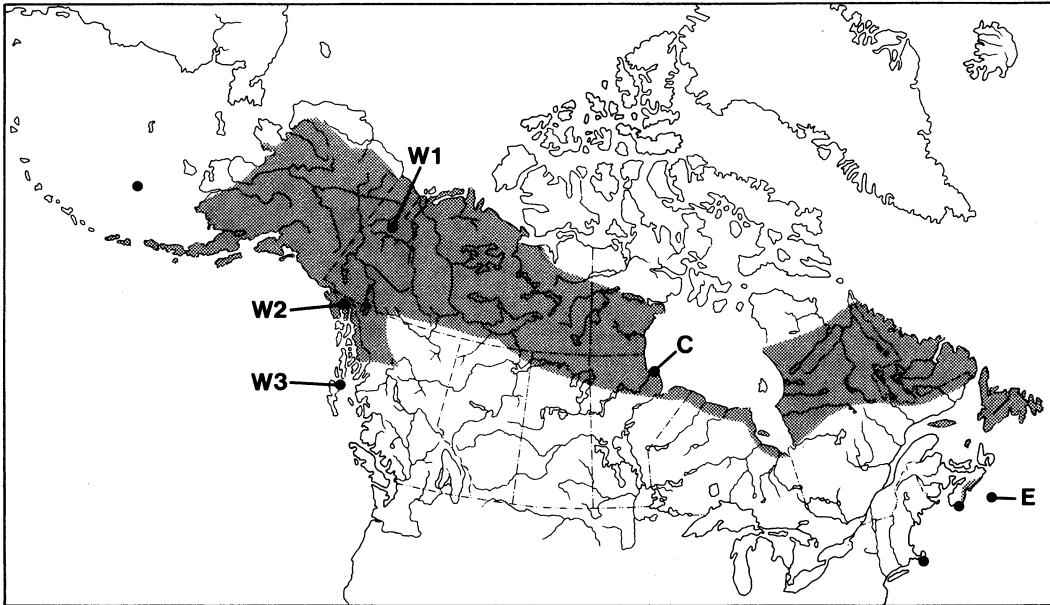
FIG. 1. Map showing approximate breeding range of least sandpipers and locations where birds recorded. Unlabelled symbols are for isolated breeding locations (that in the Bering Sea is for the Pribilof Islands). W1, W2, and W3 are Western samples; C is Central sample; and E is Eastern sample. Distribution based on Anderson (1980), Godfrey (1986), B. Kessel (pers. comm.) and D. D. Gibson (pers. comm.), with modifications for Canada from D. F. Hatler (pers. comm.), I. A. McLaren (pers. comm.), and my unpublished observations (Southampton Island; Queen Charlotte Islands).

7098. Frequency calibrations produced by the machines were examined periodically, but variations were minor.

Song and Chatter were less suitable than RRCs for quantitative analysis because they were much more variable, even within single utterances, and adequate sample sizes from individual birds were hard to obtain. In this paper, I present only general descriptions of Song and Chatter.

Temporal and frequency measurements on RRCs were made on spectrograms prepared over the frequency range 80 to 8,000 Hz, with 300- and 45-Hz analyzing filter bandwidths. RRCs that occurred at the beginning of call sequences or during interruptions, or that preceded song or descent, differed somewhat from those in unbroken rhythmical sequences, so only the latter were used (Miller, 1983a, 1984). For such calls, the following measurements were taken (Fig. 2): (a) Temporal variables (measured on wide-band spectrograms). T1, interval preceding call; T2,

duration of initial element; T3, time from the end of the initial element to the end of the final element; T4, interval following call. The intermediate elements shown in Figure 2 were often very faint so could not be measured reliably. (b) Frequency variables (measured on narrow-band spectrograms). F1, peak frequency of initial element; F2 to F7, frequencies of the terminal element measured at equal time intervals up to its peak frequency (F8). The intervals were established by trial and error so they would apply to all males. The six intervals preceding F8 totalled 96 msec, so each was 16 msec long.

The 13 points shown in Figure 2 (five points delimiting four temporal variables and eight points for frequency variables) were estimated with a transparent overlay and were entered into a data file directly from a HIPAD digitizing tablet (Houston Instrument Division of Bausch and Lomb). Temporal and frequency variables were computed from the coordinates. Variable
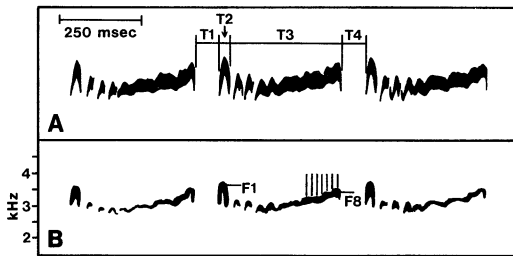
FIG. 2. Diagram of three Rhythmically Repeated Calls (RRCs) of least sandpipers, showing variables used in this study. Temporal variables are horizontal distances between vertical lines. Frequency variables are vertical distances between baseline (not depicted) and horizontal markers. Horizontal markers for F2 to F7 not shown; they would intersect vertical lines in B at appropriate midpoints of trace. Figure is an ink tracing of first harmonic overtone. Analyzing filter bandwidths (A) 300 Hz and (B) 45 Hz.

T4 was omitted from analyses because it was equivalent to T3 for the next call in many cases.

Most analyses were done with standard statistical packages (BMDP, SPSS-X, SAS). Nested analysis of variance (ANOVA) was used to estimate variance components attributable to variation among calls of individual males, among males within localities, and among localities.

Heterogeneity among coefficients of variation (V, following the symbolism of Sokal and Rohlf [1981]) within geographic samples was evaluated by Friedman's test for randomized blocks (Sokal and Braumann, 1980; Bird et al., 1981; Sokal and Rohlf, 1981). Each geographic sample was examined in turn, with variables considered as "treatments" and individual males as "groups." A significant test indicates two things: (1) "the rank of the coefficient of variation of a character tends to be the same" among males at each locality; and (2) there are significant differences among Vs within the variability profile for the locality under consideration (Bird et al., 1981:62). My application differs slightly from that of Bird et al. (1981), who set localities as groups.

Differences among Vs for individual variables were tested for by the Scheffé-Box (log-ANOVA) test for homoscedasticity (Sokal and Rohlf, 1981). This test may

be preferable to others because it is less sensitive to departures from normality (Sokal and Braumann, 1980). Sokal and Rohlf (1981:406) pointed out that the number of subsamples should approximate $n^{1/2}$ and that the sizes of the subsamples should be nearly equal. I used three geographic samples with sample sizes of 26 (W), 24 (C), and 30 (E), and subdivided these into subsamples of: 5, 5, 5, 5, and 6 (W); 5, 5, 5, 5, and 4 (C); and 5, 5, 5, 5, and 5 (E). This set of subdivisions also satisfied the recommendation that subsamples should be nearly equal in size (Sokal and Rohlf, 1981:406).

Individual-differences scaling is a potentially valuable method in bioacoustic studies. The method originated as a metric one for the analysis of perceptual differences (Carroll and Chang, 1970) on the assumption that people have common perceptual dimensions but these differ in relative importance among individuals (Shepard, 1980). Data used in such analyses take the form of a series of proximity matrices, one for each subject. Commonly, the proximity measures are the judged (pairwise) similarities between N stimuli, such as sounds, tastes, or colors. By analogy, I used 80 matrices (one per male) of correlations among acoustic characters (with the nonmetric implementation afforded by PROC ALSCAL; Takane et al., 1977; Carroll and Arabie, 1980). My data describe the acoustic space of individuals, not their perceptual space. However, auditory perception in birds is fairly conservative (Dooling, 1982; but see Okanoya and Dooling [1985]), so I assume that acoustic space is related to perceptual space in a similar way across populations of a single species.

Systematic variation among individuals or groups of them (e.g., by gender or age) can be revealed by individual weights on the perceptual (in this case, acoustic) dimensions, and a test analogous to analysis of variance has been developed for group comparisons (analysis of angular variation, or ANAVA; Schiffman et al., 1981). In my analysis, matrices were grouped into the three geographic samples and the vectors of males in "subject weight space"
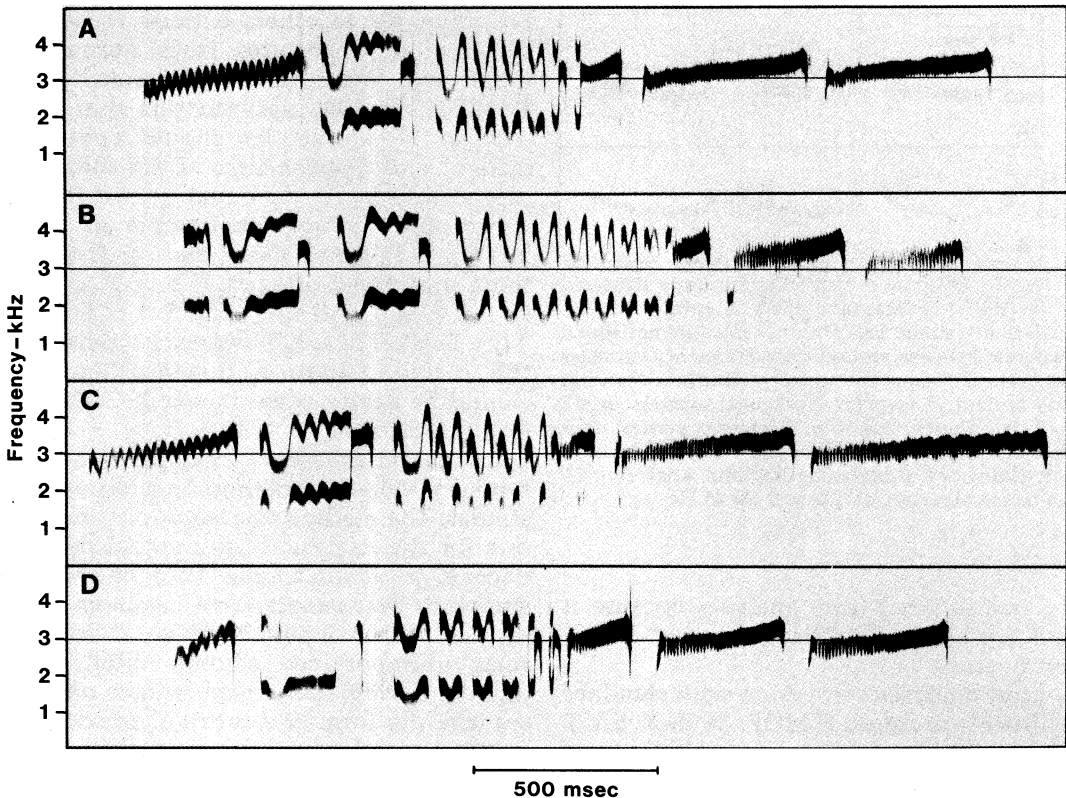
FIG. 3. Sound spectrograms (analyzing filter bandwidth of 300 Hz) of Song of least sandpipers from (A) Queen Charlotte Islands, (B) Yukon Territory, (C) northern Manitoba, and (D) Sable Island.

were subjected to ANAVA on that basis. Riska (1985) used a different approach for comparing correlation matrices among geographic samples.

RESULTS

General structure of display flights.—Display flights had median durations of 2.15 min in the Yukon, 1.20 min in northern Manitoba, and 2.63 min on Sable Island (Miller, 1983a). Birds in display flights had a distinctive flight mode (Punctuated Fluttering or PF) in which they alternately fluttered the wings and held them motionless. The fluttering phase of PF occurred at an average rate of 26/min in the Yukon (11 min of samples), 45 in the Haines Road sample (24.5 min), 32 in Manitoba (54.7 min), and 37 on Sable Island (81.3 min). Thus, there was considerable variation among geographic samples but rate of fluttering, as well as display-flight activity and duration, were influenced by time of day, date, wind, and other variables (Miller, 1979a, 1983a). Thus, little can be concluded from the observed differences.

Song and Chatter.—Detailed descriptions of Song and Chatter, with behavioral observations, are presented elsewhere (Miller, 1979b, 1983a, 1985). In those papers, I did not emphasize the fact that Song comprises Song *units*, one to several of which are repeated in a string. This organization of Song is identical to that of long- and short-billed dowitchers (*Limnodromus scolopaceus* and *L. griseus*; Miller et al., 1983, 1984). A sample of 203 Songs from the Haines Road contained 87% of Songs composed of a single Song unit, 11% of two, 1% of three, and 0.5% of four units.
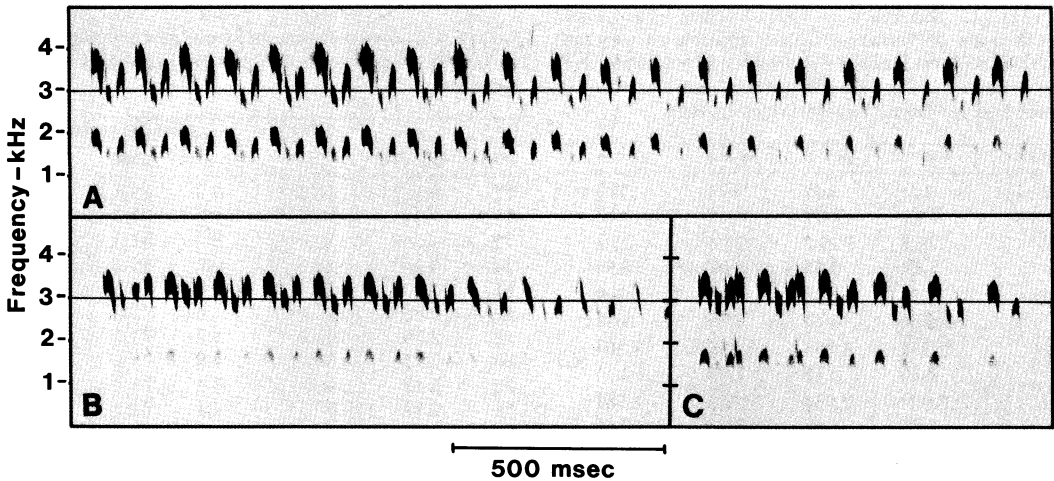
Song and Chatter were very similar

FIG. 4. Sound spectrograms (analyzing filter bandwidth of 300 Hz) of Chatter of least sandpipers from (A) Queen Charlotte Islands, (B) northern Manitoba, and (C) Sable Island.

throughout the range. Each Song unit comprised four types of elements (Fig. 3): (1) an introductory one with rhythmic frequency modulation (FM) superimposed on a gently rising carrier frequency; (2) one to several repetitions of an element characterized by a well defined harmonic structure, an initial dip then recovery in frequency followed by a constant-frequency portion (sometimes with rhythmic FM), and a rapid terminal jump in frequency; (3) a series of brief elements very similar to the beginning of element type (2), but becoming successively briefer throughout the series; and (4) several long calls with strong rhythmic amplitude modulation (approaching pulsing) and a slight increase in carrier frequency over their length (Fig. 3). These four element types were present in this sequence in nearly all songs. The number of each element type, except type (1), varied according to context. I detected no qualitative differences in sound spectrograms among the sample localities and could distinguish no differences "by ear."

Chatter was composed of repeated element groups, usually triplets (Fig. 4). The number of elements per group, their frequency, and their amplitude all varied within particular utterances and across

contexts (Miller, 1979a, 1983a). Chatter, like Song, was qualitatively similar in all samples.

Character variation among populations. — Temporal characteristics of RRCs were very similar across geographic samples, with differences being less than about 5% of the grand mean in each case (Table 1, Fig. 5). Frequency variables were very similar too, though Western birds averaged higher than Central birds on each variable, and Central birds averaged higher than Eastern birds. Each difference was less than 4% of the grand mean, and only one variable (F1) showed significant variation among localities (Table 2).

The curves shown in Figure 5 were significantly concordant (Kendall's $W \approx 1$), which resulted partly from high correlations among the frequency variables. Correlations among frequency variables (based on means for each male) ranged from 0.795 to 0.996; in contrast, correlations among temporal variables ranged from -0.159 to 0.124. These differences among variables are reflected in the factor loadings in principal components analysis: frequency variables loaded heavily and similarly on the first dimension, whereas T1 to T3 loaded more variably on the second (Fig. 6A). Not surprisingly, Eastern, Central and

TABLE 1. Summary of means (upper figures) and coefficients of variation (lower figures; in percent) for 11 variables. Figures not weighted by sample sizes for different males (means for temporal variables in msec and for frequency variables in Hz).

Variable	Western	Central	Eastern	Totals
T1	103	103	104	103
	7.96	9.09	8.67	8.57
T2	24.4	25.7	25.4	25.2
	7.81	6.55	6.51	6.96
T3	339	348	341	342
	4.36	4.23	3.73	4.11
F1	3,357	3,334	3,236	3,304
	2.30	2.17	1.96	2.14
F2	3,004	2,954	2,930	2,961
	2.75	2.68	2.37	2.60
F3	3,000	2,960	2,923	2,959
	2.81	2.65	2.44	2.63
F4	3,070	3,034	2,993	3,030
	2.68	2.61	2.35	2.55
F5	3,054	3,022	2,972	3,014
	2.76	2.66	2.43	2.62
F6	3,117	3,098	3,036	3,081
	2.83	2.59	2.37	2.60
F7	3,164	3,139	3,078	3,124
	2.77	2.44	2.36	2.52
F8	3,266	3,227	3,170	3,218
	2.66	2.35	2.27	2.43
n (males)	26	24	30	80
n (calls)[a]	670–673	822–837	736–740	2,228–2,250

[a] Variation resulted from missing values.

TABLE 2. Summary of frequency estimates and percent variance components from nested analysis of variance on each variable (calls within males within locations).[a]

Vari-able	MS_L/MS_M	MS_M/MS_C	Percent of variance		
			Location	Male	Call
T1	0.117	42.3***	0.0	59.8	40.2
T2	1.49	79.9***	1.0	73.1	25.9
T3	0.582	128.0***	0.0	82.0	18.0
T4	0.180	40.6***	0.0	59.1	40.9
F1	4.20*	170.3***	9.0	78.1	12.9
F2	2.88	105.7***	5.0	75.0	20.0
F3	2.79	106.0***	4.7	75.2	20.0
F4	2.71	106.4***	4.5	75.4	20.0
F5	2.67	107.9***	4.4	75.7	19.8
F6	2.57	107.3***	4.1	75.9	20.0
F7	2.57	111.4***	4.2	76.4	19.4
F8	2.78	127.5***	4.8	77.9	17.2

[a] MS = mean square; L = location; M = male; C = call. Degrees of freedom for all ratios in the second column are 2 and 77, for which $F_{0.05}$ = 3.89. Degrees of freedom for ratios in third column vary from 77 and 2,125 to 77 and 2,170; $F_{0.001}$ < 2 for this range (*, P < 0.05, ***, P < 0.001).

Western samples were separated along component I only weakly (Fig. 6 [right panels]; note also the locations of the centroids in Fig. 6 [left panel]).

Variance components and taxonomic distances among males.—RRCs varied little within each male but varied greatly among males within each geographic sample. The among-male component of variance ranged from 60 to 82% across variables in nested ANOVAs (Table 2). A related measure is the added variance component among males within each population, based on one-way ANOVAs for the different variables. Trends in added variance components paralleled those summarized in Table 2, as expected: values ranged from 58 to 84% for temporal variables (extremes were for T1 and T3 in the Western sample); and 75 to 87% for frequency variables

(extremes were F2 in the Western and F1 in the Eastern samples).

The acoustic similarity among males within each population can be estimated with a measure (taxonomic distance) used commonly in studies of ecomorphology and "phenetic packing" (e.g., Findley, 1973), which is simply the Euclidean distance between two points in an n-dimensional space (here n = 11). Taxonomic distances among males were computed on variables "ranged" by Gower's expression (Sneath and Sokal, 1973:153). Average
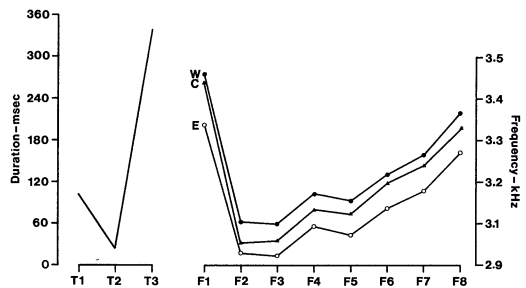

FIG. 5. Graph of unweighted mean values per variable for the different geographic samples (W = Western, C = Central, E = Eastern). Samples not distinguished for temporal variables because they are so similar.
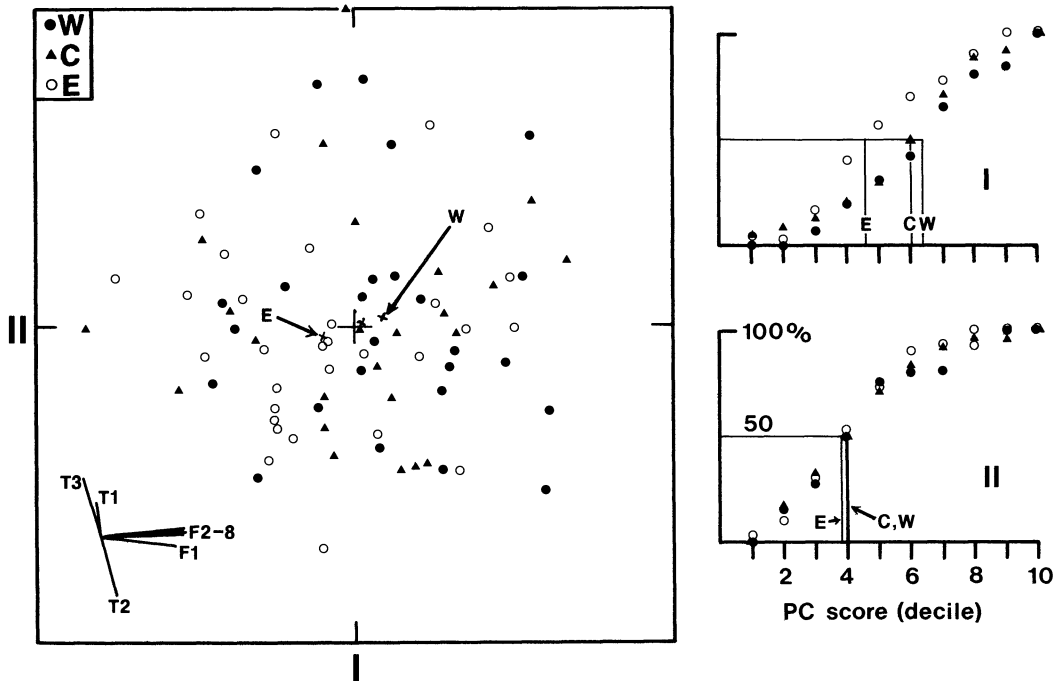
FIG. 6. Left panel depicts a two-dimensional principal components solution (with varimax rotation) based on mean values per variable for each male. Symbols represent individual males. Western (W), Central (C), and Eastern (E) samples represented by different symbols; centroids of W and E samples also indicated (C lies between them). Component loadings summarized as vectors in bottom left corner. Right panels include cumulative plots of scores on PC-I and PC-II for each of three geographic samples. Ranges for scores subdivided into deciles for the plots.

taxonomic distances were very similar in the Central and Eastern samples but were significantly greater in the Western sample; estimates (±SE) were: 36.6 ± 0.848, 32.0 ± 0.885, and 31.7 ± 0.720 for Western, Central, and Eastern samples, respectively.

Variation in the coefficient of variation.—Vs of temporal variables ranged only from 3 to 9% and showed no systematic trends across geographic samples (Table 1, Fig. 7). Variation within and among frequency variables was less (2–3%), and Vs were highest for Western birds and lowest for Eastern ones on all variables. However, no Vs differed significantly among localities: Scheffé-Box tests provided estimates of F from 0.214 to 1.924 for the different variables ($P > 0.05$; for each test, df = 2,13). Similarly, multivariate Vs did not differ significantly among localities, using van Valen's (1974, 1978) expression of

$$V_p = (100\sigma_p)/|\mu|, \qquad (1)$$

where $|\mu|$ is the multivariate joint mean; the jack-knifed estimates were 2.71 ± 0.136, 2.53 ± 0.127, and 2.35 ± 0.208 for Western, Central, and Eastern samples, respectively.

Heterogeneity of Vs among characters was investigated for each locality separately by Friedman's method for randomized blocks (Sokal and Rohlf, 1981). In each case there was a highly significant effect of "treatment" (=variable) upon "groups" (=individual males), whether frequency and temporal variables were considered jointly or separately ($P < 0.001$ in each case). These patterns were very similar across geographic samples: the variability profiles in Figure 7 were significantly concordant with one another overall, or when frequency and temporal variables were considered separately (for frequency vari-
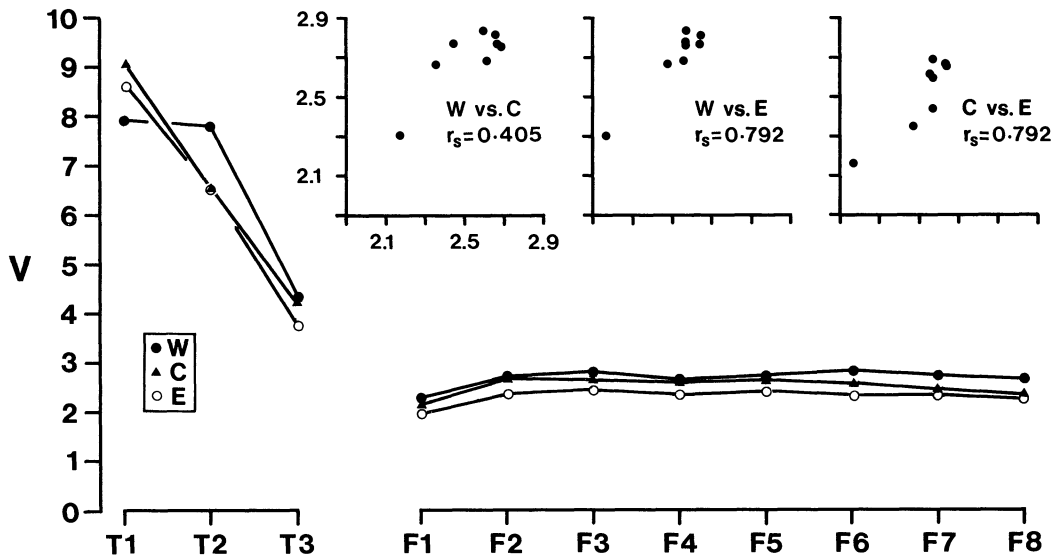
FIG. 7. Variability profiles showing mean coefficient of variation (V) per variable for different geographic samples (W = Western, C = Central, E = Eastern). V estimates not weighted by sample sizes for individual males. In insets, plots of V estimates for frequency variables show similarities across geographic samples (r_s = Spearman's rank-correlation coefficient).

ables, Kendall's $W = 0.77$, df $= 7$, $P < 0.025$; for temporal variables, $W = 1.00$, $P < 0.05$). Concordance among variability profiles for frequency variables was investigated further through pairwise comparisons among localities; two of the three comparisons revealed significant correlations between Vs for the same variables (insets, Fig. 7). Among frequency variables, F1 consistently varied the least, F8 varied most, and intervening variables were intermediate.

V appeared to be inversely related to frequency, but this was statistically significant only for one of the three samples (Fig. 8). Kendall's τ for the data (grand means) plotted in Figure 8 was 0.43 ($P > 0.10$) for Western, 1.00 ($P < 0.01$) for Central, and 0.29 ($P > 0.10$) for Eastern samples. Similar trends appeared when Vs and mean frequencies for particular variables for individual males were examined—V was significantly negatively correlated with frequency variables for the Central sample only. For example, r was -0.407 ($P < 0.05$) for F1, -0.621 ($P < 0.01$) for F5, and -0.535 ($P < 0.01$) for F8 in the Central sample (df $= 22$ in each case), but did not

differ significantly from 0 in the other samples or when all samples were combined. Thus, in the Central birds, RRCs began and ended at high frequencies that varied little from call to call, and the regular increase in frequency over the course of the long element in each RRC was accompanied by regularly decreasing variation.

ALSCAL was applied to the 80 correlation matrices of individual males. The vectors of males described an arc in subject weight space, with most in the bottom part (Fig. 9). The mean vectors for the different geographic samples were very similar in position and length, and the samples differed insignificantly from one another (Tables 3, 4).

DISCUSSION

Acoustic character variation.—Variation in least sandpiper calls agrees with a general trend for temporal attributes of bird calls to vary more than frequency attributes (Fig. 10). Estimates for the least sandpiper are at the low end of the ranges for species plotted. Whether the reported quantita-
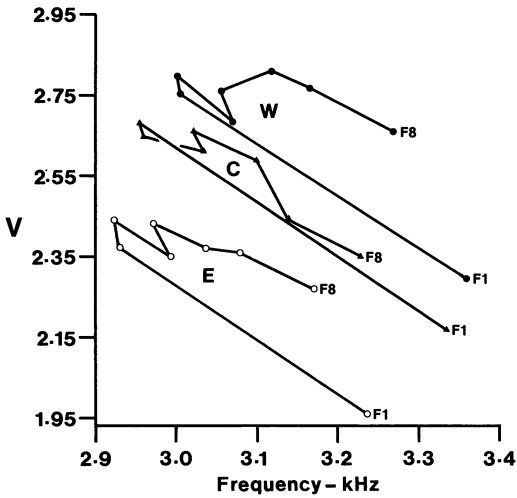
FIG. 8. Relationship of V to frequency for three geographic samples. Consecutive frequency variables connected for each sample.

TABLE 3. Descriptive statistics from analysis of angular variation (ANAVA).

Sample	n	Vector lengths	SD	Mean directions[a]	
				1	2
Western	26	0.978	0.393	0.867	0.453
Central	24	0.974	0.428	0.854	0.469
Eastern	30	0.955	0.576	0.807	0.512
Total	80	0.968	0.482	0.840	0.480

[a] Dimension coordinates.

tive differences among species are biologically significant is difficult to assess because of differences in procedures and measurement errors. This is particularly true of frequency measures for which procedural differences often contribute to overestimates of V. Many frequency estimates have been made from wide-band sonagrams or on poorly defined midpoints

or peaks of calls that were smeared in the frequency plane (e.g., broadband calls; calls with rapid and pronounced frequency modulations). Because of this bias, the relatively higher variation in temporal attributes must be even greater than that shown in Figure 10. It seems unlikely that such a strong trend is due to differing selection pressures, for both frequency and temporal characteristics are often species-specific and important for species discrimination (Becker, 1982). It is more likely that the trend reflects general constraints on the mechanisms or control of voice production. The low estimate of V for T3 relative to T1 and T2 may be because it is a compound variable (Lande, 1977).

Estimates of variance components can provide insights into the hierarchical structure of local or geographic variation in bird sounds and can establish quantitative standards for comparative studies, so it is surprising that ANOVAs and related techniques have been used relatively little (Miller, 1982). Such approaches should be coupled with other analyses of variation; both are needed to adequately investigate the structure of behavioral variation.

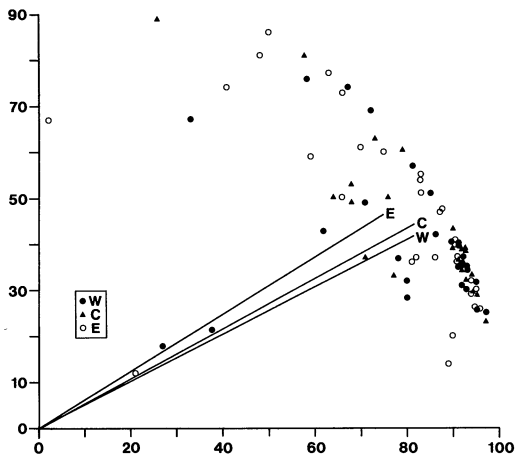*Ecogeographic variation.*—Least sandpiper calls did not vary geographically in any

FIG. 9. Subject weight space for 80 males (from ALSCAL) with geographic samples distinguished by different symbols. Mean vectors also shown for each location.

TABLE 4. Analysis of angular variation (ANAVA) table for vectors of individual males in subject weight space (grouped by geographic sample).

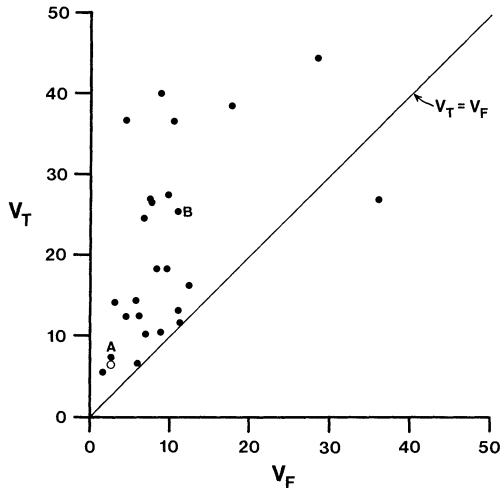| Source	Sum of squares	Degrees of freedom	Mean square	F
Among samples	0.052	2	0.026	0.787
Within samples	2.522	77	0.033	
Total	2.574	79		

FIG. 10. Bivariate plot of V for temporal and frequency variables (V_T and V_F, respectively) for different taxa of birds. Points marked "A" and "B" represent separate estimates for *Junco hyemalis* using data from Tables 1 and 2 of Konishi (1964). Hollow circle for least sandpiper. For other sources of data, see Appendix.

characters except frequency (which is inversely related to body size; Table 5) in: univariate or multivariate variability; variance components; similarities among males; or correlational relationships among call variables. This uniformity was unexpected in light of the species' extensive nesting range, philopatry, nest-site fidelity, fidelity to migration routes, and exposure to geographically diverse abiotic and biotic conditions—factors that should predispose the species to some adaptive or nonadaptive differentiation in call structure or variation. In the subarctic environment near Churchill, Manitoba, least

sandpipers nest at high density, have a brief nesting period, and are locally sympatric with several congeners plus other Scolopacidae (Jehl and Smith, 1970). On Sable Island, Nova Scotia, the species also nests at high density, but has a nesting period twice as long as at Churchill and is the only breeding calidridine (the spotted sandpiper [*Actitis macularia*], the only other scolopacid breeding there, nests in low numbers; Miller, 1983c). If call structure is adapted for distinctiveness in the presence of related species, then total character variance should be lower near Churchill and individual males should overlap more (i.e., be more similar) and/or should exhibit reduced character variance compared with Sable Island. None of these predictions was met. Similar examples could be developed by comparing other study locations.

Predictions about adaptation to geographically varying physical conditions or habitat features are less clear. However, habitat influences breeding densities and spacing, which in turn set distances over which vocal communication must occur. Sounds are degraded and suffer frequency-dependent attenuation with distance travelled, so their spectral properties, dominant frequency, and temporal organization should be adapted for passage over typical transmission distances (Wiley and Richards, 1982). Least sandpipers nest at high densities on the Queen Charlotte Islands, in northern Manitoba, and on Sable Island, and in much lower densities in northwestern British Columbia and central Yukon, but RRCs in these populations

TABLE 5. Geographic variation in culmen length of least sandpipers.[a]

Breeding locality	Culmen length (mm)		Source
	Male	Female	
Queen Charlotte Islands, British Columbia[b]	17.2 ± 0.08 (41)	18.7 ± 0.10 (39)	Miller, unpubl. data
Churchill, Manitoba	17.4 ± 0.11 (45)	18.9 ± 0.12 (43)	Jehl, 1970; Jehl and Smith, 1970
Sable Island, Nova Scotia	17.8 ± 0.09 (37)	19.5 ± 0.13 (33)	Miller, 1979c

[a] Measurements are listed as $\bar{Y}$ ± SE (n). All measurements refer to breeding birds.
[b] Measurements on museum specimens from California, British Columbia, and Alaska are: males, 17.0 ± 0.08 (43); females, 18.7 ± 0.12 (46) (Page, 1974). Sample presumably included many migrants.

do not differ in dominant frequency, or frequency profile (spectral properties were not studied in detail).

Bird vocalizations usually vary geographically (e.g., Goldstein, 1978; Mundinger, 1982; Kroodsma, 1981). Local learning of song attributes is a major reason for geographic variation in many bird species and the process often leads to geographic differences that are arbitrary or nonadaptive with respect to the physical environment, the general biological sound environments, or the presence of related species (see Baker and Cunningham [1985] and associated discussion papers). The absence of detectable geographic variation in least sandpiper calls is open to various interpretations, but it is reasonable to conclude that vocal learning is of minor significance throughout the species' range.

RRCs of least sandpipers are not under strong selective pressure to be distinct from related species. Indeed, RRCs may have become distinctive enough during speciation so that adaptive modification in the presence of related species always has been unnecessary. RRCs are widely distributed as a sound class and in many of their attributes throughout the Calidridini (Miller, 1983b), so their antiquity and phylogenetic conservatism may account for my observations on low variation at the species level. Comparative studies on other calidridines, especially across well differentiated subspecies or across closely related species, would shed light on this possibility.

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APPENDIX

Sources of Data for V Estimates Plotted in Figure 10

Most data points in Figure 10 represent mean values of V computed from estimates of SD, SE, or V listed in the following sources: Konishi, 1964 (tables 1, 2; four species; including two separate estimates for Junco hyemalis); King, 1972 (table 1); Miller and Gottlieb, 1976 (table 5); Goldstein, 1978 (table 1); Miller, 1978 (table 1); Payne, 1978 (table 1); Winkler and Short, 1978 (table 5; averages for 15 species of Picoides); Blacquiere, 1979 (table 3); Payne and Budde, 1979 (table 1); Johnson, 1980 (table 6); Cosens, 1981 (table 3); Nuechterlein, 1981 (table 4); Baptista et al., 1983 (table 1); Bowman, 1983 (table 31); Miller et al., 1983 (table 2); Thielcke, 1983 (table 3); Shy, 1984 (table 1); Conner, 1985 (table 1); Gaddis, 1985 (table 1); Pietz, 1985 (table 1); Zann, 1984 (table 1).