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GEOGRAPHIC VARIATION IN PLUMAGE PATTERN AND COLORATION OF SAVANNAH SPARROWS

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ABSTRACT.—We used principal coordinates analysis to analyze variation in 11 plumage characteristics of 1,722 Savannah Sparrows (*Passerculus sandwichensis*) breeding at 55 different sites from throughout the species' range in Canada, Mexico, and the United States. There is clinal interpopulational variation in size with considerable overlap among localities. Savannah Sparrows resident along the Pacific coast of southern California and Baja California, and those from along the coast of Sinaloa and Sonora (i.e., saltmarsh Savannah Sparrows) differ from those throughout the rest of their range (i.e., non-saltmarsh). Variation among populations of non-saltmarsh Savannah Sparrows was clinal with the exception of those from Sable Island, Nova Scotia, which are consistently more pallid than birds from the adjacent mainland. Western Savannah Sparrows are more pallid than those in the east. The median crown stripe of eastern Savannah Sparrows is distinct, whereas the median crown stripe of western Savannah Sparrows generally is indistinct or narrow. Savannah Sparrows, with the exception of those on Sable Island, are also more pallid in relatively hot and dry areas than in cool mesic sites, following the general prediction of Gloger's Rule. There is clinal variation of saltmarsh populations along the Pacific coast with those in the north being relatively dark in coloration, and with more yellow in the supercilium than those farther south. There is also clinal variation among the populations from the east coast of the Gulf of California with pallid birds in the north, where vegetation is sparse, and darker birds to the south; these coastal birds have indistinct median crown stripes and little yellow in the supercilium. *Received 16 June 2008. Accepted 3 November 2008.*

Savannah Sparrows (*Passerculus sandwichensis*) are among the most widespread and geographically variable New World songbirds. They breed from the Aleutian Islands east across Alaska and mainland Canada and the United States, north to the Arctic Ocean and Hudson Bay, and south to Pennsylvania, northern New York, and northwestern Georgia (in the Appalachian Mountains), central Ohio, Indiana, Illinois, and Iowa, northern Nebraska, western Colorado and New Mexico, and in the west from Alaska south to California. They are resident in the interior of Mexico and south in the highlands to southern Mexico (and perhaps to Guatemala), and along the Pacific coast in saltmarshes from California to southern Baja California (Rising and Beadle 1996). The American Ornithologists' Union (AOU 1957) recognized 16 subspecies of Savannah Sparrows in addition to the Ipswich Sparrow (*P. princeps*) which has more recently has been treated as a subspecies of the Savannah Sparrow (AOU 1998). Paynter and Storer (1970) recognized 21 subspecies (including *P. s. princeps*). Hellmayr (1938) listed 15 subspecies (including *P. s. princeps*) for the world, and Miller et al. (1957) listed 15 subspecies from Mexico. This large number of subspecies is a reflection of the species' considerable geographic variation in size, proportions, and, most especially, coloration (Peters and Griscom 1938, Aldrich 1940, Hubbard 1974). Rising (2001) summarized geographic variation in size of this species, but discussed variation in coloration only in passing. Rising (2007) proposed that only six subspecies be recognized. The objectives of this paper are to: (1) provide a quantitative account of geographic variation among populations of Savannah Sparrows throughout their range, and (2) describe the relationship of patterns of plumage variation to local climatic environments, as well as to latitude, longitude, and elevation at each sampling site.

METHODS

Collections.—JDR collected and analyzed samples of Savannah Sparrows from sites covering nearly the entire breeding range of the species (Fig. 1, Appendix; Rising 2001). All specimens were collected just prior to, or during, the breeding season and are assumed to have been collected near their breeding site.

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FIG. 1. Distribution of collections of Savannah Sparrows in North America.

Adults of this species undergo a complete Prebasic molt (partial in first-year birds) in the fall that occurs, at least in part, in breeding areas after breeding (Pyle 1997). The molt may be suspended during migration if it is not completed in breeding areas, although this has not been studied. The timing of the molt also may vary geographically. There is a limited Prealternate molt in spring that involves principally head feathers, but may also result in the replacement of some tertials and central rectrices. Thus, birds collected in the breeding season have worn plumage, whereas sparrows collected in autumn have unworn plumage. Fall- and winter-taken specimens are of unknown geographic origin and are not useful for analyses or geographic variation in color. Both males and females were collected at each site, and each was prepared as a skin-and-skeletal specimen (Rising 2001). The skins were all prepared in the same way: roughed out in the field, and then cleaned and stuffed in the museum. These specimens are housed in the Royal Ontario Museum in Toronto, Ontario, Canada.

Plumage Quantification.—Savannah Sparrows are streaked and spotted birds, and we decided it would be difficult to obtain repeatable estimates of spectral reflectance. Thus, JDR selected 14 quantitative multistate characters to quantify variation in plumage pattern and coloration. Each was scored on a scale of 1 to 6 or 1 to 4 with 1 being the lowest value for each feature (size or extent of spotting, palest color, etc.) and 4 or 6 being the highest. Each specimen scored was compared to a reference series of 18 birds, selected to show most of the variation in the species. JDR scored all of the specimens once, and then each was scored a second time in an effort to decrease variation in the scoring. Only 11 features were selected for the second scoring as three features could not be scored in a consistent manner; all colors follow Smithe (1975). These 11 features are:

spot size (the size of the ventral spots; 1 = small and 6 = large),
spot color (the color of the ventral spots; 1 = fawn [color 25] and 6 = dusky brown [19]),
spot extent (the extent of the ventral spotting; 1 = few, restricted to upper breast with few on the flanks, and 6 = extensive streaking),
background color (the ventral background color; 1 = whitish and 6 = pale horn [92]),
throat color (1 = white and unspotted and 4 = spotted with dark spots),
undertail covert color (1 = white and no beige patches and 4 = with large patches),
supercilium color (the amount of yellow in the supercilium; 1 = none and 6 extensively, bright spectrum yellow [55]),
mantle color (the color of the centers of the mantle feathers and scapulars; 1 = pale tawny [38] and 6 = dusky brown or black),
margin color (brightness) (the color of the edges of the mantle feathers; 1 = hoary and 6 = dark),
crown stripe (the distinctiveness of the median crown stripe; 1 = distinct, and 6 = absent), and
spot width (the width of the lateral crown stripe spots; 1 = small and 6 = broad).

The scores were selected *a priori* to cover the possible range of variation. Only specimens that could be scored for all 11 characters were used in the analyses.

Statistical Analyses.—We calculated the Euclidean distances among all pairs of birds to examine the extent of similarity among specimens for the combination of characters. We performed principal coordinates analysis (PCoA) using NTSYS-pc 1.8 software (NTSYS-pc 1993) to reduce the complexity of the resulting matrix. All other statistical calculations were performed using SAS software (SAS Institute Inc. 1988). These samples were divided into two groups on the basis of morphology (Rising 2001), ecology, and behavior: those resident in saltmarshes on the west coast (i.e., the saltmarsh sparrows), and those that do not breed in saltmarshes (i.e., the non-saltmarsh or typical sparrows). Three sets of sparrows were used for analyses: (1) all 1,722 specimens (from 55 locations); (2) 1,497 specimens of non-saltmarsh sparrows (from 47 non-saltmarsh localities); and (3) 225 specimens of saltmarsh sparrows (from 9 locations) (Appendix). Savannah Sparrows are sexually monomorphic in color (Wheelwright and Rising 1993, Pyle 1997), and males and females were combined in analyses. Treating the males and females separately had no significant effect on the general results, and reduced sample sizes.

The sample from Morro Bay was included in both the saltmarsh and non-saltmarsh groups because this group of sparrows is intermediate morphologically (Rising 2001), and often have been classified with non-saltmarsh sparrows even though they are resident in saltmarshes. The first two axes from the PCoA of the matrix containing all populations and the matrix containing the saltmarsh populations were non-trivial (Jackson 1993). Additional axes were important in the analysis of the non-saltmarsh populations, and six were retained from each of the solutions. We used discriminant functions analysis (DFA) (SAS, Procedure DISCRIM) using the first six principal coordinate scores as variables to examine if there were multivariate differences among the groups.

We calculated the mean, range, and standard deviation for PCoA I and PCoA II scores, and used Pearson's product-moment

correlations to identify the correlations (factor loadings) between the raw scores for each plumage and each of the two PCoA scores. This allowed us to ascertain the magnitude and dimension that best explained the variation for each plumage characteristic. We used Pearson's (parametric) and Spearman's (nonparametric) correlations to assess the pattern of variation in relation to geography and climate between the first two PCoA scores of each of the following: (1) latitude, (2) longitude, (3) elevation of the collecting localities, (4) mean annual precipitation, (5) mean June precipitation, (6) mean minimum summer air temperature (Jun–Aug), (7) mean maximum summer air temperature, (8) extreme minimum summer air temperature, and (9) extreme maximum summer air temperature. We used climatic data from the nearest recording weather station to each locality listed by Environment Canada (1973) and NOAA (1983). The environmental data used are in Rising (2001). Climatic data were not available for all samples, and samples without climatic data were omitted from the correlation analyses.

RESULTS

Multivariate Measures of Plumage Variables.—The discriminant functions analysis (DFA) using all 55 localities revealed there were highly significant differences among samples in multivariate space. Most of the differences between individual samples also were statistically significant (data not presented) (1,444 of 1,485 different comparisons). Those 41 comparisons that did not differ significantly were generally geographically close to each other. Some samples were significantly different from all others: for example, all of the saltmarsh samples were statistically different from all other samples. There was substantial overlap among the samples and, with the exception of Sable Island, in *a posteriori* analyses only a small overall percentage of individuals was correctly identified to their correct group. About 89% of the birds from Sable Island were correctly identified as being from Sable Island, whereas in all samples combined, only ~21% of the individuals were identified into the correct sample. Misidentified specimens were often, but not always, placed in a close geographical area. For example, birds from St. Andrews, New Brunswick were identified as being from Atlantic Canada, but also from geographically distant places such as Kuujjuaq, Quebec; Manitoba; Alberta; Northwest Territories; and Lerma, Mexico. Birds from Lerma were identified as being from Kuujjuaq, Quebec, northern Ontario, the Magdalen Islands, Quebec, and Sheridan, Wyoming.

There is one less axis in principal coordinates analysis than the number of individuals in the analysis, each explaining less of the total variation among individuals than that preceding. We concentrated only on the first two principal coordinates to simplify analyses and to present results with minimal loss of information. These two coordinates together explain 43.4 to 59.6% of the total variance (Table 1); addition of more axes would lead to little clarification of the data. The correlation between PCoA I and PCoA II, and the 11 variables for the three analyses (All, Non-saltmarsh, and Saltmarsh) varied (Table 1). The correlation vectors in these three analyses are quite different, indicating the patterns of covariation of saltmarsh and non-saltmarsh birds differ substantially (Table 1).

The correlations between PCoA I and all characters except for *median crown stripe* for the non-saltmarsh birds are negative (correlations between the coordinate and *ventral background color* and *undertail covert color* are essentially 0). Thus, individuals with large PCoA I scores are rather pallid with limited spotting, little yellow in the supercilium, and an indistinct or narrow medium crown stripe. Birds with large PCoA II scores tend to have heavily spotted throats and an indistinct crown stripe (Table 1).

The correlations between PCoA I and plumage characteristics among saltmarsh birds are similar to those of non-saltmarsh birds except the correlation between *ventral background color* is −0.72 (cf. −0.07 for non-saltmarsh birds) and, overall, the correlations are stronger. Individuals with large PCoA II scores tend to have small ventral spots with pale background color, extensive throat spotting, broad crown spots, and little yellow in the supercilium.

The relationship among the samples in the bivariate space defined by PCoA I and PCoA II scores varied (Fig. 2). Saltmarsh birds are

TABLE 1. Pearson's correlations between PCoA I and PCoA II and 11 measures of plumage variation among populations of Savannah Sparrows.

Variable	All (n = 1,738)			Non-saltmarsh (n = 1,530)			Saltmarsh (n = 225)		
	I	II	%[a]	I	II	%	I	II	%
Ventral spot size	0.30	−0.71	59.4	−0.54	0.14	31.2	−0.59	−0.53	62.9
Ventral spot color	−0.21	−0.51	30.4	−0.42	0.04	17.6	−0.84	−0.17	73.5
Extent of spotting	0.36	−0.66	56.6	−0.50	0.21	29.4	−0.41	−0.13	18.5
Ventral background color	0.25	−0.44	25.7	−0.07	0.19	3.6	−0.72	−0.52	78.8
Throat spotting	−0.17	−0.69	50.5	−0.61	0.69	84.8	−0.54	0.36	32.2
Undertail covert color	0.17	−0.26	9.7	−0.12	0.19	3.7	−0.09	−0.27	8.1
Yellow in superciliuim	−0.75	−0.23	61.6	−0.71	−0.25	56.7	−0.69	−0.05	47.9
Back spot color	−0.55	−0.46	51.5	−0.59	−0.03	34.8	−0.86	0.24	79.8
Color of back feather edges	−0.87	0.05	76.0	−0.42	−0.23	22.9	−0.83	0.21	73.3
Median crown stripe	0.86	−0.18	77.2	0.48	0.63	62.7	0.37	−0.32	23.9
Crown spot width	−0.73	−0.18	56.5	−0.58	−0.13	35.3	−0.56	0.52	58.4
variance explained (%)	40.5	17.3		28.4	15.0		47.7	11.9	

[a] Percentage of variable explained in the two PCoA axes.

clustered away from the others (Fig. 2A), and differ from typical Savannah Sparrows by having little yellow in the supercilium, pale edges to the back feathers, and an indistinct or thin median crown stripe with small crown spots. Birds with large PCoA II scores are pallid with reduced spotting (Sable Island and Puerto Peñasco), whereas those with small scores are darkly colored with extensive spotting (San Diego and Guerrero Negro). The sample from Sable Island is an outlier on Axis I, and Morro Bay on Axis II (Fig. 2B) when the saltmarsh birds (with the exception of Morro Bay) are removed and the principal coordinates recalculated.

Saltmarsh Savannah Sparrows.—Three localities were sampled from along the east coast of the Gulf of California (Fig. 2C): Puerto Peñasco (northern Sonora), Bahía Kino (central Sonora), and El Molino (central Sinaloa). There are five samples from the Pacific coast (Fig. 2C): Morro Bay (central California), San Diego (southern California), Bahía San Quintin (northern Baja California), Guerrero Negro (southern Baja California), and Bahía Magdalena (central Baja California Sur). The San Benito sample is from Islas San Benito, 140 km west of Guerrero Negro in the Pacific Ocean. These are the only Savannah Sparrows in this region that are not found in saltmarshes with the exception of a small population on Islas Todos Santos off Ensenada, northwestern Baja California. Instead their habitat consists of sparse xerophylic vegetation. Thus, they are ecologically different from the mainland saltmarsh-dwelling individuals, but presumably descended from saltmarsh colonists.

The discriminant functions analysis (DFA) of the nine saltmarsh samples revealed highly significant differences. The first six PCoA scores, which were used as variables in this analysis, explain 80% of the plumage variation among these samples (Fig. 2C). Overall, the DFA correctly identified ~69% of the 225 individuals to the correct localities with 100% of the individuals correctly identified in three of the samples: Puerto Peñasco, Bahía Kino, and Islas San Benito (Table 2). Two of the specimens from El Molino were identified as being from Bahía Kino (north along the Gulf Coast), and one from Bahía Magdalena (the southern-most from Baja California) while

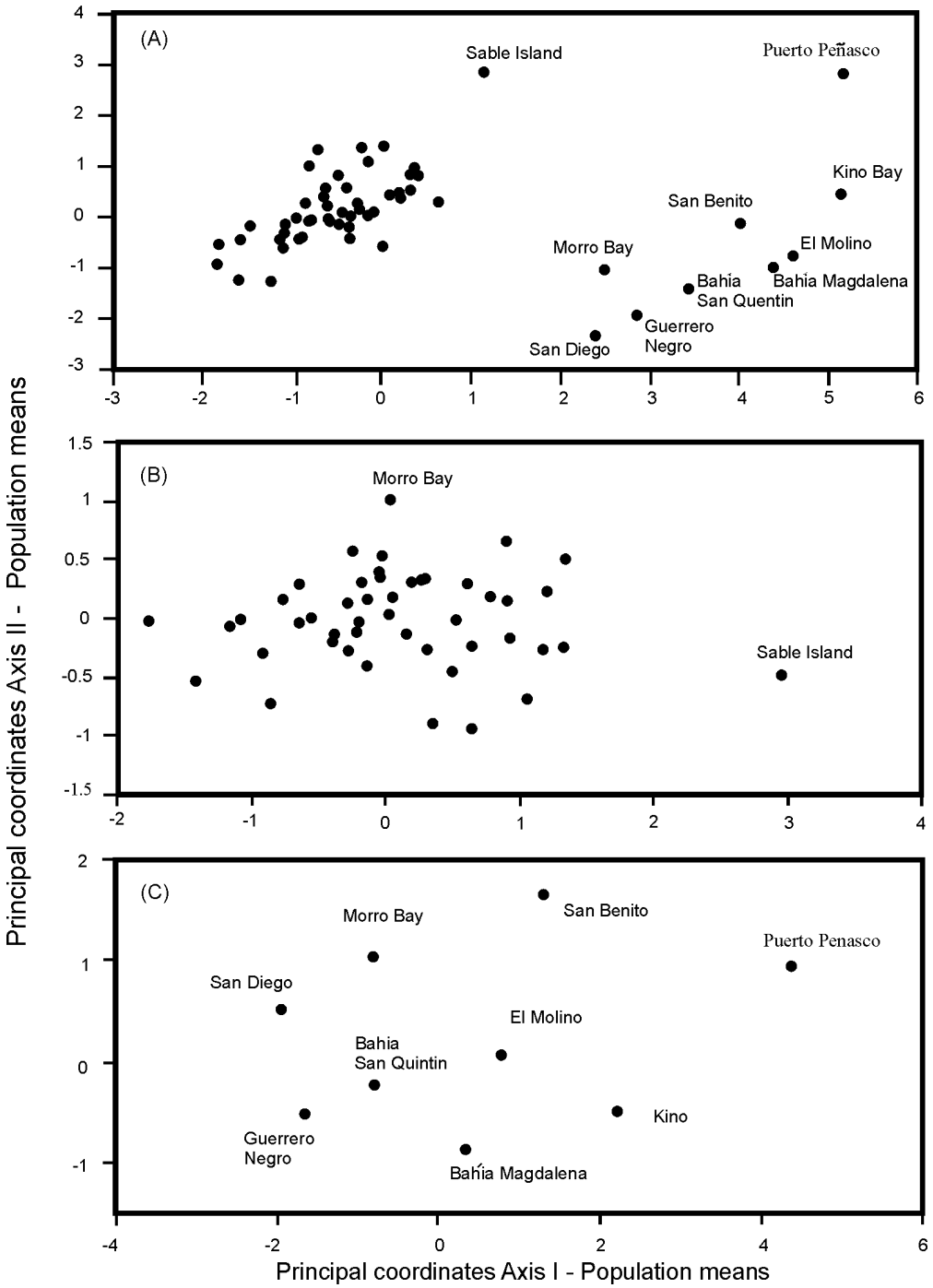

FIG. 2. (A) Bivariate plot of all 55 samples of Savannah Sparrows in the space defined by the first two principal coordinate axes; (B) bivariate plot of only the non-saltmarsh samples of Savannah Sparrows; and (C) bivariate plot of only the saltmarsh samples of Savannah Sparrows. Morro Bay in included in both (B) and (C).

TABLE 2. Actual vs. predicted identification of Saltmarsh Savannah Sparrows.

		Predicted group membership								
Actual group	*n*	Pto. P	Kino	Molino	Mag.	G. N.	San Q.	San D.	Morro	San B.
Pto. Peñasco	14	14	0	0	0	0	0	0	0	0
Bahía Kino	25	0	25	0	0	0	0	0	0	0
El Molino	22	0	2	17	1	0	0	0	2	0
B. Magdalena	32	0	1	5	19	1	2	4	0	0
Guerrero Negro	37	0	0	1	3	24	6	2	1	0
B. San Quintin	31	0	0	0	2	8	15	5	1	0
San Diego	33	0	0	1	6	3	3	18	2	0
Morro Bay	17	0	0	1	1	0	2	3	10	0
I. San Benito	14	0	0	0	0	0	0	0	0	14

two were identified as being from Morro Bay. The sample from Bahía San Quintin had the lowest number correctly identified, but most of the misidentified individuals were identified as being from adjacent areas (i.e., San Diego, California and Guerrero Negro, Baja California). None of the birds from Guerrero Negro was identified as being from Islas San Benito.

The sparrows from coastal Sinaloa and Sonora in the plots of PCoA I versus PCoA II (Fig. 2C) are plotted to the right on PCoA I. They are relatively pale with indistinct median crown stripes (Fig. 2C, Table 1). Variation on the PCoA I axis is clinal along the coast of the Gulf of California with birds from Puerto Peñasco the palest and those from El Molino the darkest. The birds from Islas San Benito and Bahía Magdalena are similar to those from El Molino on this axis; the sparrows from San Diego and Guerrero Negro are the darkest with the most distinct crown stripes and relatively more yellow in the supercilium. The birds with positive values on PCoA II tend to have small ventral spots with pale ventral coloration, an indistinct median crown stripe, and spotted throats. There is a progressive decrease in the values of PCoA II scores along the Pacific coast from Morro Bay south to Bahía Magdalena. Birds from Islas San Benito are distinct in coloration and differ from those from Guerrero Negro on the adjacent mainland, which are darker overall (especially ventrally) and have large ventral spots. The Islas San Benito birds also have little, if any, yellow in their supercilium as opposed to mainland Pacific coastal birds; this variation is not reflected on PCoA II.

Relationship Between Plumage and Environmental Variation.—The analyses of the relationship between plumage variation and climate are limited to samples collected from non-saltmarsh sites (in these correlations, Morro Bay is not included with the non-saltmarsh sites), due to the lack of climatic data for many sites in Mexico. There is little variation in the geographical characters (latitude, longitude, elevation) among the saltmarsh localities (all are from the west coast, near sea level), and these samples are not analysed with the others.

There was little latitudinal variation in PCoA I scores (Table 3). However, there was significant positive correlation (Spearman's correlation) with longitudinal variation. Western Savannah Sparrows tend to be more pallid than eastern ones and have relatively indistinct or narrow median crown stripes. Sable Island, at 60° longitude, has the largest PCoA I score of all of the non-saltmarsh birds and is the exception; others with relatively large values include those from Utah, Nevada, eastern Washington, and eastern California (i.e., in the Great Basin). There is also a positive correlation between elevation and PCoA I scores, probably because most of the western localities, which have relatively high scores, are at high elevations. However, Sable Island, which is near sea level, is again the exception. None of the correlations between average annual rainfall and PCoA scores is significant, but there is a significant negative correlation between average June rainfall and PCoA I (Fig. 3A); Savannah Sparrows are relative pallid where there is little summer rainfall (i.e., in the Great Basin). PCoA I scores are positively correlated with all of the measures of summer temperature (Table 3, Fig. 3A, B, C), as they are pale where it is hot (and dry; Table

TABLE 3. Pearson's and Spearman's correlations (exact probability) between latitude, longitude, elevation, and climatic variables and sample averages of the first two PCoA axes (I, II) of Savannah Sparrows from non-saltmarsh localities.

Variable	*n*	Pearson's		Spearman's	
		I	II	I	II
Latitude	46	−0.10 (0.49)	0.40 (0.01)	−0.18 (0.23)	0.41 (0.01)
Longitude	46	0.20 (0.19)	0.39 (0.01)	0.34 (0.02)	0.38 (0.01)
Elevation	46	0.33 (0.03)	−0.38 (0.01)	0.40 (0.01)	−0.24 (0.11)
Average annual rainfall	42	−0.08 (0.62)	−0.07 (0.67)	−0.17 (0.29)	−0.14 (0.38)
Average June rainfall	42	−0.25 (0.11)	−0.26 (0.09)	−0.31 (0.04)	−0.35 (0.02)
Average minimum summer temperature[a]	42	0.41 (0.01)	−0.27 (0.09)	0.43 (0.005)	−0.33 (0.04)
Average maximum summer temperature	42	0.45 (0.01)	−0.31 (0.04)	0.50 (0.001)	−0.44 (0.01)
Extreme minimum summer temperature	42	0.41 (0.01)	0.08 (0.63)	0.39 (0.01)	0.07 (0.68)
Extreme maximum summer temperature	42	0.28 (0.07)	−0.46 (0.01)	0.38 (0.01)	−0.40 (0.01)

[a] June, July, and August.

3) although these correlations (especially with rainfall) are not particularly high. Coloration of birds from Sable Island is the exception to these trends; they are pallid, but summer weather conditions there are cool and mesic.

Savannah Sparrows with relatively large PCoA II scores have a heavily spotted throat and a relatively indistinct median or narrow crown stripe (Table 1). PCoA II scores were positively correlated with latitude and longitude, and sparrows with these features tend to be found in the north and in the west (Table 3). There is a negative correlation between PCoA II scores and average June rainfall (Fig. 3A), and three measures of June temperature (Fig. 3B, 3C, and 3D). Savannah Sparrows tend to exhibit sparse throat spotting and a distinct crown stripe where it is hot and dry in the summer.

DISCUSSION

Non-saltmarsh Savannah Sparrows.—The sample of Savannah Sparrows from Sable Island, Nova Scotia, is clearly separable from the others on the basis of plumage characters used in these analyses. However, considerable clinal variation exists among the other samples of non-saltmarsh Savannah Sparrows, and there is overlap among localities. This is especially true among geographically contiguous samples. This is not surprising because, with the exception of birds nesting along the California coast, all of the populations are migratory and site fidelity is not particularly high (except in island populations) (Bédard and LaPointe 1984, Wheelwright and Rising 1993). Moreover, in many parts of their range they nest in habitats that are transitional and ephemeral (recent burns, pastures, etc.), necessitating dispersal.

Savannah Sparrows are relatively pale and have little yellow in their supercilium where summers are hot and relatively dry, especially in the Great Basin, specifically in Utah, Nevada, eastern California, and eastern Washington. They are also relatively pale at high elevations, but this is likely an artifact of western samples being taken at relatively high elevations in relatively hot and dry places. Vegetation in those areas tends to be sparse and soils tend to be pale. Savannah Sparrows are ground-feeding birds and are likely selected to match their background, which is relatively pale in arid areas and dark in mesic ones. The pallid birds from Sable Island would appear to be an exception as that location is neither xeric nor hot. However, Sable Island is composed of white sand and supports sparse vegetation, and Savannah Sparrows that breed there winter only in coastal dunes along the northern Atlantic coast where the background color is pale. Thus, although climatic correlates are different, in both cases it would seem that evolution of pallor reflects selection for crypsis. Hence, these birds follow the trend described by Gloger's Rule (Zink and Remsen 1986).

Savannah Sparrows also tend to have distinct median crown stripes and spotted throats in the east and at high latitude, and indistinct crown stripes and reduced spotting on the throat in the west and at low latitude, where

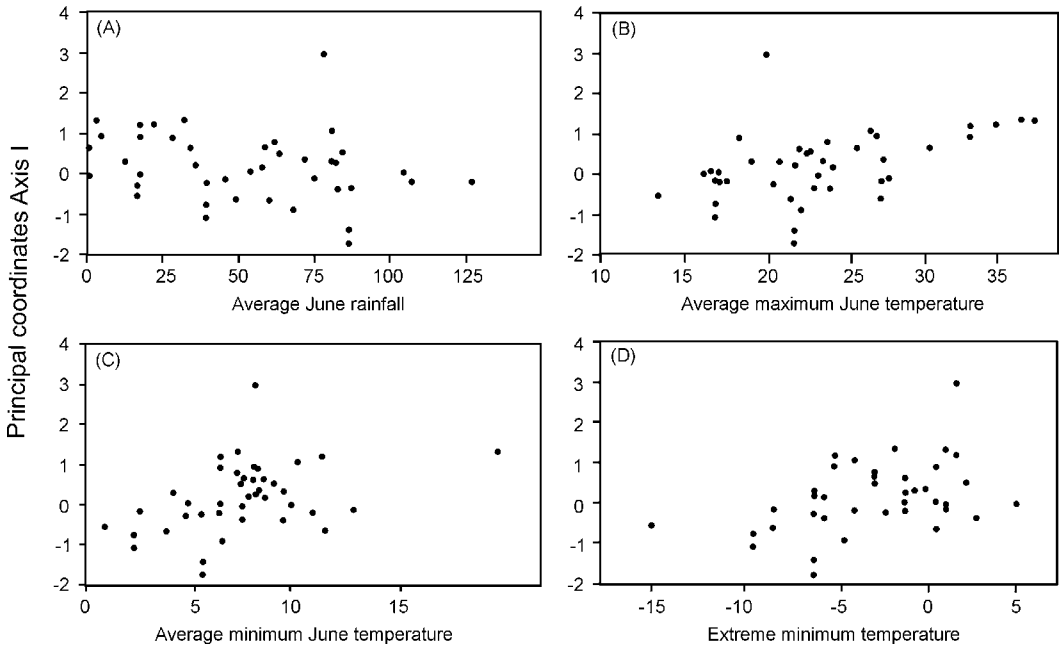

FIG. 3. Plots of the principal coordinate I scores vs. measures of: (A) June rainfall (mm); (B) average maximum June temperature (°C), (C) average minimum June temperature, (D) extreme minimum June temperature.

it is relatively hot and dry in summer. This may reflect crypsis, but an explanation based on habitat is not obvious.

Saltmarsh Savannah Sparrows.—Populations of saltmarsh Savannah Sparrows are much more clearly separated from each other than those in non-saltmarsh habitats. This is not surprising as they are generally sedentary, and live in habitat that is discontinuous and relatively permanent. Post-breeding large-billed Savannah Sparrows wander south to Sinaloa and Cabo San Lucas, Baja California Sur and to the islands in the Gulf of California, and *P. s. rostratus*, from the Gulf of California, winter north to the coast of southern California and the Salton Sea (van Rossem 1947, Rising and Beadle 1996).

The pale sparrows (*P. s. rostratus*) along the xeric coast of northern and central Sonora occur in sparse halophytes (*Frankenia*, *Allenrolfia*, *Atriplex*, *Salicornia*, *Suaeda*, *Cressa*, *Distichlis*, *Monanthochloe*, and *Batis*), whereas other populations of saltmarsh sparrows, with the exception of those on Islas San Benito, occur in dense marsh vegetation (in Bahía Magdalena they also occur in mangroves [*Rhizophora mangle*]). The pallid coloration of birds from coastal Sonora doubtless reflects the openness of the vegetation; Savannah Sparrows there are frequently seen on the ground between patches of vegetation and, on occasion, away from saltmarshes. The birds from Islas San Benito are more pallid than those from the adjacent mainland (140 km east at Guerrero Negro). These islands are rocky with sparse vegetation and no saltmarshes. These sparrows are commonly seen in coast desert thorn (''frutilla'', probably *Lycium californicum*), and occasionally along the beach feeding in the wrack. They differ structurally (large billed) and in plumage from mainland birds. They seemed to feed exclusively on *Lycium* (the plants did not have their red fruit, and the material in the gut was greenish with small black seeds) during the third week of April 1999 (JDR, pers. obs.), whereas birds at Guerrero Negro were eating animal matter (JDR, pers. obs.). Thus, ecology and behavior of Savannah Sparrows from the island is strikingly different from that of mainland Savannah Sparrows, and they do not appear to breed at the same time, at least during

some years. JDR found birds nesting in late April with active nests in May at Guerrero Negro. Nesting is much earlier on Islas San Benito (Jan–Feb; van Rossem 1947) in some years, but in 1999 nesting did not seem to have started by the third week of April and no fledged young were seen (JDR, pers. obs.).

Traditionally, Savannah Sparrows from Morro Bay have been placed in the subspecies *P. s. alaudinus*, which breeds from Humboldt Bay south to Morro Bay along the California coast (AOU 1957). Birds from Humboldt Bay in this study were not from saltmarshes, although Savannah Sparrows breed in saltmarshes along the coast of northern California. Morphologically, birds from Morro Bay are intermediate between birds from Humboldt Bay and San Diego, but closer to San Diego (Rising 2001). We included Morro Bay birds, for these reasons, both with the saltmarsh and non-saltmarsh birds in this study. We found them to be more like the saltmarsh birds from southern California than typical Savannah Sparrows.

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APPENDIX. Sample localities and numbers of Savannah Sparrows scored for coloration.

Locality	*n* (M)	*n* (F)	Subspecies	Latitude	Longitude	Elev.(m)
Nova Scotia: Sable Island	24	12	*princeps*	44.00	60.00	16
Nova Scotia: Halifax Co., Lawrencetown Beach, Seaforth	12	10	*savanna*	44.67	63.67	16
Nova Scotia: Pictou Co., River John	22	12	*savanna*	45.84	63.00	16
Newfoundland: Pasadina, Steady Brook, Doyles	12	10	*labradorius*	49.00	57.67	61
Newfoundland: Parson's Pond, Bellburns	12	7	*labradorius*	50.00	57.67	16
Prince Edward Island: Prince Co., Bedeque	21	6	*savanna*	46.33	63.67	3
New Brunswick: Charlotte Co., St. Andrews	20	15	*savanna*	45.15	67.00	16
Quebec: Matane Co., Matane	15	13	*savanna*	48.84	67.5	305
Quebec: Magdalen Islands	26	13	*savanna*	47.50	61.75	3
Quebec: Terr. Nouveau Quebec, Kuujjuaq (Fort Chimo)	16	21	*labradorius*	58.16	68.33	34
West Virginia: Preston Co., Brandonville	20	11	*savanna*	39.58	79.58	610
Ontario: Peel Co., Wildfield, and Kleinburg	37	7	*savanna*	43.84	79.67	120
Ontario: Lampton Co., Wallaceburg	33	14	*savanna*	42.67	82.33	183
Ontario: Algoma Dist., Sowerby	21	9	*oblitus*	46.33	83.24	183
Ontario: Kenora Dist., Sutton Ridges	12	2	*labradorius*	54.50	84.92	100
Ontario: Cochrane Dist., Moosonee	40	28	*labradorius*	51.33	80.67	9
Ontario: Kenora Dist., Attawapiskat	31	20	*labradorius*	53.00	82.33	6
Ontario: Kenora Dist., Winisk	44	20	*labradorius*	55.33	85.16	8
Ontario: Thunder Bay Dist., Kaministikwia	14	7	*oblitus*	48.45	89.67	45
Manitoba: Delta	25	12	*nevadensis* > *oblitus*	50.16	98.33	260
Manitoba: The Pas	19	6	*oblitus* > *nevadensis*	53.84	101.33	275
Manitoba: Gillam	17	6	*oblitus*	56.33	94.67	150
Manitoba: Churchill	28	16	*oblitus*	58.84	94.16	30
Northwest Terr.: Yellowknife	13	9	*anthinus* > *nevadensis*	62.50	114.33	180
Nunavut: Kugluktuk (Coppermine)	30	14	*anthinus*	67.84	115.16	30
Northwest Terr.: Norman Wells	13	9	*anthinus*	65.33	126.84	72
Northwest Terr.: Inuvik	13	10	*anthinus*	68.33	133.67	30
Saskatchewan: Maple Creek, Consul, Estuary	18	0	*nevadensis*	50.00	109.50	1,100
Saskatchewan: Courval, Dundurn, Gurn	16	4	*nevadensis*	50.00	106.00	880
Alberta: Milk River	24	7	*nevadensis*	49.16	111.67	1,050
Alberta: Grande Prairie	28	17	*nevadensis*	55.16	118.84	670
Alaska: Fairbanks	14	3	*anthinus*	65.00	147.67	305
Alaska: Wasilla	25	19	*anthinus*	61.16	150.00	15
Alaska: Aleutian Is., (Umnak Island)	28	23	*sandwichensis*	55.33	168.00	61
Alaska: Cold Bay	11	7	*sandwichensis*	55.00	163.00	15
Alaska: Port Heiden	16	13	*sandwichensis* > *anthinus*	56.83	159.00	15
Alaska: Middleton Island	16	15	*anthinus*	59.50	146.33	17
Wyoming: Sheridan Co., Sheridan	24	15	*nevadensis*	44.78	107.17	1,372

APPENDIX. Continued.

Locality	*n* (M)	*n* (F)	Subspecies	Latitude	Longitude	Elev.(m)
Utah: Rich Co., Woodruff	42	13	*nevadensis*	41.50	111.16	1,921
Utah: Utah Co., Elberta	16	3	*nevadensis*	40.00	111.92	1,402
Nevada: Elko Co., Halleck	24	7	*nevadensis*	40.87	115.33	1,646
Washington: Lincoln Co., Creston	14	15	*nevadensis*	47.67	118.50	700
California: Inyo Co., Owens Lake, 27 km S Lone Pine	16	13	*nevadensis*	36.50	118.00	1,085
California: Humboldt Co., Eureka	22	11	*alaudinus*	40.67	124.22	3
California: San Luis Obispo Co., Morro Bay	10	7	*alaudinus* > *beldingi*	35.33	120.84	3
California: San Diego Co., Soledad Creek and Rio Santa Margarita	18	15	*beldingi*	33.33	117.84	3
Baja California N.: Bahia San Quintin	18	13	*beldingi*	30.33	116.00	3
Baja California N.: Islas San Benito	6	8	*sanctorum*	28.33	115.50	10
Baja California S.: Guerrero Negro	24	13	*anulus*	28.00	114.16	3
Baja California S.: Bahia Magdalena, San Carlos and Estero Salinas	14	18	*magdalenae*	24.33	111.16	3
Sonora: Puerto Peñasco	11	3	*rostratus*	31.33	113.33	3
Sonora: Bahia Kino	13	12	*atratus*	28.84	112.00	3
Sinaloa: El Molino	16	6	*atratus*	24.50	107.40	3
Jalisco: Charco Redondo, 32 km W Ojuelos de Jalisco (Cienega de Mata)	16	6	*rufofuscus*	21.67	101.84	2,100
México: 1/2 km N. Lerma (Lerma Marshes)	21	6	*rufofuscus*	19.33	99.50	2,560
Totals (55 samples)	1,111	611				