

SPECIFIC LIMITS AND DISTRIBUTION OF MEADOWLARKS OF THE DESERT GRASSLAND

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THE polytypic Eastern Meadowlark (*Sturnella magna*) has a breeding range that extends throughout eastern North America westward to Ontario, Nebraska, Texas, and Arizona, and southward through Central and South America as far as northern Brazil. A monotypic sibling species, the Western Meadowlark (*Sturnella neglecta*), breeds only in western North America eastward to the Great Lakes region, Missouri, and Texas, and southward on the Mexican plateau to northern Jalisco. A poorly differentiated northwestern race, *S. neglecta confluenta*, is currently recognized by the A.O.U. *Check-list* (1957).

The breeding ranges of these species overlap broadly throughout the north-central United States, from Oklahoma northeastward into Ontario. Their behavioral and ecological interrelationships within this zone of sympatry have been described elsewhere (Lanyon, 1953, 1956, 1957). A similar analysis of their sympatric relationship in the southwestern United States and in Mexico has been delayed because of the (1) considerable confusion that exists even among contemporary ornithologists as to the specific identification of the meadowlarks breeding in these regions and, owing to this confusion, (2) a lack of reliable distributional data for these areas. The Mexican *Check-list* states, for example, that the southern limits of the breeding ranges of *S. neglecta* and *S. magna lilianae* are not known (Miller *et al.*, 1957). The objectives of this paper are (1) to present the specific limits for those populations of the two species that are involved in the area of geographical overlap in the southwestern United States and Mexico, and (2) to summarize the distributional data for this area based on a reexamination of the material currently available. A preliminary discussion of their ecological relationships in this zone is included. A map of the breeding ranges of the populations under consideration here is presented in Figure 1.

On the basis of evidence reviewed during this study, the current taxonomic treatment of the breeding populations within the area of geographical overlap in the southwestern United States and in Mexico appears adequate (Miller *et al.*, 1957), with two races of *magna* and the monotypic *neglecta* involved. The breeding ranges of the three races appear to be as follows (cf. Figure 1): (1) *Sturnella magna lilianae* Oberholser breeds from north-central Arizona east to central eastern New Mexico and south to northern Sonora, Chihuahua, and the Big Bend region of Texas; (2) *S. magna auropectoralis* Saunders breeds from Sinaloa and central Durango southward, intergrading with *S. m. alticola* south of the area of sympatry;

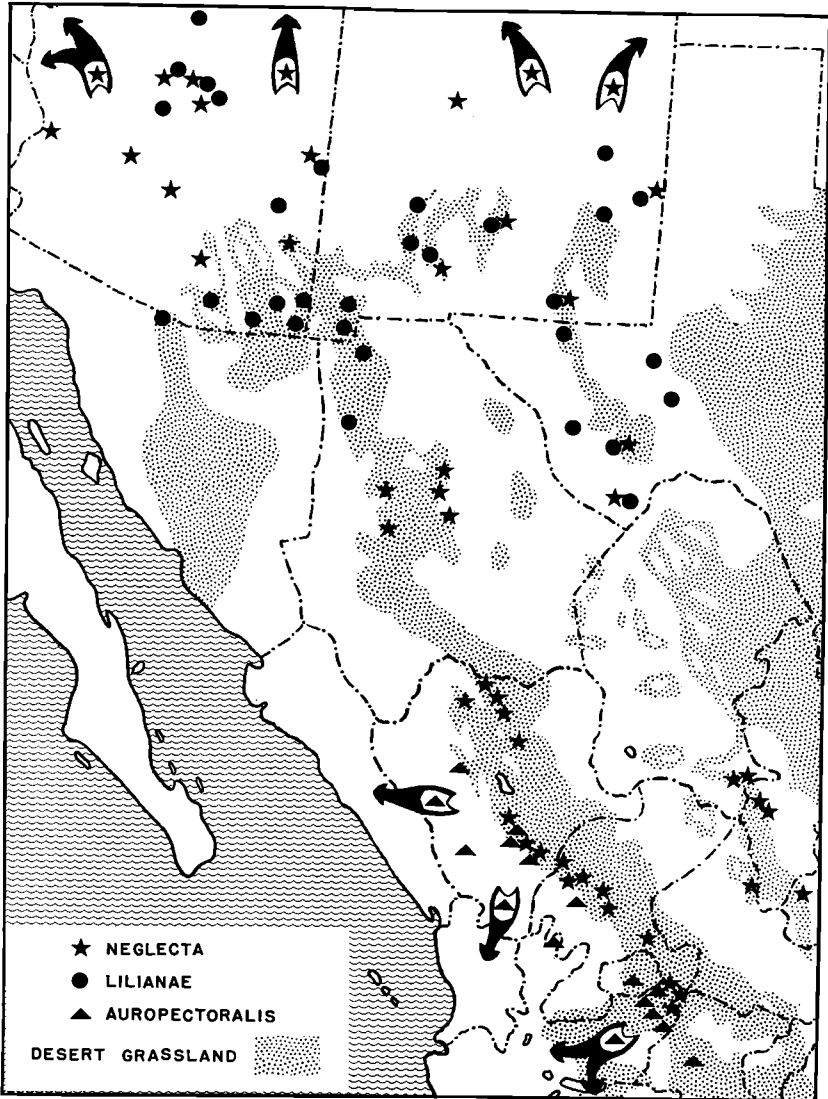


Figure 1. Localities of breeding specimens examined. The distribution of desert grassland has been adapted from maps by Shantz and Zon (1923) and Leopold (1951).

(3) *S. neglecta*, entering the area of sympatry from its main range to the north, breeds south to southeastern Arizona (locally) and the Big Bend region of Texas and on the Mexican plateau south to northern Jalisco and southwestern Tamaulipas. It is apparent from the localities of breeding

specimens examined (Figure 1) that the geographical overlap of the breeding ranges of the two species in this region is closely coincident with the distribution of the desert grassland, as interpreted by Shantz and Zon (1923) and Leopold (1951).

METHODS

Field observations and recordings were made in Arizona and northern Chihuahua during the summers of 1956 and 1957, and in southwestern Texas in June 1960. Other Mexican populations, in Coahuila, Nuevo León, San Luis Potosí, Jalisco, Zacatecas, Durango, and Chihuahua, were studied during May and June of 1959 and 1960. Emphasis in these field studies was placed on collecting a series of specimens of known sex, vocalizations, habitat preference, and mate preference. Tape recordings were made of representative vocalizations of most of the breeding populations visited, using a Magnemite recorder at 15 inches per second, a preamplifier, and an Altec 660B microphone mounted in a 24-inch parabolic reflector. These recordings involved 25 individuals, from San Luis Potosí northward to Arizona. All recordings were analyzed by ear in the laboratory, and subsequently over 150 representative vocal patterns were selected for analysis with a sound spectrograph. The spectrograms presented here were chosen to demonstrate the extremes of variation evident from this analysis. Comparisons were made between these spectrograms and those produced in connection with studies of other populations of *Sturnella* (Lanyon, 1957, unpubl. ms; Lanyon and Fish, 1958).

Over 200 museum specimens of *Sturnella* from populations in the southwestern United States and the Mexican plateau were examined and analyzed for morphological variation. Over 400 additional specimens from extralimital populations were examined for comparative purposes. Linear measurements, in millimeters, were taken as follows: wing, flattened; "tarsus," with calipers, taken as the diagonal distance from the lowest depression at the rear of the joint between the tibia and metatarsus to the lower edge of the lowest undivided scute on the front of the junction of the metatarsus with the bases of the third and fourth toes. The wing-to-tarsus ratio was derived by dividing the wing length by the tarsal length. To determine the extent of encroachment of the yellow coloration of the throat on to the cheek region, the feathers of the cheek were arbitrarily parted from those of the throat by projecting a line posteriorly from the mandibular ramus. Data were accumulated with regard to the extent of yellow coloration between this arbitrary line and the eye. The extent of white in the rectrices was determined by the presence or absence of pigmentation in that portion of the vanes immediately bordering the rachis of the fifth and sixth rectrices (outer two). Additional morphological characters considered were the general coloration of the upper parts, especially the crown stripes, and the nature of the darker markings on the remiges and rectrices, *i.e.*, whether distinctly barred or whether confluent.

In diagramming statistical analyses, 1.3 times the standard deviation has been plotted on each side of the mean (forming a solid rectangle). Thus, when comparing two samples, nonoverlap of the solid rectangles indicates the probability that at least 90 per cent of the individuals of one sample are separable from 90 per cent of the individuals of the other sample with respect to the particular character being analyzed.

MORPHOLOGICAL VARIATION

Sexual dimorphism, pronounced seasonal variation in both species, and a remarkable geographical variation within *Sturnella magna* are factors

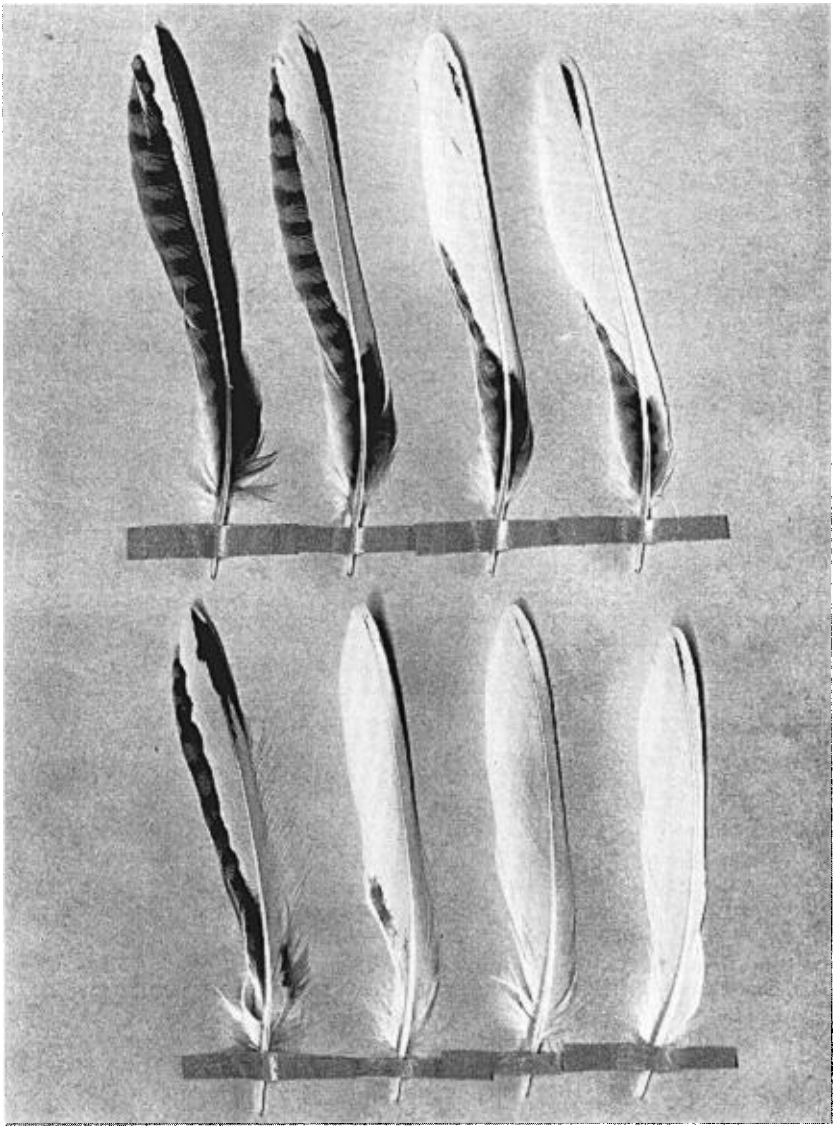


Figure 2. Rectrix patterns in meadowlarks of the desert grassland. Rectrices three through six are arranged from left to right. Top row—*S. neglecta*, male, Cienega de las Vacas, Durango, Mexico, 27 March 1903 (AMNH 92364). Bottom row—*S. magna lilianae*, male, Sásabe, Sonora, Mexico, 21 October 1948 (AMNH 326489).

contributing to the problem of devising specific limits, based on morphology alone, that will apply to all populations of these species throughout their respective breeding ranges. Fortunately, the problem is somewhat simpler if one limits the discussion to those breeding populations occupying a more restricted area, such as that being considered in this study.

Rectrix pattern. The most objectively determined and the most reliable morphological distinction between the species within the study area is the extent of white in the rectrices. Both *S. magna lilianae* and *S. m. auropectoralis* have consistently more white in the tail than does *S. neglecta*, with no overlap noted in the series examined. This distinction is easily determined by noting the extent of white in that portion of the inner and outer vanes immediately bordering the rachis of the fifth and sixth rectrices (outer two), as illustrated in Figure 2. All specimens of *S. magna* (including both sexes) examined from the study area have had white bordering the entire length of the rachis in at least one of the following vanes: (a) inner vane of the sixth rectrix; (b) outer vane of the fifth rectrix; and (c) inner vane of the fifth rectrix. About 85 per cent of the series of *S. magna* specimens had white bordering the entire length of the rachis in all three of these vanes. I have yet to examine a specimen of *S. neglecta* from anywhere in its range that has white bordering the entire length of the rachis in any rectrix vane. This character is especially valuable as a specific criterion, since, unlike all other morphological characters, there is no sexual dimorphism. Caution must be exercised in the use of this character to identify individuals outside of the study area, since other races of *S. magna* approach the typical pattern of *S. neglecta* in this respect.

Cheek coloration. The second most reliable morphological distinction between these species within the study area involves the extent to which the yellow coloration of the throat extends on to the cheek. When a line is projected posteriorly along the ramus of the lower mandible (cf. Figure 3), the feathers of the cheek can be parted from those of the throat. Males of *S. neglecta*, regardless of locality, have an extensive area of yellow above this arbitrary line, *i.e.*, for a distance of two mm or more toward the eye. Males of *S. magna* from the study area (as well as from all populations of the species in the United States and Canada) may have a fringe of yellow above this line, involving up to a dozen feathers at most, but this fringe area was not found to extend for a distance of more than one mm above the line in the series examined. On general inspection, then, *S. magna lilianae* and *S. magna auropectoralis* have white cheeks while *S. neglecta* has a yellow cheek (see Figure 3). In both species, the encroachment of yellow on to the cheek is less extensive in the females than in the males. In the series examined, none of the females of *S. magna* had any yellow feathers above this line, whereas all females of *S. neglecta* have some yellow

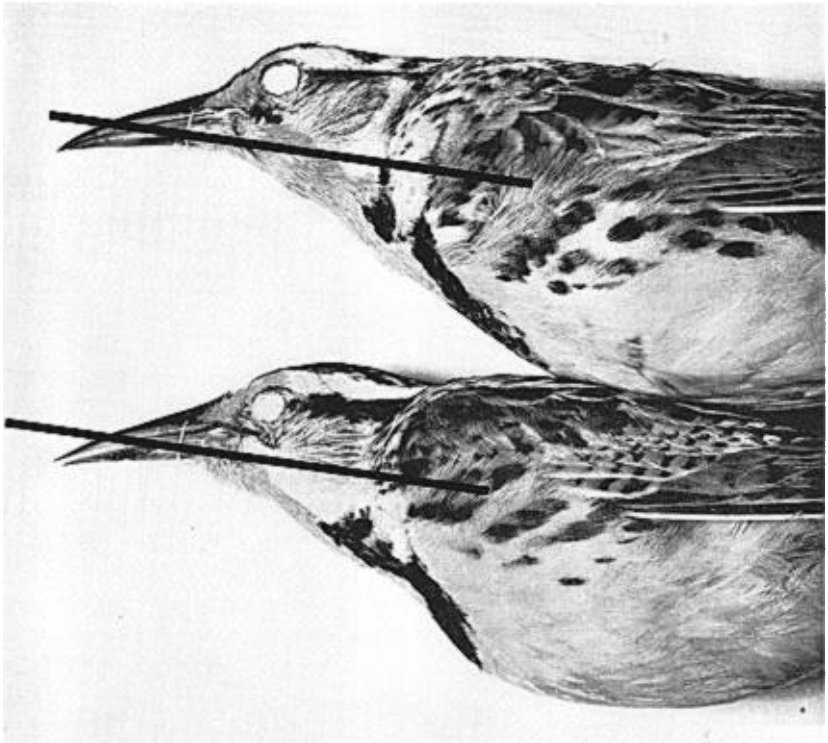


Figure 3. Cheek coloration in meadowlarks of the desert grassland, as determined by encroachment of yellow of the throat above arbitrary line projected posteriorly along the ramus of the lower mandible. Top—*S. neglecta*, male, El Casco, Durango, Mexico, 7 June 1959 (AMNH 766744). Bottom—*S. magna auropectoralis*, male, Durango, Durango, Mexico, 8 May 1960 (AMNH 766735).

feathers in this area. Caution should be exercised with fresh-plumaged birds in which the cheek feathers are tipped with buff. The extent of the yellow area in these specimens must be determined by inspection of the bases of the cheek feathers.

Although there was no overlap noted in the series examined, with respect to cheek coloration, the use of this character lacks the degree of objectivity with which the rectrix pattern may be determined. It has been the misuse of this character, among others, that has led to much of the confusion over the identification of meadowlarks. It must be determined with care and one must recognize the fact that males of *S. magna*, even in the Atlantic coastal states, frequently have a fringe of yellow feathers at the extreme lower portion of the cheek, as noted above. It is of interest to note that those populations of *S. magna* not sympatric with *S. neglecta*,

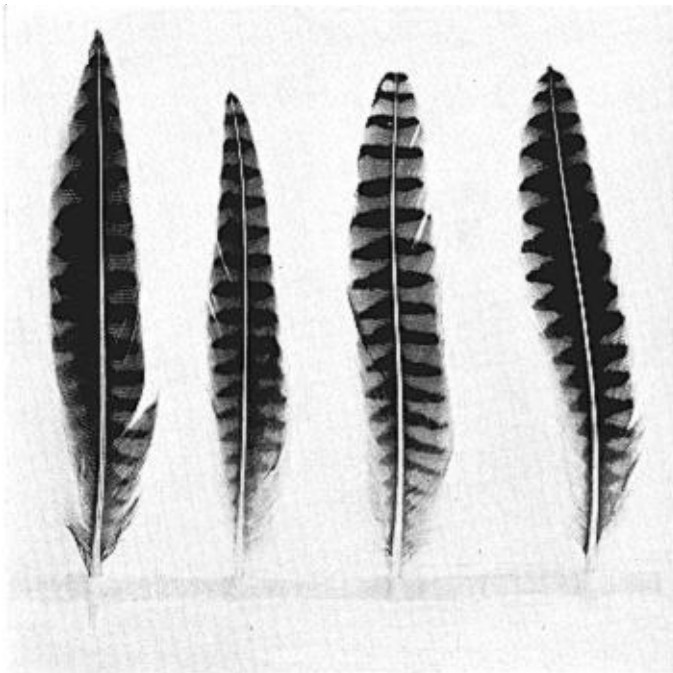


Figure 4. Geographical variation within the two species of meadowlarks with respect to the nature of the markings on the first left rectrix. Left to right—(1) *S. magna magna*, male, Queens, New York, 27 October 1887 (AMNH 6544); (2) *S. magna lilianae*, male, Sásabe, Sonora, Mexico, 21 October 1948 (AMNH 326490); (3) *S. neglecta*, male, Guadalajara, Jalisco, Mexico, 9 November 1891 (AMNH 521417); (4) *S. neglecta*, male, British Columbia, Canada, 19 October 1889 (AMNH 47581).

such as in southern Mexico southward to Brazil, more closely approach the sibling species with respect to this character.

Coloration of crown and back. *S. neglecta* shows essentially no geographical variation in coloration. By contrast, *S. magna* is quite variable, with those breeding populations of the arid grasslands of the southwestern United States and northwestern Mexico exhibiting a markedly paler coloration than is evident elsewhere in the species' range. This convergence in general coloration where the two species meet in this particular portion of the zone of sympatry reduces the effectiveness of general coloration in species identification. Pronounced seasonal variation and sexual dimorphism in plumage coloration further complicate the use of such a character in establishing specific limits. It was found that comparison of specimens with respect to coloration of the lateral crown stripes was a convenient and reliable technique, providing one had access to a reference series of birds

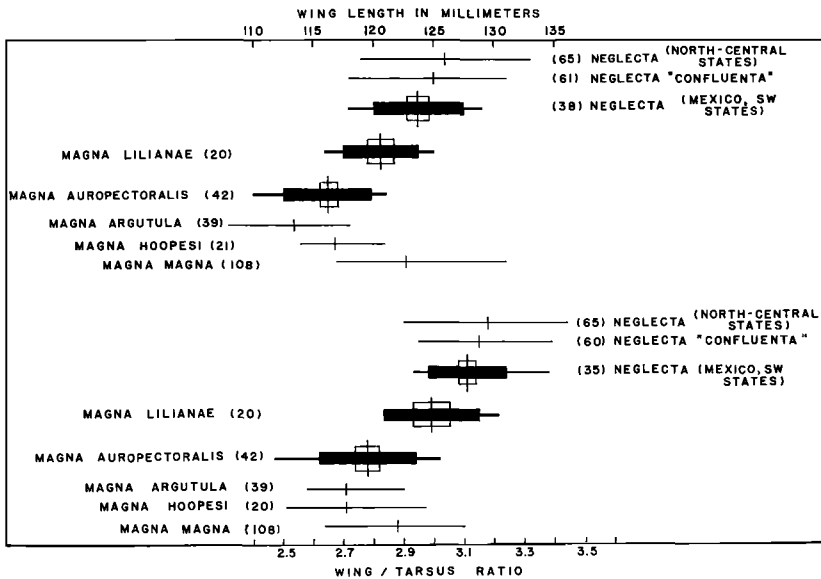


Figure 5. Statistical analyses of wing length and wing/tarsus ratio in male meadowlarks of the desert grassland. Numbers in parentheses indicate sample size. Horizontal lines represent range; means are indicated by vertical lines; open rectangles indicate twice the standard error of the mean; solid rectangles indicate 1.3 times the standard deviation. Range and mean alone are given for samples of additional meadowlark populations for comparative purposes.

of the same geographical area, same sex, and equivalent condition of feather wear. The comparatively paler coloration of the upper parts of *S. neglecta* and the darker coloration of the upper parts of *S. magna lilianae* are evident even when comparing a worn (darker) specimen of *neglecta* with a fresh (paler) specimen of *lilianae*. In the absence of a reference series for comparative purposes, the coloration of crown and back can be used effectively to supplement the more objectively determined rectrix pattern character.

Other differences in plumage coloration. The nature of the markings on the remiges and rectrices—*i.e.*, whether distinctly barred or confluent—is frequently cited in the literature as being a reliable specific character for distinguishing between these siblings. It is not. These markings are highly variable, geographically and individually, and there is complete specific overlap in them. This is especially true in the desert grasslands, where, presumably through selection under arid conditions, *S. magna* approximates the "barred pattern" that is generally characteristic of *S. neglecta* (see Figure 4).

There are a number of other specific differences in plumage coloration, all of which involve somewhat more arbitrary appraisals of differences in richness or hue, as for example the color of the breast, flanks, and crissum. Use of these characters is not recommended, however, without access to an adequate reference series.

Mensural characters. There is no significant geographical variation in the size of *S. neglecta*. A tendency toward longer wings in the breeding birds of the north-central United States is no doubt correlated with the more migratory behavior of those populations as compared with the Mexican birds, and this variation appears to be clinal. By contrast *S. magna* exhibits pronounced variation in size throughout its extensive range. Although this variability is also clinal in nature, the gradients are steep in zones of racial hybridization. Consequently, contiguous subspecies of *S. magna* are characteristically identified by significant differences in body size.

Wing length has the lowest coefficient of variability within populations of both species and is the most useful of the mensural characters in determining specific limits (see Table 1 and Figure 5). But since there is extensive overlap in the wing lengths of sympatric populations of these species, this character is of only supplemental value at the individual level. In both species the males have substantially longer wings than do the females, this being the most practical means of sexing specimens at any season.

Since *S. neglecta* averages a longer wing but a shorter tarsus than *S. magna*, it seemed likely that the ratio of wing length to tarsal length might be a useful morphological character. However, an analysis revealed as much statistical overlap between populations with regard to this ratio as when compared with respect to wing length (Figure 5). Furthermore, this ratio was found to be more variable within populations than either wing length or tarsal length alone.

Bill length and tail length were found to be too variable for discriminating between these populations of meadowlarks.

VARIATION IN VOCALIZATIONS

Call notes. The most characteristic and most frequently heard call note of *S. neglecta* in the north-central United States is the *chupp*, a single, explosive note in which the sound energy is concentrated in the 2.0- to 3.0-kilocycle range (Lanyon, 1957). Further study elsewhere within the range of the species suggested that there was no consistent geographical variation in this note (Lanyon and Fish, 1958). An analysis of the spectrograms of this call note made from recordings of representative breeding birds from the desert grasslands of the Mexican plateau supports

TABLE 1
MEASUREMENTS OF MEADOWLARKS OF THE DESERT GRASSLAND

| | <i>S. neglecta</i> | | <i>S. magna lilianae</i> | | <i>S. magna auropectoralis</i> | |
|--------------------|---------------------------|----------------|--------------------------|---------------|--------------------------------|----------------|
| | Males | Females | Males | Females | Males | Females |
| Wing length (mm) | | | | | | |
| Range | 118-129 (38) ¹ | 108-118 (14) | 116-125 (20) | 105-115 (7) | 110-121 (42) | 101-110 (18) |
| Mean, S.E. | 123.7 ± .47 | 112.9 ± .83 | 120.6 ± .53 | 110.7 ± 1.34 | 116.2 ± .44 | 105.4 ± .62 |
| S.D. | 2.91 | 3.10 | 2.39 | 3.55 | 2.83 | 2.64 |
| C.V. | 2.35 | 2.74 | 1.98 | 3.20 | 2.43 | 2.50 |
| Tarsal length (mm) | | | | | | |
| Range | 37-41 (35) | 34-40 (14) | 37-42 (20) | 37-40 (9) | 39-47 (42) | 37-42 (19) |
| Mean, S.E. | 39.8 ± .20 | 37.2 ± .46 | 40.4 ± .33 | 38.9 ± .39 | 41.9 ± .26 | 39.1 ± .31 |
| S.D. | 1.18 | 1.72 | 1.47 | 1.17 | 1.66 | 1.35 |
| C.V. | 2.95 | 4.62 | 3.63 | 3.00 | 3.97 | 3.46 |
| Wing/tarsus ratio | | | | | | |
| Range | 2.93-3.38 (35) | 2.80-3.29 (14) | 2.83-3.21 (20) | 2.76-2.89 (7) | 2.47-3.02 (42) | 2.50-2.87 (18) |
| Mean, S.E. | 3.11 ± .02 | 3.04 ± .04 | 2.99 ± .03 | 2.84 ± .02 | 2.78 ± .02 | 2.71 ± .02 |
| S.D. | 0.10 | 0.15 | 0.13 | 0.04 | 0.12 | 0.11 |
| C.V. | 3.22 | 4.87 | 4.21 | 1.41 | 4.39 | 3.87 |
| Body weight (gm) | | | | | | |
| Range | 88.3-114.0 (8) | 74.1-79.6 (3) | 104.0-110.9 (3) | 88.1-94.2 (2) | 88.1-102.5 (2) | 75.0 (1) |
| Mean | 101.5 | 75.9 | 107.0 | 91.2 | 95.3 | 75.0 |

¹ Sample size.

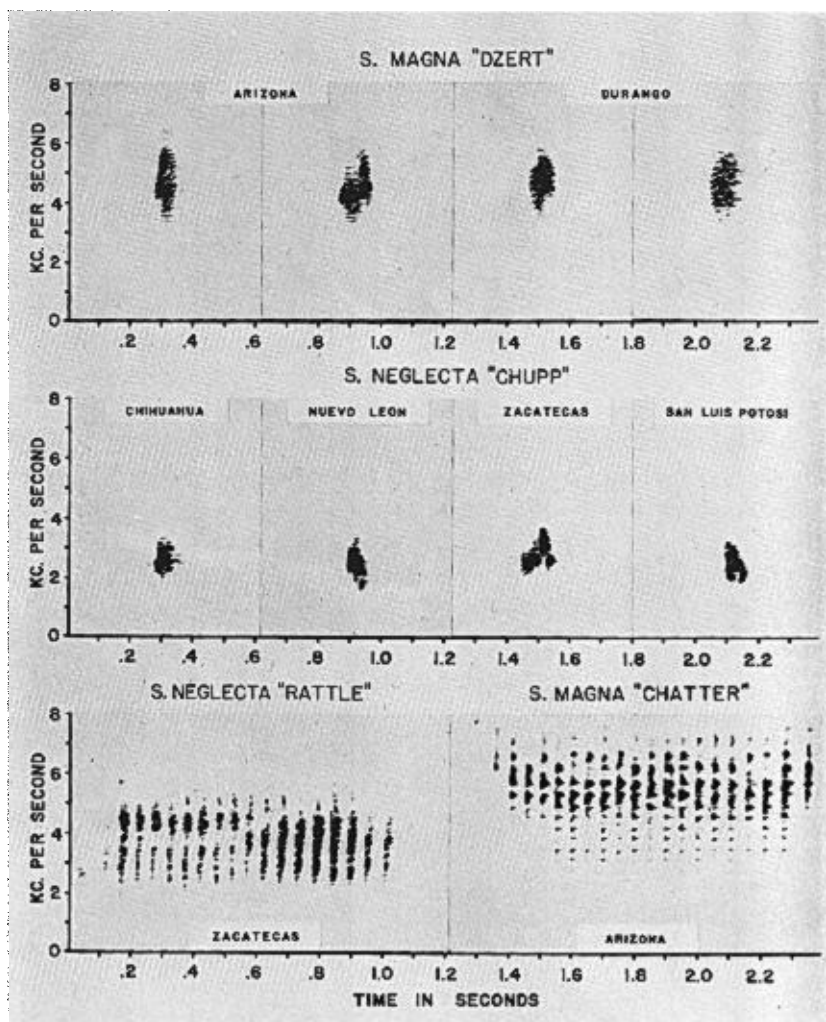


Figure 6. Sound spectrograms of diagnostic call notes of meadowlarks of the desert grassland. Note the specific differences in frequency (kc per second). Recording localities and dates: *magna* "dzert" notes from Bernardino, Arizona (one male, June 1959), Durango City, Durango (male, 8 May 1960) and near Vicente Guerrero, Durango (male, 7 May 1960); *neglecta* "chupp" notes from Santa Ana Babicora, Chihuahua (male, 15 June 1957), La Paz, Nuevo León (male, 5 May 1960), Sombrerete, Zacatecas (male, 7 May 1960), and Matchuala, San Luis Potosí (male, 6 May 1960); *neglecta* "rattle" from Fresnillo, Zacatecas (female, 7 June 1959); *magna* "chatter" from Sonoita, Arizona (male, May 1956).

this conclusion (Figure 6). Variation between widely separated populations was no greater than that exhibited by a given individual in reaction to environmental stimuli of varying intensities. The *chupp* rendered by *S. neglecta* of the desert grasslands is at once recognized by the field observer who is familiar with the species elsewhere from California to the Great Lakes.

The *chupp* of *S. neglecta* has its counterpart in the *dzert* note of *S. magna*, likewise a single, explosive note but with the sound energy concentrated at sufficiently higher frequencies that permit the use of both calls in the specific identification of birds in the field. In the Wisconsin study (Lanyon, 1957) the *dzert* note of *S. m. magna* was reported as typically occurring in the 3.0- to 4.0-kilocycle range. A frequency range of 3.0 to 4.5 kilocycles is actually covered by the spectrograms of the *dzert* notes recorded and analyzed during that study. Subsequently, additional recordings have been made of that race in Ohio and in New York (Lanyon, ms), which suggest that this note may regularly contain frequencies up to 5.5 kilocycles. Likewise, the spectrograms made recently from recordings of *S. m. alticola*, from the Isthmus of Tehuantepec south to Costa Rica, suggest that the *dzert* note may regularly consist of higher-frequency components than formerly supposed (Lanyon, ms). Spectrograms of the *dzert* notes given by representative males of *S. m. lilianae* and *S. m. auropectoralis* are shown in Figure 6. These patterns exhibit energy in the 3.0- to 6.0-kilocycle range, thus conforming to what is now known of the specific limits for this call note. Variation within the individual with regard to the configuration and frequency of this note is as great as the geographical variation between *lilianae* of Arizona and *auropectoralis* of Durango. Note the variability in the two spectrograms from Arizona, both made from recordings of the same male (Figure 6). The meadowlarks of the desert grasslands can be specifically differentiated, then, on the basis of the pitch of their most characteristic and most frequently heard call note: the *dzert* of *S. magna* centering on a frequency some two kilocycles higher than the average frequency of the *chupp* of *S. neglecta*.

As suggested in the Wisconsin study (Lanyon, 1957), the *rattle* of *S. neglecta* is a common female call note and is only rarely given by a male. This appears to apply to *neglecta* of the desert grasslands as well. That it is the most frequently rendered vocalization of female *neglecta* makes it, potentially, a valuable means of specific identification. The *chatter* call note of *S. magna*, unlike the analogous *rattle* of *neglecta*, is commonly rendered by both sexes in an identical pattern (Lanyon, 1957). An analysis of the spectrograms of these analogous call notes (Figure 6) recorded from

a desert grassland population of each species reveals the same specific limits for these vocal patterns as determined for the populations of the north-central states. The *rattle* of *neglecta* females within the study area is a homogeneous note made up of a repetitive series of component elements, variable in number, with frequencies from 2.0 to 5.0 kilocycles. The *chatter* of both *S. m. lilianae* and *S. m. auropectoralis* (there is no racial distinction in the call note) is of a configuration similar to that of the *neglecta* counterpart but with frequencies from 2.0 to 8.0 kilocycles. The *chatter* is characteristically higher in frequency and covers a greater range of frequencies than the *rattle*.

Primary song. The primary song of *S. magna* of the desert grasslands (Figures 7 and 8) is characterized by a series of gently downward-sloping elements, commonly three to four in number (to the human ear) and ranging in frequency from 2.0 to 8.0 kilocycles. Often the components range as high as 6.0 kilocycles or higher. In all respects, *i.e.*, configuration of component elements, frequency, and duration in time, the primary song of *S. m. lilianae* (Figure 7) and of *S. m. auropectoralis* (Figure 8) falls within the specific limits exhibited by populations in the north-central states (Lanyon, 1957) and in southern Mexico and Central America (Lanyon, ms). This lack of geographical variation in the basic characteristics of primary song is of special interest in view of the rather marked morphological variation among the races of this species.

The primary song of *S. neglecta* has been shown to retain certain basic, common characteristics among widely separated breeding populations of the species (Lanyon, 1957; Lanyon and Fish, 1958). The spectrograms made of songs recorded from the desert grassland populations of *neglecta* (Figures 9 and 10) conform in all respects with these specific limits: (1) sound energy concentrated in the range of 1.0 to 5.0 kilocycles, with components rarely going as high as 6.0 kilocycles; and (2) a division of the song into phases, an introductory phase of rather pure tones or whistles, and a concluding group of more complex, "steep slope elements." It is the presence of the latter-type element that makes the primary song of *neglecta* more melodious and of a richer quality than *magna*.

As elsewhere within the zone of overlap of these siblings, the pronounced specific differences in their primary song constitute the most practical means for their field identification in the desert grasslands. The apparent conservativeness of their primary songs, geographically, is of particular interest in view of the evidence that the complete manifestation of these specific characteristics is dependent, in both species, upon learning from experienced individuals of their own kind during a critical developmental period (Lanyon, 1957, 1960).

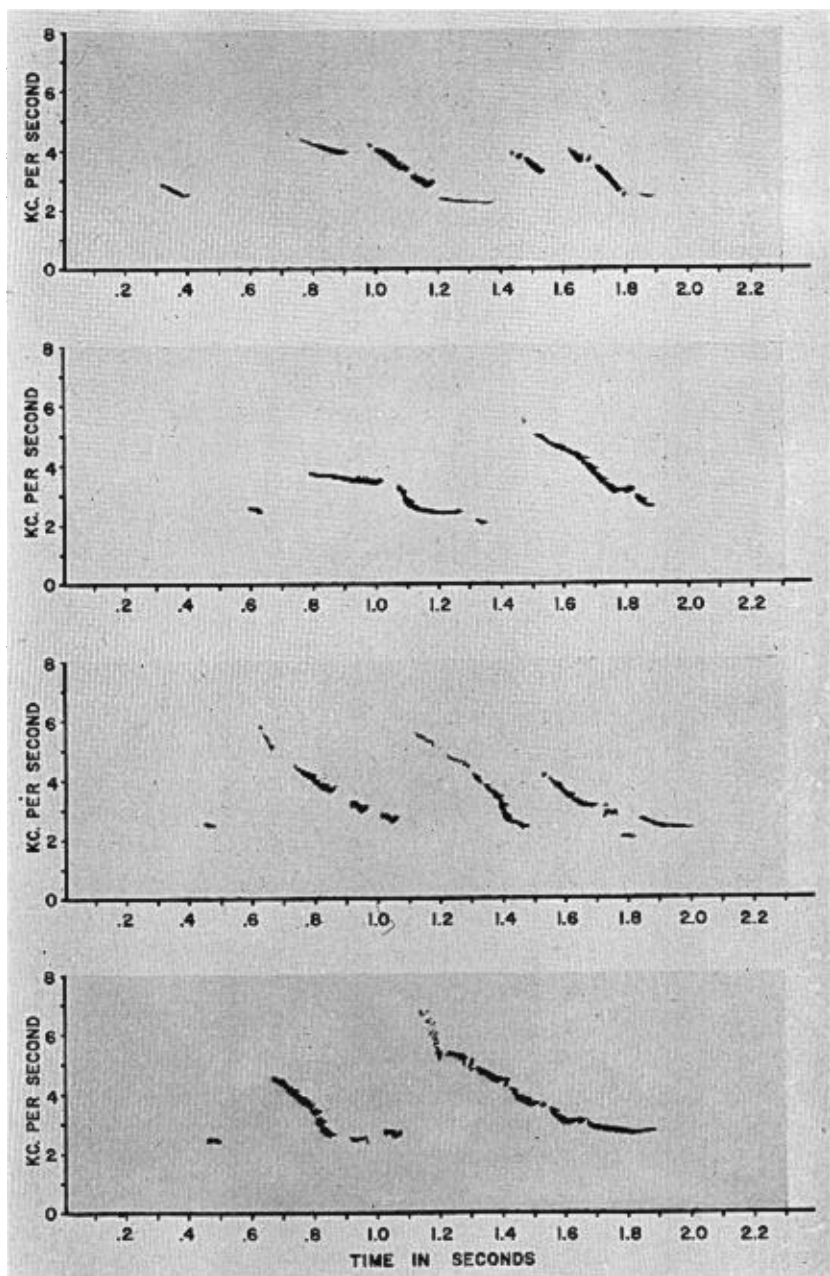


Figure 7. Sound spectrograms of primary songs of *S. magna lilianae*. Top song recorded at Bernardino, Arizona (June 1959); others recorded at Sonoita, Arizona (May 1956).

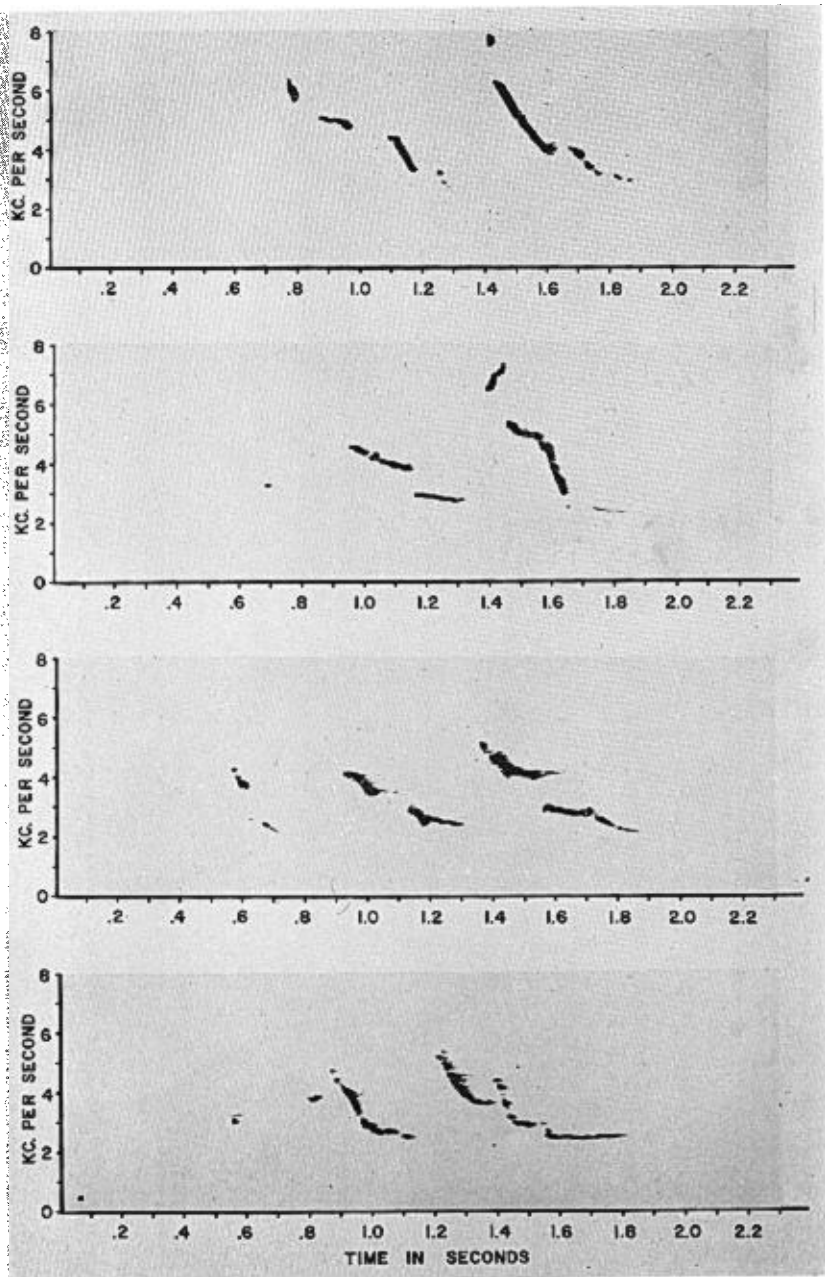


Figure 8. Sound spectrograms of primary songs of *S. magna auropectoralis*. Top song recorded at Durango City, Durango (8 May 1960); others recorded at Vicente Guerrero, Durango (7 May 1960).

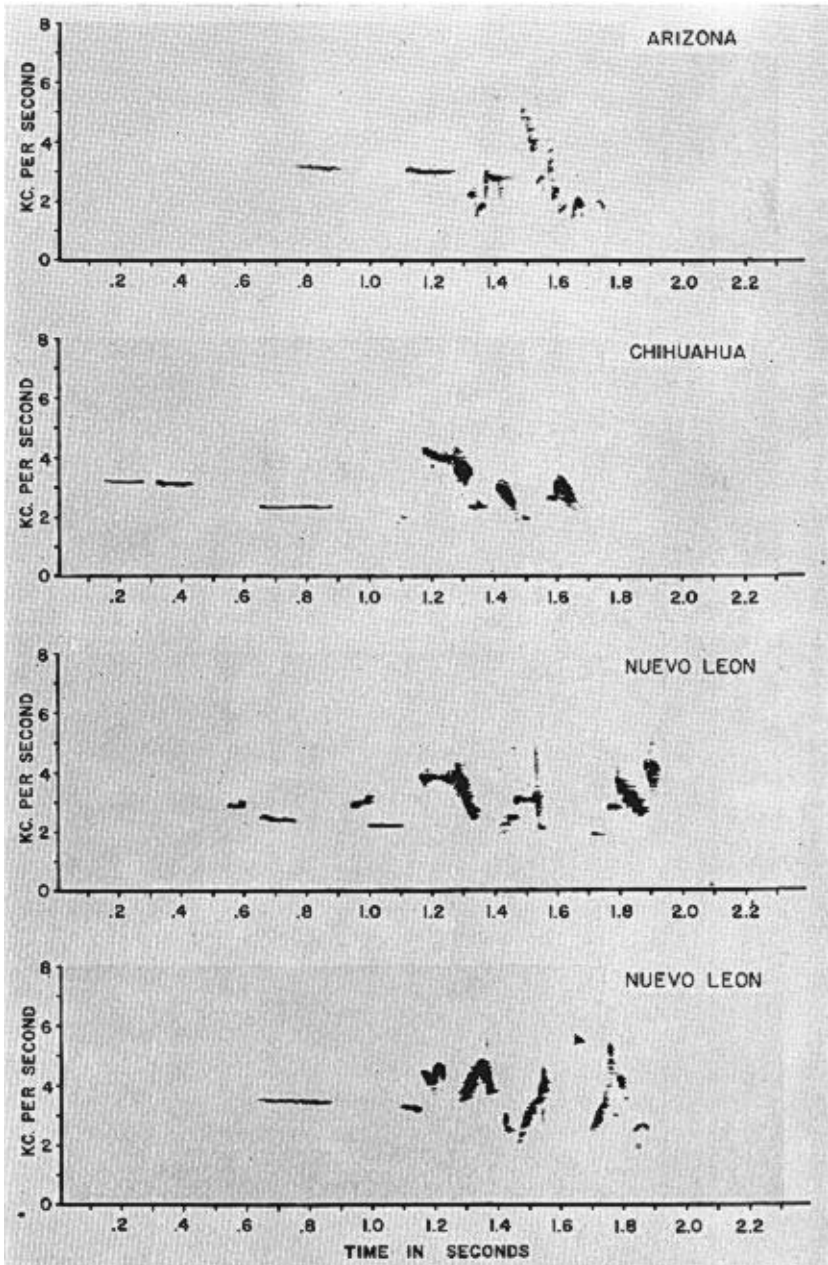


Figure 9. Sound spectrograms of primary songs of *S. neglecta* in the desert grassland. Recording localities and dates: Tucson, Arizona (April 1956); Santa Ana Babicora, Chihuahua (15 June 1957); La Paz, Nuevo León (one bird, 5 May 1960).

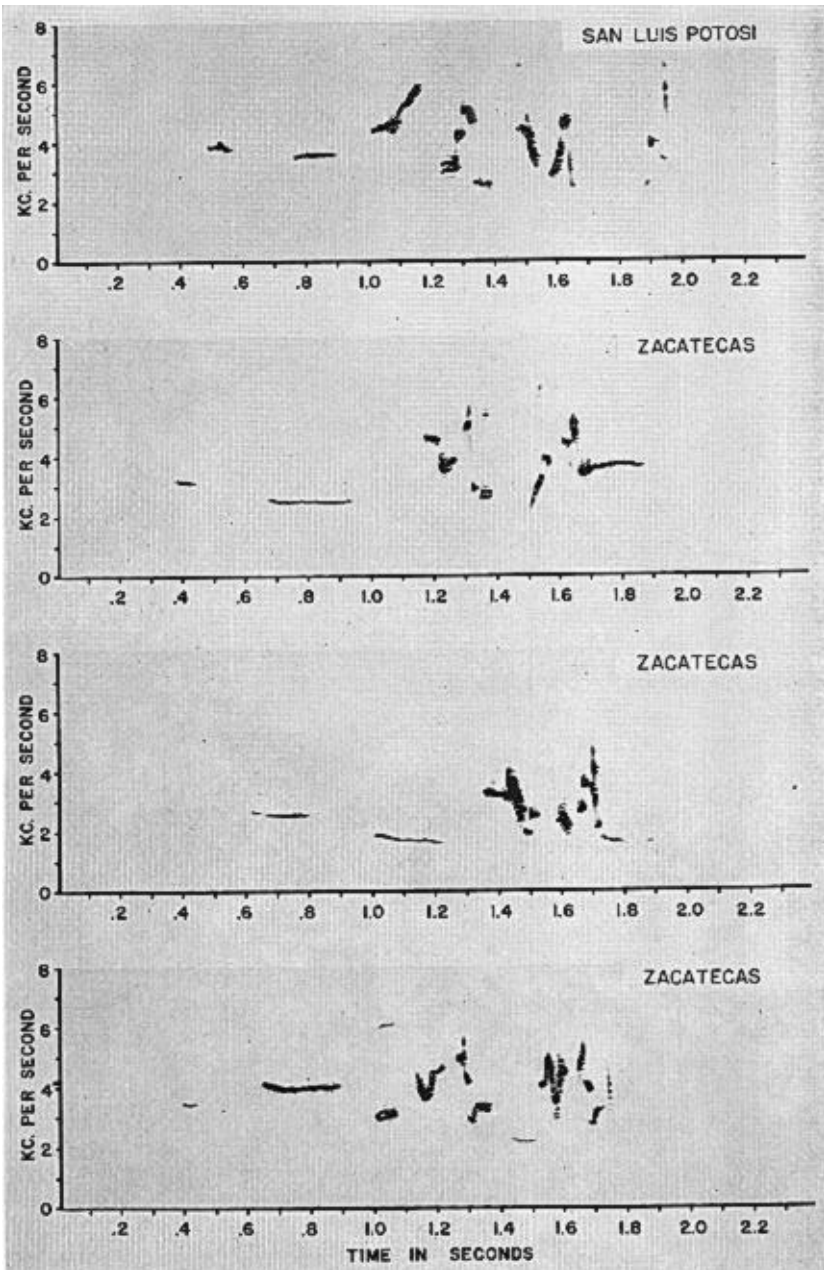


Figure 10. Sound spectrograms of primary songs of *S. neglecta* in the desert grassland. Recording localities and dates: Matehuala, San Luis Potosí (6 May 1960); Fresnillo, Zacatecas (7 June 1959); Sombrerete, Zacatecas (7 May 1960); Fresnillo, Zacatecas (7 June 1959).



Figure 11. Desert grassland along Highway 45, just south of Sombretete, Zacatecas, 7 May 1960. *S. neglecta* is the only meadowlark that breeds on these arid plains.

DISTRIBUTION AND ECOLOGICAL RELATIONSHIPS

A reexamination of the existing series of breeding meadowlarks, based upon the smaller series taken in this study, has now revealed a reasonably adequate picture of the breeding range of *S. neglecta* in Mexico (see Figure 1). The largest numbers are to be found within the broad belt of desert grassland along the eastern base of the Sierra Madre Occidental, notably in central Chihuahua, Durango, and Zacatecas (see Figure 11). The dominant grasses in this community are grammas of the genus *Bouteloua*,

with shrubs and cacti generously interspersed (*Acacia* sp., *Prosopis* sp., *Opuntia* sp., and *Yucca* sp.). The specimens taken in Chihuahua, Durango, and Zacatecas are no doubt representative of a fairly continuous breeding population, extending from a point some 85 km north of Chihuahua City southward at least as far as Matanzas, Jalisco. In May 1960, I heard over a dozen males along a 17-km stretch of Highway 80, just north of Matanzas, and these constitute the southernmost breeding population of the species to my knowledge. There is a good series of specimens in the Moore collection taken in June about 35 km west of Ojuelos, which would be about 25 km north of Matanzas. South of Matanzas the grassland soon disappears. However, an undated but worn specimen in the U.S. National Museum (USNM 78108), from Silao, Guanajuato, may possibly have been a breeding bird. Smaller, more restricted breeding populations are also associated with similar desert grassland communities along the western base of the Sierra Madre Oriental, in extreme southeastern Coahuila, southern Nuevo León, northwestern San Luis Potosí, and southwestern Tamaulipas. The latter populations are almost certainly discontinuous with those to the west because of the vast intervening areas of desert where grass cover is too sparse to provide suitable nesting substrate for meadowlarks. I doubt the occurrence of *neglecta* as a breeding bird in Mexico other than on the central plateau, except for the area about the Colorado River delta in extreme northwestern Sonora. As a species, *S. neglecta* winters commonly throughout much of northern Mexico, as far south as Michoacán, México, and Veracruz.

The breeding populations of *S. neglecta* in Mexico appear to be isolated geographically from those populations breeding in the southwestern United States. The southeastern Coahuila birds are separated ecologically from those of the Big Bend region of Texas by intervening desert. The hiatus of breeding *neglecta* from north-central Chihuahua northward to the latitude of Tucson, Arizona, and Las Cruces, New Mexico, seems to be well established, but it is questionable that this particular distributional gap can be explained solely on the basis of an ecological barrier. The desert grassland of southeastern Arizona and southwestern New Mexico would not appear to differ, physiognomically or otherwise, from the grassland of Durango or Zacatecas, yet the only breeding meadowlark of the former region is *S. magna lilianae*. The absence of *neglecta* in this portion of the desert grassland is further accentuated by its presence as a breeding bird on irrigated ranch land near Tucson and elsewhere in central and eastern Arizona.

The largest breeding populations of *S. magna lilianae* are to be found in the desert grassland of southeastern Arizona (see Figure 12), southern New Mexico, and the trans-Pecos region of Texas. In north-central and

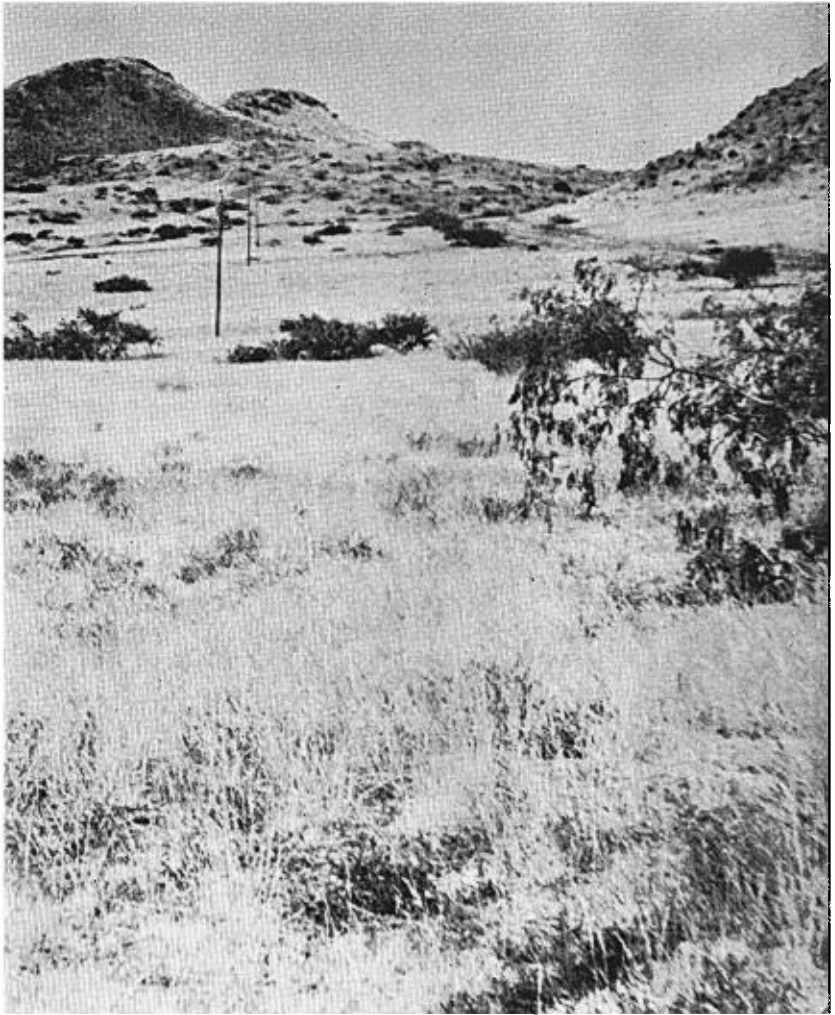


Figure 12. Desert grassland in Cochise County, southeastern Arizona, October 1955. *S. magna lilianae* breeds here, whereas *S. neglecta* prefers irrigated land in central and eastern Arizona, thus reversing their ecological relationships as exhibited elsewhere in the zone of geographical overlap.

central eastern Arizona it has invaded some of the higher mountain prairies as well. Although successful at the northern limit of the desert grassland, *S. m. lilianae* is not found farther south on the Mexican plateau. The southernmost Mexican breeding specimens to my knowledge (AMNH 56792 and 56793) were taken at San Diego, Chihuahua, some 130 km

northwest of the northernmost known breeding locality for *neglecta* in that state.

In contrast to the many areas where *S. m. magna* and *S. neglecta* breed contiguously in the north-central United States, there are comparatively few areas where both *lilianae* and *neglecta* can be found breeding. Van Tyne and Sutton (1937) reported both species breeding "side by side" in the grasslands near Marathon, Texas. Apparently drought conditions since then have disturbed this picture, for I found only *lilianae* breeding in this region in June 1960. Both species have bred in the past in the Milnesand area of central eastern New Mexico (J. S. Ligon, *in litt.*, 1954). Only rarely do they nest in close proximity in Arizona, as where irrigated farmland and desert grasslands are contiguous in north-central and central eastern Arizona (A. R. Phillips and G. Monson, pers. comm.). In June 1956 I worked the region between Eagar and McNary, in central eastern Arizona, and found *neglecta* breeding on the irrigated farmland and *lilianae* breeding on the drier, upland grasslands. The habitat preferences exhibited by these birds at the northern limits of the desert grassland, *i.e.*, *neglecta* in irrigated land and *magna* in the more arid, natural grass communities, are reversals of their usual ecological relationships noted elsewhere in the zone of sympatry (Lanyon, 1953, 1956). No satisfactory explanation comes to mind, although historical factors are no doubt involved.

A considerable hiatus may exist between the ranges of *S. m. lilianae* and *S. m. auropectoralis* for I have seen no breeding *magna* from central or southern Sonora and Chihuahua. *S. magna auropectoralis* is essentially confined to the Pacific lowlands and foothills of the Sierra Madre Occidental, from Sinaloa to Michoacán. It penetrates the desert grasslands of the Mexican plateau only insofar as it has followed the major river systems to their headwaters, as in central Durango, Zacatecas, and north-eastern Jalisco. The northernmost locality in Durango for which I have a specimen of *auropectoralis* (taken by Nelson and Goldman, August 1888) is Santiago Papasquiari. Other populations of *auropectoralis* closely associated with *neglecta* at the edge of the desert grasslands have been documented by specimens from: San Juan del Río, Durango City, Nombre de Dios, and Vicente Guerrero, in central and southeastern Durango (American Museum of Natural History, and the Moore collection); Laguna Valderama, in central Zacatecas (California Academy of Sciences); 35 km west of Ojuelos, in northwestern Jalisco (Moore collection); and near Ibarra, northern Guanajuato (Moore collection). An additional breeding population was located 25 km north of Lagos de Moreno, Jalisco, on 8 May 1960, and identified on the basis of voice.

The small, peripherally breeding populations of *S. magna auropectoralis* that occur at the edge of the Mexican plateau appear to be associated

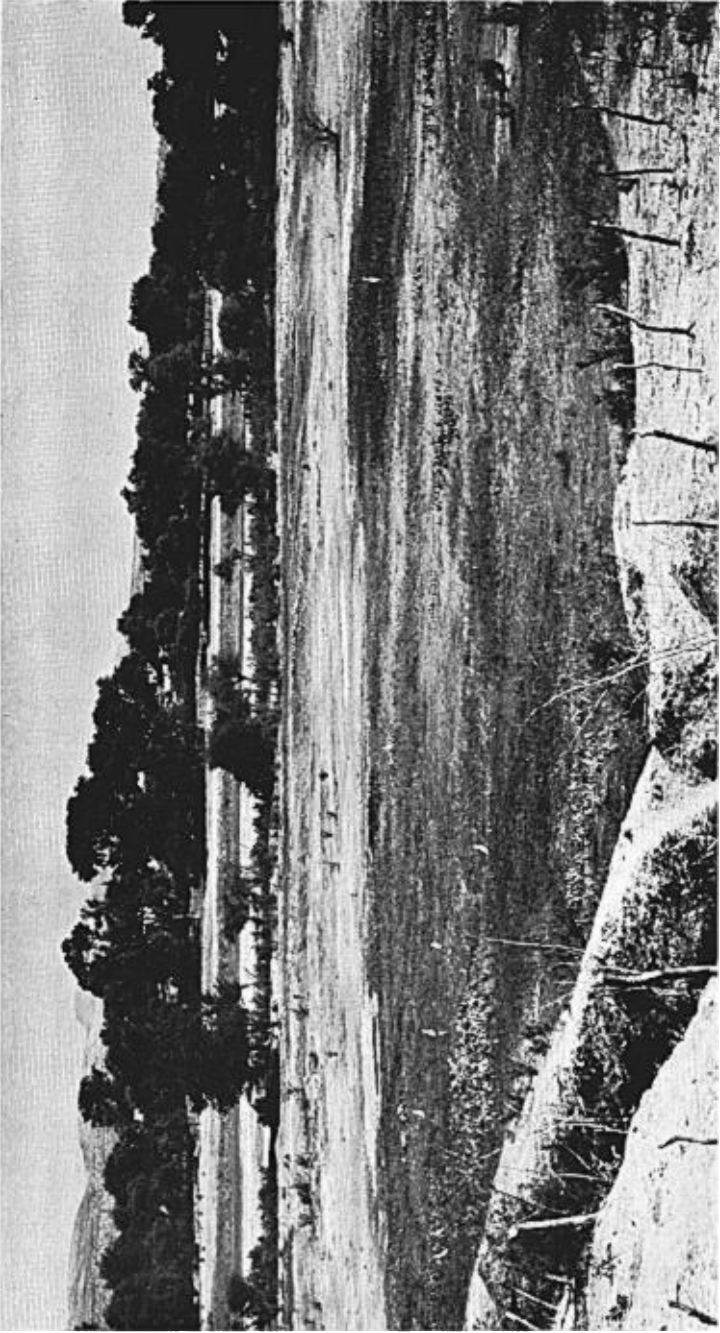


Figure 13. A peripheral population of *S. magna auropectoralis* breeds in the grassland bordering this *ciénega* along the Rio Coapanco near Nombre de Dios, Durango (photo taken 7 May 1960). The surrounding desert grassland is occupied exclusively by *S. neglecta*, reflecting the usual habitat preferences of these species in the zone of overlap in the north-central United States.

with irrigated farmland and the grassland bordering *ciénegas* and ponds. I visited four of these peripheral colonies in May 1960: (1) on irrigated farmland in the valley of the Rio Graceros, near Vicente Guerrero, Durango; (2) near a *ciénega* at the northern edge of Nombre de Dios, Durango (see Figure 13); (3) at the edge of a *ciénega* just east of Durango City; and (4) near a series of large, artificial ponds 25 km north of Lagos de Moreno, Jalisco. The desert grassland surrounding these populations was inhabited exclusively by *S. neglecta*. It would seem, then, that the ecological relationship between *S. m. auropectoralis* and *S. neglecta* at the southern end of the desert grassland is similar to that between *magna* and *neglecta* in the zone of overlap in the north-central United States, with *neglecta* occupying the drier uplands and *auropectoralis* exhibiting a preference for the more moist grassland environments.

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SUMMARY

1. Specific limits for morphological and vocal characters are presented for those populations of the two species of meadowlarks that breed in the desert grasslands of the southwestern United States and the Mexican plateau. The current taxonomic treatment of these populations is accepted.

2. Specimens in the hand can be readily identified as to species according to the extent of white in the rectrices. Both races of *magna* have consistently more white in the tail than does *neglecta*, with no overlap noted in the series examined.

3. Useful supplemental morphological characters are the greater extent of yellow on the cheek of *S. neglecta* (if determined properly), and the darker, lateral crown stripes and general upper parts of *S. magna* (reference series required). There is overlap in all mensural characters.

4. The two species can be readily distinguished in the field on the basis of consistent differences in their respective call notes and primary songs. The breeding populations of the desert grasslands were found to have the same basic vocal characters exhibited by the other populations of these species that have been studied thus far. These vocal characters appear to be more conservative, geographically, than are the morphological characters, and this is especially evident in the wide-ranging *S. magna*.

5. In Mexico, breeding *S. neglecta* are confined to the desert grasslands of the central plateau and are geographically isolated from those populations in the southwestern United States. *S. m. lilianae* is not found farther south on the Mexican plateau than northwestern Chihuahua. Few areas have been found where both *lilianae* and *neglecta* breed. The habitat preferences of these species at the northern limits of the desert grassland, *i.e.*, *S. neglecta* in irrigated land and *S. magna* in the more arid, natural grassland, is a reversal of their usual ecological relationship elsewhere within the zone of sympatry.

6. *S. m. auropectoralis* has penetrated the southern limit of the desert grassland only insofar as it has followed the major river systems of the Pacific lowlands to their headwaters at the western edge of the central plateau. Four of these peripheral colonies were visited, and all were associated with irrigated farmland and the grassland bordering *ciénegas* and ponds. The desert grassland surrounding these populations was inhabited exclusively by *S. neglecta*, thus reflecting the ecological relationship reported for the two species in the north-central United States.

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