1963, Zink and Remsen 1986). The considerable debate about these "ecogeographic rules" (McNab 1971, Zink and Remsen 1986) has focused on two separate and unrelated issues: (1) do these trends occur in birds (and mammals) more often then we would expect to find by chance, and (2) if so, why? It is surprisingly difficult to answer the first question, both because it is, in practice, difficult to measure body size (Rising and Somers 1989) and because there have been few in-depth studies of geographic size variation, especially across the entire range of a species. However, at least so far as North American birds are concerned, it does appear that the majority of species that show geographic variation in size follow Bergmann's Rule, and this is especially so for non-migratory species, although many species show the trend only weakly (James 1970, Zink and Remsen 1986). The traditional answer to the second question has been that an individual that has a relatively large body and relatively small appendages has a thermoregulatory advantage in cold climates, and conversely one with a relatively slight body and large appendages has a similar advantage in warm ones (Mayr 1963). However, it has been argued that body size is far more significantly influenced by food size and abundance (McNab 1971), and by interspecific competition (Schoener 1969, McNab 1971), the latter being taken as perhaps the principal reason why populations on islands tend to be larger on average than their mainland counterparts (Case 1978).

Because the Savannah Sparrow breeds in a wide range of climates, occurs both in species-rich and species-poor sparrow guilds, and is found on the American mainland as well as on several islands, it is an ideal species to use to test these hypotheses about the evolution of geographic variation in size and shape in birds.

MATERIALS AND METHODS

I measured a total of 2281 Savannah Sparrows (1459 males, 822 females) that were collected from 65 different sites from virtually throughout the species' range (Fig. 1; Table 1). These birds were all collected during the breeding season, had little fat, and had enlarged and apparently active gonads; in all probability, most if not all were breeding birds that were collected at their breeding site.

Each was prepared as a skin and skeletal specimen, and is in the collection of the Royal Ontario Museum. I made 24 skeletal measurements on each specimen, to the nearest 0.1mm. These were skull length (to the tip of the premaxilla; all measures were maxima), skull width, premaxilla length and depth, narial, premaxilla, and interorbital widths, mandible length, gonys length, mandible depth, coracoid and scapula length, femur length and width, tibiotarsus, tarsometatarsus, humerus, ulna, carpometacarpus, and hallux lengths, sternum length and depth, keel length (from apex to posterior margin), and synsacrum width. I made all measurements, and they are the same that I have used in other studies (Rising 1987, 1988). These measurements are illustrated in Robins and Schnell (1971). I also took five measurements on the skins, and noted the weight of each specimen. Some of these data are published elsewhere (Wheelwright and Rising 1993, Rising 1996). When it was not possible to measure all 24 skeletal variables, I estimated missing or broken elements using multiple regression (BMDP Statistical Software, Method = Twostep; Dixon 1983); if a specimen was missing more than three measurements, the specimen was omitted from multivariate analyses that involved any of the missing values.

The Savannah Sparrow is sexually dimorphic in size (Rising 1987) so I have assessed patterns of geographic variation for the two sexes separately. ANOVA was used to test for geographic variation for each variable; for these analyses, only reasonably large samples ($N > 9$) were used. I identified statistically homogeneous subsets of samples using an *a posteriori* Student-Newman-Kuels (snk) multiple range test (SAS PROC ANOVA; SAS Institute 1985).

To reduce the dimensionality and complexity of the data, I used a Principal Components Analysis, operating on the matrix of correlations among the 24 characters (Rohlf et al. 1982); this is a standard procedure in morphometric analyses, and makes little difference in practice whether a correlation or covariance matrix is used (Rising and Somers 1989). ANOVA was used to test for geographic variation in each of the first three Principal Components (PCs), again using only the larger samples. I did not use additional PCs as their eigenvalues were small and were of similar magnitude.

To assess the significance of differences among populations in multivariate space, I used Discriminant Functions Analysis (DFA; SPSSX Program Discriminant; SPSS 1986). To do DFA among the larger samples (excluding those from saltmarsh localities, see below), I reduced the number of variables to 12, using skull length and width, premaxilla length and width, and mandibular, gonys, coracoid, femur, tibiotarsus, ulna, hallux, and keel lengths. I selected these variables because they had relatively low within-group variances, and included measures of the different parts of the birds' bodies (e.g. head size, bill size, wing size, and leg size). Birds missing any of these variables were omitted from analyses, and only samples with $N > 12$ were used: for males, this included 1152 individuals from 47 different localities; for females, 501 individuals from 27 localities.

With the exception of the sample from Morro Bay, California (which is intermediate in size between the resident "Belding's" sparrows of the saltmarshes of southern California and Baja California and non-saltmarsh sparrows), the Savannah Sparrows from the saltmarshes of southern California (San Diego), Baja California, Sinaloa, and Sonora were not included in these analyses as they are very different in size and shape (see RESULTS). Because several of the saltmarsh samples are relatively small, to assess the significance among differences among these, I used a step-wise DFA, limiting the number of steps to eight. The Morro Bay sample was included in both sets of analyses to facilitate comparisons. For males, the eight variables selected in the step-wise analysis were: premaxilla depth and width, mandible length and depth, tibiotarsus and ulna length, sternum depth, and synsacrum width. For females: premaxilla length and depth, mandible depth, tarsometatarsus, ulna, sternum, and keel lengths, and synsacrum width.

To relate patterns of variation to the climatic environment and geography, I calculated Spearman's non-parametric correlations and regressed multivariate measures of size and shape from the Principal Component (PC) and Discriminant Function (DF) analyses (see RESULTS), namely PC 1, PC 2, DF 1, and DF 2 scores, with measures of the (1) average annual precipitation, (2) average June precipitation, (3) average minimum summer (June–August) temperature, (4) extreme low summer temperature, (5) extreme high summer temperature, (6) latitude, (7) longitude, and (8) elevation. The climatic data for each site were based on the nearest weather station of similar elevation, and were obtained from Canadian and United States government sources (Environment Canada 1973, National Oceanic and Atmospheric Administration 1983), and are given in Table 1. I also related these to four measures of "sparrow" diversity: (1) the number of potentially competing species (e.g., other sparrows [Emberizinae], Bobolinks [*Dolychonyx oryzivorus*], meadowlarks [*Sturnella* spp.]) that I found in the fields with Savannah Sparrows ("All Species"), (2) the number of species of sparrows in these fields ("Sparrows"), (3) a measure of the abundance of potentially competing species that I found in the fields ("Abundance"; using my field notes, the abundance of each species was scored as: 3, abundant; 2, common; or 1, present, but not common, and the sum of all of the species present was used in these analyses), and (4) the number of species of Fringillidae reported breeding in the general vicinity of the collecting site ("Cook's Index"; Cook 1969). The Fringillidae of Cook (1969) included the Cardinalini, Emberizini, and Carduelini of Sibley and Monroe (1990), or the Emberizidae, Cardinalidae, and Fringillidae of the AOU Check-list (1998); that is, an apparently paraphyletic assemblage of phenetically similar, conical-billed birds. If competition were to affect the evolution of body size and shape, phenetically similar species (whether closely related or not) represent potential competitors. In these analyses I omitted the samples from Lerma and Charco Redondo, Mexico, as I did not have comparable information on the environment or species diversity for those sites.

Because the environmental variables selected are to varying degrees correlated with each

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