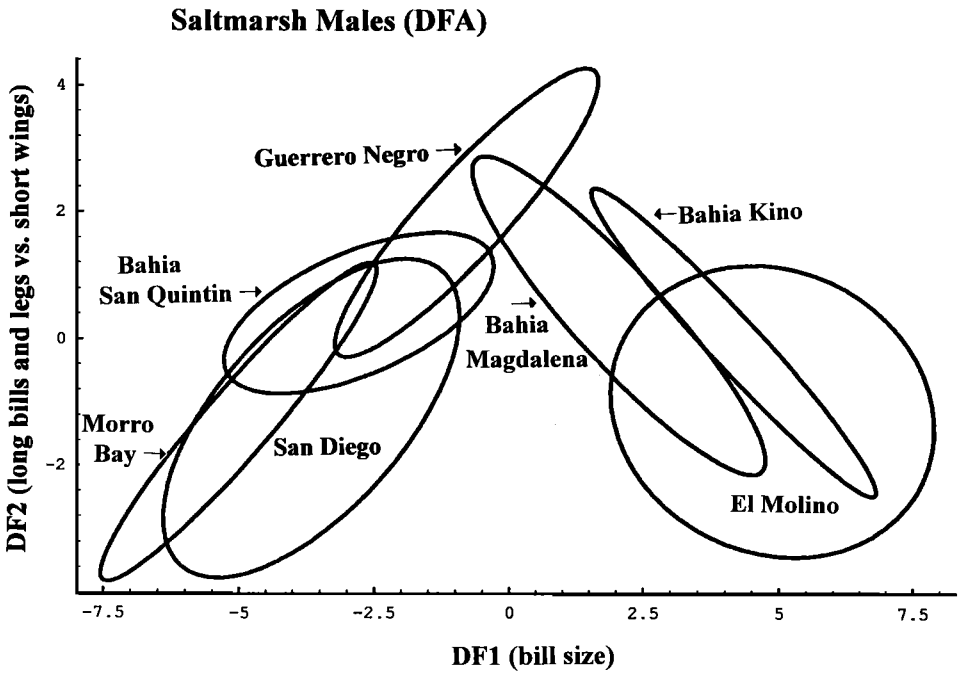

FIGURE 21. Samples of male Savannah Sparrows from coastal saltmarsh sites (95% confidence ellipses) in the space defined by DF 1 and DF 2. DF 1 explains 84.9% of the total variance and contrasts bill size and leg length with measures of wing size. DF 2 explains an additional 9.5% of the variance, and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

body size of *Anolis* and the number of species of *Anolis* (and other potentially competing lizards) on West Indian islands.

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 passerine bird that nests, 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 habitat. The Song Sparrows and rosy-finches on the Aleutians also have notably large body size (J. D. Rising, pers. obs.). 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 Savannah Sparrows in habitat, and Song Sparrows are common as well. On Middleton Island, Fox Sparrows (*Passerella iliaca*) and Lapland Longspurs are both common, as are Savannah Sparrows. (Although I have not analyzed them here, the Savannah Sparrows from the Islas San Benito, Baja California, Mexico, are also large in size, and they are the only sparrow-like species that breeds on those islands.) Thus, while Savannah Sparrows do tend to be small where species diversity is highest (see discussion below), this alone does not appear to be an adequate explanation for their large body size on islands. One common feature of all of the islands on which Savannah Sparrows live is that they have long, cool, moist summers; this may result in a predictable and fairly rich food supply. On Sable Island, the length of the breeding season seems to permit them to be multi-brooded (commonly three or four broods in a season) and also polygynous (Stobo and McLaren 1975), perhaps leading to enhanced competition for high quality territories. This is apparently generally true for islands in the Maritimes (Wheelwright and Rising 1993). Either competition with conspecifics for food or territories seemingly selects for large body size on these islands.

Murphy (1938) noted that 78% of insular races of North American songbirds have larger bills than their mainland counterparts, and cites Savannah Sparrow (both from the Aleutian Islands and Sable Island) as among those species illustrating this trend. My results confirm this for Savannah Sparrows, but it would appear that the bills are large because the birds are large; the bills are not noticeably larger relative to body size.

Savannah Sparrows are also somewhat larger from the mainland at Halifax, Nova Scotia, than in other maritime sites. This may reflect gene flow from Sable Island as "Ipswich" sparrows are sometimes reported in the Halifax area mated to mainland birds, although I know of no proof that any of these "mixed" pairs have successfully fledged young (Stobo and McLaren 1975; I. A. McLaren, pers. comm.). Other maritime Savannah Sparrows are also relatively large, but not so large as the Halifax ones.

The correlation analyses show that 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 are true even with the samples of the largest birds removed

from the analyses. The significant negative relationship between body size and species diversity supports hypotheses that relate body size with 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 seem to follow the trend described by Bergmann's Rule. Although the Bergmann trend is shown by many species that are migratory (James 1970), it is less prevalent among these than among sedentary species (Zink and Remsen 1986).

There is clinal variation in size eastward from the Aleutian Islands down the Alaska Peninsula, with the birds at the tip of the Peninsula (Cold Bay) being nearly as large as those from the Aleutians, and those from Port Heiden, midway down the Peninsula, being intermediate in size between the larger birds and those from the Alaskan mainland. This suggests that there is selection for large birds on the Aleutians and probably also on the Alaskan Peninsula, and selection for smaller birds on the mainland, and gene flow among these populations.

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. They also have notably large bills. Fiddler-crabs (*Uca*) are abundant in these marshes, and stomach analyses reveal that the Savannah Sparrows there commonly eat *Uca,* at least during the breeding season (February–March; J. D. Rising, pers. obs.). The large bill would seem to facilitate handling these relatively large prey items. *Uca* are also abundant in the marshes around Bahía Magdalena where the sparrows are also large-billed.

Interpopulational variation in wing length is related to migratory status: sedentary populations or 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. Rising (1988) supplied indirect, phenetic, evidence that in fall migration, birds tend to move more or less south, so that birds that breed in the Maritimes and northeast probably generally winter in the southeastern United States, whereas those that breed in the Great Plains probably generally winter from central Texas and California south into Mexico. A sparrow migrating from Coppermine in the northern Northwest Territories (near the northern-most part of their range in the western arctic) to northern Mexico would fly at least 4000 km, whereas one flying from Kuujjuaq in northern Quebec (near the northern-most part of their range in the eastern arctic) to northern Florida would fly about 3000 km. Banding data (although limited) do indicate that migratory movement is principally in a north to south direction (Brewer et al. 2000)

The arrangement of the two inland Mexican populations is somewhat surprising. Lerma, México, clusters with the samples from northeastern North America, and populations from Charco Redondo, Jalisco, with birds from the Northwest Territories. These two sites, however, are quite different ecologically; Lerma is higher in elevation and considerably more mesic than Charco Redondo. The separation between these two samples is on the PC 1 axis (Fig. 3); that is, the birds differ in size, but not shape. The sample collected at Charco Redondo was collected 7–8 May, and may have contained some migratory birds, although that is unlikely as many of the males were singing and had recrudescing testes, and all

had little fat. The sample from Lerma was collected on 11 May, and the condition of the birds was similar to that of the birds from Charco Redondo.

My results confirm that there is an east to west trend in bill size, with western birds tending to have more slender bills than eastern ones. There is, however, a tremendous amount of overlap among populations, and the total range of variation is slight.

There is also clinal variation in both body size and bill size among the populations in saltmarshes along the Pacific Coast, from Morro Bay, San Luis Obispo County, California, south to Bahía Magdalena, Baja California Sur, with the birds from Morro Bay and San Diego being the smallest, with relatively gracile bills, and those from Bahía Magdalena being the largest, with stout bills. The latter birds are intermediate in size and shape between the birds from Guerrero Negro and those from along the coast of the Gulf of California in Sonora and Sinaloa.

CONCLUSIONS

Savannah Sparrows show clinal variation in size, with birds from the northeast being slightly larger than those from the west. Additionally, they are strikingly larger on islands than from mainland sites. This is not obviously related to species diversity as the diversity of sparrows is high on some islands, and low on others. I speculate that the rather long breeding season and predictability of the weather select for individuals to be multibrooded, and this, in turn, may select for large body size. Savannah Sparrows tend to be larger in cool, moist areas, and small where it is hot and dry. They also tend to be smallest where they co-occur with several other sparrow species. They do not follow Bergmann's Rule. In general, measures of the climatic environment (summer temperature, precipitation) explain well patterns of morphological size variation.

Bill proportions vary subtly, with birds from the northeast having bills that average slightly more conical than those from the west.

Savannah Sparrows from isolated saltmarshes in California, Baja California, and coastal Sonora and Sinaloa show a great deal of interpopulational variation, with a clinal increase in body size from north to south along the Pacific Coast, and to a lesser extent along the east coast of the Gulf of California. Relative to other Savannah Sparrows, they have short wings and large bills, with the birds from the Gulf coast having the largest bills. As with body size, there is clinal variation with regard to these features, with an increase in bill size relative to body size from north to south along the Pacific Coast.

TAXONOMIC COMMENTS

Sixteen subspecies of Savannah Sparrows were recognized in the 5th edition of the AOU Check-list of North American Birds (AOU 1957). In addition, they treated the Ipswich Sparrow as a separate species, *Passerculus princeps.* More recently, *P. princeps* has been treated as a subspecies (AOU 1998), *P. s. princeps,* bringing the number of subspecies recognized to 17. These subspecies were described on the basis of a variety of attributes relating to size, shape, and coloration.

Philosophically, I do not see much value in delimiting subspecies on the basis of clinal variation, unless there are well-defined steps in the clines. Chopping clinal variation into subspecies results in more or less arbitrarily delimiting overlapping groups on a phenetic continuum. I see no virtue in naming subspecies