

GEOGRAPHIC VARIATION IN SEX RATIOS AND BODY SIZE IN WINTERING FLOCKS OF SAVANNAH SPARROWS (*PASSERCULUS SANDWICHENSIS*)

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ABSTRACT.—I examined geographic variation in the sex ratio of Savannah Sparrows (*Passerculus sandwichensis*) in wintering flocks from 22 different localities. The percentages of males in relatively large samples ($N > 20$) range from 45 to 70%; overall, 55% of wintering birds collected were male. There is no discernible geographic pattern to the interpopulational variation in sex ratio. I also examined patterns of size (PC1) and shape (PC2) variation among 542 wintering Savannah Sparrows. The largest Savannah Sparrows of both sexes tend to winter in the east and in the north; the east-west trend is more pronounced than the north-south one. In both sexes, individuals with relatively small bills and large wing bones tend to winter in the west. I suggest that the variability in bill size reflects geographic differences in the seeds available in winter, for it is only during that time that Savannah Sparrows are primarily granivorous. Variation in the relative size of the bones of the pectoral girdle may reflect variation in the distances migrated (which are probably longer on average in the west than in the east).

For this data set a principal component analysis done on the raw data, using the matrix of correlations among variables, provides a more satisfactory result than an analysis using log-transformed data and the variance-covariance matrix. Canonical correlations analysis provides a clearer description between the relationships among morphometric and environmental variables than does stepwise multiple regression analysis. The latter technique, because it uses partial correlations, sometimes identifies variables as being significant that have low univariate correlations. For Savannah Sparrows, wing length is not a good measure of body size. *Received 27 Jan. 1987, accepted 28 Dec. 1987.*

Most studies of geographic variation in the size of birds have dealt with comparisons among breeding populations of nonmigratory species. It is generally assumed that patterns of variation in size and shape reflect adaptations of the birds to geographic variation in environmental conditions (James 1970, Power 1970, Johnston and Selander 1971, Niles 1973, Mengel and Jackson 1977, Aldrich 1984, Zink 1986), perhaps augmented by direct environmental influences (James 1983). Often, for birds, the average body size is greatest where the ambient temperature is lowest—the pattern described as Bergmann's Rule. However, the percentage of migratory species that conform to Bergmann's Rule is not significantly different from those that do not (Zink and Remsen 1986). Evidence supporting Bergmann's Rule is often taken to reflect direct adaptations for temperature regulation (e.g., James 1970, Power 1970), but it may reflect

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adaptations to other environmental factors such as interspecific competition, prey availability, predatory pressures (Ray 1960, McNab 1971, Case 1978), the conditions under which the young were raised (James 1983), or various combinations of these.

It is easier to correlate body size with environmental factors in non-migratory species than in migratory ones, not only because the annual range of environmental conditions to which resident individuals are exposed can be determined, but also because the relative conditions among sites are generally similar from season to season: a site that is cold relative to others in summer is probably cold relative to others in winter as well. Consequently, most ornithologists have studied geographic variation in species that either are resident or that migrate little. There are, nonetheless, a few studies of size variation among wintering populations of birds. Ketterson and Nolan (1976) and Nolan and Ketterson (1983), for example, found no within-sex latitudinal variation in wing length in Dark-eyed Juncos (*Junco hyemalis*). They (1983) did find latitudinal variation in the body mass of juncos, with heavier birds tending to winter farther north; visible fat stores were also greater in birds wintering at higher latitudes, and they suggested that this, rather than variation in body size, probably explained the trend they found. James et al. (1984) found a clinal increase in median wing length (unflattened primary length; humerus length) among populations of male Red-winged Blackbirds (*Agelaius phoeniceus*) wintering in the southeastern U.S.

Here I report patterns of geographic variation among wintering populations of migratory Savannah Sparrows (*Passerculus sandwichensis*), and relate these to the variation in environmental conditions on the wintering grounds of the species. King et al. (1965) and Ketterson and Nolan (1979) reported that male western White-crowned Sparrows (*Zonotrichia leucophrys*) and eastern Dark-eyed Juncos tend to winter farther north than females. In both species males average larger in body size than females. On average, therefore, larger individuals of these species are wintering in the coldest parts of the wintering range. There is experimental evidence that migratory western male White-crowned Sparrows can fast longer than can females, presumably because of their greater mass (Ketterson and King 1977). This, however, apparently is not true for juncos and Tree Sparrows (*Spizella arborea*) (Stuebe and Ketterson 1982).

Ketterson and Nolan (1983) note that individuals wintering relatively farther north are closer to their breeding grounds than are others from the same populations that winter farther south, and therefore not only have a shorter distance to migrate, but also are perhaps better able to assess the conditions on their breeding grounds. This might permit more northerly wintering individuals to return and establish territories earlier

in spring than conspecifics wintering farther south. If so, it might select for males to winter as far north as possible, for in these species males compete for territories, and arrive on the breeding grounds well before females, probably as a consequence of this competition. They further suggest that individuals not constrained to winter in the north by other factors, such as the benefits of early return, may travel farther south to avoid higher densities in the north.

Savannah Sparrows breed across North America from Labrador to Alaska, and south to Massachusetts, central Ohio and Nebraska, in the Appalachians south to eastern Tennessee, and in the Cordilleras south into central Mexico and (formerly?) Guatemala (AOU Checklist 1983). With the exception of those birds that breed in southwestern saltmarshes, Savannah Sparrows are migratory. In winter, they are found east of the Appalachians, from Nova Scotia, and especially New Jersey south to Florida, and from Arkansas, Oklahoma and central New Mexico, central Arizona, and Oregon, south through most of Mexico. In winter, they are especially common from the coastal Carolinas south through Florida, west across southern Mississippi, and throughout Texas. They are moderately common, at least during some years, north to Oklahoma, and in southern New Mexico and Arizona, and very common in southern California and locally in the Mexican highlands. The approximate abundance and wintering range in the United States are shown in Fig. 1. I have samples from most regions in the United States where Savannah Sparrows are common in winter.

Using the data on wintering Savannah Sparrows, I address two questions: (1) do male Savannah Sparrows winter farther north than do females, and (2) do larger individuals (of either or both sexes) winter farther north than smaller ones. I also correlate interpopulational patterns of morphological variation with environmental variables in an effort to clarify the significance of morphological variability in the species.

An additional objective of this study is to use these data to assess empirically different methods of measuring "size" variation in a species. When many different variables are analyzed, as here, it is useful to create various combinations of these to simplify the perception of the patterns of interpopulational variation. Commonly, principal component analyses (PCA) are used to reduce the number of dimensions in multivariable studies. N components can be extracted from a matrix of N variables for each specimen; in morphometric studies of birds, most of the variance in the N variables usually can be explained in only two or three components (those with the largest eigenvalues). The PCA approach has advantages. It accounts for the covariation among the variables and reduces the number of "significant" dimensions. The components themselves,

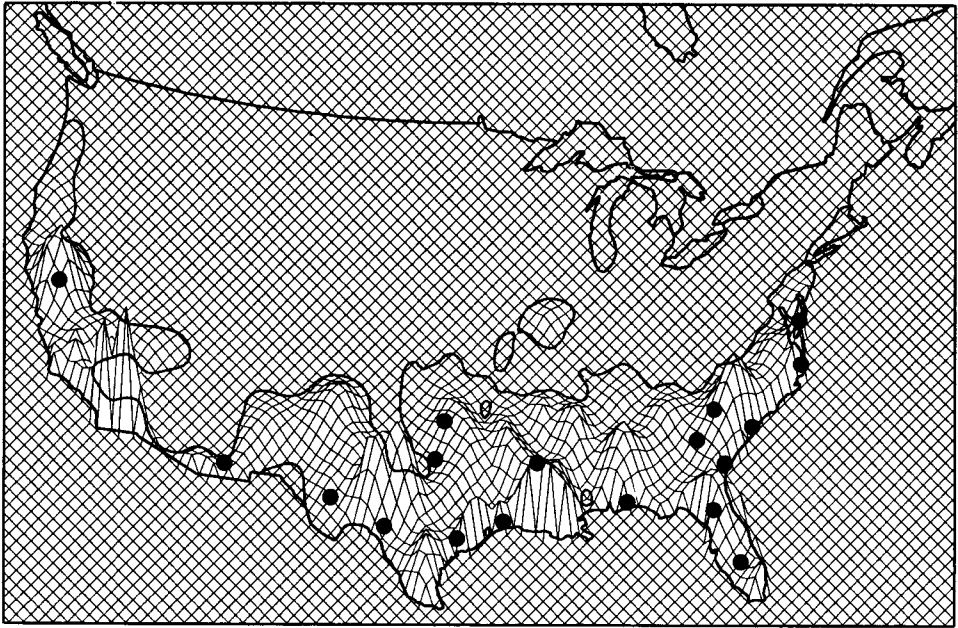


FIG. 1. Map of the abundance of Savanna Sparrows (*Passerculus sandwichensis*) based on Christmas Bird Count data. The height of the peaks indicate the relative abundance. The dots indicate sites from which I obtained wintering samples. However, the two sites from High Island, Texas, coastal South Carolina, North Carolina, and Delaware are indicated by only a single dot. Contour map courtesy of T. Root.

however, can be difficult to interpret. PC1, in such studies, contains a great deal of information about overall size (large animals have large parts), but also contains information about shape (Gibson et al. 1984, Somers 1986). Mosimann and James (1979) recommend log transformation of data in morphometric studies, and the use of the geometric mean of the log transformed data as a measure of overall size, and of various ratios as measures of shape (e.g., bill length divided by bill depth). However, as Bryant (1986) notes, the use of a log transformation equilibrates variances within suites of highly correlated characters, but not among suites of such characters. If a data matrix contains two or more such suites of characters, log transformations may change the multivariate structure in the data matrix. Thus, Bryant recommends no single transformation of data when intercorrelations among the traits are likely to differ. McGillivray and Johnston (1987) use the sum of the unstandardized measures of an individual as a measure of body size. This approximates PC1 scores derived from a matrix of correlations among raw measures, but gives greater weight to measures which relatively high variances.

Here, I present results from two PCA analyses, one using untransformed data, and the other using log transformed data. Traditionally, wing length (approximately the length of the longest primary wing feather) has been used as an approximate measure of body size. This is, in part, because it is easy to measure on museum study skins as well as on living birds—indeed, it is virtually the only measure of “size” that one can make on such material. Also, as Mosimann and James (1979:455) note, “wing length is easy to visualize.” Inasmuch as both skins and skeletons are available for most of the birds I examined here, I assess the value of wing length as a measure of body size in Savannah Sparrows. The wing feathers of these wintering sparrows show little sign of wear.

MATERIALS AND METHODS

I obtained samples of migratory Savannah Sparrows from wintering flocks from several different localities (Table 1). Although some of these specimens were shot, the majority were caught in mist nets. None was captured at feeding stations or at otherwise baited localities. I think this procedure introduced minimal bias in the sex ratios in the samples. Each specimen was sexed, when possible. Of 568 sparrows collected for this research, only 26 could not be sexed; thus, bias due to any differences in the difficulty of determining the sexes could have only a slight effect on the results. (The unsexed birds were not used in any of these analyses, and are not included in the numbers in Table 1.) All birds were collected from mid-December through mid-February, except for 32 specimens from Dewey Beach, Delaware that were collected in early April. The April birds from Dewey Beach are probably birds that wintered there; at least, in sex ratio and size they are like Savannah Sparrows collected there in February. Collections were made from 1971 through 1979, but mostly between 1975 and 1979 (Table 1).

Each specimen was preserved as a skin and skeleton, and is in the Royal Ontario Museum, with the exception of those from Isabel Valley, California, which are in the Delaware Museum of Natural History. I measured 24 variables (Table 2) on the skeleton of each bird, and wing length (longest primary on the unflattened wing) on the skin. The size of broken or missing bones was estimated by multiple regression (BMD, Dixon 1983); birds for which wing length could not be measured (including the entire sample from Isabel Valley, California) were not used in analyses involving wing length. To summarize size variation, I used two different PCA models (using NTSYS/FACTOR, Version IV, Rohlf et al. 1982). First I calculated the first three components from a matrix of correlations among the unstandardized 24 skeletal measures. PCAs using raw data and correlation matrices have been widely used in morphometric studies (Schnell 1970, Johnston et al. 1972, Leisler and Winkler 1985). Second, I calculated the first three components from a covariance matrix among the log-transformed skeletal measures. Such an approach, which is particularly appropriate for species showing indeterminate growth, or when growth is specifically being studied, has been used widely (Fleischer and Johnston 1982, Zink 1986). Birds from all samples listed in Table 1 were used in the PCA. Additionally three specimens from Padre Island, Texas, and one from San Francisco, California, were included, for a total of 542 (299 males and 243 females). Following Mosimann and James (1979), I calculated bill length/bill depth for each specimen as a direct measure of bill shape, and in some analyses I used tibiotarsus and humerus lengths as direct measures of leg and wing lengths. Individuals from all samples were pooled, but the sexes were analyzed separately.

TABLE 1
COLLECTING LOCALITIES, COLLECTION DATES, SAMPLE SIZES, AND
PERCENTAGES OF MALES IN WINTER SAMPLES OF SAVANNAH SPARROWS
(*PASSERCULUS SANDWICHENSIS*)

Locality	Latitude	Longitude	Date(s) collected	N	% Males
St. David, Cochise County, Arizona	32°30'	109°30'	30 Dec 1973	29	55
Isabel Valley, Santa Clara County, California	37°30'	122°15'	9 Nov 1974	19	(68) ^a
Dewey Beach, Sussex County, Delaware (winter)	38°45'	75°06'	21 Feb 1975	40	45
			16 Dec 1977		
			16 Feb 1978		
Dewey Beach, Sussex County, Delaware (April)	38°36'	75°06'	15-16 Apr 1974	32	47
			13 Apr 1976		
Fieldsboro, New Castle County, Delaware	39°24'	75°42'	15 Dec 1977	14	(43)
Gainesville, Alachua County, Florida	29°36'	82°18'	17 Feb 1975	23	48
Molino, Escambia County, Florida	30°42'	87°30'	19 Dec 1971	26	69
Basinger, Okeechobee County, Florida	27°18'	81°06'	18 Feb 1975	17	(24)
Waynesboro, Burke County, Georgia	33°00'	82°00'	15 Feb 1975	13	(31)
Jekyll Island, Glynn County, Georgia	31°06'	81°24'	20 Feb 1975	22	64
Mississippi State, Oktibbeha County, Mississippi	33°18'	89°00'	17 Feb 1979	35	63
Norman, Cleveland County, Oklahoma	35°06'	97°18'	28 Feb 1979	6	(83)
Nags Head, Dare County, North Carolina	36°00'	75°42'	15 Feb 1978	14	(64)
Harbinger, Currituck County, North Carolina	36°03'	75°48'	15 Feb 1978	23	58
Charleston, Charleston County, South Carolina	32°48'	79°54'	17 Dec 1977	26	50
Folly Beach, Charleston County, South Carolina	32°48'	79°54'	18 Dec 1977	12	(42)
Clemson, Pickens County, South Carolina	34°45'	82°45'	13 Feb 1978	28	61
High Island, Chambers County, Texas (coastal)	29°18'	94°00'	19 Feb 1979	15	(33)
High Island, Chambers County, Texas (inland)	29°18'	94°00'	20 Feb 1979	28	57
Goliad, Goliad County, Texas	29°00'	97°00'	21-22 Feb 1979	30	70
Ft. Davis, Jeff Davis County, Texas	31°00'	103°30'	26 Feb 1979	37	62
Graham, Young County, Texas	33°00'	97°30'	27 Feb 1979	12	(67)
Crystal City, Zavala County, Texas	29°30'	100°06'	25 Feb 1979	37	54
Overall				538	55

^a Percentages based on small samples (N < 20) in parentheses.

TABLE 2
 SPEARMAN CORRELATIONS BETWEEN PERCENT OF MALE SAVANNAH SPARROWS
 (*PASSERCULUS SANDWICHENSIS*) IN WINTER FLOCKS AND ENVIRONMENT

Environmental variable	Correlation	Significance (<i>P</i>)
Latitude	-0.27	0.18
Longitude	0.30	0.16
Coldest winter temperature	0.00	0.50
Average winter temperature	-0.13	0.34
Average annual snowfall	-0.09	0.38
Average annual precipitation	0.09	0.38
Sparrow abundance	0.04	0.45
Sparrow diversity	0.17	0.29

In an effort to identify the possible adaptive nature of size and shape variation among wintering Savannah Sparrows, I correlated patterns of morphometric variation with geographic patterns of environmental variation, using stepwise multiple regression (SPSSX/REGRESSION, SPSSX 1986), and canonical correlations analysis (SAS/CANCORR procedure; SAS 1982). In multiple regression, the probability required to include an independent variable was set at 0.05. The measures of size and shape used were: PC1 and PC2 scores (from untransformed data), and in multiple regression, bill shape (length/depth), tibiotarsus length (skeletal measure of leg length), and humerus length (skeletal measure of wing length). The "environmental" variables used were: (1) coldest extreme temperature, (2) average temperature in the coldest month, (3) average annual snowfall, (4) average annual precipitation, (5) latitude, (6) longitude, (7) abundance of wintering Emberizinae, and (8) diversity of wintering Emberizinae. The climatic data are from the U.S. Department of Commerce ("Local Climatological Data" from nearest reporting station of comparable elevation); the data on abundance and diversity of Emberizinae are from Bock and Lepthien's summary of Christmas Bird Count data (1976: Figure 3). Because the univariate measures of size contribute to the calculation of the PC scores, in canonical correlations analysis only PC1 and PC2 scores were used as dependent measures. Sexes were analyzed separately, and only data from localities where at least eight individuals were measured were used. There were 19 such localities for females, and 16 for males. Fewer than eight males were available from four sites where sufficient females were available, and sufficient females were not available from one locality where there were sufficient males. Thus 15 localities were used in analyses for both sexes, but the results are not directly comparable because somewhat different suites of localities were used for the male and female data.

Both canonical correlations analysis and multiple regression have been used to relate patterns of morphometric variation with patterns of climatic variation (O'Rourke et al. 1985, Zink 1986). Canonical correlations derive the linear functions of a vector of morphological variables with a vector of environmental variables that have maximal covariance. This may be preferable to multiple regression, which is more commonly used, because in multiple regression assumed independent (environmental) variables are entered into the equation on the basis of partial correlations, which can differ substantially in similar data sets (Pimentel 1979).

I used Spearman's rank correlations to quantify the univariate relationships among the

PC scores and the eight environmental variables. I also used Spearman's correlations between the percentages of males in the 13 samples in which the total sample size was greater than 20, and the latitude, longitude, and environmental variables listed above to describe those relationships.

RESULTS

Variation in sex ratios.—Overall, 55% of the Savannah Sparrows from wintering flocks that could be sexed are males, and although the percentage varies considerably among localities (from 45–70% in samples of more than 20 individuals; Table 1), there is no conspicuous geographic pattern. None of the Spearman correlations between the sex ratio and the environmental variables are even close to being significantly different (Table 2). In studies of breeding populations, males have been found to outnumber females. For example, Bédard and LaPointe (1984) found that, on average, about 60% (range 56–63%) of the birds in a breeding population at Isle Verte, Quebec, were males. It thus seems probable that males outnumber females in this species, but that there is no geographic pattern to the variation in the proportions of each sex in wintering flocks, at least within the latitudinal range covered by this study.

Principal component analyses.—Univariately, analysis of variance shows that there is significant interpopulational variation in all of the variables measured and for both sexes, with the exception of scapula length of females ($P = 0.08$). Five of the 24 components from the PCA, based on a matrix of correlations among 24 unstandardized variables among 299 males and four from the 243 females have eigenvalues of 1.0 or greater. However, PC3, PC4, and PC5 from the male data have eigenvalues of nearly equal size (1.3, 1.2, 1.0), and thus there is little discernible structure in these three dimensions. Similarly, PC3 and PC4 of females are of similar magnitude (1.5 and 1.2), and cannot be reliably interpreted (Cattell and Vogelman 1977, Gibson et al. 1984). Univariate correlations between the variables and PC1 are positive and large for both sexes (Table 3); thus, I interpret this component as being primarily a measure of overall size variation among individuals. PC2, for both sexes, contrasts bill size with wing size. An individual with a large value on this component has a relatively small bill and large flight apparatus (humerus, ulna, carpo-metacarpus, keel). Average PC1 and PC2 scores for 22 samples are given in Table 4.

From the PCA using the log transformed data and covariance matrix, PC1 explains 38.4% and PC2 12.7% of the total variance for the males, and PC1 explains 37.9% and PC2 13.5% of the total variance for the females. For both sexes, the loadings on PC1 are all of the same sign, indicating that it is a general measure of size. The scores of individuals on this axis approximate the geometric means of the 24 measures. In both

TABLE 3
CORRELATIONS BETWEEN VARIABLES AND PRINCIPAL COMPONENT SCORES FROM
A PCA OF THE CORRELATION MATRIX OF THE RAW MEASUREMENTS OF WINTERING
SAVANNAH SPARROWS (*PASSERCULUS SANDWICHENSIS*)^a

Variable	Males			Females		
	PC1	PC2	PC3	PC1	PC2	PC3
Skull length	0.78		0.31	0.73		
Skull width	0.74			0.68		
Premaxilla length	0.53	-0.40		0.49	-0.44	
Premaxilla depth	0.44	-0.39	-0.42	0.52	-0.31	
Narial width	0.54	-0.30	-0.45	0.57		-0.40
Premaxilla width	0.56	-0.44		0.64	-0.38	
Interorbital width	0.37		-0.37	0.41	-0.32	-0.33
Mandible length	0.71	-0.35	0.33	0.68	-0.37	
Gonys length	0.51	-0.49	0.34	0.48	-0.50	
Mandible depth	0.57	-0.49		0.55	-0.57	
Coracoid length	0.82	0.30		0.82	0.30	
Scapula length	0.76	0.33		0.71	0.38	
Femur length	0.81			0.79		0.31
Femur width	0.46			0.45		-0.30
Tibiotarsus length	0.84			0.79		0.42
Tarsometatarsus length	0.81			0.77		0.46
Humerus length	0.80	0.34		0.78	0.33	
Ulna length	0.78	0.45		0.80	0.33	
Carpometacarpus length	0.71	0.39		0.69	0.37	
Hallux length	0.72			0.65		0.34
Sternum length	0.75			0.74	0.34	
Sternum depth	0.65			0.66		-0.41
Keel length	0.70	0.33		0.65	0.47	-0.34
Synsacrum width	0.70			0.64		
Eigenvalue	11.2	2.3	1.3	10.6	2.5	1.5
% Variance explained	46.5	9.5	5.4	44.0	10.4	6.3

^a Correlations <0.30 are not included.

TABLE 4
 LOCALITY MEAN PRINCIPAL COMPONENT SCORES FROM A MATRIX OF
 CORRELATIONS AMONG RAW DATA FOR WINTERING
 SAVANNAH SPARROWS (*PASSERCULUS SANDWICHENSIS*)

Locality	Male		Female	
	PC1	PC2	PC1	PC2
Arizona, St. David	-0.47	0.19	-0.31	0.25
California, Isabel Valley	-0.38	0.06	(-0.07) ^a	(0.18)
Delaware, Dewey Beach	0.68	-0.08	0.61	-0.30
Delaware, Fieldsboro	(0.85)	(-0.12)	(0.17)	(-0.30)
Florida, Gainesville	0.15	-0.08	-0.30	-0.33
Florida, Molina	-0.11	-0.11	(-0.20)	(-0.22)
Florida, Basinger	[-0.57]	[-0.20]	-0.10	-0.25
Georgia, Waynesboro	[0.32]	[-0.34]	(0.11)	(-0.13)
Georgia, Jekyll Island	0.38	-0.07	(-0.09)	(-0.13)
Mississippi, Mississippi State	-0.18	0.02	-0.32	0.13
Oklahoma, Norman	(-0.13)	(0.14)	[-0.29]	[0.23]
North Carolina, Nags Head	(0.57)	(-0.13)	(0.07)	(-0.10)
North Carolina, Harbinger	0.05	-0.10	0.03	-0.12
South Carolina, Charleston	0.28	-0.09	0.27	0.02
South Carolina, Folly Beach	-0.16	0.00	0.23	-0.07
South Carolina, Clemson	0.27	-0.07	-0.05	-0.05
Texas, High Island (coastal)	(0.54)	(0.15)	0.12	0.35
Texas, High Island (inland)	0.12	-0.03	-0.22	0.10
Texas, Goliad	-0.64	0.13	(-0.06)	(0.03)
Texas, Ft. David	-0.50	0.22	-0.52	0.23
Texas, Graham	(-0.33)	(-0.07)	[-0.68]	[0.39]
Texas, Crystal City	-0.32	0.17	-0.33	0.21

^a Samples with N < 10 in parentheses; N < 5 in brackets.

sexes, PC2 is essentially a measure of interorbital width, the one variable not well "explained" by PC1 in any of the PC analyses (e.g., see Table 3). Although interorbital width has relatively low correlations with the other variables, the adaptive significance, if any, of variation in this feature is not apparent. In the log transformed data, PC3 contrasts bill size with pectoral element size, and is thus similar to PC2 in the raw data analysis. PC3 explains 9.8% and 11.3% of the variance among males and females, respectively.

The squared correlations among the first three components from each of the analyses (PCA/correlation matrix/raw data; PCA/covariance matrix/log transformed data), and wing length are in Table 5. The correlations between the respective PC1 scores are quite high for both sexes ($r = 0.92$ and 0.94). The correlations between the corresponding PC2 and PC3

TABLE 5
 RELATIONSHIPS (R^2) AMONG COVARIANCE AND CORRELATION
 COMPONENTS AND WING LENGTH IN WINTERING SAVANNAH SPARROWS
 (DATA FOR MALES ABOVE THE DIAGONAL, FOR FEMALES BELOW)^a

	Cov1 (38.4%)	Cov2 (12.7%)	Cov3 (9.8%)	Cor1 (46.5%)	Cor2 (9.5%)	Cor3 (5.4%)	Wing
Cov1 (37.9%)	—	0.00	0.00	0.88	0.07	0.01	0.01
Cov2 (13.5%)	0.00	—	0.00	0.03	0.00	0.23	0.03
Cov3 (11.3%)	0.00	0.00	—	0.06	0.77	0.07	0.03
Cor1 (44.0%)	0.85	0.10	0.07	—	0.00	0.00	0.06
Cor2 (10.4%)	0.09	0.21	0.58	0.00	—	0.00	0.07
Cor3 (6.3%)	0.04	0.07	0.06	0.00	0.00	—	0.03
Wing	0.04	0.04	0.07	0.10	0.08	0.01	—

^a N (males) = 299 (268 for comparisons with wing length); N (females) = 243 (220 for comparisons with wing length). Percentages of variance explained for females under variables in left-hand column, for males under variables across top.

values are quite low (range = 0.00–0.48). The correlations between PC2 (correlation matrix) and PC3 (covariance matrix), however, are high (0.88 and 0.76), indicating that they reflect similar shape variation. As previously stated, PC2 of the covariance/log matrix is a unique component summarizing variation in interorbital width. Some of this variation is incorporated into PC3 from the analysis of the correlations matrix of raw data, yet based on the percent of the total variation explained, PC3 is relatively unimportant (Table 3), and as mentioned above, cannot be reliably interpreted.

Wing length is essentially uncorrelated with any of the PC variables, but is significantly correlated with several of the original measures and mass (Table 6). Not surprisingly, the highest correlations with wing length are with various measures of the pectoral girdle, but even these correlations are not impressively high. In both sexes, wing length best predicts carpometacarpus length (the bone to which the primary wing feathers insert), but these correlations are only 0.47 and 0.45. At best wing length explains only about 20% of the variation in any bone measure, and, at least in Savannah Sparrows, wing length, though positively correlated with body size, is not a good measure of it, regardless of how estimated. Of the 139 studies of geographic variation in North American birds summarized by Zink and Remsen (1986), 80% used measures of study skins, and must have based assessment of body size on measures of wing length.

Because more of the total variance is explained by PC1 and PC2 from the correlation/raw data analyses than from the covariance/log analyses, I use PC scores based on the raw data in analyses of geographic variation

TABLE 6
CORRELATIONS BETWEEN WING LENGTH AND 25 OTHER
MEASUREMENTS IN WINTERING SAVANNAH SPARROWS^a

Variable	Females (N = 209)	Males (N = 251)
Skull length	0.20	0.22
Skull width	0.25	0.18
Premaxilla length	0.08	0.07
Premaxilla depth	0.06	0.02
Narial width	0.12	-0.06
Premaxilla width	0.13	-0.01
Interorbital width	0.10	-0.03
Mandible length	0.16	0.18
Gonys length	0.03	0.05
Mandible depth	-0.02	-0.08
Coracoid length	0.30	0.27
Scapula length	0.34	0.25
Femur length	0.15	0.22
Femur width	0.13	0.04
Tibiotarsus length	0.14	0.23
Tarsometatarsus length	0.18	0.21
Humerus length	0.31	0.20
Ulna length	0.40	0.26
Carpometacarpus length	0.47	0.45
Hallux length	0.08	0.19
Sternum length	0.40	0.24
Sternum depth	0.30	0.24
Keel length	0.41	0.22
Synsacrum width	0.15	0.27
Mass (gm) ^b	0.41	0.33

^a Correlations >0.11 are statistically significant ($P < 0.05$).

that follow. Also, as discussed above, the log/covariance analysis produced a PC2 that is essentially a measure of a single variable (interorbital width), whereas the interesting shape variation described by PC2 from the raw/correlation analysis is found in PC3 of the covariance matrix.

Relationship between size and environment. — For both sexes, there was one significant canonical axis. PC1, plus average winter temperature, snowfall, and precipitation are positively correlated with this axis for both sexes, although the standardized canonical coefficients between the axis and PC1 scores for males are not large (Table 7). In contrast, PC2 scores are highly negatively correlated with this axis. Thus, there is a weak tendency for relatively large birds to winter where it is relatively mild and mesic, and, because PC2 is negatively correlated with bill size and pos-

TABLE 7
STANDARDIZED CANONICAL COEFFICIENTS FROM CANONICAL CORRELATION
ANALYSIS OF WINTERING SAVANNAH SPARROWS (*PASSERCULUS SANDWICHENSIS*)

Characteristic	Females	Males
Average PC scores		
PC1 Score	0.51	0.29
PC2 Score	-0.73	-0.77
Climatic measures		
Latitude	0.34	0.29
Longitude	-0.39	-0.02
Coldest temperature	-0.49	-0.66
Average winter temperature	0.74	0.91
Average annual snowfall	0.30	0.23
Average annual precipitation	0.20	0.97
Sparrow abundance	-0.16	0.25
Sparrow diversity	-0.17	-0.04
Canonical correlation	0.94	0.95
Significance	$P = 0.001$	$P = 0.04$

itively correlated with pectoral size, sparrows with relatively large bills and small pectoral elements tend to winter where it is relatively mild and mesic.

Multiple regression shows similar relationships, although to a certain extent different variables are emphasized because partial correlations are used instead of covariances (Table 8). For females, PC1 is positively correlated with snowfall, and in males negatively correlated with longitude. This effectively describes an east to west pattern of size variation in both sexes, with the largest birds found in the east or northeast (where snowfall is greatest). In both sexes, PC2 is negatively correlated with precipitation (Fig. 2), which is correlated with many other variables, such as longitude and the species diversity of wintering sparrows (Table 9). Relatively long-legged sparrows of both sexes are found in the north, and also (in males) in the east. Although the relationship between tibiotarsus length of females and the abundance of other sparrow species is identified by multiple regression as being highly significant, the univariate correlations are so low that it is doubtful that this is biologically important (Tables 8 and 9). Humerus length of males is negatively correlated with longitude (Tables 8 and 9). Both average PC1 and average PC2 scores for both sexes are highly correlated with longitude and (in males) with average annual precipitation, which is highly correlated with longitude. Other than

TABLE 8
TEN MULTIPLE REGRESSIONS OF MEASURES OF MORPHOLOGY VS. ENVIRONMENT
FOR WINTERING SAVANNAH SPARROWS (*PASSERCULUS SANDWICHENSIS*)

Morphological variable	Environmental variable	Simple r	Cumulative r^2	F
Females (19 locs.)				
PC1	Average snowfall	0.56	0.31	7.7 ^a
PC2	Longitude	-0.72	0.52	18.4 ^c
	Sparrow diversity	0.58	0.66	15.8 ^c
Bill shape	Average temperature	0.61	0.38	10.3 ^b
	Longitude	0.49	0.53	9.2 ^b
Tibiotarsus length	Latitude	0.59	0.35	9.3 ^b
	Abundance	-0.07	0.54	9.2 ^b
Humerus length	None significant			
Males (16 locs.)				
PC1	Longitude	-0.79	0.63	23.5 ^c
PC2	Average precipitation	-0.80	0.64	24.4 ^c
	Latitude	-0.37	0.75	19.0 ^c
Bill shape	None significant			
Tibiotarsus length	Longitude	-0.69	0.48	13.0 ^b
	Latitude	0.53	0.66	12.4 ^c
Humerus length	Longitude	-0.83	0.69	31.8 ^c

^a $P < 0.05$.

^b $P < 0.01$.

^c $P < 0.001$.

precipitation, however, other direct measures of the climatic environment are not significantly correlated with the PC scores (Table 9).

Thus, the best environmental predictor of PC2 variation is average annual precipitation (Fig. 2), although the correlation for the female data is reduced by several outlying points that may represent sampling artifacts. The females from High Island (coastal), Texas and Fieldsboro, Delaware, have the largest residuals, and these averages are based only on 10 and 8 individuals, respectively. The male sample with the largest residual is from Graham, Texas, and likewise is based on a small sample ($N = 8$). In males, PC2 scores also decrease latitudinally (Table 8), but univariately this relationship is not statistically significant (Table 9). "Bill shape" (length/width) is not correlated either with PC2 or precipitation, but in females is significantly correlated with temperature and snowfall (Table 9). Thus, sparrows with relatively small bills are found where it is relatively dry. Female Savannah Sparrows with relatively long, narrow bills ("bill shape") are found where it is relatively warm, and in the west (Tables 8 and 9).

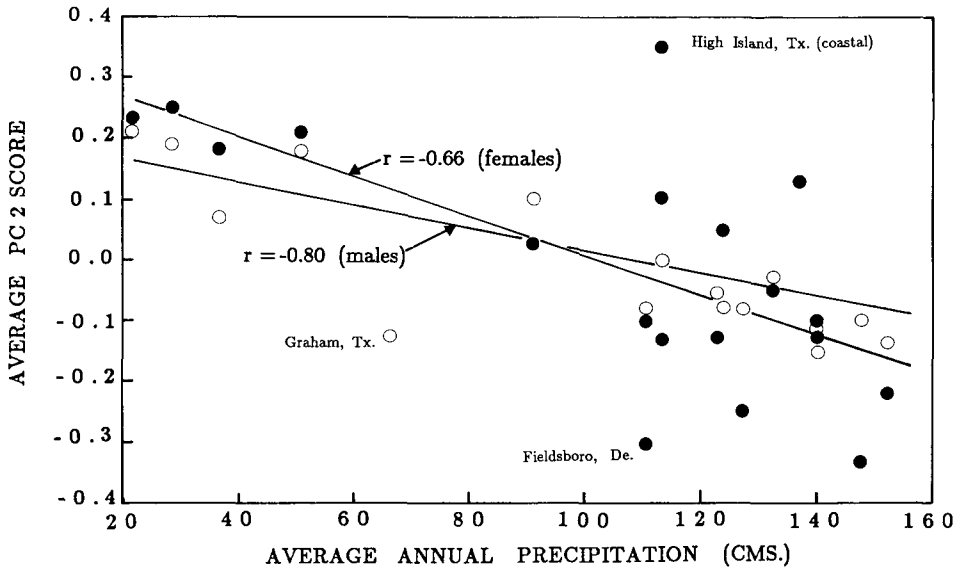


FIG. 2. Bivariate plot of PC2 scores and average annual precipitation. Birds with relatively large PC2 scores have relatively small bills and relatively large pectoral skeletal elements.

DISCUSSION

In contrast with studies of two other species of Emberizinae, eastern Dark-eyed Juncos and western White-crowned Sparrows, I find no evidence that male Savannah Sparrows tend to winter farther north than do females. The reason for this difference is not obvious. I have no data on sex ratios in populations of Savannah Sparrows that winter in Mexico (they winter commonly in the northern and central highlands), and thus it is possible that there is a latitudinal trend that I cannot detect. This seems unlikely, however, for two reasons: (1) the overall ratio of approximately 55 males to 45 females that I find is a reasonable reflection of the overall sex ratio in the species, and (2) I find no trend in the birds wintering north of Mexico. Unlike the White-crowned Sparrow and Dark-eyed Junco, which winter in weedy woodland edge and rank oldfields, Savannah Sparrows winter in open fields and would probably be more severely threatened by heavy snowfall. Savannah Sparrows, in fact, winter south of regions where there is persistent snow and, in general, farther south than White-crowned Sparrows and especially juncos. Thus, in the

TABLE 9

SPEARMAN RANK CORRELATIONS AMONG VARIABLES USED IN CANONICAL CORRELATION AND MULTIPLE REGRESSION ANALYSES
(CORRELATIONS AMONG 16 MALE SAMPLES ARE ABOVE THE DIAGONAL AND THOSE AMONG 19 FEMALE SAMPLES ARE BELOW)

Variable	Latitude	Longitude	Coldest	Average Temperature	Snowfall
Latitude	—	-0.35	-0.53 ^a	-0.56 ^a	0.49 ^a
Longitude	-0.43 ^a	—	0.02	0.04	-0.32
Coldest temperatures	-0.69 ^c	0.22	—	0.88 ^c	0.60 ^b
Average wint. temperatures	-0.70 ^c	0.17	0.90 ^c	—	-0.64 ^b
Average snowfall	0.64 ^c	-0.42 ^a	-0.64 ^b	-0.69 ^c	—
Average an. precipitation	0.00	-0.52 ^a	0.24	0.24	-0.13
Spar. abundance	0.51 ^a	0.33	-0.58 ^b	-0.67 ^c	0.49 ^a
Spar. diversity	-0.47 ^a	0.50 ^a	0.17	0.21	0.06
PC1	0.46 ^a	-0.67 ^c	-0.29	-0.18	0.27
PC2	-0.14	0.69 ^c	-0.01	-0.07	-0.02
Bill shape	-0.49 ^a	0.56 ^b	0.49 ^a	0.55 ^b	-0.65 ^c
Tibiotarsus length	0.61 ^b	-0.63 ^b	-0.46 ^a	-0.34	0.38
Humerus length	0.00	-0.14	-0.08	0.02	-0.10

^a $P < 0.05$.

^b $P < 0.01$.

^c $P < 0.001$.

U.S., the winter range of the Savannah Sparrow is more latitudinally compressed, and the average distances traveled in migration are greater than those of the other species of sparrows that have been studied. Possibly, within the region where Savannah Sparrows usually winter there is little size-differential mortality. As well, inasmuch as my data were gathered from several different winters, it is possible that in any given year there is a geographic pattern that is obscured by pooling information from several years.

The interpretation of patterns of size variation among wintering Savannah Sparrows is complicated because there is a high degree of intercorrelation among the various measures of environmental variation used. For example, the diversity and abundance of sparrows is highest in the southwest; snowfall is greatest in Delaware; precipitation shows an east to west pattern; and average winter temperature is highest in Florida. Thus east-west or north-south clines will be "explained" by several different measures of environmental variation that may or may not be of any significance to the birds. Nonetheless, some of the relationships are suggestive.

In both sexes, birds with relatively small bills and large pectoral skeletal

TABLE 9
CONTINUED

Precipitation	Abundance	Diversity	PCI	PC2	Shape	Tibiotarsus	Humerus
0.08	0.33	-0.62 ^b	0.35	-0.37	-0.04	0.43 ^a	0.28
-0.72 ^c	0.53 ^a	0.48 ^a	-0.84 ^c	0.70 ^c	0.38	-0.82 ^c	-0.88 ^c
0.25	-0.51 ^a	0.17	-0.08	0.04	0.13	-0.15	-0.15
0.20	-0.58 ^b	0.22	-0.08	0.04	0.27	-0.06	-0.17
-0.14	0.34	0.08	0.35	-0.22	-0.22	0.27	0.38
—	-0.61 ^b	-0.53 ^a	0.57 ^a	-0.73 ^c	-0.11	0.52 ^a	0.52 ^a
-0.50 ^a	—	0.06	-0.40	0.43 ^a	0.07	-0.44 ^a	-0.33
-0.42 ^a	0.05	—	-0.42	0.52 ^a	-0.07	-0.47 ^a	-0.34
0.12	-0.30	-0.20	—	-0.62 ^b	-0.16	0.93 ^c	0.91 ^c
-0.57 ^b	0.46 ^a	0.63 ^b	-0.27	—	-0.02	0.56 ^a	-0.48 ^a
-0.07	-0.24	0.18	-0.29	0.06	—	-0.11	-0.48 ^a
0.13	-0.11	-0.32	0.78 ^c	-0.31	-0.34	—	0.86 ^c
0.00	-0.30	0.25	0.56 ^b	0.22	0.01	0.48 ^a	—

elements winter in the west, where there is little rainfall and where several other species of sparrows commonly winter. In summer, Savannah Sparrows predominantly eat insects, whereas in winter seeds comprise the bulk of their diets (pers. obs.). In Darwin's Finches (*Geospiza*) bill size influences the efficiency with which birds can handle and crack seeds. Birds with large bills can eat both small and large seeds, although they may handle the small seeds less efficiently than birds with smaller bills. *Geospiza* with relatively small bills eat seeds of less varied sizes than ones with relatively large bills, and this is true both among and within species (Grant 1986). This is probably true for seed-eating birds in general (Puliam 1985). The existence of an east-to-west cline in relative bill size of wintering Savannah Sparrows therefore indicates that there are differences in the foods available to them in different parts of their range, and specifically that large seeds are not so available in the west as in the east. This could be either because there is greater competition from other species in the southwest for relatively large seeds (the species diversity of wintering sparrows is high there), or because relatively few large seeds are produced there. If the variety of food produced is greater in mesic than in xeric habitats, there is support for either of these explanations in the data: PC2 scores correlate significantly with indices of sparrow abundance

and diversity, that is, bill sizes are relatively small where other species of sparrows commonly winter, as well as where it is dry.

All of the longitudinal trends in geographic variation among wintering populations that I have discussed reflect similar trends among breeding populations (Rising, unpubl. data) in general, eastern Savannah Sparrows: (1) are larger than western ones, (2) have relatively larger and stouter bills, and (3) smaller pectoral appendages. Thus, the trends among wintering populations of Savannah Sparrows are consistent with the hypothesis that the breeding birds simply move south in winter, and north again in the spring. Although it is reasonable to assume that western-breeding Savannah Sparrows winter in the west, and eastern-breeding birds winter in the east, there is little direct evidence of paths of migratory movement for the species. There are, for example, only nine records of Savannah Sparrows banded during the summer and subsequently recaptured in winter, or vice versa. Of these, four are of apparently resident individuals from coastal California. The others are: banded 10 August 1932 in northern Michigan, and recovered 24 January 1933 in Alabama; banded 28 August 1954 in central Vermont, and recovered in December 1954 on Long Island, New York; banded in central Wisconsin 16 August 1956, and recovered in southern Maine on 25 December 1956; banded 25 July 1968 on Kent Island, New Brunswick, and recovered in eastern New York in early December 1968; and banded 10 February 1970 in east-central Florida, and recovered in July 1970 in New Brunswick. These banding data point to a north-south pattern, as well as some movement of birds from the interior to winter on the east coast.

The well-marked "Ipswich" sparrows, Savannah Sparrows that breed on Sable Island, Nova Scotia, are known to winter along the Atlantic coast, where they are virtually never found away from the dune grass of outer beaches (Stobo and McLaren 1975, pers. obs.). Ipswich sparrows are substantially larger than other eastern Savannah Sparrows. Indeed, there are a few Ipswich sparrows in my sample from Dewey Beach, Delaware (winter), although the inclusion of these birds has not significantly affected the results presented here. Other maritime breeding sparrows are somewhat larger than more inland ones (Rising, unpubl. data); if they, like the Ipswich sparrows, tend to winter along the coast, this could at least partially explain the longitudinal trend in body size and perhaps the latitudinal one as well. In the data presented here, there is some indication that larger individuals tend to winter closer to the coast than do smaller ones at the same latitude (Table 4). The two samples from North Carolina are from localities that are close to each other, one (Nags Head) in coastal dune grass and the other (Harbinger) just inland, in oldfield habitat. Similarly, the two samples from High Island, Texas, are from a coastal and

nearby inland site. In both cases, the birds in the coastal sample average larger than those from the inland sample, although the samples are small. The males from Folly Beach (coastal) South Carolina are small relative to those from Charleston (dump) and Clemson, but there are only five males in the Folly Beach sample.

If the conical bills of sparrows have evolved for granivory, I propose that winter selection has dominated the evolution of the cline in bill size (PC2 and to a lesser degree bill shape). Variation in the relative size of the pectoral elements could reflect differences in migratory distances as it is likely that western birds fly, on average, farther than eastern ones if they tend to move due south in the winter (it is about 4500 km from central Alaska to southern Arizona, and 3500 km from Ungava or southern Keewatin to central Florida).

Although it made little difference whether I used log-transformed data and the covariance matrix or raw data and the correlation matrix, more of the variance was explained by the first few (2 or 3) principal components in the raw-correlation analysis than in the log-covariance analysis. As well, the first few components from the raw-correlation analysis could be more easily interpreted as meaningful measures of size and shape than those from the log-covariance analysis. In a study such as this, the features measured are important. Wing length, for example, does not accurately reflect size or shape as defined by single measures of bones or PC scores. Although wing length may be the best measure of "size" available in many cases, my analyses suggest that it is a poor measure of size, explaining at most 20% of the variation in a long bone measure.

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LITERATURE CITED

- ALDRICH, J. W. 1984. Ecogeographical variation in size and proportions of Song Sparrows (*Melospiza melodia*). Ornithol. Monogr. 35.
- AMERICAN ORNITHOLOGISTS' UNION. 1983. Check-list of North American birds. 6th edition, American Ornithologists' Union, Washington, D.C.

- BÉDARD, J. AND G. LAPOINTE. 1984. The Savannah Sparrow territorial system: can habitat features be related to breeding success? *Can. J. Zool.* 62:1819–1828.
- BOCK, C. E. AND L. W. LEPHIEN. 1976. A Christmas Count analysis of the Fringillidae. *Bird-Banding* 47:263–272.
- BRYANT, E. H. 1986. On use of logarithms to accommodate scale. *Syst. Zool.* 35:552–559.
- CASE, T. J. 1978. A general explanation for insular body size trends in terrestrial vertebrates. *Ecology* 59:1–18.
- CATTELL, R. B. AND S. VOGELMANN. 1977. A comprehensive trial of the scree and KG criteria for determining the number of factors. *J. Mult. Behav. Res.* 14:289–325.
- DIXON, W. J. (ED.) 1983. *BMDP Statistical Software*. Univ. California Press, Berkeley, California.
- FLEISCHER, R. C. AND R. F. JOHNSTON. 1982. Natural selection on body size and proportions in house sparrows. *Nature* 298:747–749.
- GIBSON, A. R., A. J. BAKER, AND A. MOEED. 1984. Morphometric variation in introduced populations of the Common Myna (*Acridotheres tristis*): an application of the jackknife to Principal Component Analysis. *Syst. Zool.* 33:408–421.
- GRANT, P. R. 1986. *Ecology and evolution of Darwin's Finches*. Princeton Univ. Press, Princeton, New Jersey.
- JAMES, F. C. 1970. Geographic variation in birds and its relationship to climate. *Ecology* 51:365–390.
- . 1983. Environmental component of morphological differentiation in birds. *Science* 221:184–186.
- , T. ENGSTROM, C. NESMITH, AND R. LAYBOURNE. 1984. Inferences about population movements of Red-winged Blackbirds from morphological data. *Am. Midl. Nat.* 111: 319–331.
- JOHNSTON, R. F., D. M. NILES, AND S. A. ROHWER. 1972. Hermon Bumpus and natural selection in the House Sparrow *Passer domesticus*. *Evolution* 26:20–31.
- AND R. K. SELANDER. 1971. Evolution in the House Sparrow. II. Adaptive differentiation in North American populations. *Evolution* 25:1–28.
- KETTERSON, E. D. AND J. R. KING. 1977. Metabolic and behavioral responses to fasting in the White-crowned Sparrow (*Zonotrichia leucophrys gambelii*). *Phys. Zool.* 50:115–129.
- AND V. NOLAN, JR. 1976. Geographic variation and its climatic correlates in the sex ratio of eastern-wintering Dark-eyed Juncos (*Junco hyemalis hyemalis*). *Ecology* 57:679–693.
- AND ———. 1979. Seasonal, annual, and geographic variation in sex ratio of wintering populations of Dark-eyed Juncos (*Junco hyemalis*). *Auk* 96:532–536.
- AND ———. 1983. The evolution of differential bird migration. Pp. 357–402 in *Current ornithology*. Vol. 1 (R. F. Johnston, ed.). Plenum Press, New York, New York.
- KING, J. R., D. S. FARNER, AND L. R. MEWALDT. 1965. Seasonal sex and age ratios in populations of the White-crowned Sparrow of the race *gambelii*. *Condor* 67:489–504.
- LEISLER, B. AND H. WINKLER. 1985. Ecomorphology. Pp. 155–186 in *Current ornithology*. Vol. 2 (R. F. Johnston, ed.). Plenum Press, New York, New York.
- MCGILLIVRAY, W. B. AND R. F. JOHNSTON. 1987. Differences in sexual size dimorphism and body proportions between adult and subadult House Sparrows in North America. *Auk* 104:681–687.
- McNAB, B. K. 1971. On the ecological significance of Bergmann's Rule. *Ecology* 52: 845–854.
- MENGEL, R. M. AND J. A. JACKSON. 1977. Geographic variation in the Red-cockaded Woodpecker. *Condor* 79:349–355.

- MOSIMANN, J. E. AND F. C. JAMES. 1979. New statistical methods for allometry with application to Florida Red-winged Blackbirds. *Evolution* 33:444-459.
- NILES, D. M. 1973. Adaptive variation in body size and skeletal proportions of Horned Larks of the southwestern United States. *Evolution* 27:405-426.
- NOLAN, V., JR. AND E. D. KETTERSON. 1983. An analysis of body mass, wing length, and visible fat deposits of Dark-eyed Juncos wintering at different latitudes. *Wilson Bull.* 95:603-620.
- O'ROURKE, D. H., B. K. SUAREZ, AND J. D. CROUSE. 1985. Genetic variation in North Amerindian populations: covariance with climate. *Am. J. Phys. Anthro.* 67:241-250.
- PIMENTEL, R. A. 1979. *Morphometrics*. Kendall/Hunt Publ., Dubuque, Iowa.
- POWER, D. M. 1970. Geographic variation of Red-winged Blackbirds in central North America. *Univ. Kansas Publs. Mus. Nat. Hist.*
- PULLIAM, H. R. 1985. Foraging efficiency, resource partitioning, and the coexistence of sparrow species. *Ecology* 66:1829-1836.
- RAY, C. 1960. The application of Bergmann's and Allen's rules to the poikilotherms. *J. Morphol.* 106:85-108.
- ROHLF, F. J., J. KISHPAUGH, AND D. KIRK. 1982. NT-SYS. Numerical taxonomy system of multivariate statistical programs. Tech. Rep. State Univ. New York at Stony Brook, Stony Brook, New York.
- SAS INSTITUTE INC. 1982. *SAS user's guide: statistics*. SAS Institute, Cary, North Carolina.
- SCHNELL, G. D. 1970. A phenetic study of the suborder Lari (Aves) I. methods and results of principal components analyses. *Syst. Zool.* 19:35-57.
- SOMERS, K. M. 1986. Multivariate allometry and removal of size with principal components analysis. *Syst. Zool.* 35:359-368.
- SPSSX. 1986. *SPSSX guide*, ed. 2. McGraw-Hill Book Co., New York, New York.
- STOBO, W. T. AND I. A. McLAREN. 1975. *The Ipswich Sparrow*. Nova Scotia Institute Sci., Halifax, Nova Scotia.
- STUEBE, M. M. AND E. D. KETTERSON. 1982. A study of fasting Tree Sparrows (*Spizella arborea*) and Dark-eyed Juncos (*Junco hyemalis*): ecological implications. *Auk* 99: 299-308.
- ZINK, R. M. 1986. Patterns and evolutionary significance of geographic variation in the *schistacea* group of the Fox Sparrow. *Ornithol. Monogr.* 40.
- AND J. V. REMSEN, JR. 1986. Evolutionary processes and patterns of geographic variation in birds. Pp. 1-69 in *Current Ornithology*. Vol. 4 (R. F. Johnston, ed.). Plenum Press, New York, New York.