Studies in Avian Biology No. 23:1–65, 2001.

ABSTRACT

I analyzed variation in 24 measurements on the skeletons of 2281 breeding Savannah Sparrows (*Passerculus sandwichensis*) from 65 different localities to describe patterns of geographic variation in size and shape. The samples come from virtually throughout the species' breeding range, from northern Canada and Alaska, south to the northeastern United States, central Great Plains, and in the highlands of the west, south to central Mexico.

For the most part, the interpopulational variation in size is clinal, with considerable overlap among geographically contiguous populations. The most striking finding of this study is that Savannah Sparrows are large on islands, as would be predicted by some theory.

The largest Savannah Sparrows are from Sable Island, Nova Scotia, and the Aleutian Islands, Alaska. Although both are islands, these two areas are ecologically different in many ways. On Sable Island, the Savannah Sparrow is the only breeding passerine, whereas on the Aleutians, Lapland Longspurs (*Calcarius lapponicus*) as well as Savannah Sparrows are abundant, and seemingly found in the same habitat; Song Sparrows (*Melospiza melodia*) and Gray-crowned Rosy-Finches (*Leucosticte tephrocotis*) also breed there, but generally in different habitats. Thus, one site is sparrow poor, and the other relatively sparrow rich. Savannah Sparrows are also relatively large on the Magdalen Islands, Quebec, and on Middleton Island, Alaska. On the Magdalen Islands, Nelson's Sharp-tailed Sparrows (*Ammodramus nelsoni*) and Swamp Sparrows (*M. georgiana*) overlap with Savannah Sparrows in habitat use, and Song Sparrows are common as well. On Middleton Island, Fox Sparrows (*Passerella iliaca*) and Lapland Longspurs are both common, as are Savannah Sparrows. Thus, while Savannah Sparrows tend to be small where species diversity is highest (see below), this alone does not appear to be an adequate explanation for their large body size on islands. One characteristic of all of these islands is that they have long, cool, and moist summers; this may result in a predictable and fairly rich food supply. On Sable Island, Savannah Sparrows are often socially polygynous, which, at least in many species, leads to enhanced competition for high quality territories and enhanced body size, at least in males, but sexual size dimorphism is not enhanced there.

There is also significant geographical variation in bill shape, with western Savannah Sparrows having relatively more slender bills. Variation in bill shape, however, is clinal and slight, and there is a great deal of overlap among populations.

I calculated correlations between various multivariate measures of size and shape (derived from Discriminate Function and Principal Component analyses) and a variety of measures of climatic variation, latitude, longitude, elevation, and species diversity. Savannah Sparrows tend to be large where it is moist, and small where it is hot and dry. They are also smallest in the west and at high elevations, and large where they coexist with few other sparrow-like birds. These trends remain even when the samples from islands, which are outliers, are removed from the analyses. The significant negative relationship between body size and species diversity supports hypotheses that relate body size to interspecific competition. Overall, there is no significant relationship between body size and latitude, and although they tend to be small where maximum summer temperatures are highest, the species does not follow the trend described by Bergmann's Rule. This is true when all samples are considered as well as when the eastern and western samples are analyzed separately

Savannah Sparrows from the coastal saltmarshes of Sinaloa and Sonora also have large body sizes. They are the only sparrow-like birds that breed in these saltmarshes, and they are abundant in them. They also have notably large bills, probably reflecting their diet, which includes fiddler-crabs (*Uca*).

Interpopulational variation in wing length is related to migratory status: birds from sedentary populations, where only short-distance movement occurs, have relatively short wings; those that presumably migrate the greatest distances have relatively long wings. The birds with the relatively longest wings are from the northern Great Plains and high elevations.

The location of the two inland Mexican populations in multivariate space is interesting, in that Lerma, México, is close to the samples from northeastern North America, whereas Charco Redondo, Jalisco, is close to birds from the Northwest Territories. Although Lerma and Charco Redondo are only about 500 km apart, Lerma is higher in elevation and more mesic than Charco Redondo.

There is also clinal variation in both body size and bill size among the non-migratory populations in saltmarshes along the Pacific Coast; the smallest birds are from Morro Bay, San Luis Obispo County, California, and the largest from Bahía Magdalena, Baja California Sur. The birds from coastal California have relatively gracile bills whereas those from Bahía Magdalena have stout bills.

Seventeen subspecies of Savannah Sparrows are generally accepted. Many of these have been named on the basis of coloration, which is not examined here, as well as body size and bill shape. *P. s. princeps,* from Sable Island, is large (and pale in coloration); my results show that they are significantly larger in size than birds from the adjacent mainland, but not different in shape, thus supporting this subspecific separation. *P. s. sandwichensis* from the Aleutian Islands and the tip of the Alaskan Peninsula are also significantly larger than (but similar in coloration to) those from the mainland, but

there is clinal variation down the Alaskan Peninsula; it is my opinion, therefore, that these should not be recognized as subspecifically distinct because there is no benefit to more or less arbitrarily delimiting taxa that overlap on a phenetic continuum. Viewed in this way my analyses support the recognition of only one subspecies of Savannah Sparrow from North America, *P. s. sandwichensis,* other than *P. s. princeps* and the birds resident in west coastal saltmarshes. The nine subspecies of saltmarsh Savannah Sparrows all seem to be clearly separable, and my analyses support the retention of these as valid and distinct taxa.

Key Words: Bergmann's Rule, geographic variation, islands, morphology, *Passerculus sandwichensis,* Savannah Sparrow, subspecies.

INTRODUCTION

Evolutionary biologists use studies of geographic variation as a means of testing hypotheses about adaptation, because the evolution of variation among populations of a species across its range, where is it exposed to a variety of different environments, reflects changes that could take place in a single population, exposed to changing environments, through time (Gould and Johnston 1972). Patterns of geographic variation within a species allow us to test hypotheses about adaptations to different environmental conditions, and thus by inference to environmental changes (biotic and abiotic) over time. Why, for example, do features such as body size, wing length, or bill size and shape differ across a species' range? If these differences reflect adaptations to the different environments to which the species is exposed, what are the selection agencies that have resulted in them? This perhaps cannot ever be answered by field studies, but correlations with environmental factors may point to possible experiments that could clarify these questions.

The Savannah Sparrow (*Passerculus sandwichensis*) is one of the commonest and most wide-spread of American songbirds. It breeds from Alaska, west to the Aleutian Islands (Amukta Island), eastward across northern Canada, south of the Arctic Archipelago and central Nunavat ("Northwest Territories"), south (in mountains) to eastern Tennessee and northern Georgia, southern Ohio, central Indiana, central Iowa (formerly or irregularly south to western Missouri and northwestern Arkansas), central Nebraska, and locally in the western mountains south in the Mexican highlands to Guatemala, and along the Gulf coast of Sonora and Sinaloa, and the Pacific Coast to southern Baja California (south to Bahía Magdalena; Rising 1996) (Fig. 1). Savannah Sparrows have been the subject of a number of systematic reviews, most importantly by Peters and Griscom (1938), van Rossem (1947), and Hubbard (1974), and a large number of subspecies have been described, indicating that there is considerable geographic variation in the species. The 5th Edition of the AOU Check-list (1957) recognized the "Ipswich" Sparrow (*P. princeps*), which breeds on Sable Island, Nova Scotia, as a separate species, and listed 16 subspecies of other Savannah Sparrows from Baja California, Canada, and the United States; a 17th subspecies has been described from Guatemala, but where breeding has not been confirmed. Most current lists (Sibley and Monroe 1990, AOU 1998) merge the Ipswich Sparrow with the other Savannah Sparrows. Most populations of Savannah Sparrows are migratory (Rising 1988, Wheelwright and Rising 1993). There are, however, resident populations in coastal saltmarshes in California and Baja California (five or six subspecies in the *P. s. beldingi* group), and coastal Sonora and Sinaloa (two subspecies in the *P. s. rostratus* group). Preliminary analyses of mitochondrial DNA indicate that the *P. s. rostratus* birds may best be recognized as a distinct species, and little if any