

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

when the only way they can be reliably separated is on the basis of locality. Trying to identify to subspecies migratory and wintering individuals of such subspecies is problematic and leads to circularity.

EASTERN SAVANNAH SPARROWS

Four subspecies of eastern Savannah Sparrows are generally recognized: *P. s. princeps*, which breeds on Sable Island, Nova Scotia, and winters along the Atlantic coast; *P. s. labradorius*, which breeds in Labrador, Newfoundland, and northern Quebec; *P. s. oblitus*, which breeds in northern Ontario west to eastern Keewatin; and *P. s. savanna*, which breeds south of *P. s. labradorius* and *P. s. oblitus*. Aldrich (1940) split *P. s. savanna* into *P. s. savanna* and *P. s. mediogriseus*, restricting the range of the former to Nova Scotia; *P. s. mediogriseus* was not recognized in the AOU Check-list (AOU 1957).

P. s. princeps are significantly larger than any other eastern Savannah Sparrows (Fig. 4); these birds are also noticeably more pallid in color than other Savannah Sparrows (J. D. Rising, pers. obs.).

P. s. labradorius was described by Howe (in Todd 1963) because of its supposed larger size on the basis of only three specimens from Labrador. The distinctiveness of *P. s. labradorius* was debated for some years until Austin (1932), on the basis of 18 adult specimens from Labrador, concluded that *P. s. labradorius* was both larger and darker than *P. s. savanna*, although his assessment of size appears to have been qualitative. Peters and Griscom (1938:452) examined over 150 specimens of this subspecies and upheld its validity as "A dark Savannah Sparrow with relatively stout bill, its depth more than half the length of the culmen." However, they examined only 30 birds from Newfoundland and Labrador, the rest being migrating or wintering birds. Todd (1963) noted that birds from the interior of Labrador are also, on average, dark as are those from the James Bay and Hudson Bay lowlands, and he extended the range of *P. s. labradorius* westward to Churchill, the type locality of *P. s. oblitus*, a subspecies named by Peters and Griscom in 1938 as a "... gray Savannah Sparrow with relatively stout bill, its depth more than half the length of the culmen ... [S]imilar ... to *P. s. labradorius* ... , but the browns much paler and reduced in area" (Peters and Griscom 1938:455). Todd (1963:673-674), on comparing series from Churchill and the Labrador Peninsula, commented that "the general more grayish tone of the upperparts [of the birds from Churchill], as against the more brownish appearance in the latter series [from Labrador] is apparent, but it is quite possible to select specimens from one series which resemble some in the other." *P. s. savanna* is said to be a "brown Savannah Sparrow with relatively stout bill; its depth equal to or exceeding half the length of the culmen. Similar to *P. s. oblitus* ... but browner throughout" (Peters and Griscom 1938:450).

My analyses show that there is clinal variation in size, with a decrease from east to west; birds from Churchill, southern Ontario, and West Virginia are significantly smaller than those from the northeast, but there is a great deal of overlap of individuals from different samples (Figs. 6 and 9). My measures of bill size are based on skeletal features (Appendices 1 and 2), and thus are not comparable to those used by Peters and Griscom (1938). The ratio of premaxilla length to premaxilla depth for birds from the northeast range from 1.7 to 1.8. The bill proportions of the sample from Kuujuaq, in Labrador, is 1.8; that from Churchill

1.7. Although no one (including myself) has published a quantitative analysis of color variation (J. D. Rising, in prep.), my studied opinion supports that of Todd (1963), namely that there is subtle clinal variation in color, but that intrapopulational variation is great, obfuscating even the clines. Thus, there seems to be little to support any of these eastern subspecies except for *P. s. princeps*, which is distinctive

WESTERN SAVANNAH SPARROWS

Other than the Savannah Sparrows that breed in coastal saltmarshes, six subspecies of western Savannah Sparrows are generally recognized. *P. s. sandwichensis* breeds in the Aleutian Islands and the western Alaskan Peninsula. *P. s. anthinus* breeds from the base of the Alaskan Peninsula east across Canada to Nunavut, and south to central Saskatchewan and Alberta. These are replaced to the south by *P. s. nevadensis* of the northern and central Great Plains and the Great Basin, south to central New Mexico and Arizona (Hubbard 1974). *P. s. brooksi* breeds on Vancouver Island, along the southwestern coast of British Columbia, south through western Washington to northwestern California. *P. s. brunescens* (= *P. s. rufofuscus*; Hubbard 1974) breeds on the Central Plateau of Mexico. *P. s. wetmorei* is known only from the type series of five birds, which were collected in Guatemala in 1897; I have not seen these birds, and no one has reported Savannah Sparrows from Guatemala since 1897.

P. s. sandwichensis is nearly as large in size as *P. s. princeps* from which it differs on both the PC2 and DF2 axes (Figs. 2 and 4), as well in coloration, which is like that of other "typical" Savannah Sparrows. There is clinal variation on the Peninsula with the largest birds at the western tip (Cold Bay), and birds from Port Heiden intermediate in size between *P. s. sandwichensis* and *P. s. anthinus*. Birds from Middleton Island, Alaska, are also large, and probably best placed in *P. s. sandwichensis*. *P. s. sandwichensis* are said to be slender-billed, with the "... depth at base about one-half the length of the culmen" (Peters and Griscom 1938). The ratio of premaxilla length to premaxilla depth of birds from Umnak Island is 1.7; that of birds from Cold Bay 1.7; that of birds from Port Heiden 1.8; that of birds from Middleton Island 1.7; and that of birds from Wasilla (*P. s. anthinus* from near Anchorage) 1.8. Thus, there is little justification for separating these two subspecies on bill shape, but the size difference is considerable.

Peters and Griscom (1938:461) characterize *P. s. brooksi* as being "Smallest of the races . . . ; bill intermediate between the stout-billed and slender billed forms; depth of bill averaging just about one-half of length of culmen." My sample from Hoquiam, in western Washington (which on geographical grounds would be *P. s. brooksi*), certainly is not one of notably small-sized Savannah Sparrows, the birds from the Great Plains and Great Basin being the smallest (Figs. 7 and 10). The premaxilla length to depth ratio of this sample is 1.6; that of the sample from Eureka, northwestern California is 1.7, again not indicating a different bill shape. Peters and Griscom (1938:461) write, "In spring general coloration nearest *nevadensis*, averaging very slightly browner . . .," that is, the supposed differences in coloration are slight. Also, spring birds may well be migrants of unknown breeding provenance.

P. s. nevadensis is a pale gray Savannah Sparrow, paler than *P. s. anthinus*, and with less streaking below. The yellow supercilium is frequently pale. They

are said to be relatively slender billed (Peters and Griscom 1938), but in this group, as with others, variation in bill shape is slight. Hubbard (1974) places the birds from the southwestern United States in *P. s. nevadensis*.

According to Hubbard (1974) *P. s. brunnescens* do not differ mensurally from *P. s. nevadensis* and in my analyses the sample from Charco Redondo, Jalisco, is close to birds from the Canadian north (*P. s. anthinus*) and the sample from Lerma, México, with birds from the northeast (*P. s. savanna*). Savannah Sparrows from the interior of Mexico are said to be reddish brown in upperpart color and streaking, compared to the grayer and duller birds from the southwest United States (Hubbard 1974); to my eye, the difference is slight.

SALTMARSH SAVANNAH SPARROWS

The nine subspecies of saltmarsh Savannah Sparrows all seem to be clearly separable; here I have examined material for seven of these.

P. s. alaudinus breeds from Humboldt Bay south to Morro Bay, in California. *P. s. beldingi* breeds from Santa Barbara south to northwestern Baja California; my samples from San Diego and Bahía San Quintin, on geographic grounds, belong to this subspecies. Phenetically, the birds from Morro Bay are intermediate between the birds from Humboldt Bay (Eureka) and San Diego, which are, in turn, intermediate between Morro Bay and Bahía San Quintin. The birds that I collected at Humboldt Bay, although from along the coast, were not in a saltmarsh, whereas all birds I collected and examined from along the coast south of there were. I am inclined to place the birds from Morro Bay in the same subspecies as the birds from San Diego and Bahía San Quintin as they all overlap in the discriminant functions analysis (Fig. 21). In the San Francisco Bay area there are populations that do breed in saltmarsh habitats (Mailliard 1916, 1917; Squires 1916; J. D. Rising, pers. obs.), but there also are birds in non-saltmarsh habitats. Apparently, the birds in these two habitats are very similar in appearance, although the upland individuals may be lighter in coloration; I have not examined material from the San Francisco area.

P. s. annulus breed in the marshes around Bahía Viscaíno, where my Guerrero Negro sample was collected; these are phenetically intermediate between the birds from Bahía San Quintin and those from Bahía Magdalena, where *P. s. magdalanae* breed. Bahía Magdalena is the southern-most place on the coast of Baja California where Savannah Sparrows breed. I have not rigorously examined material from Laguna San Ignacio, where *P. s. guttatus* are resident, but I have seen them in the field and they appear to be very like *P. s. annulus*, as Van Rossem (1947) asserts. The birds from the Islas San Benito where *P. s. sanctorum* are resident are quite distinctive.

From north to south along the coast there is clinal variation in bill size (Appendices 1 and 2): premaxilla length of males increases from 5.7 mm at Humboldt Bay, which is like the bill size of typical Savannah Sparrows, to 7.1 mm at Bahía Magdalena. The length of the bill relative to its depth (premaxilla) also increases from north to south, with the premaxilla length/premaxilla depth ratio being 1.7 at Humboldt Bay, typical for the species, and 1.9 at Bahía San Quintin and Guerrero Negro. It is 1.8 at Bahía Magdalena.

The samples from Bahía Kino, Sonora, and El Molino, Sinaloa, represent *P. s. atratus*. These are darker in coloration than *P. s. rostratus* from the coast of

northwestern Sonora; I measured a sample from Puerto Peñasco, Sonora, which is not included in the figures as I have only nine male and four female specimens. On the basis of my specimens, these have somewhat smaller bills than *P. s. atratus*. I feel that we should defer changing the taxonomy of the saltmarsh Savannah Sparrows until additional information is available.

In conclusion, I see no justification in retaining either *P. s. oblitus* or *P. s. brooksi*. Careful field work along the coast of northern California is needed to clarify the status of the saltmarsh birds there. Many of the other subspecies are poorly differentiated, and all of the geographic variation among the non-saltmarsh localities is clinal. A careful analysis of plumage variation is needed. I suspect that it will appear reasonable to recognize only three subspecies of non-saltmarsh Savannah Sparrows, *P. s. sandwichensis* (large size), *P. s. savanna* (typical Savannah Sparrows), and *P. s. princeps* (large and pallid). However, because *P. s. sandwichensis* merges clinally into *P. s. savanna* (as defined above), I would prefer to recognize only two subspecies of non-saltmarsh Savannah Sparrows, *P. s. sandwichensis* and *P. s. princeps*. As mentioned in the introduction, a preliminary study (Zink et al. 1991) suggests that the large-billed Savannah Sparrows (*P. S. rostratus*) may be specifically distinct; the same may be true for "Belding's" sparrows. Biochemical studies (J. D. Rising and R. M. Zink, in prep.) of the typical Savannah Sparrows may help us better understand the relationships among the populations.

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