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GEOGRAPHIC VARIATION IN THE SAVANNAH SPARROWS OF THE INLAND SOUTHWEST, MEXICO, AND GUATEMALA

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INTRODUCTION

Savannah Sparrows (*Ammodramus sandwichensis*) breed in inland southwestern North America southward locally to the highlands of Guatemala. Although the extensive review of Peters and Griscom (1938) treated geographic variation in several of these populations, there have been no studies that emphasize all of them and none that are recent. Several collections, particularly of fresh, autumn-plumaged birds, have been made in recent years, providing the basis for at least this preliminary review of the breeding birds of the region. The populations treated are mainly those extending from the highlands of extreme southwestern Guatemala northward through Arizona, New Mexico, and Colorado. Other populations dealt with are those ranging northward into the Great Basin, Rocky Mountains, and Great Plains (all presently assigned to *A. s. nevadensis*), with Nevada and adjacent California birds serving as especially useful comparison samples. Names applied most recently (Paynter, 1970) to these populations are: *wetmorei* (Guatemala), *brunnescens* (southern Mexico), *rufofuscus* (northern Mexico, Arizona, and New Mexico), and *nevadensis* (Colorado, etc.). Northern birds are probably largely migratory and southern ones resident, although no detailed studies have been made to verify their status.

MATERIALS AND METHODS

Specimens of probable breeding or resident birds examined are as follows (numbers in parentheses are molting or fresh-plumaged birds from late summer to December): California—67 (9), Nevada—40 (1), Colorado—25 (21), Arizona—21 (4), New Mexico—10, Chihuahua—7, Durango—27 (7), Nayarit—4, Jalisco—2 (2), Michoacán—4 (4), Guanajuato—2 (1), State of Mexico—28 (12), Distrito Federal—17 (3), Hidalgo

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—5 (1), Veracruz—5, Tlaxcala—2, Puebla—15 (3), Guatemala—5. These total 286 specimens, to which may be added 21 juveniles: California—11, Nevada—5, Arizona—1, State of Mexico—1, Hidalgo—1, Puebla—2. I also examined two score of specimens from Idaho, Oregon, Washington, Wyoming, British Columbia, and Alberta, mainly of breeding-plumaged adults.

My major emphasis is the detailing of variation in color and pattern, as measurements revealed no significant geographic differences over the area. For color and pattern comparisons, geographical samples of specimens were sorted by dates and degree of wear and then examined in series in both natural and artificial light. The most important comparisons are those involving autumn plumage, even though the series of 68 specimens is relatively small. Specimens in active molt and those taken early in the season can be considered with certainty to be from the breeding grounds, but the origin of molt-completed or later-season birds is sometimes open to question. In general, I have assumed a local origin if specimens conform to observed or expected patterns of geographic variation for a population. Obviously, some margin for error exists in this approach, and I have pointed this out whenever possible. Late spring and summer birds which are not badly worn are also of value in color and pattern comparisons. Late summer and late winter to early spring birds are often too worn for comparisons, although some of these birds provide information on populational plumage characteristics.

Another factor besides wear affecting the assessment of coloration in specimens is how long ago they were collected. In general, the browns become redder with age (or "fox") in these sparrows, as is true in many other species. In most cases I have been able to detect the change simply by comparing older with more recently collected specimens from a locality. Only in the Guatemala series was this impossible, as only the type series (collected in 1897) is available. As a rule, foxing is not so drastic in better-cared-for material, but in some old birds the shift in color is marked. I might also add that birds in molt, especially the postnuptial molt, tend to be somewhat darker and browner while the feathers are growing than just after.

Mensural characters used were wing chord, length of culmen (from nostril), height of bill at the base, and lean body weight.

PLUMAGE COMPARISONS

Juvenal Plumage

My series of juveniles is not extensive enough to make more than superficial assessment of the geographic variation, and only in the Great Basin is even a partial review possible. From that locality I assembled the

following specimens for study: CALIFORNIA: Mono Co., Convict Creek, Long Valley, 6900'—2 ♂♂, 16–17 July 1922; Sierra Co., Campbell Hot Springs—♂, 18 July 1919; Inyo Co., Farrington Ranch, Laws—sex?, 6 July 1917; Lassen Co., 1 mile south of Red Rock P.O.—3 ♂♂, 2 sex?, 11–22 July 1928. NEVADA: Fish Lake, Fish Springs Valley—sex?, 16 July 1933; Elko Co., west side of Ruby Lake and Ruby Mts. (Secret Pass, 6200')—2 ♂♂, 2 sex?, ♀, 10 July–2 August 1927.

Additional material from farther south consists of the following: ARIZONA: Apache Co., Crescent Lake, 21 miles south of Springerville, 9100'—sex?, 11 August 1935. STATE OF MEXICO: 1 mile southwest of Almoloya del Río, south of Lerma—sex?, 10 September 1961. HIDALGO: Lago de Tecocomulco—♀, 2 November 1956. PUEBLA: Laguna del Carmen—2 ♂♂, 2 September 1961.

The Great Basin series of juveniles is quite variable, even among specimens at similar developmental stages and from single localities. The ground color of the upperparts varies from grayish white to pale orange-buff, with some birds having a mixture of these. Most specimens with buff above also have at least some whitish edgings on the back, and all have the superciliary whitish. The dorsal streaking varies from light to medium brown, with the extent and width variable but usually moderate. The underparts are generally whitish, and all but three specimens have at least a tinge of buff on the breast. The breast streaking varies from light gray to brown, with the extent light to moderate and the width narrow (and spotlike) to moderate. The wing edgings (tertials and inner secondaries) are mainly light rufous, except for the innermost, which are usually whitish. These edgings are also present in the autumn plumage.

From the preceding description, the Great Basin series of juveniles obviously is not subject to succinct characterization. This is contrary to the contention of Grinnell (1910:312–314), who implied that the population was homogeneous in this plumage and actually used a juvenile as the type of *A. s. nevadensis* (type locality: Soldier Meadows, Humboldt Co., Nevada).

Farther southward, the lone Arizona specimen is essentially identical to the darker and more heavily streaked Great Basin specimens and thus cannot be distinguished from them. The single specimen from the State of Mexico is somewhat younger than other specimens examined, although not to the point of precluding comparison. It is similar to the buffier Great Basin birds, but it is somewhat darker and richer than any of those. Three Hidalgo and Puebla specimens differ from the State of Mexico specimen; they are similar *inter se* and in turn to Great Basin specimens. They differ from the latter in being slightly less heavily streaked on the crown, and the wing edgings are also somewhat more extensive and darker rufous—as is the State of Mexico specimen. In es-

sence, then, the Arizona, Hidalgo, and Puebla juveniles are similar to certain Great Basin birds, whereas the State of Mexico specimen is darker and richer in color. In view of the variability of the Great Basin series and the paucity of more southern specimens, no statement on the variation in juvenal plumage seems justified at present.

Adult Plumage

The Savannah Sparrow has two plumages each year: the *autumn* (or *basic*) *plumage*, which is obtained in the late summer and early autumn through a complete postnuptial (prebasic) molt (adults) or a partial postjuvinal (prebasic) molt (immatures), and the *breeding* (or *alternate*) *plumage*, which is obtained in late spring and early summer by a partial prenuptial (prealternate) molt. I have not made a detailed study of the molts in this species; in particular, a question exists as to how variable the extent of feather replacement is in the prenuptial molt, both in and between populations. In the specimens I examined, all birds appear to have at least some feather replacement prior to breeding, and in some this is quite extensive.

I have segregated the specimens from inland, southwestern North America into the seven samples (see Map): *Guatemala*, *Puebla* and vicinity (including Tlaxcala, Veracruz, and adjacent Hidalgo), *Valley of Mexico* (Distrito Federal and adjacent, easternmost State of Mexico), *Lerma* area (remainder of the State of Mexico and adjacent Guanajuato, Michoacán, and Jalisco), *Northern Plateau* (Durango, Chihuahua), *Southwest* (Colorado, Arizona, and New Mexico), and, for comparative purposes only, the *Great Basin* (Nevada and adjacent easternmost California). These lines of demarcation are based on natural geographic boundaries and on similarities in the aggregations of specimens themselves. These samples will be described in sequence from south to north, with each being compared to Great Basin birds and to populations to the south of it to avoid repetition. Thus, to see how a southern sample differs from a more northern one, consult the latter one.

GUATEMALA

Specimens

AUTUMN-WINTER: None available.

SPRING-SUMMER: Dept. of Huehuetenango: Hacienda Chancol, 10,000'; 2♂♂, 3♀♀ (all somewhat worn), 11–17 June 1897.

Description

BREEDING PLUMAGE: Upperparts light reddish to almost ruddy brown, with dorsal streaking dark reddish brown, moderate in width and extent;



Samples of Savannah Sparrows. A, Great Basin (a = type locality of *A. s. nevadensis*); B, Southwest; C, Durango (c = type locality of *A. s. rufofuscus*); D, Lerma; E, Valley of Mexico (type locality of *A. s. brunnescens*); F, Puebla; G, Guatemala (type locality of *A. s. wetmorei*).

edgings of back feathers pale brown to whitish; crown stripe pale buff to yellowish white; superciliary yellowish white posteriorly and medium yellow anteriorly; wing edgings medium rufous; ventral streaking medium to dark gray, moderate in extent and width.

Comparisons

BREEDING PLUMAGE: Compared to Great Basin specimens, those from Guatemala are darker and more reddish (much less grayish) brown above, with the dorsal streaking darker, redder brown, and more extensive. The yellow of the superciliary is also darker and more extensive than in Great Basin birds, the rufous wing edgings are darker, and the light streaking of the back is buffier (less whitish to grayish). I would emphasize that in spite of the age of the Guatemalan specimens, they do not appear unduly foxed; thus, comparisons with them are probably valid. (Other comparisons are discussed under the populations that follow.)

Comments

These specimens, taken by W. B. Richardson and now in the British Museum (Natural History), remain unique in that there seem to be no subsequent records of Savannah Sparrows summering in the Guatemalan highlands. There is no question about their validity, as during the same period Richardson took a series of the endemic *Dendroica coronata goldmani* in the same area.

PUEBLA

Specimens

AUTUMN-WINTER: *Puebla*: Laguna del Carmen—♀ and ♂, 23 September 1964 and 12 November 1958.

SPRING-SUMMER: *Puebla*: Laguna del Carmen—4 ♂ ♂, 16 May 1962; 2 miles east of El Carmen—♀, 11 August 1956; 1.5 miles northwest of Zaragoza—♂, 25 April 1958; 50 miles east of Puebla—♂, 30 July 1943; 1 mile east of Ocojala, M. de Chignahuapán—♂, ♀, 16 August 1958; Chalchicomula—2 ♂ ♂, ♀, 9–14 April 1893; Atlixco—3 ♂ ♂, 2 ♀ ♀, 23 July–27 August 1893 and 17 June 1903. *Tlaxcala*: Apixco—♂, 9 April 1893; 5 miles west of Tlaxcala—♂, 18 April 1958. *Veracruz*: Perote—4 ♂ ♂, 26 May 1939; 9 kilometers north of Perote—♀, 12 July 1970. *Hidalgo*: Irolo—♀, 3 March 1893; Tulancingo—3 ♂ ♂, 3 ♀ ♀, 18–24 August 1893; Lago Tecocomulco—♀, 22 May 1958.

Description

AUTUMN PLUMAGE: Upperparts light grayish brown, with dorsal streaking medium dark brown, moderate in width and extent; back feathers edged with pale grayish buff; crown stripe and superciliary pale grayish buff, pale yellowish over eye and anteriorly; wing edgings gray-

ish rufous to light reddish brown; ventral streaking medium brown, rather narrow and moderate in extent; buff of breast and sides pale and limited.

BREEDING PLUMAGE: Upperparts more grayish brown, with streaking and light edgings more prominent; yellow of superciliary more conspicuous; central streaking grayer and less conspicuous, buff mainly absent.

Comparisons

AUTUMN PLUMAGE: Compared to Great Basin specimens, the two in this series are somewhat browner (less grayish) on the upperparts, with browner streaking and buffier (less grayish to whitish) edgings on the dorsum. Moreover, they have deeper rufous wing edgings and ventrally they are generally more heavily streaked. One Great Basin specimen (Calif.: Modoc Co., ♂, 4 August 1910) is very similar to the two Pueblan specimens, but it is somewhat less heavily streaked above. (There are no autumn-plumaged Guatemalan specimens available for comparison.)

BREEDING PLUMAGE: Compared to Guatemalan specimens, the Pueblan birds are definitely paler and grayer (less reddish) above, with paler, narrower, and less extensive dorsal streaking. The ventral streaking in Guatemalan birds is also somewhat darker and heavier, the wing edgings deeper rufous, and the patterns of the head more contrasting. Compared to Great Basin specimens, those of the Puebla series are somewhat browner above (less grayish), with narrower, browner streaking and less whitish edgings on the dorsum (ventral streaking is similar).

VALLEY OF MEXICO

Specimens

AUTUMN-WINTER: *Distrito Federal:* southwest corner of Lago Texcoco, near Airport—3 ♂ ♂, 25 October 1962; Tlalpam—♀, 8 December 1892. *Mexico:* north shore of Lago Texcoco—2 ♂ ♂, ♀, 4 October 1959. *Hidalgo:* Tula—sex?, 14 December 1958.

SPRING-SUMMER: *Distrito Federal:* southwest corner of Lago Texcoco, near Airport—3 ♀ ♀, ♂, 6 May 1962; Ixtacalco—4 ♂ ♂, ♀, 25 June 1904; Peñón—♀, 17 June 1933 and 2 ♀ ♀, ♂, 21 August 1933; no locality—♀, 15 April 1930. *Hidalgo:* Requeña Reservoir, near Tepejé del Río—♀, 2 July 1954; Tula—♀, 11 March 1893. *Mexico:* 7 miles east of Chalco—♂, 15 August 1965; San Pedro Techuchulco—♀, ♂, 5 June 1964.

Description

AUTUMN PLUMAGE: Upperparts light olive-brown, with broad and extensive dark brown streaking; back feathers edged light grayish brown to light buff; crown stripe and superciliary pale brown to pale grayish buff, generally with tinge of yellowish over eye and sometimes anterior-

ly; wing edgings grayish rufous to medium rufous, sometimes giving way to whitish; ventral streaking medium to dark brown, moderate in width and extent; buff of breast and sides pale to light and moderate in extent.

BREEDING PLUMAGE: Upperpart similar, but dorsal streaking more grayish brown and narrower; yellow over eye more prominent and buff absent below.

Comparisons

AUTUMN PLUMAGE: Compared to Puebla birds, those from the Valley of Mexico have the upperparts slightly darker and redder brown (lacking grayish cast), with the dorsal streaking richer brown, broader, and more extensive. Furthermore, the ventral streaking is broader and more extensive; and, as a rule, the buff on the breast and sides is more pronounced. The Tula specimen is actually an intergrade toward Puebla specimens, with its somewhat grayish brown upperparts and narrow streaking on the back. Compared to Great Basin specimens, those from the Valley of Mexico are distinctly browner (less grayish) and darker above, with darker brown, wider, and more extensive dorsal streaking; browner or buffier (less grayish or whitish) edgings on the back; and more and darker rufous wing edgings. Ventrally, Valley of Mexico birds are buffier, with broader and more extensive streaking.

BREEDING PLUMAGE: Compared to Guatemalan specimens, those from the Valley of Mexico are somewhat paler and less reddish (more olive-brown) above and have the dorsal and ventral streaking slightly paler. Compared to Pueblan specimens, those from the Valley of Mexico are darker and less grayish brown above, with broader and more extensive streaking above and below. There is some overlap or approach in these characters, involving one Lago Texcoco and two Puebla (Ocojala and Zaragosa) specimens. Compared to Great Basin birds, those from the Valley of Mexico are distinctly darker and browner above, with darker rufous wing edgings, and browner and more extensive dorsal streaking; the ventral streaking also averages broader.

Comments

I have been able to examine three of the original specimens used by Butler (1888) in his description of the race *A. s. brunnescens* (type locality: Valley of Mexico). I agree with Peters and Griscom (1938:471) that the type series is heterogeneous and does not represent a pure sample of that breeding population. Butler's No. 30 (now Carnegie Museum No. 4156), a female taken on 8 December 1879, is apparently a migrant from the Great Basin; i.e., *A. s. nevadensis*. Butler's No. 3 (now in the R. L. Dickerman Collection), a male taken on 20 November 1879, also appears to be a northern migrant, probably *A. s. anthinus*. Although

foxing has reddened its coloration to some degree, the specimen has the streaking too pallid to represent a Mexican bird. Butler's No. 29 (USNM 113,558), a male taken on 8 December 1879, was designated the lectotype of *A. s. brunnescens* by Peters and Griscom (1938:472). Although it undoubtedly represents a bird of the breeding population of that general area of Mexico, its characteristics would seem to make the exact origin of the specimen open to question.

Compared to five autumn-winter birds from the Valley of Mexico, the lectotype is redder brown above, with darker dorsal streaking and more conspicuous buff edgings on the back. On the other hand, a closer resemblance exists to Lerma and Northern Plateau specimens, of which eight and seven respective specimens were compared. Compared to the latter, the lectotype is somewhat paler above (especially on the nape), with the crown in particular less heavily streaked and the ventral streaking generally paler. The lectotype differs from most Lerma specimens in that it is more darkly streaked and has buffier edges above, giving it an intermediate appearance between Northern Plateau and Lerma birds. Perhaps the best agreement is with a Lerma bird (imm. ♀, near Almoloya del Río, Mexico, 25 November 1962), although the lectotype is somewhat more extensively marked with buff above and is more pallidly streaked below than that specimen. Based on these comparisons, it is my guess that the lectotype is from farther north in Mexico, perhaps as a stray (or possible migrant) to the Valley of Mexico. (The specimen cannot be considered typical of Valley of Mexico autumn-plumaged birds, although one cannot rule out its being a variant of that population.) Clearly the lectotype is too dark and reddish to represent the Puebla, Southwest, and Great Basin populations, and the possibility is extremely unlikely that it represents the Guatemalan population.

LERMA SAMPLE

Specimens

AUTUMN-WINTER: *Mexico*: Hacienda Atenco, etc., in vicinity of Almoloya del Río—2 ♀♀, ♂, 25 November 1962 and ♂, 26 November 1961; kilometers 100–108, State of Mexico-Morelia Highway—2 ♂♂, 16 November 1962 and ♀, ♂, 27 November 1958. *Michoacán*: 4.7 miles west of Álvaro Obregón—2 ♂♂, ♀, 1 December 1958. *Guanajuato*: Yuriría—♂, 21 November 1956. *Jalisco*: Lagos—♀, 27 November 1896.

SPRING-SUMMER: *Mexico*: Hacienda Atenco, near Almoloya del Río—11 ♀♀, ♂, 28 May 1961; Lerma—♀, 4 July 1904; 25 kilometers south of Toluca—♂, 10 August 1946; kilometers 100–104, Mexico-Morelia Hwy.—4 ♂♂, 1 unsexed, 6–8 June 1961 and 27 May 1954. *Guanajuato*:

Yuriría—♀, 8 May 1958. *Jalisco*: La Barca—2 ♂♂, 29 June 1903; Charco Ojuelos—5 ♂♂, 23–24 August 1947.

Description

AUTUMN PLUMAGE: Upperparts medium light brown to reddish brown, with broad and extensive dark reddish brown streaking dorsally; edgings of back feathers light brownish to buff and whitish; crown stripe and superciliary light grayish buff to light buffy brown, with at least a tinge of yellowish over the eye and sometimes anteriorly; wing edgings light to medium rufous, sometimes giving way to light gray or whitish; ventral streaking medium to dark brown, moderate to relatively broad and moderate to heavy in extent; buff of breast and sides pale to light, limited to moderate in extent (wears off progressively into winter).

BREEDING PLUMAGE: Upperparts tend to be grayer brown, with some specimens notably grayish brown; streaking above and below grayer (less brownish), generally narrower and less extensive; buff generally absent ventrally; yellow around eye more conspicuous.

Comparisons

AUTUMN PLUMAGE: Compared to Valley of Mexico birds, those from the Lerma region are generally more richly colored above, being more reddish (less olive) brown, with the dorsal streaking darker brown and tending to be more extensive, especially on the crown. One Valley of Mexico specimen (D. F., Lago Texcoco, ♂, 25 October 1962) is very similar to less reddish Lerma birds in respect to the upperparts, and the few least reddish specimens from the Lerma series also show an approach to Valley of Mexico birds. The two Puebla specimens are notably paler and grayer than Lerma specimens, with paler, narrower, and less extensive streaking above and below. Lerma specimens differ from those of the Great Basin in being distinctly darker and more reddish (less grayish) brown above, with the dorsal streaking darker and browner, broader, and more extensive; the edging to the back feathers browner or buffier (less whitish to grayish); and the wing edgings deeper rufous. Lerma specimens are also more darkly and broadly streaked below and have the buff more extensive and darker.

BREEDING PLUMAGE: In comparing Lerma with Valley of Mexico birds, one finds considerable overlap and many specimens cannot be segregated. There is a tendency for Lerma birds to be more reddish (less olive) brown above, but some Lerma birds are so grayish above as to be difficult to distinguish on this basis even from Puebla birds. The latter tend to be less heavily streaked above and below, with the breast streaking often paler as well. Guatemalan birds are quite similar to Lerma birds, although the latter average slightly less ruddy and less

heavily streaked on the upperparts (there is much overlap). Compared to Great Basin birds, those from the Lerma series are darker and browner (less grayish) above, with browner (less gray) streaking above, browner or buffier (less whitish) edgings on the back, deeper rufous wing edgings, and darker, broader ventral streaking.

Comments

The Lerma series is the most variable of those yet discussed, both in autumn-winter and spring-summer plumages. One might assume that part of the variability is due to heterogeneity in the geographic origins of specimens in the sample. This may be the case in autumn-winter specimens (taken over the period 16 November to 1 December), possibly as the result of the infusion of migrants. However, in the spring-summer sample, variability is still high, e.g., in the 12 specimens from Almoloya del Río, Mexico, taken on 28 May and almost certainly on the breeding grounds. The question can be resolved only by more collecting, especially in late summer and early autumn.

NORTHERN PLATEAU

Specimens

AUTUMN-WINTER: *Durango*: Laguna de Santiaguillo—4 ♂♂, 3 ♀♀, 15–18 November 1971. *Chihuahua*: Madera—♀, 7 October 1921.

SPRING-SUMMER: *Chihuahua*: Babicora—2 ♂♂, ♀, 15 June 1902; 17 miles east of La Junta—3 ♀♀, ♂, 31 May–7 June 1949. *Durango*: 12 miles northeast of Durango—♀, 25 May 1946; Laguna de Santiaguillo—17 ♂♂, 2 ♀♀, 19–24 April 1972. *Nayarit*: 2 ♂♂, 2 ♀♀, Laguna San Pedro Lagunillas, 24–25 May 1962.

Description

AUTUMN PLUMAGE: Upperparts medium light reddish brown; dorsal streaking dark brown, broad, and extensive, especially on the sides of the occiput; edgings on back grayish white to buff; crown stripe and superciliary pale brown to buff, pale yellow over the eye and anteriorly; wing edgings pale to medium rufous, sometimes giving way to pale grayish or buffy white; ventral streaking medium brown to blackish, relatively narrow to medium width, light to moderate in extent; buff of breast and sides generally pale and limited in extent.

BREEDING PLUMAGE: Upperparts as in autumn plumage but tending toward paler brown or grayish brown in some specimens; yellow over eye more extensive and brighter; ventral streaking grayer and paler, buff generally lacking below.

Comparisons

AUTUMN PLUMAGE: Compared to Lerma birds, Northern Plateau specimens are equally dark but the upperparts are slightly browner (less reddish), the dorsal streaking is somewhat darker and generally heavier on the crown, and the crown stripe and superciliary are paler and buffier. The effect is of more contrastingly marked dorsal plumage in Northern Plateau specimens, with a brighter aspect (less dull) overall. Ventrally the two series are similar. Compared to Valley of Mexico birds, Northern Plateau specimens are darker and brighter above, with darker dorsal streaking and a more contrasting patterning, especially on the occiput. Northern Plateau specimens are distinctly darker, richer, and more contrastingly marked above than the two Puebla specimens, with darker and broader streaking and greater buff ventrally. Compared to Great Basin specimens, those from Northern Plateau are notably darker and more reddish (less grayish) brown above, with darker brown, broader, and more extensive dorsal streaking (especially on the crown); buffier crown and superciliary stripes and back edgings; darker and broader rufous wing edgings; and broader, darker, and more extensive ventral streaking.

BREEDING PLUMAGE: Northern Plateau specimens are similar to Lerma and Valley of Mexico birds, but tend to be more richly brown above and with heavier dorsal streaking, especially on the crown. Northern Plateau birds are distinctly darker and more richly brown above compared to Puebla specimens, with streaking more pronounced throughout. Compared to Guatemalan birds, those from Northern Plateau average somewhat darker on the upperparts, and the dorsal and ventral streaking is generally darker and more extensive.

Comments

I include here specimens from as far south as Nayarit, which almost certainly represent breeding birds, having been collected in late May. Some specimens of the Lerma series also approach Northern Plateau specimens (e.g., GTO, Yuriría—♀, 8 May 1958), but whether these represent breeding birds or possible migrants is not presently known.

SOUTHWEST

Specimens

AUTUMN-WINTER: *Arizona:* Apache Co., White Mountains and vicinity (Sheep Crossing, Basin Lake, Springerville)—2 ♀♀, ♂, 4 September 1953 and 9 September 1934. *Colorado:* Adams Co., Barr Lake and Barr—5 ♀♀, 4 ♂♂, 22 August–13 September 1936 and ♀, 9 September 1909;

Jackson Co., N. Platte River—3 ♂♂, 31 August 1913; Jackson Co., Mt. Zirkel—3 ♂♂, 13 September 1913; Park Co., Buffalo Creek—3 ♂♂, unsexed, 9 September 1956; Douglas Co., southwest of Woolhurst—♂, 6 September 1913.

SPRING-SUMMER: *Arizona*: Apache Co., White Mountains and vicinity (Big Lake, Marsh Lake, Becker Lake, Springerville)—4 ♂♂, ♀, 24 June–5 August 1914; 3 ♂♂, 2 ♀♀, 7 June–10 August 1915; ♂, ♀, sex?, 8–10 June 1934; ♀, 14 July 1954. *New Mexico*: Rio Arriba Co., Burford Lake—2 ♀♀, ♂, 23 May 1971; Rio Arriba Co., 11.5 miles northeast of Chama—♀, 14 August 1952; Taos Co., Taos—♀, ♂, 14 July 1904; Colfax Co., 3–5 miles south of Eagle Nest—2 ♂♂, 1 August 1940; Maxwell area—3 ♂♂, 17 May–21 June 1971. *Colorado*: Grand County, Sulphur Springs—♂, 1 June 1909; Denver Co. (Berkeley Lake)—♂, 9 May 1903; Summit Co., Breckenridge—♀, 15 June 1890; Jackson Co., Walden—♂, 15 August 1936.

Description

AUTUMN PLUMAGE: Upperparts light grayish brown to medium olive-brown, streaking medium to dark brown, generally moderate in width and extent; edgings of back light buff to pale brown; crown and superciliary stripes pale buff to light brown, tinge of yellow over eye; wing edgings light to medium rufous, giving way sometimes to pale gray or whitish; ventral streaking medium brown, narrow, and light to moderate in extent; buff of breast and sides pale and limited in extent.

BREEDING PLUMAGE: Upperparts somewhat grayer brown than above, with streaking and edges of dorsum more prominent; ventral streaks grayer (less brownish) and generally narrower.

Comparisons

AUTUMN PLUMAGE: Compared to Northern Plateau birds, those from the Southwest are distinctly paler and more grayish (less reddish) brown above, with grayer brown dorsal streaking that is less extensive, especially on the crown; the edgings of the back are grayer (less buffy), the wing edgings paler rufous, and the head less bright and less contrasty. Compared to *Lerma* specimens, they are notably more grayish (less reddish) brown, with grayer brown dorsal streaking, white or grayer (less buffy) edgings on the back, and paler rufous wing edgings. The Southwest series is similar to that from the Valley of Mexico, but the latter is somewhat browner (less grayish brown) above and in its streaking. The Puebla birds are more similar yet to the series from the Southwest, but the former are slightly grayer in their upperpart color and dorsal streaking and have the latter somewhat less extensive than in the Southwest series. Compared to Great Basin birds, the Southwest series is distinctly

darker and more brownish (less grayish brown) in upperpart color and dorsal streaking and has the ventral streaking somewhat darker.

BREEDING PLUMAGE: Compared to Northern Plateau specimens, the Southwest species are generally grayer and duller (less brightly reddish) brown in upperpart color and streaking (the latter also is less pronounced, especially on the head) and tend to have the ventral streaking paler and narrower. Compared to Lerma and Valley of Mexico specimens, those from the Southwest are generally grayer (less reddish) brown in the upperpart color and dorsal streaking (with the latter usually less extensive); the ventral streaking is paler and less pronounced. Southwest specimens are quite similar to the grayer Lerma specimens and those from Puebla, although from the latter they tend to differ in having the central streaking heavier and broader. Compared to Great Basin specimens, those from the Southwest are generally darker and less grayish (more brownish) in upperpart color and dorsal streaking, with the light edging of the back less contrasting and the ventral streaking averaging darker. Guatemalan specimens differ from Southwest specimens in being darker and ruddier brown above, with the streaking more extensive and darker; the yellow of the superciliary also tends to be darker and more extensive.

Comments

Certain Colorado autumn-plumage specimens show varying degrees of approach toward Great Basin specimens, although on the average the series of 21 specimens is more similar to Southwest (Arizona) than to the California-Nevada birds. Some of the Great Basin type do occur in the Colorado series (e.g., North Platte River—2 ♂♂, 31 August 1913), but other specimens are of a dark extreme that even shows an approach to Durango birds (e.g., Buffalo Creek, 2 ♂♂, 9 September 1956). This tendency toward rather dark and more rich coloration is also found in Idaho, as in a series from Fremont County (6 ♀♀, ♂, 17–31 August 1930), where five of the specimens differ slightly and two differ distinctly from the Great Basin series in that direction. The tendency toward darker and more richly colored birds appears to extend even farther north in the Rockies and vicinity, as evidenced by the findings of Peters and Griscom (1938).

As already mentioned, among the populations treated to this point, only those of the United States are known to be migratory. Of particular interest in this regard are two specimens that appear to represent migrants from the rather distinctive Southwest population: Arizona, Tucson—♂, 1 January 1938, and New Mexico, Mora Co., La Cueva Ranch—♀, 20 April 1940. The Arizona specimen has been identified elsewhere (Phillips et al., 1964:192) as *A. s. alaudinus*, a California coastal race,

but Phillips has corrected the identification (pers. comm.) and I concur. I have seen two other specimens that may represent Southwest birds, but both are so old and foxed as to be only tentatively identifiable: Texas, Ft. Clark—♀, 2 April 1898, and Texas, locality?—♀, 11 January 1880.

MENSURAL COMPARISONS

Mensural comparisons (Table 1) reveal that in wing length, culmen from nostril, and bill depth at the base considerable overlap exists be-

Table 1: Measurements of Breeding Ground Savannah Sparrows

SAMPLES	SEX	WING LENGTH			CULMEN LENGTH			BILL DEPTH			BODY WEIGHT		
		N	Mean	SD	N	Mean	SD	N	Mean	SD	N	Mean	SD
			(range)			(range)			(range)			(range)	
Guatemala	♂ ♂	2	68.5	—	2	7.5	—	2	5.6	—		—	
			(68.0–69.0)			(7.4–7.6)			(5.5–5.7)				
	♀ ♀	3	64.0	—	2	7.2	—	1	5.6	—		—	
			(62.5–65.5)			(6.8–7.6)			(—)				
Puebla	♂ ♂	10	71.0	1.9	11	7.7	0.3	10	5.5	0.3	1	17.5	—
			(68.0–74.0)			(7.3–8.5)			(5.2–6.1)			(—)	
	♀ ♀	8	66.8	1.8	5	7.7	0.3	4	5.2	—	4	17.4	—
			(64.5–69.5)			(7.2–8.2)			(4.9–5.5)			(14.9–18.9)	
Valley of Mexico	♂ ♂	12	70.2	2.4	4	8.1	—	1	5.0	—	6	18.6	1.2
			(66.5–74.5)			(7.8–8.8)			(—)			(17.0–19.8)	
	♀ ♀	7	65.3	0.9	6	7.6	0.4	5	5.3	0.2	4	17.9	—
			(64.5–67.0)			(6.9–8.0)			(5.0–5.6)			(16.2–19.6)	
Lerma	♂ ♂	8	68.9	2.3	6	7.7	0.5	4	5.7	—	7	19.2	0.8
			(64.5–72.0)			(7.2–8.6)			(5.4–5.9)			(18.1–20.2)	
	♀ ♀	15	66.4	1.7	10	7.7	0.4	9	5.5	0.2	6	17.8	1.5
			(64.0–69.0)			(7.2–8.1)			(5.3–5.8)			(15.8–20.2)	
Northern Plateau	♂ ♂	24	69.1	1.4	24	7.7	0.3	22	5.4	0.2	17	17.6	1.3
			(66.0–72.0)			(7.1–8.5)			(5.1–5.6)			(15.0–20.0)	
	♀ ♀	9	65.1	1.4	9	7.7	0.3	7	5.3	0.2	5	15.6	1.1
			(63.5–67.5)			(7.5–8.1)			(5.1–5.7)			(14.0–17.0)	
South-west	♂ ♂	20	71.1	1.7	11	7.7	0.2	8	5.4	0.2	5	17.5	1.2
			(67.5–74.5)			(7.4–8.2)			(5.2–5.8)			(16.0–19.0)	
	♀ ♀	8	66.8	1.7	5	7.4	0.3	5	5.3	0.3	5	16.6	0.6
			(64.0–69.0)			(7.0–7.8)			(4.8–5.5)			(16.0–17.3)	
Great Basin	♂ ♂	19	70.1	1.5	19	7.6	0.4	13	5.2	0.2		—	
			(68.0–74.0)			(7.1–8.5)			(4.9–5.5)				
	♀ ♀	7	66.2	1.6	8	7.5	0.5	7	4.8	0.2		—	
			(64.0–68.0)			(6.7–8.2)			(4.4–5.1)				

Wing length (chord), culmen (from nostril), and bill depth (at base) are in millimeters; body weight is in grams.

tween all populations and means are similar throughout. Mann-Whitney U tests (Steel and Torrie, 1960) of selected samples show that no significant differences exist among the means of the characters ($P > .05$). In body weight average differences exist among some samples, with Valley of Mexico and Lerma specimens being the heaviest. Again, Mann-Whitney U tests revealed no significant differences among samples.

Within samples mean wing lengths of males are 2.6 to 4.9 mm. greater than those of females, and in comparisons the differences between the sexes are significant ($P < .05$). There are also slight differences in weight, with females averaging lighter; but only in the Durango series is the difference significant ($P < .05$). Perhaps with larger series of weights the other samples might also have shown a significant difference in the weight of the sexes.

Table 2: Indices of Separability (See Text) of Breeding Ground Savannah Sparrows (Expressed as Percentages)

	GUATE- MALA	PUEBLA	VALLEY OF MEXICO	LERMA	NORTH- ERN PLATEAU	SOUTH- WEST	GREAT BASIN
Guatemala							
A (0)	----	----	----	----	----	----	----
B (5)	----	100.0	85.0	61.4	77.6	93.3	100.0
Puebla							
A (2)	----	----	90.7	100.0	100.0	83.3	61.1
B (11)	100.0	----	90.9	91.5	98.9	71.7	83.4
Valley of Mexico							
A (6)	----	91.7	----	83.5	97.6	66.7	85.7
B (4)	85.0	90.9	----	53.5	91.2	61.1	90.9
Lerma							
A (7)	----	100.0	83.3	----	79.6	85.7	100.0
B (14)	61.4	91.5	53.5	----	68.4	71.4	96.1
Northern Plateau							
A (7)	----	100.0	97.6	79.6	----	95.2	100.0
B (17)	77.6	98.9	91.2	68.4	----	93.5	99.3
Southwest							
A (6)	----	83.3	66.7	85.7	95.2	----	76.3
B (9)	93.3	71.7	61.1	71.4	93.5	----	77.8
Great Basin							
A (9)	----	61.1	85.7	100.0	100.0	76.3	----
B (11)	100.0	83.4	90.9	96.1	99.3	77.8	----

A = autumn plumage; B = breeding plumage. Numbers in parentheses are sample sizes.

In summary, slight mensural differences existing between populations are not significant at the .05 level (and generally not at the .01 level). On the other hand, males are significantly longer winged than females in all samples, and in the Northern Plateau sample males are heavier than females.

DISCUSSION

Breeding populations of Savannah Sparrows of the inland Southwest, Mexico, and Guatemala differ *inter se* in coloration but not mensurally, except perhaps in weight. Succinctly, the seven populations studied here can be segregated into four coloration types: *pale* (Great Basin, Puebla), *moderately dark* (Southwest, Valley of Mexico), *dark* (Lerma, Guatemala), and *very dark* (Northern Plateau). In general, adjacent populations tend to form clines of increasing or decreasing darkness, although between the Southwest and Northern Plateau and especially between Puebla and Guatemala the transition is quite stepped.

For the purpose of delimiting subspecies among these populations, I have used an index of separability (Table 2). To calculate the index, I compared each specimen in a sample with each in another sample. Then the total number of specimens that were separable in the two was divided by the overall total of comparisons. For example, in comparing the five Guatemala birds with the 11 from Puebla, I found that all were separable. Thus I divided that total of separable birds (5×11 , or 55) by the overall total of comparisons (also 5×11 , or 55), for an index separability of 100 percent. The indices of separability (Table 2) among adjacent populations can be summarized as follows (autumn plumage index and breeding plumage index):

Great Basin from Southwest	= 76.3 and 77.8%
Southwest from Northern Plateau	= 95.2 and 93.5%
Northern Plateau from Lerma	= 79.6 and 68.4%
Lerma from Valley of Mexico	= 83.5 and 53.5%
Valley of Mexico from Puebla	= 90.7 and 90.9%
Puebla from Guatemala	= — and 100.0%

In order to apply these indices, I have used a form of the "75 percent rule" suggested by Mayr et al. (1953); i.e., to be worthy of recognition subspecies should differ by about 75 percent from about 100 percent in compared samples. This is equivalent to about 90 percent inter-sample separability, which is the level at which the indices above are gauged. On this basis, one finds that four groups emerge as potential subspecies, i.e., are 90 percent or greater in their separability. These are the Great Basin-Southwest, the Northern Plateau-Lerma-Valley of Mexico, the

Puebla, and the Guatemala samples or groups of samples. Of these, the highest degrees of separability among adjacent samples are between the Puebla and Guatemala samples (100 percent of breeding birds) and between the Southwest and the Northern Plateau samples (95.2 of autumn and 93.5 percent of breeding birds). The level of separability between the Valley of Mexico and Puebla samples (90.7 of autumn and 90.0 percent of breeding birds) is borderline, and I will discuss that situation further on. For the moment, we can accept three definite groups as meriting subspecific recognition, and for each a name is already available.

For the Guatemala population the name *A. s. wetmorei* (van Rossem, 1938), type locality Hacienda Chancol, Department of Huehuetenango, is applicable, as is *A. s. nevadensis* (Grinnell, 1910), type locality Soldier Meadow, Humboldt County, Nevada, for Great Basin birds. For the populations from the Valley of Mexico to the Northern Plateau, two names have been applied: *A. s. brunnescens* (Butler, 1888), type locality Valley of Mexico, and *A. s. rufofuscus* (Camras, 1940), type locality Babicora, Chihuahua. As already mentioned, the lectotype of *brunnescens*, selected by Peters and Griscom (1938), agrees more with Lerma birds than with those from the Valley of Mexico in its characters. However, as no question exists of these two populations being subspecifically separable, the exact origin of the type does not matter—the name *brunnescens* is applicable regardless. Furthermore, the Northern Plateau population, to which *rufofuscus* was originally applied, must also be included in *brunnescens*, as the former sample and that from Lerma are not subspecifically distinguishable.

The name *rufofuscus* has also been extended to the breeding birds of Arizona and New Mexico (Duvall, 1943) and recently by Allan R. Phillips to those of parts of Colorado (Bailey and Niedrach, 1965). However, my study places these populations closer to Great Basin *nevadensis*, although as a whole the Southwest sample is an intergrade population, between that race and *brunnescens* (*sensu lato*).

Actually, in some ways the Southwest population is distinctive, although the index of separability shows that its recognition as a separate race would be unjustified. Undoubtedly this distinctiveness is what led Duvall and, later, Phillips to ally the birds with Mexican populations, and it is clear that Peters and Griscom (1938) were also aware of this variational trend. I say "aware" advisedly, because for unknown reasons those authors did not even mention Arizona and New Mexico breeding birds (which were certainly available); however, they did detect the browner tones in birds from Colorado to Montana and Idaho. They even singled out birds from the eastern slope of the Rockies (Colorado and Montana) as being very similar to the northerly *anthinus* (type locality on Kodiak Island, Alaska), although their final assessment was to call

them minutely nearer *nevadensis*. Because they were unaware of the situation in Arizona and New Mexico, and in the absence of data on the yet-to-be-discovered breeding birds of Durango and Chihuahua, their taxonomic assessment is understandable. They also faced a dilemma in that had they called Rocky Mountain birds *anthinus*, the range of that race would have been disjoined (in at least southern British Columbia) and would in turn have disjoined Great Basin *nevadensis* from that of the Great Plains. (Peters and Griscom rejected the naming of Great Plains birds as a distinct race, i.e., *campestris* Taverner [1932]). Their nomenclatural course of action avoided these disjunctions, but the fact remains that Rocky Mountain populations are browner than those to the east and west—regardless of what one chooses to call them. I have already expressed my preference as *nevadensis* toward *brunnescens*, but eventually a population-by-population review of more northerly birds will be needed to elucidate possible links with *anthinus*.

The final matter to discuss is possible subspecific status for the Puebla population. As already mentioned, the index of separability of this sample compared to the adjacent Valley of Mexico (*brunnescens*) population is about 90 percent. This level is right on the borderline of acceptance, and in view of this fact and the small samples that were available, I opt for a conservative approach and retain Puebla birds in *brunnescens*. With additional material, perhaps the present index of separability level can be accepted or might improve and a new race could be described.

SUMMARY

The geographic variation in breeding or resident Savannah Sparrows of the inland Southwest, Mexico, and Guatemala was studied. No mensural differences were found among populations, but color differences exist, mainly in the darkness and hue (grayish to reddish) of the upperparts and the streaking of the adults. Juveniles were not widely available, but at least in the Great Basin these appear to be quite variable. I recommend the recognition of three subspecies: *wetmorei* (van Rossem) of Guatemala, *brunnescens* Butler of Mexico (which includes *rufofuscus* [Camras] and provisionally the pale birds of Puebla), and *nevadensis* (Grinnell) of the Great Basin and the Southwest (the latter area actually intergrades toward *brunnescens*).

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