I did principal components analyses on these, and then correlated the Environmental PC scores with the Phenotypic PC scores.

Lastly, to determined the association between the Environmental PC scores and the Phenotypic PC scores I used the average morphological data for males from the 42 samples for which I had good climatic data and the climatic data set (not including latitude, longitude, elevation, or the measures of species diversity). I used a redundancy analysis (SAS PROC CANCOR; SAS Institute 1985), which links the morphological data with the climatic data with a canonical correlation analysis. This can be done both ways (morphological data vs. climatic data, or climatic data vs. morphological data) with parallel principal components analyses between the two data sets where the correlation between them is maximized. Lastly, for a multivariate measure of the concordance between these two matrices, I used Procrustes Analysis (PROTEST; Jackson 1995; D. A. Jackson, pers. comm.); many more commonly used procedures for such comparisons are unsuitable because of non-linearity among locality and environmental data. I looked at the residuals from a Procrustian analysis of the two largest axes combined from both the morphological and climatic data principal components to identify from which localities the morphology was least well explained by the climatic variation.

RESULTS

The patterns of variation in the saltmarsh Savannah Sparrows from the coast of southern California and Baja California, and Sonora and Sinaloa are substantially different, and are discussed separately. I included the sample resident in the saltmarshes near Morro Bay, California, in both groups because they are phenetically intermediate (Fig. 2; see discussion below).

NON-SALTMARSH SAVANNAH SPARROWS

Univariate analyses of size

The ANOVA's (which are not presented here) showed significant geographic variation with regard to all 24 skeletal variables for both sexes. Appendices 1 and 2 list means, ranges, and standard deviations for the larger samples of males and females, respectively. The patterns of variation for the two sexes are similar, and a number of overlapping statistically homogeneous (snk) subsets were identified. I will only describe general trends.

Birds from Sable Island, Nova Scotia, and Umnak Island in the Aleutians are the largest (Figs. 1 and 4; Appendices 1 and 2). There is clinal variation along the Alaska Peninsula, with large birds, nearly as large on average as those on Umnak Island, at the tip (Cold Bay), intermediate birds at Port Heiden, about half-way eastward down the Peninsula, and small birds at Wasilla, Alaska (near Anchorage). Birds from Middleton Island, Alaska, in the north Pacific, are also large, nearly comparable in size to birds from Cold Bay. Savannah Sparrows from the coast of maritime Canada, including those from the Magdalen Islands, Quebec, in the Gulf of St. Lawrence, are larger than those from farther inland. "Ipswich" sparrows (*P. s. princeps*) from Sable Island, Nova Scotia, are especially large and are comparable in size (although slightly larger) with birds from the Aleutian Islands. At the other end of the spectrum, the smallest birds are from the interior of California (Owens Lake), Washington (Creston, Hoquiam), and from Nevada (Elko, Alamo), Utah (Elberta), Alberta (Milk River, Grande Prairie), Wyoming (Sheridan), the interior of Alaska (Koyuk, Wasilla, Fairbanks), and the Mackenzie River Valley, Northwest Territories (Norman Wells, Inuvik). It needs to be emphasized, however, that, with the exception of birds from Sable Island, Umnak

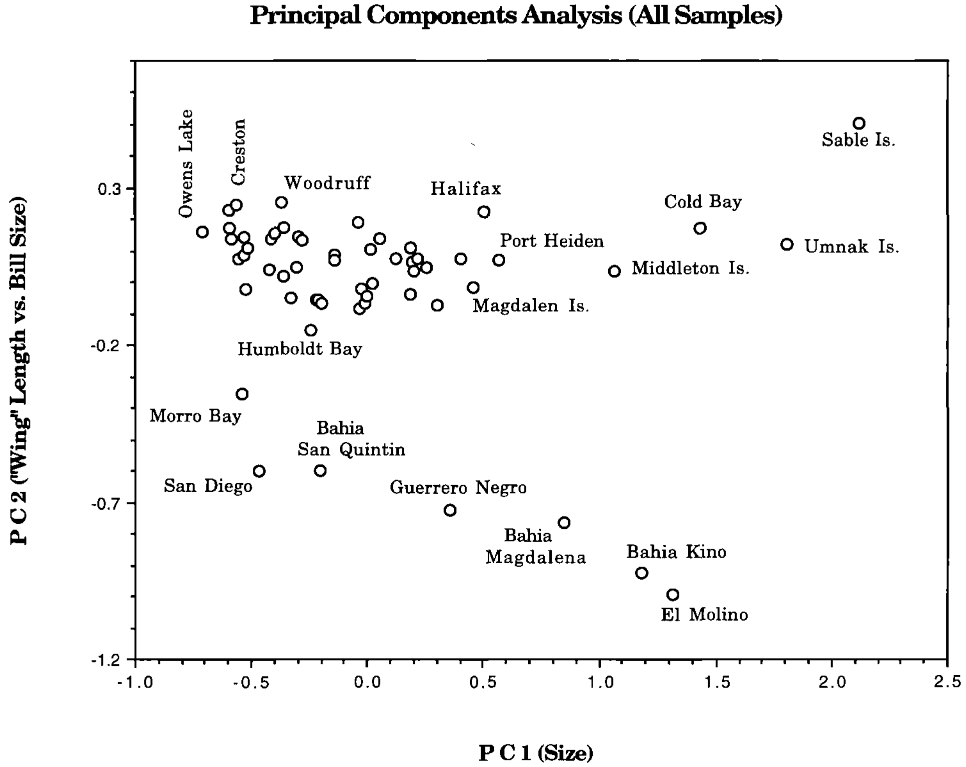

FIGURE 2. Sample averages of male Savannah Sparrows in the space defined by principal components 1 and 2 from a principal component analysis based on the correlations among 24 variables. PC 1 explains 52.4% of the total variance, and represents increasing overall size. PC 2 accounts for 12.9% of the total variance; increasing scores are associated with increasing wing size and decreasing bill size.

Island, and the Alaska Peninsula, the differences in size are small, and there is an enormous amount of overlap in all dimensions (see Appendices). For example, the tibiotarsus length (a good univariate measure of size; i.e., it is highly correlated with PC 1 [Table 2]) of males from Halifax, Nova Scotia (where they are relatively large), range from 29.4–30.6 mm (average = 30.0 mm), those from Woodruff, Utah, (where they are relatively small) range from 25.3–29.5 mm (average = 28.0 mm), and those from Churchill, Manitoba, (where they are intermediate in size) range from 27.2–29.6 mm (average = 28.5 mm); males from Sable Island range from 30.3–32.7 mm (average = 31.7 mm); those from Umnak Island, Aleutian Islands, range from 29.2–32.2 mm (average = 30.8 mm), and those from Wasilla, near Anchorage, Alaska, range from 26.9–29.3 mm (average = 28.2 mm; Appendix 1).

Bill size also varies geographically, with birds from both coastal and the interior of California, the Great Basin, the Great Plains, and north into the Northwest Territories having generally more gracile bills than birds from the northeast or central Mexico (Lerma). Again, however, the amount of interpopulational variation is slight. The ratio of premaxilla depth to premaxilla width ranges only between 0.55 and 0.61, with almost all 0.58–0.60 (see Appendices). Thus, although there is interpopulational variation in bill proportions, the variation is slight.

TABLE 2. CORRELATIONS BETWEEN VARIABLES AND PRINCIPAL COMPONENT SCORES FROM A PCA OF THE CORRELATION MATRIX OF THE RAW MEASUREMENTS OF 1459 MALE AND 822 FEMALE SUMMER-TAKEN SAVANNAH SPARROWS (*Passerculus sandwichensis*)[a]

	Males		Females	
Variable	PC 1	PC 2	PC 1	PC 2
Skull length	0.85	−0.37	0.83	−0.40
Skull width	0.81	—	0.79	—
Premaxilla length	0.66	−0.55	0.60	−0.66
Premaxilla depth	0.72	−0.37	0.66	−0.43
Narial width	0.64	—	0.67	—
Premaxilla width	0.74	−0.37	0.73	−0.40
Interorbital width	0.47	—	0.49	—
Mandible length	0.82	−0.40	0.79	−0.47
Gonys length	0.68	−0.49	0.61	−0.62
Mandible depth	0.72	−0.50	0.71	−0.54
Coracoid length	0.78	0.40	0.77	0.42
Scapula length	0.67	0.47	0.70	0.48
Femur length	0.85	—	0.88	—
Femur width	0.48	—	0.58	—
Tibiotarsus length	0.88	—	0.90	—
Tarsometatarsus length	0.86	—	0.85	—
Humerus length	0.78	0.36	0.79	0.38
Ulna length	0.75	0.47	0.77	0.47
Carpometacarpus length	0.74	0.41	0.78	0.42
Hallux length	0.68	—	0.71	—
Sternum length	0.69	0.47	0.73	0.44
Sternum depth	0.59	0.35	0.58	0.36
Keel length	0.57	0.55	0.59	0.54
Synsacrum width	0.77	—	0.78	—
Eigenvalue	12.6	3.1	12.7	3.6
% variance explained	52.4%	12.9%	52.9%	15.1%

[a] Correlations <0.30 are not included.

Principal components analysis

The correlations between all 24 skeletal measurements of male and female Savannah Sparrows and the first principal component (PC 1) are all relatively large and positive (Table 2), and therefore PC 1 can be taken to be a multivariate measure of overall size (Rising and Somers 1989). Thus, individuals with large PC 1 values are relatively large. The correlations between the measures of bill size (including skull length, which includes the entire premaxilla length) and PC 2 are negative and all greater than 0.36, whereas the correlations between the eight measures of wing and sternum length and PC 2 are all positive and 0.35 or larger. Thus, PC 2 is a measure of shape: individuals with large PC 2 values have relatively large pectoral bones (wings) and small bills, whereas individuals with small PC 2 values have relatively large bills and small wings (Table 2). The first two principal components, taken together, explain 65.3 % (males) and 68.0% (females) of the total variance in the correlation matrices (Table 2); all of the other principal components individually explain less than 7% of the total variance, and are not discussed here.

In two-dimensional, PC 1 vs. PC 2 space, the saltmarsh birds (Morro Bay, San Diego, Bahía San Quintin, Guerrero Negro, Bahía Magdalena, Bahía Kino, and El Molino) are separated on the PC 2 axis from the others because they have relatively large bills and short wings (Fig. 2). The birds from El Molino and

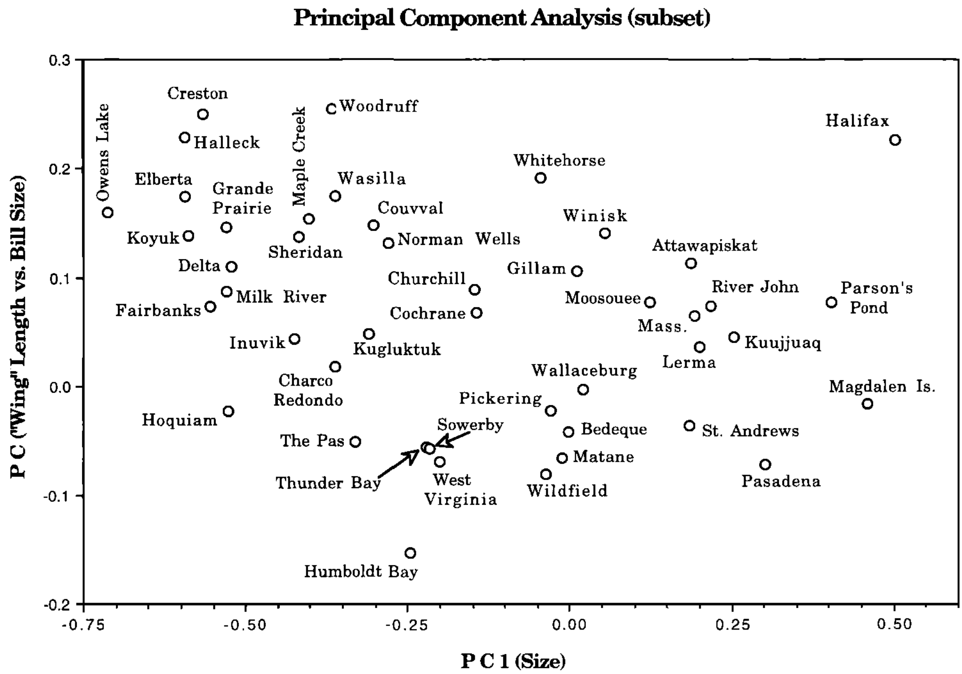

FIGURE 3. Male Savannah Sparrows in PC 1 vs. PC 2 space with the samples from Sable, Umnak, and Middleton islands, and Cold Bay and Port Heiden, Alaska, and the saltmarsh localities removed (see Fig. 2).

Bahía Kino are, in the broad sense, the "large-billed" Savannah Sparrows (the "*rostratus*" group; van Rossem 1947, Rising 1996); they are relatively large as well as large-billed.

The individuals on the islands (Sable Island, Umnak Island, and Middleton Island) as well as Cold Bay (at the tip of the Alaskan Peninsula) are larger than the other non-saltmarsh birds. There is a clear size cline from the Aleutian Islands eastward along the Alaskan Peninsula, with the largest individuals coming from the Aleutians (Umnak Island), then Cold Bay, then Port Heiden (about mid-Peninsula; Fig. 2).

To get a clearer picture of the variation among the remaining populations, I removed the seven saltmarsh samples, plus the samples from Sable, Umnak, and Middleton islands, Cold Bay, and Port Heiden (Fig. 3). For this, no new analyses were done. Rather the "outlier" populations were removed from the figure to give a clearer view of the arrangements of the remaining populations in the principal component ordination. This figure shows a basically east to west cline in body size, with the largest birds being from Halifax (on mainland Nova Scotia, about 300 km west of Sable Island), the Magdalen Islands in the Gulf of St. Lawrence, and Parson's Pond on the west coast of Newfoundland. Although the sparrows on the Aleutians, Middleton Island (in the north Pacific, southeast of Anchorage, Alaska), and the Alaskan Peninsula are large, those from the coastal mainland or inland Alaska are small (Wasilla, near Anchorage; Koyuk, on Norton Bay; Fairbanks).

On the PC 2 axis, Humboldt Bay (coastal northern California) is separate from

TABLE 3. STANDARDIZED CANONICAL DISCRIMINANT FUNCTION COEFFICIENTS FROM A DFA OF 12 MEASUREMENTS OF 1152 MALE SAVANNAH SPARROWS (*Passerculus sandwichensis*) FROM 47 LOCALITIES AND 501 FEMALES SAVANNAH SPARROWS FROM 27 LOCALITIES

	Males		Females	
Variable	DF 1	DF 2	DF 1	DF 2
Skull length	0.15	−0.17	0.13	−0.22
Skull width	0.33	−0.05	0.24	−0.16
Premaxilla length	0.00	0.23	0.10	0.40
Premaxilla width	0.26	0.18	0.31	0.13
Mandible length	0.23	−0.13	0.24	−0.07
Gonys length	0.17	0.26	0.13	−0.26
Coracoid length	0.01	0.34	−0.07	0.11
Femur length	0.12	0.05	0.18	0.09
Tibiotarsus length	0.34	−0.38	0.48	−0.33
Ulna length	−0.36	0.84	−0.34	1.00
Hallux length	0.27	−0.75	0.22	−0.44
Keel length	−0.02	0.12	−0.11	0.38
Eigenvalue	3.53	0.77	4.43	0.70
% variance explained	59.7%	13.0%	66.7%	10.5%
Canonical Correlation	0.88	0.66	0.90	0.64

the others (Fig. 3), intermediate on this axis between the saltmarsh birds and the others (Fig. 2). There is clinal variation, south to north, along the Pacific Coast, from San Diego, Morro Bay, and Humboldt Bay. Hoquiam, on the Washington coast, is widely separated from Humboldt Bay on the PC 2 axis (Fig. 3). The same applies to the two inland Mexican populations (Charco Redondo, Jalisco, and Lerma, México), but they differ only on the PC 1 (size) axis (Fig. 3).

Discriminant functions analysis

Non-saltmarsh males.—The discriminant functions (DF) analysis of the 1152 male Savannah Sparrows from the 47 large (N > 12) non-saltmarsh samples identified 10 significant functions. The first explains 59.7% of the total variance; the second an additional 13.0%; the third and forth 6.8% and 6.0%, respectively; and the remaining ones less than 4% (Table 3). I will discuss variation only in the first two DF dimensions. The ellipses in Figs. 4–10 are 95% confidence ellipses (i.e., 95% of the individuals in the sample are found within the ellipse). Figure 4 shows the positions of all 47 samples; the standardized discriminant function coefficients of the 12 variables used in these analyses are shown in Table 3. The DF 1 coefficients for premaxilla length, coracoid length, and keel length are very small and, with the exception of ulna length and keel length (both measures of the size of the pectoral girdle), all of these are positive. Thus samples to the right in Fig. 4 are made up of relatively large individuals with relatively short wings. The largest DF 2 coefficients are ulna length (0.84) and hallux length (−0.75); thus samples toward the top of the figures contain individuals with relatively long wing and short toes.

The large birds from Sable Island, Cold Bay, and Middleton Island are significantly different from the other samples on the DF 1 axis. There is a great deal of overlap among the other 43 samples. I replotted these 43, with the above four samples removed, to obtain a clearer picture of the relationships among them (Fig. 5). Again, this did not involve a new analysis; the samples were removed

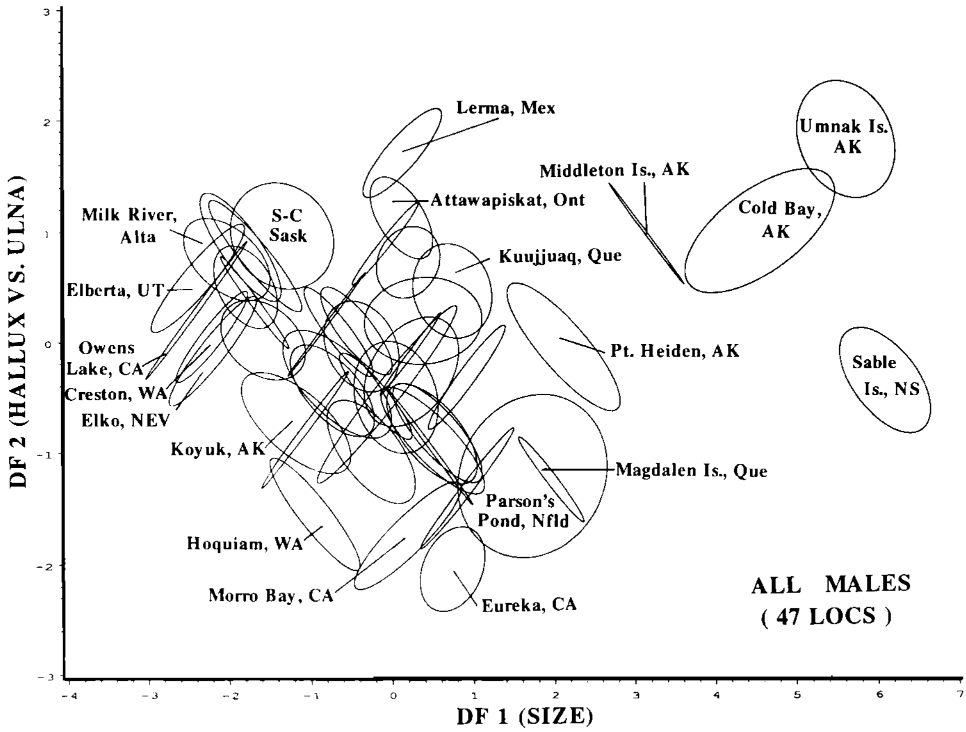

FIGURE 4. Samples of male Savannah Sparrows in the space defined by Discriminant Function (DF) 1 and DF 2; 95% confidence ellipses are shown. DF 1 explains 59.7% of the total variance and can be interpreted as summarizing size variation, with larger birds to the right; DF2 explains an additional 13.0% of the variance and contrasts hallux length with ulna length, with birds toward the top having relatively long ulnas (wings) and short halluxes.

only to better illustrate the relationships among the remaining 43 samples. Samples from Port Heiden, Alaska, the eastern maritime provinces, northern Quebec (Kuujjuaq = Ft. Chimo), northern Ontario (Attawapiskat, Moosonee), coastal California (Morro Bay, Eureka), West Virginia, and central Mexico (Lerma) are to the right in this figure, whereas the relatively small birds from the prairies and intermontane west are to the left. Birds from the north and prairies have relatively long wing and short toes, whereas those from coastal Washington and California, and Newfoundland, the Magdalen Islands, and West Virginia have relatively short wings and long toes. These trends are more clearly illustrated in plots of just the 22 eastern samples (Fig. 6) and 19 western samples (Fig. 7).

Non-saltmarsh females.—The DF results for 501 females from 27 samples are similar, with the birds from Sable and Umnak islands significantly different and substantially larger than those from the other sites. The relationships among samples, with Sable and Umnak islands removed, are shown in Fig. 8; Middleton Island is significantly larger than the other samples, and Magdalen Islands are somewhat (and significantly) larger than mainland maritime and Labrador samples (Halifax and Pictou, Nova Scotia, St. Andrews, New Brunswick, and Matane and Kuujjuaq, Quebec; Fig. 9). Among the western females, the smallest birds come

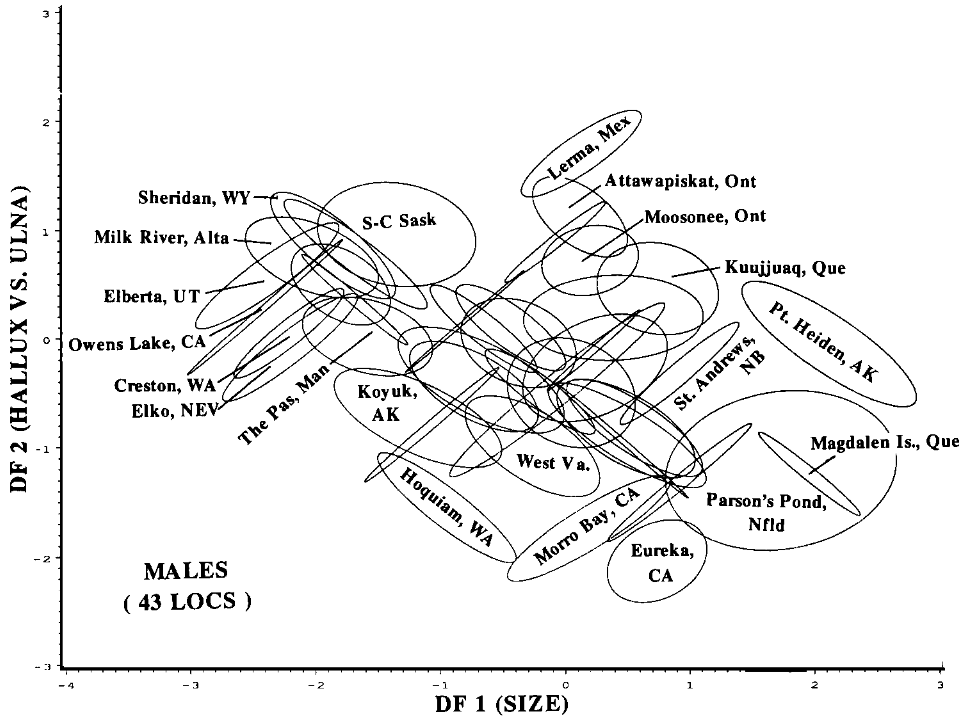

FIGURE 5. Samples of male Savannah Sparrows in the DF 1 vs. DF 2 space, with samples of larger birds removed to improve the resolution of the remaining ones (see Fig. 4).

from the arid west and Great Plains (Sheridan, Wyoming, Creston, Washington, Grande Prairie, Alberta, and Owen's Lake, California; Fig. 10).

Correlations between environmental variables and size

Spearman's correlations between principal component (PC) and discriminant function (DF) scores and a variety of environmental measures from the 45 largest ($N > 10$) male and 27 female samples from non-saltmarsh localities are given in Table 4 (only localities for which reliable environmental data were available were used in these analyses [Table 1]). Because the Savannah Sparrows from Sable Island, Nova Scotia, and Umnak Island, Middleton Island, Cold Bay, and Port Heiden, Alaska, are substantially larger than others, they are outliers in these correlation analyses. Thus, I also calculated the Spearman's correlations between male size and environmental variables, with these localities omitted, reducing the number samples of males to 40, and the number of samples of females to 25 (Table 5). Samples of females from Cold Bay, Port Heiden, and Middleton Island are small, and they are not included in either set of correlation analyses.

For both sexes, there is a significant correlation between PC 1 score (size) and both average annual precipitation and average June precipitation; that is, Savannah Sparrows tend to be large where the precipitation is high. This is true not only for all samples (Table 4), but also when the samples of especially large sparrows are omitted (Table 5). There is also a significant negative correlation between PC 1 scores and the average minimum summer temperature, average maximum sum-

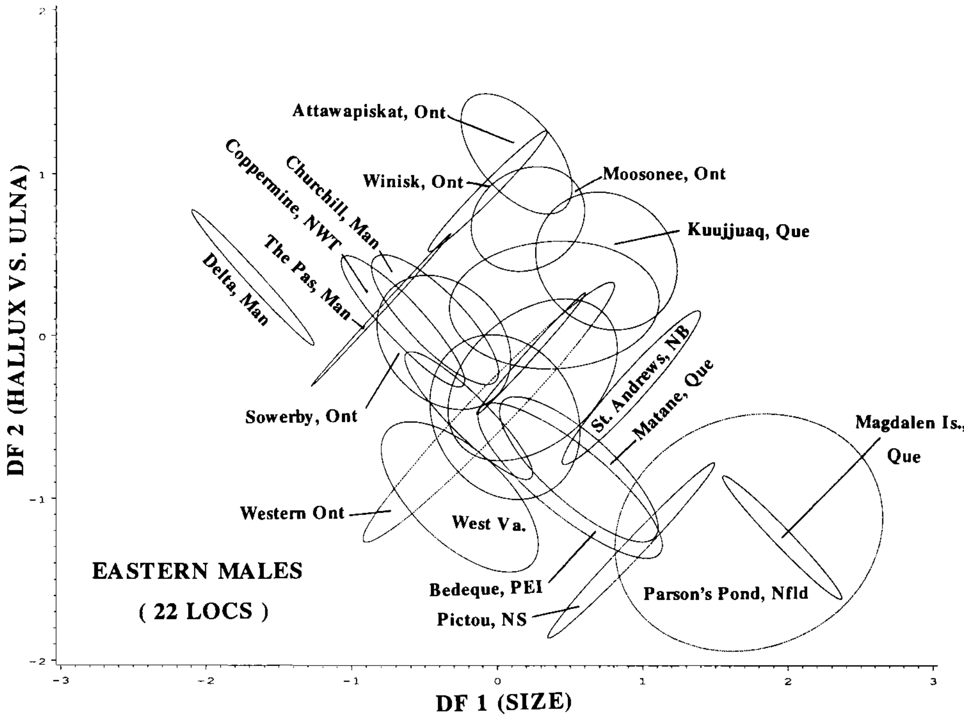

FIGURE 6. Samples of eastern male Savannah Sparrows in the DF 1 vs. DF 2 space (see Fig. 4).

mer temperature, and maximum summer temperature for males; for females, correlation values are similar, but only the last is significant (Table 4), and for both sexes these correlations similar when all of the sparrow samples are considered as well as when the largest ones are omitted (Table 5). Also, there is a significantly negative correlation between both longitude and elevation and PC (Tables 4 and 5). Thus, Savannah Sparrows are smallest in the west and at high elevations. Lastly, there is a significantly negative correlation between body size and Cook's Index, illustrating that Savannah Sparrows tend to be relatively large where they co-occur with few potential competing species.

The second principal component (PC 2) scores are negatively correlated with measures of bill size, and positively correlated with measures of pectoral girdle size (Table 2); thus, individuals with large PC 2 scores have relatively small bills and long wings. PC 2 scores are significantly negatively correlated with both average annual precipitation and average June precipitation in both sexes (Table 4). With the samples of the largest sparrows removed from the analyses, the size of the correlation between PC 2 and average annual precipitation is larger, and the same is true for females (Table 5). As well, there is a positive correlation between PC 2 score and both longitude and elevation; the correlation between elevation and PC 2 score in males is significant, and in both sexes with the largest sparrows omitted (Tables 4 and 5). Thus Savannah Sparrows from the west and high elevations have relatively small bills and long wings.

Some of these relationships in bivariate space are illustrated in Figs. 11–20. The correlation coefficients used in these figures are Pearson's correlations (cf. Tables

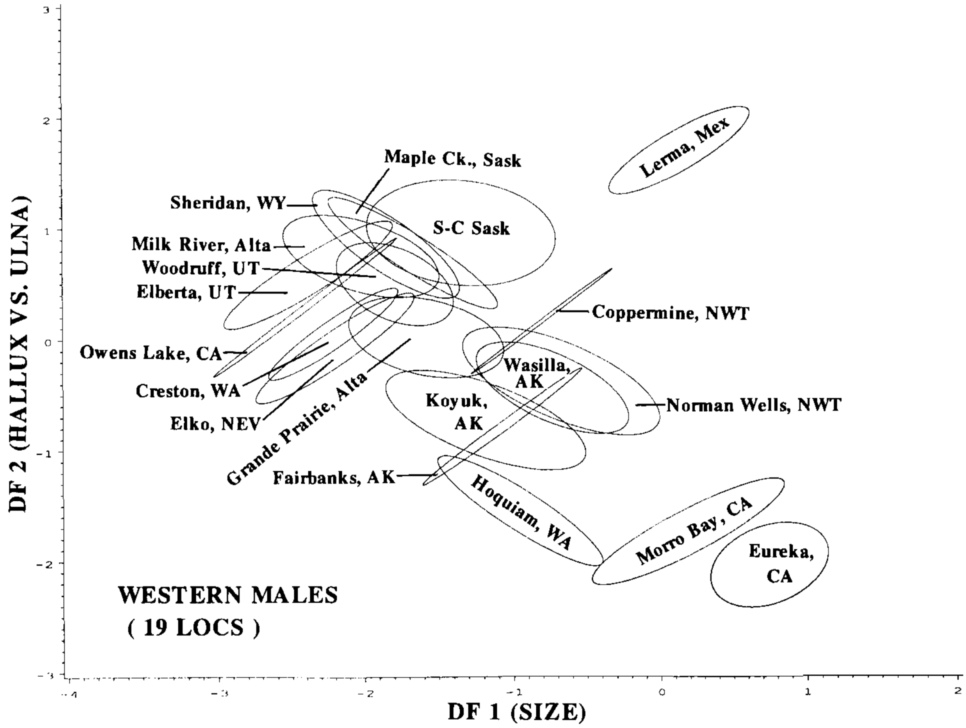

FIGURE 7. Samples of western male Savannah Sparrows in the DF 1 vs. DF 2 space (see Fig. 4).

4 and 5). There is a negative correlation between DF 1 scores (body size) of males and the maximum temperature (Fig. 11); with the three populations with the largest body size, Sable and Umnak islands and Cold Bay, removed this correlation drops from −0.69 to −0.60 (Fig. 12), but it is still statistically significant; thus, they are smallest where ambient temperatures may be high. There is a positive correlation between DF 1 scores of males and the average annual precipitation (Fig. 13). With Sable and Umnak islands and Cold Bay removed, the correlation increases from 0.56 to 0.64 (Fig. 14); both correlations are statistically significant. Females are largest (PC 1 scores) where the maximum recorded temperature is relatively low (Fig. 15); with the largest birds, those from Umnak and Sable islands, removed (Fig. 16) the correlation decreases from −0.58 to −0.46, showing that the inclusion of those samples substantially affects the apparent relationship. Females are also relatively large where the annual precipitation is high (Fig. 17), and in the east (Fig. 18). They have relatively small bills and large wing bones (PC 2) where the precipitation is low (Fig. 19). Lastly, males are relatively large (DF 1 scores) where species diversity (Cook's Index) is low (Fig. 20).

The principal components analysis of the environmental variables produced two principal components with nearly equal and large eigenvalues, which combined explained 74% (males) to 77% (females) of the variation among localities (Table 6). Environmental principal component 1 (EPC 1) is positively correlated with all of the temperature variables and rather weakly correlated with the precipitation variables; thus, localities with high values for EPC 1 tended to be warm, and

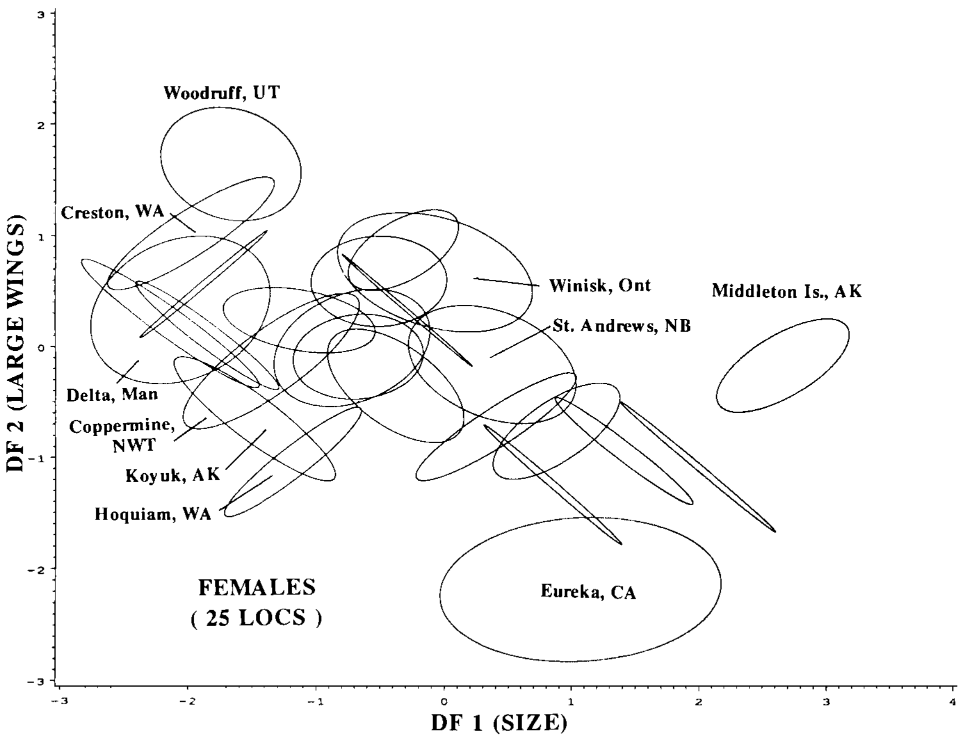

FIGURE 8. Samples of female Savannah Sparrows in the DF 1 vs. DF 2 space. Individuals to the right of the plot are relatively large; those toward the top have relatively large wings.

perhaps moister than average. EPC 2 is positively correlated with the precipitation variables and the extreme low summer temperature; thus, localities with high values for EPC 2 are moist and tend not to have extremely high summer temperatures (Table 7). Phenotypic principal component 1 (PPC 1) scores (large values for large birds) are negatively correlated the EPC 1 (that is, large birds are found where it is cool; Table 7) and positively correlated with EPC 2 (that is, large birds are found where it is moist and extreme summer high temperatures are low; Table 4). These correlations were calculated only for 45 male and 27 female samples. The correlations between PPC 2 and EPC 1 are not significant, and those between PPC 2 and EPC 2 are negative (birds in relative mesic areas have large bills and relatively small wings; Table 4).

Thus, Savannah Sparrows are smallest in the west and at high elevations. Latitudinal trends are slight and not significant, and this is so even when only the 27 eastern samples are examined (r = 0.01, ns; Sable Island not included), or the 23 western are examined (r = 0.06, ns; Umnak Island, Cold Bay, Port Heiden, and Middleton Island not included). Lastly, there is a significantly negative correlation between body size and Cook's Index, indicating that Savannah Sparrows tend to be relatively larger where they co-occur with few potential competing species (Table 4). This remains true when the samples of the largest birds (which includes three of the four island samples) are removed (Table 5).

PC 2 scores (which reflect bill size and pectoral girdle size) are significantly negatively correlated with both average annual precipitation and average June

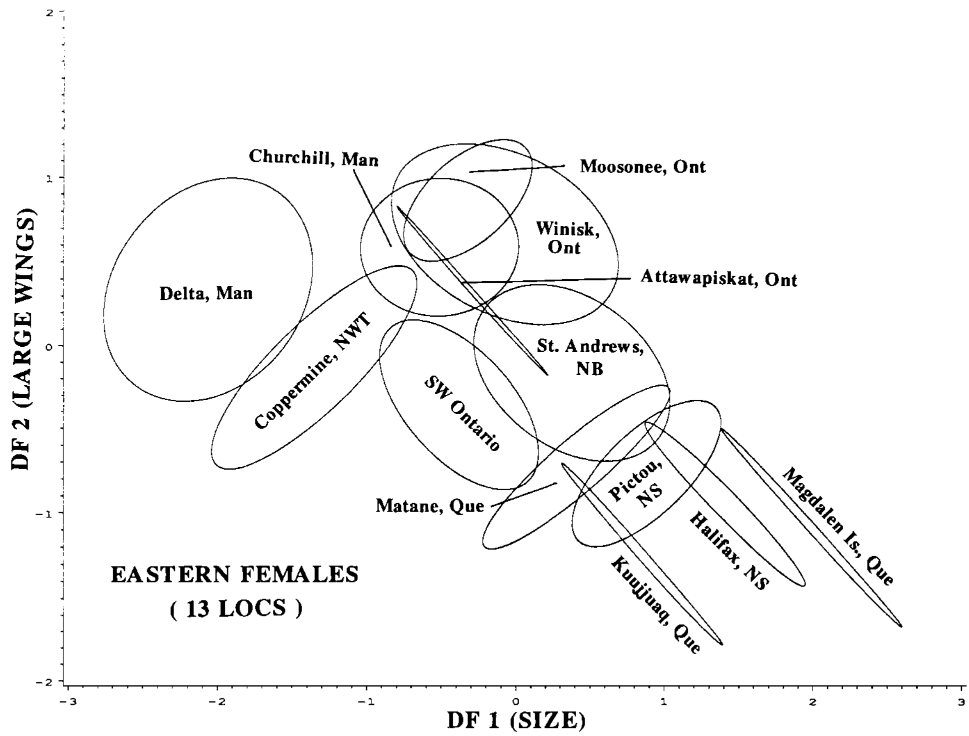

FIGURE 9. Samples of female Savannah Sparrows from eastern North America in the DF 1 vs. DF 2 space (see Fig. 8).

precipitation in both sexes (Table 4). Thus, Savannah Sparrows have relatively large bills and small wings where both annual and June precipitation are low. With the samples of the largest sparrows removed from the analyses (Table 5), the sizes of these correlations are larger. As well, there is a positive correlation between PC 2 score and both longitude and elevation; the correlation between elevation and PC 2 score is significant in males, and in both sexes with the largest sparrows omitted. Thus, Savannah Sparrows from the west and high elevations have relatively small bills and large wings.

Canonical correlations and redundancy analysis

The correlations between the morphological variables (averages for each of 42 different populations) and the first canonical variable based on the morphological canonical variable (MCV1) are all relatively high and negative, that is, large birds have small MCV1 values (Table 8). This axis, then, can be taken as a measure of size, and explains 27.9% of the morphological variance. The measures of bill size and hallux (toe) length are positively correlated with MCV2; that is, birds with relatively large bills and long toes have large MCV2 values. This second axis explains 10.2% of the variance. Lastly, measures of wing and leg length are negatively correlated with MCV3, and explains an additional 9.6% of the morphological variability.

The first climatic canonical variable (CCV1) from the analysis of the climatic variables range from relatively cool and moist localities to relatively hot and dry ones (Table 9); approximately 35.4% of the climatic variation among localities is

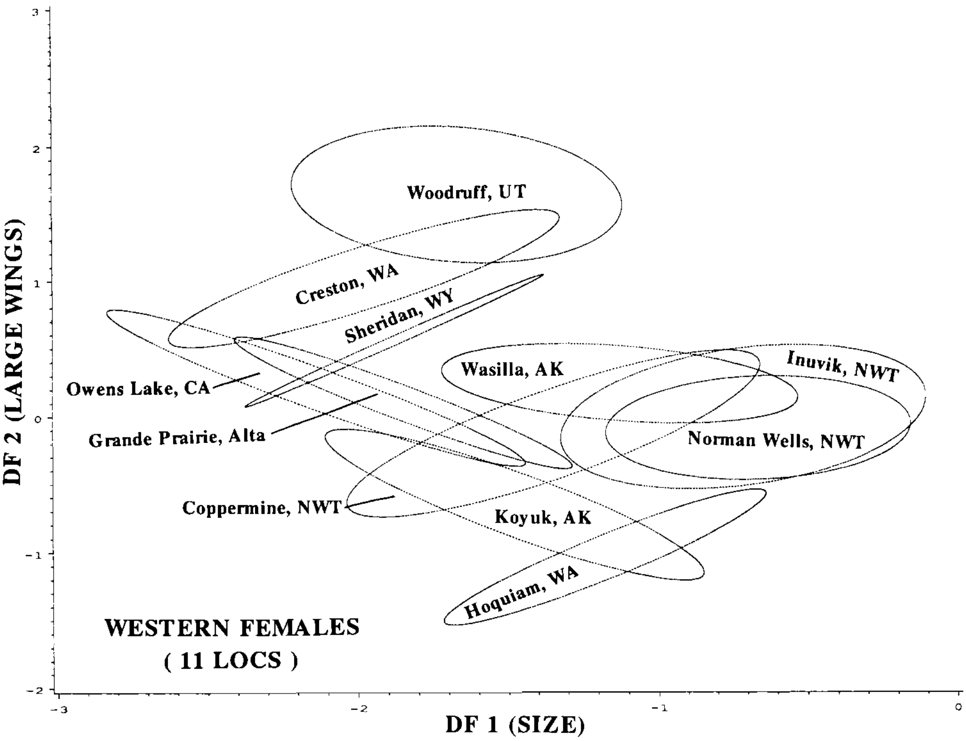

FIGURE 10. Samples of female Savannah Sparrows from western North America in the DF 1 vs. DF 2 space (see Fig. 8).

explained along this axis. CCV2 explains an additional 28.9% of the climatic variation, and contrasts localities with relatively warm and wet (as measured by rainfall) climates with those that are relatively cool. CCV3 explains 7.3% of the climatic variability, but is not particularly highly correlated with any of the climatic variables (Table 9).

For the most part, the residuals from the Procrustean analysis of the morphological and climatic principal components (two axes of each combined) are small (Table 10). The only large values are those for the localities where the birds are especially large (Sable Island, Umnak Island, and Cold Bay), two coastal localities, one of which is found in the far north (Kugluktuk and Hoquiam), and Owens Lake in east-central California (where the summers are hot and dry, but the birds are found in relatively mesic vegetation along the shores of the lake). These are, thus, either places where the birds are unusually large or where the data taken from weather stations are probably a poor indication of the environmental conditions in the microhabitat of the birds. There is strong agreement between the climatic and morphological data sets (probability of rejection is 0.0001).

SALTMARSH SAVANNAH SPARROWS

Males

There are four significant discriminant functions among the eight samples of saltmarsh Savannah Sparrow; of these, the first explains nearly 85% of the vari-

TABLE 4. SPEARMAN'S CORRELATIONS BETWEEN PRINCIPAL COMPONENTS (PC) AND DISCRIMINANT FUNCTIONS (DF) SCORES AND ENVIRONMENTAL MEASURES FOR SAVANNAH SPARROWS FROM 45 (MALES) AND 27 (FEMALES) LOCALITIES

Variable	PC 1		PC 2		DF 1		DF 2	
	Male	Female	Male	Female	Male	Female	Male	Female
Average annual precipitation	0.62	0.57	−0.66	−0.59	0.71	0.68	0.39	−0.41
	(0.0001)[a]	(0.002)	(0.0001)	(0.001)	(0.0001)	(0.0001)	(0.009)	(0.03)
Average June precipitation	0.43	0.50	−0.51	−0.39	0.44	0.47	0.21	−0.17
	(0.004)	(0.008)	(0.0005)	(0.05)	(0.003)	(0.01)	(0.18)	(0.41)
Average minimum summer[b] temperature	−0.36	−0.26	−0.13	−0.11	−0.33	−0.16	0.33	−0.21
	(0.02)	(0.19)	(0.39)	(0.59)	(0.03)	(0.43)	(0.03)	(0.29)
Average maximum summer temperature	−0.51	−0.31	0.27	0.28	−0.56	−0.45	−0.01	0.21
	(0.0005)	(0.12)	(0.08)	(0.17)	(0.0001)	(0.02)	(0.95)	(0.29)
Minimum summer temperature	0.00	0.19	−0.25	−0.28	0.08	0.30	0.25	−0.25
	(0.98)	(0.34)	(0.11)	(0.16)	(0.58)	(0.12)	(0.10)	(0.22)
Maximum summer temperature	−0.63	−0.53	−0.40	0.32	−0.67	−0.67	−0.11	0.29
	(0.0001)	(0.005)	(0.008)	(0.10)	(0.0001)	(0.001)	(0.47)	(0.14)
Environmental PC 1	−0.62	−0.41	−0.26	0.10	—	—	—	—
	(0.0001)	(0.03)	(0.09)	(0.60)				
Environmental PC 2	0.38	0.49	−0.64	−0.56	—	—	—	—
	(0.01)	(0.01)	(0.001)	(0.002)				
Latitude	0.14	−0.02	0.09	0.11	0.15	−0.04	−0.34	0.06
	(0.37)	(0.89)	(0.58)	(0.60)	(0.34)	(0.82)	(0.02)	(0.76)
Longitude	−0.40	−0.43	0.22	0.11	−0.36	−0.37	−0.30	0.13
	(0.007)	(0.03)	(0.16)	(0.59)	(0.02)	(0.06)	(0.05)	(0.53)
Elevation	−0.63	−0.56	+0.38	0.29	−0.68	−0.61	−0.26	0.33
	(0.0001)	(0.002)	(0.01)	(0.14)	(0.0001)	(0.0007)	(0.08)	(0.10)
Competitor abundance	−0.18	−0.23	+0.17	0.22	−0.17	−0.25	−0.22	−0.14
	(0.26)	(0.25)	(0.26)	(0.28)	(0.27)	(0.20)	(0.14)	(0.49)
Number of competing species	0.07	−0.13	+0.09	0.13	−0.08	−0.16	−0.28	0.19
	(0.65)	(0.51)	(0.55)	(0.51)	(0.61)	(0.43)	(0.07)	(0.33)
Number of sparrow species	0.13	0.01	+0.07	0.14	0.13	−0.03	−0.21	0.19
	(0.42)	(0.95)	(0.69)	(0.47)	(0.41)	(0.87)	(0.17)	(0.35)
Cook's Index	−0.59	−0.44	+0.20	0.04	−0.58	−0.50	0.03	0.03
	(0.001)	(0.02)	(0.19)	(0.85)	(0.0001)	(0.009)	(0.84)	(0.88)

[a] Exact probabilities are in parentheses.
[b] June, July, and August.

TABLE 5. SPEARMAN'S CORRELATIONS BETWEEN PRINCIPAL COMPONENTS (PC) AND DISCRIMINANT FUNCTIONS (DF) SCORES AND ENVIRONMENTAL MEASURES FOR SAVANNAH SPARROWS FROM 40 (MALES) AND 25 (FEMALES) LOCALITIES

Variable	PC 1		PC 2		DF 1		DF 2	
	Male	Female	Male	Female	Male	Female	Male	Female
Average annual precipitation	0.59	0.53	−0.73	−0.69	0.69	0.66	0.55	−0.55
	(0.0001)[a]	(0.007)	(0.0001)	(0.0001)	(0.0001)	(0.0003)	(0.0003)	(0.004)
Average June precipitation	0.50	0.55	−0.57	−0.44	0.51	0.51	0.26	−0.19
	(0.001)	(0.004)	(0.0002)	(0.03)	(0.0009)	(0.009)	(0.11)	(0.35)
Average minimum summer[b] temperature	−0.29	−0.29	+0.22	−0.19	−0.22	−0.16	0.23	−0.22
	(0.08)	(0.17)	(0.19)	(0.37)	(0.17)	(0.44)	(0.17)	(0.29)
Average maximum summer temperature	−0.41	−0.26	+0.30	0.30	−0.47	−0.43	−0.20	0.33
	(0.01)	(0.21)	(0.07)	(0.14)	(0.002)	(0.03)	(0.22)	(0.10)
Minimum summer temperature	−0.24	0.05	−0.25	−0.38	−0.11	0.19	0.37	−0.43
	(0.14)	(0.80)	(0.13)	(0.06)	(0.51)	(0.37)	(0.02)	(0.03)
Maximum summer temperature	−0.51	−0.43	+0.46	0.41	−0.56	−0.61	−0.33	0.54
	(0.001)	(0.03)	(0.004)	(0.04)	(0.0002)	(0.001)	(0.04)	(0.005)
Latitude	0.07	0.00	+0.18	−0.22	0.06	−0.02	−0.26	0.14
	(0.66)	(0.99)	(0.28)	(0.30)	(0.71)	(0.94)	(0.10)	(0.50)
Longitude	−0.81	−0.53	+0.48	0.30	−0.74	−0.46	−0.14	0.17
	(0.0001)	(0.007)	(0.002)	(0.15)	(0.0001)	(0.02)	(0.14)	(0.42)
Elevation	−0.64	−0.62	+0.45	0.37	−0.70	−0.68	−0.35	0.38
	(0.0001)	(0.001)	(0.005)	(0.07)	(0.0001)	(0.0002)	(0.03)	(0.06)
Competitor abundance	0.07	−0.08	−0.19	−0.34	−0.06	−0.11	0.38	0.36
	(0.66)	(0.70)	(0.25)	(0.09)	(0.73)	(0.60)	(0.02)	(0.60)
Number of competing species	0.14	−0.02	−0.11	0.26	0.10	−0.05	−0.37	0.37
	(0.41)	(0.93)	(0.49)	(0.21)	(0.53)	(0.83)	(0.02)	(0.07)
Number of sparrow species	0.29	0.11	0.10	0.28	0.26	0.05	−0.26	0.34
	(0.08)	(0.60)	(0.56)	(0.17)	(0.11)	(0.82)	(0.11)	(0.10)
Cook's index	−0.47	−0.33	−0.28	0.13	−0.45	−0.39	−0.12	0.22
	(0.003)	(0.11)	(0.09)	(0.53)	(0.004)	(0.051)	(0.47)	(0.29)

[a] Exact probabilities given in parentheses.
[b] June, July, and August.

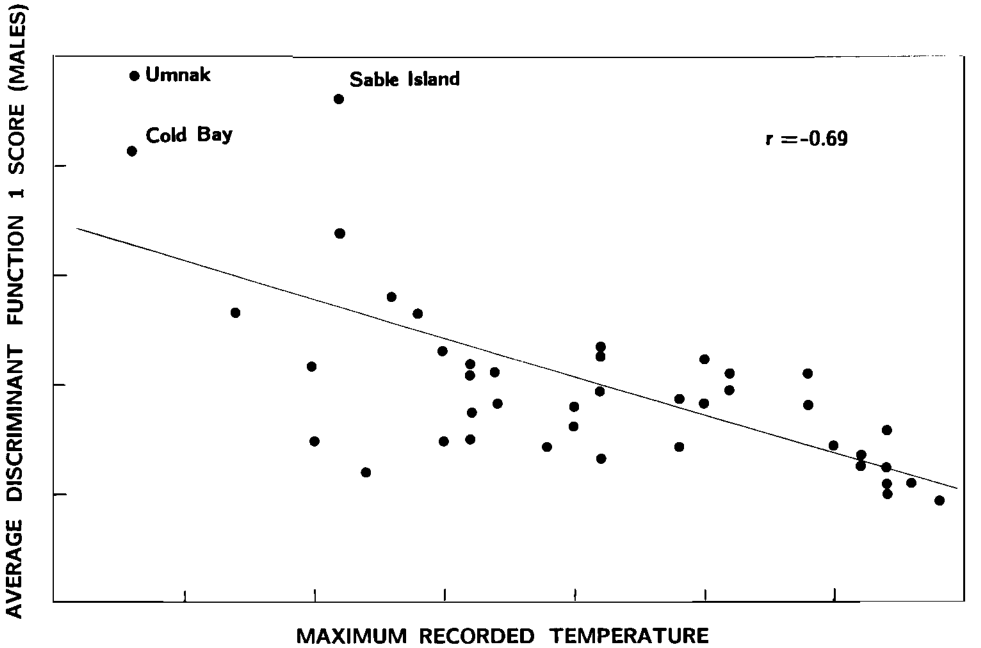

FIGURE 11. Relationship between average DF 1 score of males (Fig. 4) vs. the maximum recorded temperature. The product-moment correlation coefficient between the variables is −0.69, and it is statistically significant ($P < 0.001$).

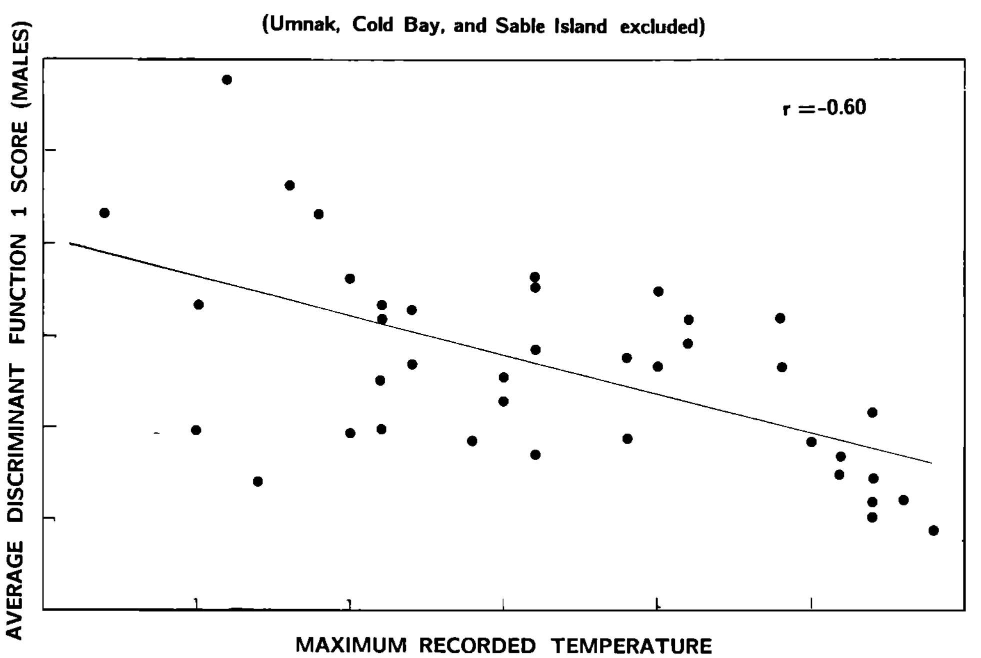

FIGURE 12. Relationship between the average DF 1 score of males (Fig. 4) vs. the maximum recorded temperature with the three samples of the largest individuals (Umnak Island, Cold Bay, and Sable Island) removed. The product-moment correlation of −0.60 is statistically significant ($P < 0.001$).

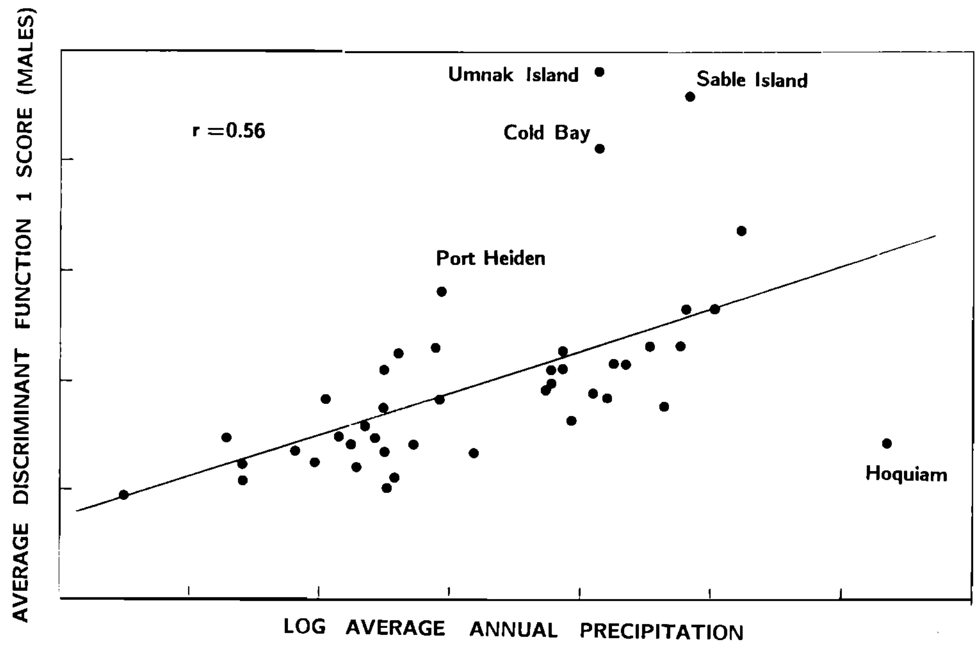

FIGURE 13. Relationship between the average DF 1 score of males (Fig. 4) vs. the log of the average annual precipitation. The product-moment correlation of 0.56 is statistically significant (P = 0.004).

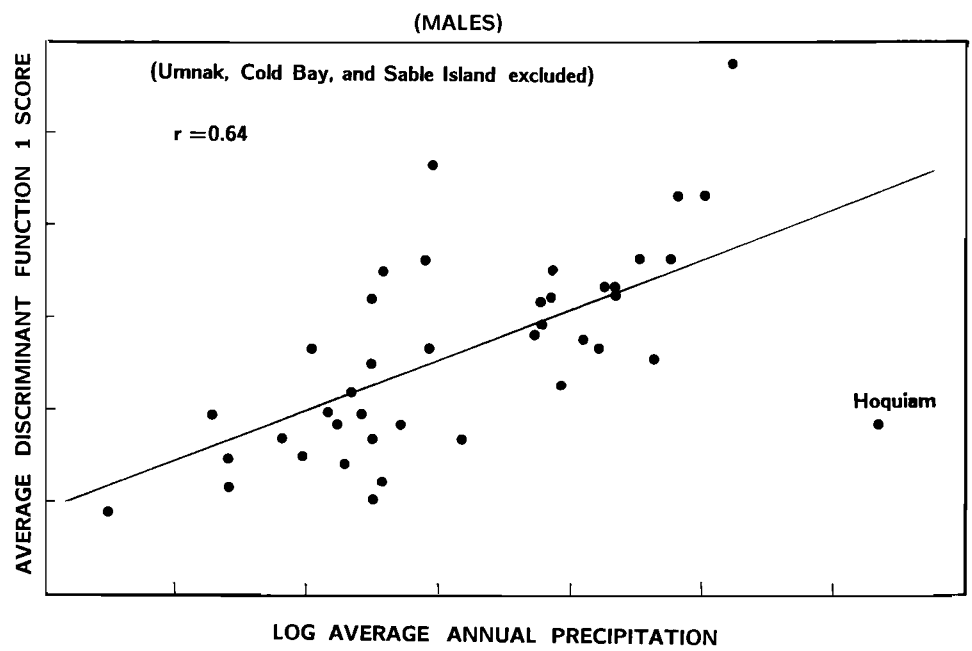

FIGURE 14. Relationship between the average DF 1 scores of males (Fig. 4) vs. the log of the average annual precipitation with the three samples of the largest individuals (Umnak Island, Cold Bay, and Sable Island) removed. The product-moment correlation of 0.64 is statistically significant P = 0.003).

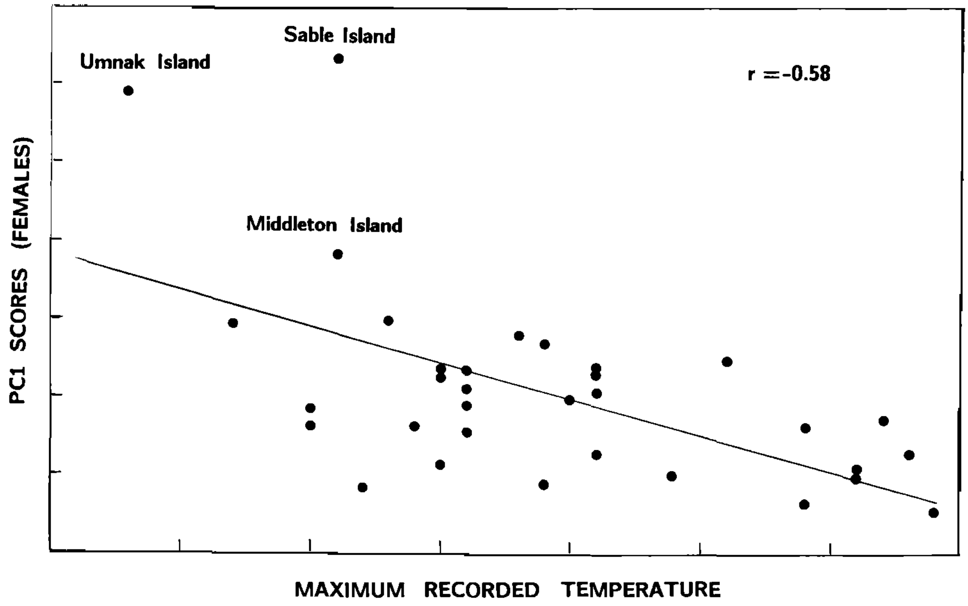

FIGURE 15. Relationship between the average PC 1 scores of female Savannah Sparrows from 33 localities vs. the maximum recorded temperature. PC 1 scores are a measure of overall body size (see text). The product-moment correlation of −0.58 is statistically significant (P = 0.002).

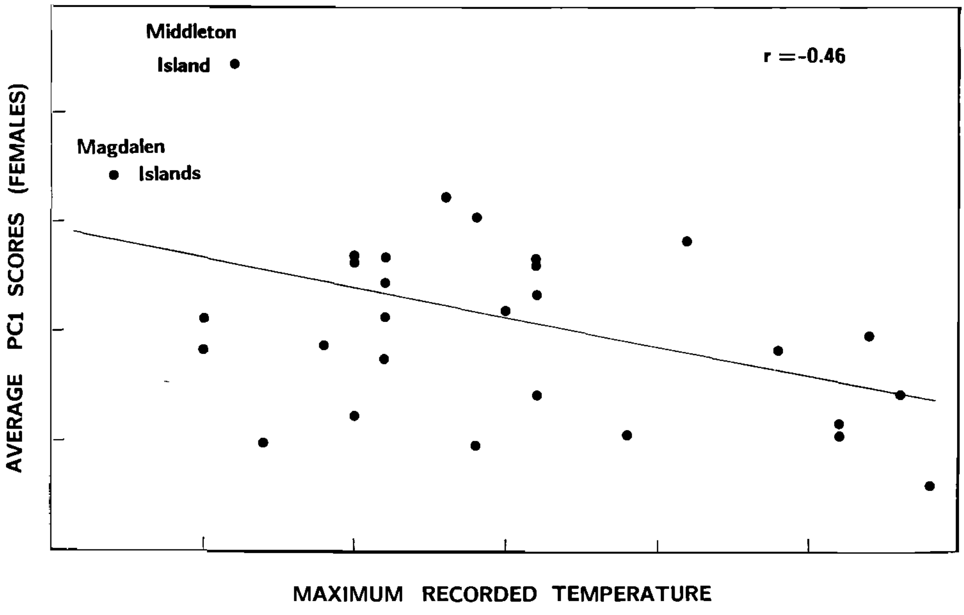

FIGURE 16. Relationship between the average PC 1 scores of female Savannah Sparrows from 29 localities (Sable and Umnak islands omitted) vs. the maximum recorded temperature. The product-moment correlation of −0.46 is statistically significant (P = 0.008).

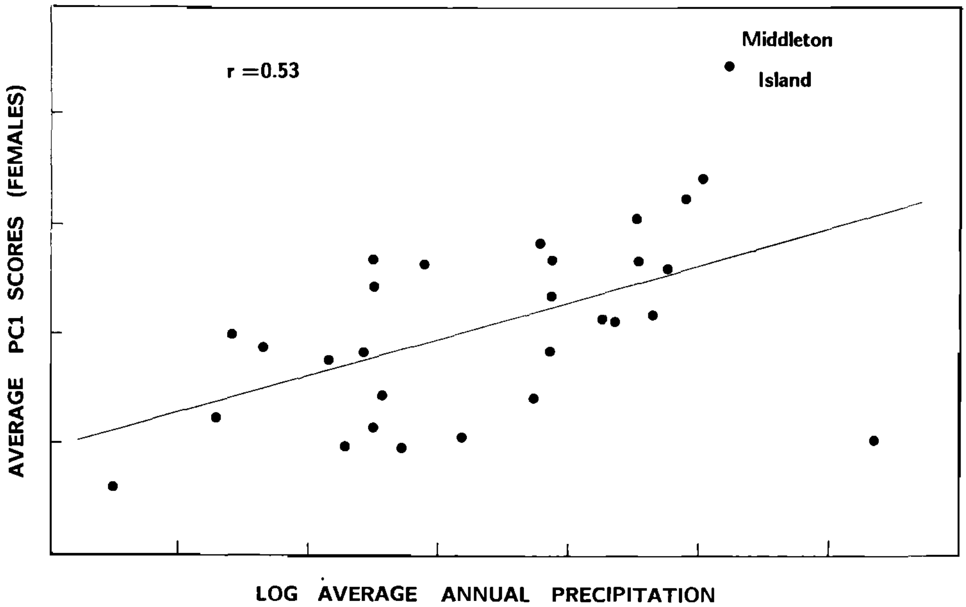

FIGURE 17. Relationship between the average PC 1 scores of female Savannah Sparrows from 29 localities vs. the log of the average annual precipitation. The product-moment correlation of 0.53 is statistically significant (P = 0.008).

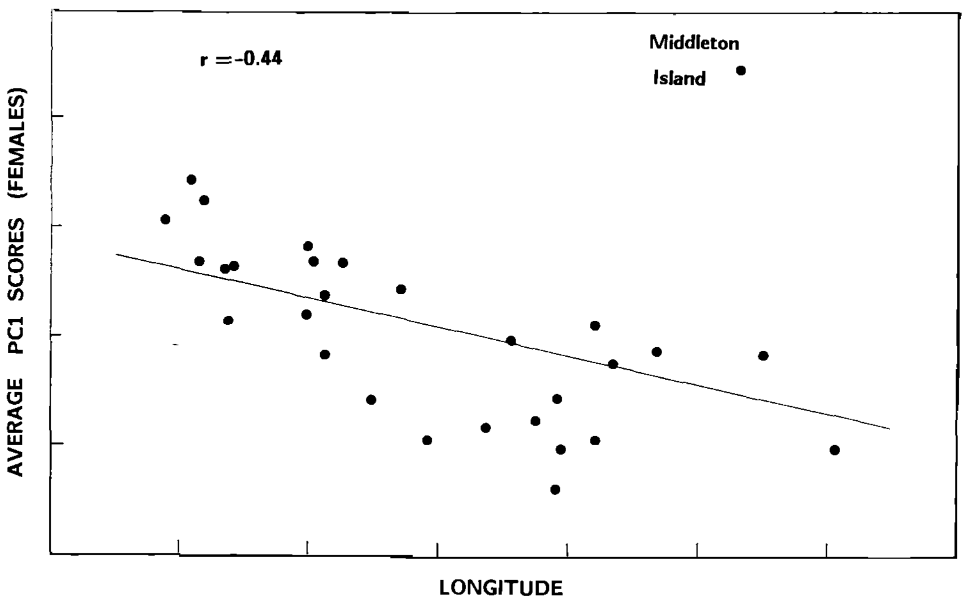

FIGURE 18. Relationship between the average PC 1 scores of female Savannah Sparrows from 29 localities vs. longitude. The product-moment correlation of −0.44 is statistically significant (P = 0.03).

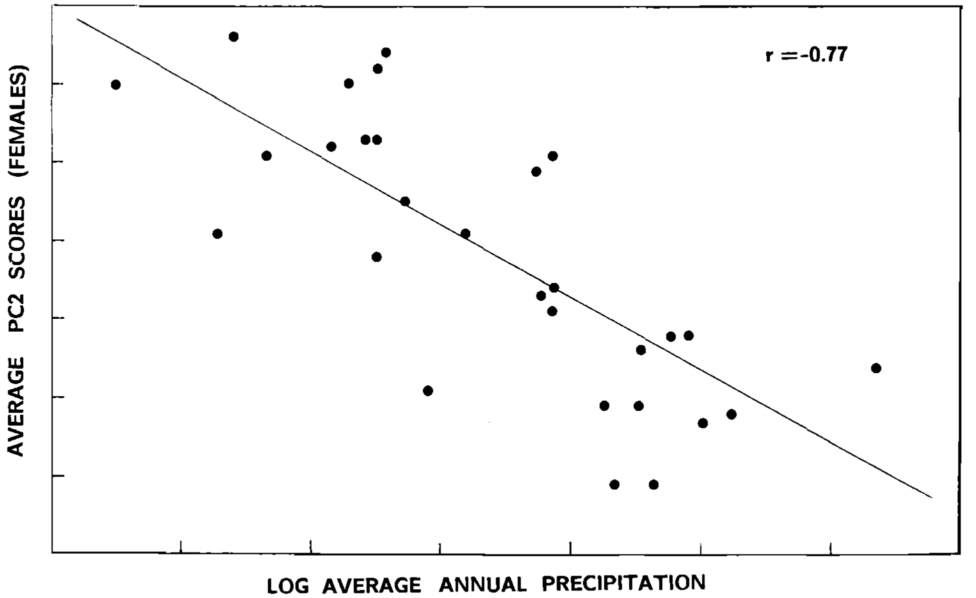

FIGURE 19. Relationship between the average PC 2 scores of female Savannah Sparrows from 29 localities vs. the log of the average annual precipitation. PC 2 scores contrast bill size with wing size (see text). The product-moment correlation of −0.77 is statistically significant (P = 0.001).

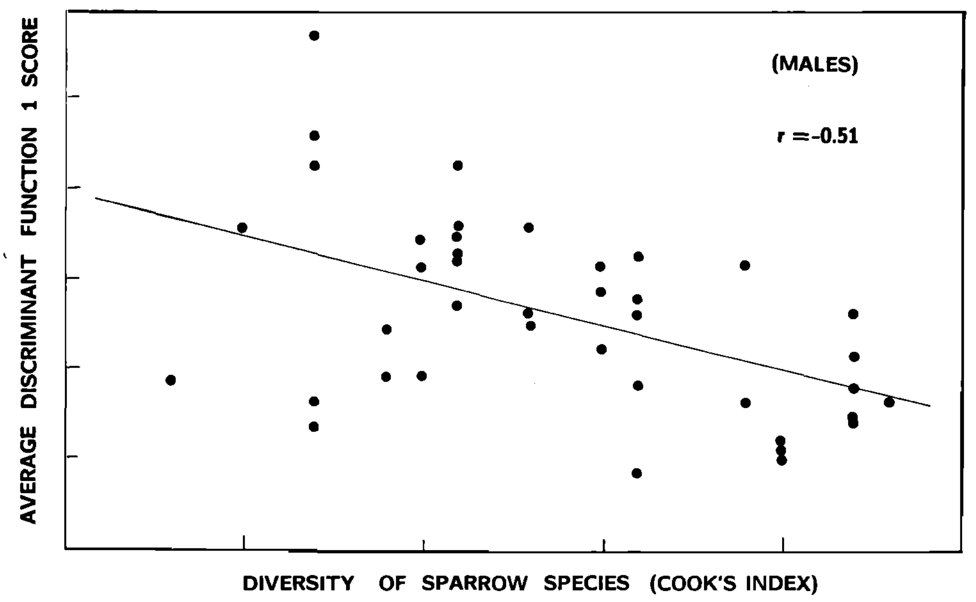

FIGURE 20. Relationship between the average DF 1 scores of male Savannah Sparrows vs. Cook's Index of sparrow species diversity (see text). The product-moment correlation of −0.51 is statistically significant (P < 0.001).

TABLE 6. STANDARDIZED CANONICAL DISCRIMINANT FUNCTION COEFFICIENTS FROM A DFA OF 8 MEASUREMENTS OF 153 MALE SAVANNAH SPARROWS FROM 8 SALTMARSH LOCALITIES AND 98 FEMALE SAVANNAH SPARROWS FROM 7 LOCALITIES

	Males		Females	
Variable	DF 1	DF 2	DF 1	DF 2
Premaxilla depth	0.48	−0.34	0.42	0.43
Premaxilla width	0.22	−0.13	0.61	0.49
Mandible length	0.34	0.43	—	—
Mandible depth	0.54	−0.01	0.66	−0.51
Tibiotarsus length	0.27	0.58	—	—
Tarsometatarsus length	—	—	0.26	0.87
Ulna length	−0.11	−1.12	−0.12	−0.73
Sternum length	—	—	−0.40	0.84
Sternum depth	−0.17	0.38	—	—
Synsacrum width	−0.15	0.77	−0.10	−0.63
Eigenvalue	9.75	1.08	12.85	0.83
% variance explained	84.9%	9.5%	87.20%	5.66%
Canonical Correlation	0.95	0.72	0.96	0.67

ance among the groups, and the second an additional 9.5% (Table 11). I will discuss only these two. The first DF separates the males principally on the basis of bill size; birds with large DF 1 scores have relatively large bills. This function separates the large-billed sparrows of coastal Sonora and Sinaloa from the small-billed birds of coastal California and Baja California. The southern-most Baja sample, that from Bahía Magdalena, is intermediate on this axis between the large-billed birds and the sample from Guerrero Negro, midway north on the Baja coast (Fig. 21; because of the small sample size, the ellipse for the birds from Puerto Peñasco is not included in the illustration). Males with large DF 2 scores have short wings, wide synsacra, long legs, and long mandibles. Samples from Baja California, especially Guerrero Negro, have relatively large DF 2 scores; the birds from Puerto Peñasco, Sonora, and Morro Bay, California, are similar on the DF 2 axis; the birds from Morro Bay and San Diego are virtually identical on this axis (Fig. 21).

Retrospectively, overall in the DFA 72.2% of the males are correctly identified as to sample. In general, misidentified individuals are grouped with the nearest population; interestingly two of the nine males from Puerto Peñasco were identified as belonging to the Magdalena Bay population, and one of the 15 males

TABLE 7. RELATIONSHIP BETWEEN MORPHOLOGICAL PRINCIPAL COMPONENTS AND ENVIRONMENTAL PRINCIPAL COMPONENTS

	Environmental			
	PC 1		PC 2	
Male				
Morphology PC 1	−0.52	P < 0.001	0.32	P = 0.04
Morphology PC 2	−0.30	P > 0.05	0.48	P = 0.001
% Variation Explained	42%		32%	
Female				
Morphology PC 1	−0.34	P > 0.05	0.45	P = 0.02
Morphology PC 2	0.45	P = 0.02	−0.48	P = 0.01
% Variation Explained	42%		35%	

TABLE 8. SQUARED MULTIPLE CORRELATIONS BETWEEN THE MORPHOLOGICAL VARIABLES AND THE FIRST THREE CANONICAL CLIMATIC VARIABLES

Morphological Variable	MCV1	MCV2	MCV3
Skull length	0.44	0.51	0.58
Skull width	0.47	0.48	0.63
Premaxilla length	0.25	0.32	0.38
Premaxilla depth	0.20	0.47	0.50
Narial width	0.15	0.55	0.61
Premaxilla width	0.23	0.44	0.49
Interorbital width	0.04	0.45	0.46
Mandible length	0.43	0.51	0.57
Gonys length	0.32	0.42	0.45
Mandible depth	0.19	0.49	0.50
Coracoid length	0.20	0.29	0.38
Scapula length	0.20	0.26	0.42
Femur length	0.18	0.28	0.38
Femur width	0.13	0.21	0.21
Tibiotarsus length	0.32	0.42	0.51
Tarsometatarsus length	0.30	0.43	0.50
Humerus length	0.08	0.14	0.20
Ulna length	0.09	0.15	0.27
Carpometacarpus length	0.22	0.24	0.37
Hallux length	0.27	0.50	0.57
Sternum length	0.19	0.28	0.35
Sternum depth	0.12	0.24	0.26
Keel length	0.12	0.21	0.32
Synsacrum width	0.35	0.42	0.49
Mass	0.26	0.34	0.39
% Morphological variation explained	27.9%	10.2%	9.6%

from Bahía Magdalena was identified with the Puerto Peñasco sample and another with the Bahía Kino sample. Otherwise, none of the coastal birds from California or Baja California were identified with the coastal Sonora and Sinaloa birds, and vice versa.

Females

There are four significant discriminant functions in the DFA of seven samples of females (the sample from Puerto Peñasco was too small for inclusion in this analysis). DF 1 explains 87.2% of the total variation among samples, and DF 2 only an additional 5.7% (Table 11); variation on only these dimensions is discussed. The first DF is sensitive to variability in bill size, especially bill depth; it

TABLE 9. CORRELATIONS BETWEEN CLIMATE VARIABLES AND THEIR CANONICAL VARIABLES (CCV)

Climatic Variable	CCV1	CCV2	CCV3
Average annual precipitation	−0.48	0.67	0.29
Average June precipitation	0.02	0.89	0.28
Average minimum summer temperature	0.49	0.37	−0.17
Average maximum summer temperature	0.88	0.05	−0.14
Minimum summer temperature	−0.16	0.46	−0.32
Maximum summer temperature	0.84	−0.15	0.33
% morphological data explained by climate axes	26.5%	8.8%	7.1%
% climatic data explained by climate axes	35.4%	28.9%	7.3%

TABLE 10. Residuals for Dimensions 1 and 2 of Procrustean Analysis of Morphological and Climatic Principal Components (2 Axes of Each) Combined

Site	Residual	Site	Residual
Sable Island, NS	0.43	Grande Praire, AB	0.12
Parsons Pond, NF	0.01	Courval, SK	0.05
Bedeque, PEI	0.05	Kaministikwia, ON	0.07
River John, NS	0.03	Owens Lake, CA	0.22
St. Andrews, NB	0.08	Brandonville, WV	0.11
Matane, PQ	0.07	Woodruff, UT	0.12
Kuujjuaq, PQ	0.16	Creston, WA	0.12
Wildfield, ON	0.09	Hoquiam, WA	0.31
Wallaceburg, ON	0.15	Morro Bay, CA	0.06
Sowerby, ON	0.09	Humboldt Bay, CA	0.12
Cochrane, ON	0.05	Koyuk, AK	0.09
Moosonee, ON	0.03	Wasilla, AK	0.11
Attawapiskat, ON	0.02	Fairbanks, AK	0.07
Winisk, ON	0.17	Umnak Is, AK	0.29
Delta, MB	0.07	Port Heiden, AK	0.10
The Pas, MB	0.05	Cold Bay, AK	0.20
Gillam, MB	0.09	Middleton Is., AK	0.10
Churchill, MB	0.19	Magdalen Is., PQ	0.10
Coppermine, NU	0.30	Halleck, NV	0.05
Norman Wells, NT	0.07	Elberta, UT	0.13
Inuvik, NT	0.16	Sheridan, WY	0.06
Maple Creek, SK	0.04	Residual sum of squares:	0.93
Milk River, AB	0.07	Probability of Rejection:	0.0001

is negatively correlated with sternum length and positively correlated with keel length. To the degree that the same variables were used in the male and female analyses, the DF coefficients on the DF 1 axis are similar between the sexes. As with the males, DF 1 separates the bird from coastal Sonora and Sinaloa from those from coastal California, with the birds from Bahía Magdalena closer to the birds from Sinaloa and Sonora than to those from coastal California. DF 2 is positively correlated with tarsometatarsus, sternum, and premaxilla lengths, premaxilla depth, and negatively correlated with ulna length, synsacrum width, man-

TABLE 11. Standardized Canonical Discriminant Function Coefficients from a DFA of 8 Measurements of 153 Male Savannah Sparrows from 8 Saltmarsh Localities and 98 Female Savannah Sparrows from 7 Localities

Variable	Males		Females	
	DF 1	DF 2	DF 1	DF 2
Premaxilla depth	0.48	−0.34	0.42	0.43
Premaxilla width	0.22	−0.13	0.61	0.49
Mandible length	0.34	0.43	—	—
Mandible depth	0.54	−0.01	0.66	−0.51
Tibiotarsus length	0.27	0.58	—	—
Tarsometatarsus length	—	—	0.26	0.87
Ulna length	−0.11	−1.12	−0.12	−0.73
Sternum length	—	—	−0.40	0.84
Sternum depth	−0.17	0.38	—	—
Synsacrum width	−0.15	0.77	−0.10	−0.63
Eigenvalue	9.75	1.08	12.85	0.83
% variance explained	84.9%	9.5%	87.20%	5.66%
Canonical Correlation	0.95	0.72	0.96	0.67

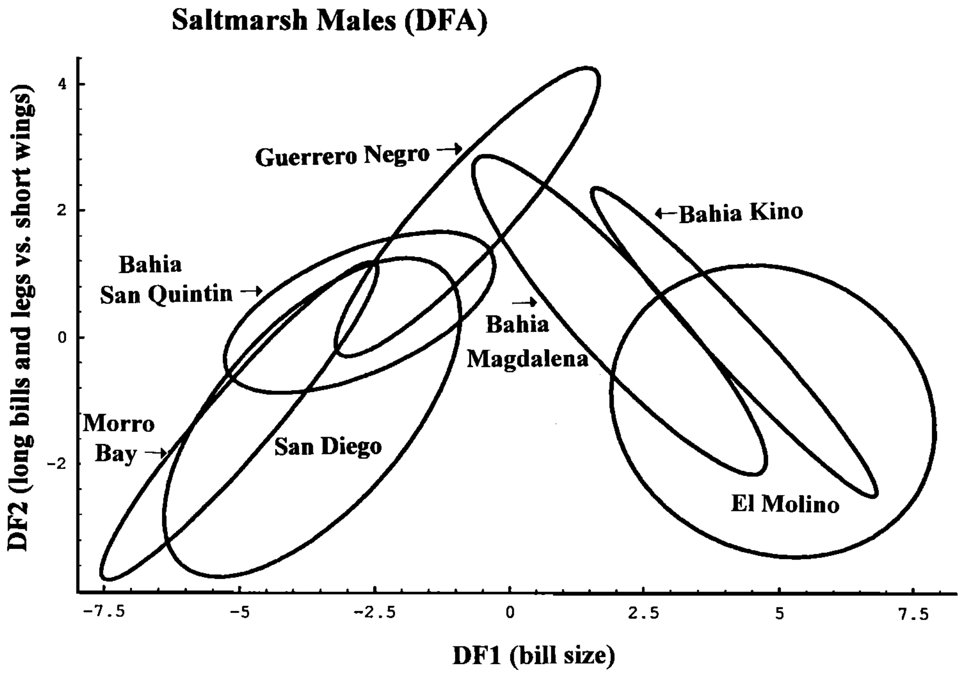

FIGURE 21. Samples of male Savannah Sparrows from coastal saltmarsh sites (95% confidence ellipses) in the space defined by DF 1 and DF 2. DF 1 explains 84.9% of the total variance and contrasts bill size and leg length with measures of wing size. DF 2 explains an additional 9.5% of the variance, and contrasts ulna length and premaxilla depth with leg length, sternum depth, and synsacrum width.

dible depth, and keel length (Table 11). Females from Bahía Magdalena have the largest DF 2 scores, whereas those from Bahía San Quintin have the smallest. Overall, 86% of the females are correctly identified in this analysis. As with the males, misidentified individuals are generally grouped with those of a geographically adjacent sample. One female from Bahía Magdalena is clustered with the Bahía Kino sample; otherwise, none of the birds from California, Baja California are identified as belonging to a sample from Sonora or Sinaloa. One bird from El Molino is clustered with the females from Bahía Magdalena.

DISCUSSION

For the most part, the interpopulational variation in size of Savannah Sparrows is clinal. The most striking finding of this study is that Savannah Sparrows are large on islands. Case (1978) argued that, unless tightly constrained by other factors, we should expect large body size to evolve on islands because (1) islands usually contain fewer competitors as well as predators, so food availability for colonists would initially be expected to be high, and (2) intraspecific interactions for food would be relatively more important for island species than mainland ones, favoring individuals with relatively large body size. Additionally, larger individuals would be able to take advantage of a larger range of foods, and are thermally more efficient. Schoener (1969) found an inverse relationship between