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Sympatry of Red-breasted Meadowlarks in Argentina, and the Taxonomy of Meadowlarks (Aves: Leistes, Pezites, and Sturnella)

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INTRODUCTION

The Greater Red-breasted Meadowlark (Pezites militaris) and Lesser Red-breasted Meadowlark (P. defilippii) have been considered variously as conspecific and as separate species. For example, de Schauensee (1966, p. 440) favored the latter treatment, but noted that P. defilippii was "perhaps a race of P. militaris." (I have followed de Schauensee in the use of scientific and vernacular names throughout this report, except at the conclusion of the taxonomic section, which see.) The Lesser Redbreasted Meadowlark is a resident of the grassland pampas of eastern Argentina, Uruguay, and southeastern Brazil (fig. 1). During the winter in the Southern Hemisphere, at least the western portion of its range is invaded by Pezites m. militaris of the Patagonian and southern Andean foothills. The migratory habits of the latter race of the Greater Redbreasted Meadowlark have made it difficult to establish whether that species breeds sympatrically with the Lesser Red-breasted Meadowlark, or not.

While en route from Buenos Aires to Neuquén, Argentina, for the purpose of studying woodpeckers in November, 1967, I sought these

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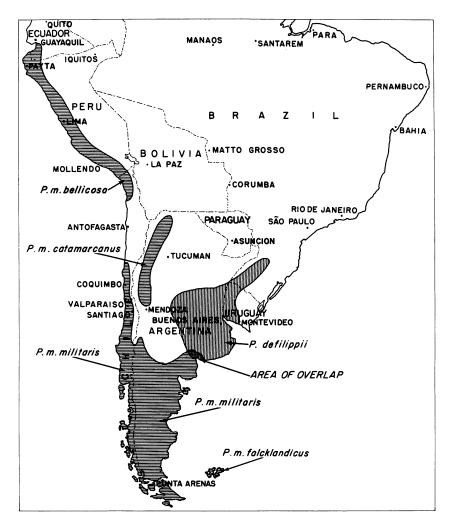


Fig. 1. Distribution in breeding season of red-breasted meadowlarks, *Pezites militaris* and its races (horizontal lines) and *P. defilippii* (vertical lines), in South America. See the text concerning the area of overlap in east-central Argentina.

meadowlarks, particularly in southern Buenos Aires Province and southern La Pampa Province. Although I did observe many individuals of *Pezites militaris* in the vicinity of Bahía Blanca, Buenos Aires Province, during November, I then had no time to investigate their status. En route back to Buenos Aires in early December, however, I was able to devote more time to the meadowlark problem. As I traveled eastward

along Federal Highway 22 on December 3, I found *P. militaris* common, apparently paired, and on territories in grassland along the edge of low, dry, *chaco* woodland at 21 kilometers west of Médanos, Buenos Aires Province. Recordings of songs and other vocalizations were obtained there. All birds encountered were in pairs; the members of presumed pairs either fed close together or perched in close proximity (unlike the northern yellow-breasted meadowlarks of the genus *Sturnella*, the sexes of the red-breasted meadowlarks are readily distinguishable, for the females are much duller than the males).

While driving along the main highway (Federal Highway 3) east of Médanos (at 23 kilometers west of Bahía Blanca) on December 4, I glimpsed a brighter, blacker, and smaller red-breasted meadowlark in open, well-drained grassland that extends north and south from the road at this point. I left the car and encountered what was apparently a male of *P. militaris* calling on a fence bordering the grassland and, beyond the fence, several individuals that were apparently *P. defilippii*, as well as several paler birds that I assumed were *P. militaris*. In a brief three-hour period I obtained moving pictures and sound recordings of some of the birds in the grassland north of the road. I also collected two male meadowlarks from adjacent territories, one of which proved to represent *Pezites defilippii*, and the other, *P. m. militaris*. Both males were adults in breeding condition.

An investigation of the entire region is necessary before the distribution of these two meadowlarks is firmly established, but it is clear that their ranges overlap in southern Buenos Aires Province (and probably La Pampa Province) during the presumed breeding season (fig. 1).

I have undertaken an analysis of this situation, which is presented below. I have also attempted an appraisal of the taxonomy of the entire group of meadowlarks, as it appears that the interaction between *Pezites militaris* and *P. defilippii* can be fully understood only after a re-evaluation of the taxonomic framework of this group.

THE SPECIMENS

The male of *Pezites defilippii* taken in the field 23 kilometers west of Bahía Blanca was collected as it sang in flight over a female perched on the ground. The female was not obtained, but it appeared small and was probably of the same species. The territory of this male (over which he flew and in which he sang many times) included about an acre of grassland. The male (figs. 2, 3) weighed 67.5 grams and had

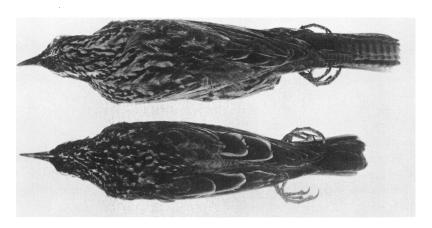


Fig. 2. Dorsal view of sympatric breeding males, collected on December 4, 1967, at 23 kilometers west of Bahía Blanca, southern Buenos Aires province, Argentina. Top: Pezites m. militaris. Bottom: Pezites defilippii.

testes measuring 9 mm. by 7 mm. and a large cloacal protuberance (one of the two discrete, testis-shaped masses of seminal tubules on each side of the cloaca measured 4 mm. by 2 mm.). The color of the soft parts was: iris brown; legs dark brown; bill black above, with silver-white tomia, and silver-white with a black tip below. Its stomach contents were entirely insects, including the large larvae of a beetle.

Immediately south of the territory of this Lesser Red-breasted Meadowlark was that of a pair of Pezites militaris. I did not determine whether or not their territories overlapped, but I suspect they did not. The territory of the Greater Red-breasted Meadowlark extended from about 80 meters north of the road south to the fence beyond the road. and it included the disturbed roadside grassy areas that were outside the fenced fields. The female of this pair was flushed with the male when I first entered the field north of the road. She generally accompanied the male about the territory, although she disappeared several times for considerable periods (about ten minutes). The female was not obtained. The male (figs. 2, 3) weighed 98.0 grams, had testes measuring 11 mm. by 6 mm., and had a very large cloacal protuberance (one of its two cloacal masses of seminal tubules measured 6 mm. by 3 mm.). The color of its soft parts was: iris brown, as in P. defilippii; legs dull brownish gray, paler than those of P. defilippii; bill identical with that of P. defilippii (see above). Its stomach contents were mainly plant material, chiefly seeds, but there were also a few insect remains. A detailed comparison of the two species is presented below, but those

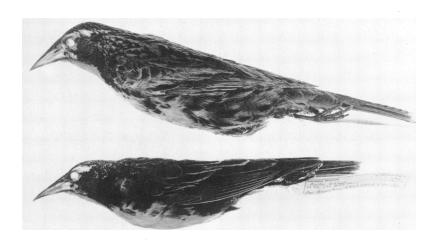


Fig. 3. Side view of sympatric breeding males, collected on December 4, 1967, at 23 kilometers west of Bahía Blanca, southern Buenos Aires Province, Argentina. Top: Pezites m. militaris. Bottom: Pezites defilippii.

features of potential use in field identification may be cited here. A sex-for-sex comparison of *P. defilippii* with *P. m. militaris* shows that the latter is larger, paler brown above, distinctly longer tailed, paler (pinker, less red) ventrally, and with less black on the sides. Additionally, flying individuals of *P. militaris* exhibit white rather than black axillar feathers.

DISTRIBUTION AND ECOLOGY

In contrast to the closely related Red-breasted Blackbird (Leistes militaris), both species of red-breasted meadowlarks seem to be birds of well-drained grasslands. Habitats in which Pezites militaris appeared to be breeding were noted in Neuquén, Río Negro, and southern Buenos Aires Province. In the Andean foothills of the former two provinces this species was found in dry level and hillside grasslands, especially in proximity to bushes and trees, and occasionally near water. For example, the species was commonly found in grassland at the edge of Nothofagus (southern or false beech) forest near San Martín de los Andes, Neuquén; among planted pines interspersed with grass east of the latter locality; and in grasslands bordering brush and low woodland along streams east of San Carlos de Bariloche, Río Negro (fig. 4). Apparently the Greater Red-breasted Meadowlark does not nest in desert grassland, for it was absent from large areas

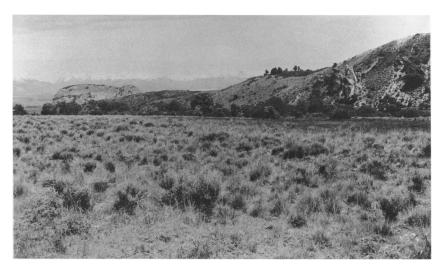


Fig. 4. The border of steppe and riparian woodland, habitat of *Pezites m. militaris*, at 16 kilometers east of San Carlos de Bariloche, Río Negro, Argentina. A stream flows at the base of the hill beyond the woods shown in the center. Part of Lake Nahuel Huapí is visible over the hill in the center, and the Andes around the lake are in the background.

of this habitat in eastern Neuquén. In southern Buenos Aires Province this species was common in cultivated fields along the road between Montes de Oca and Médanos. This region contains interspersed patches of low woods (=chaco monte), fairly dry grassland, and large cultivated (wheat) fields. At the study area 21 kilometers west of Médanos, pairs of P. militaris were scattered along the edges of cultivated fields, and especially along the grassy but brushy edges of a monte north of the main east-west highway (fig. 5). Here the males, often accompanied by females, perched and called or sang from bushes, fences, fence posts, and telephone poles. Pezites militaris was common north of Bahía Blanca in grassland. About 100 kilometers north of Bahía Blanca, however, P. militaris is replaced by P. defilippii in an area where I could detect no change in habitat.

The Lesser Red-breasted Meadowlark was observed only in southern Buenos Aires Province. Aside from the field in which it was studied in sympatry with *P. militaris, P. defilippii* was noted sporadically within 100 kilometers north of Bahía Blanca, where it was much less common, or less conspicuous than was *P. militaris*. The grasslands of this region are generally similar to those of the area of sympatry west of Bahía Blanca, although there appears to be heavier grazing and more cultivation.

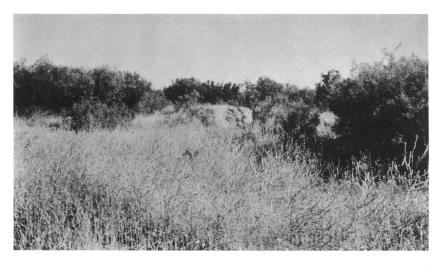


Fig. 5. The grassland edge of chaco woodland at 21 kilometers west of Médanos, southern Buenos Aires Province, Argentina, the habitat of Pezites m. militaris.

North and east of 100 kilometers north of Bahía Blanca, *P. defilippii* alone was found in similar grassland (fig. 6). On November 16 Lesser Red-breasted Meadowlarks were very common in the rather barren, dry, grassy slopes of the Sierra de la Ventana, north of Bahía Blanca, where Wetmore (1926, p. 374) had found this species "abundant." It is possible that the large population of this species inhabiting these hills forms a "reservoir" from which smaller populations "feed" south-



Fig. 6. The habitat of *Pezites defilippii* in well-drained pampas at 110 kilometers north of Bahía Blanca, southern Buenos Aires Province, Argentina.

ward and westward to come into contact with, and sporadically to occupy, areas within the range of *P. militaris*. North of the Sierra de la Ventana only *P. defilippii* is found in the better-drained areas of the pampas of central Buenos Aires Province. It is noteworthy that the vast region of wet pampas of Corrientes, Argentina, where *P. defilippii* occurs in winter in the Southern Hemisphere, is apparently not occupied by meadowlarks during the breeding season (personal observation).

Because of the limited time at my disposal, I was unable to investigate thoroughly the ecology of the two species of *Pezites* at 23

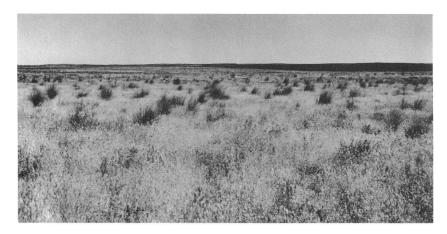


Fig. 7. The well-drained pampas at 21 kilometers west of Bahía Blanca, southern Buenos Aires Province, Argentina, where *Pezites militaris* and *P. defilippii* occur sympatrically. Parts of several territories of *Pezites defilippii* are in the foreground. In the background (to the north) is an area of low *chaco* woodland.

kilometers west of Bahía Blanca. There, in an area of mixed tall and medium grass (fig. 7), I found at least 10 pairs of P. defilippii. The habitat continues in all directions from the field of about 12 acres in which these were found; its population, therefore, is presumably much larger. At least two, and probably three, pairs of P. militaris occupied parts of this field. One pair was situated in an area from the narrow, disturbed grassy space between the fence and the main road to a short distance out into the field toward the adjacent pair of P. defilippii (see above discussion of specimens). The male of the pair of P. militaris was collected as it called on the fence north of the road. This male had sung and called from the fence, the fence posts, the tops of three small trees near the road (fig. 8), and a telephone pole

south of the road. Another pair of *P. militaris* occurred just east of this pair, but their territory extended farther north into the field. The male of this second pair also utilized the fence as a singing perch. A third male was seen in the tallest grass out in the field, surrounded by pairs of *P. defilippii*. This male called several times, but was not heard to sing. None of the males of *P. militaris* sang in flight, and all the singing males of this species utilized high perches (see above) above the grass.

In contrast, pairs of the more numerous *P. defilippii* were scattered throughout the area of grassland north of the road. The male that was

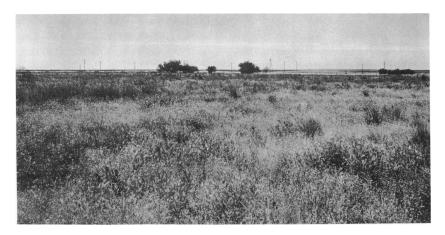


Fig. 8. Looking south toward the highway from the same spot at which figure 7 was taken. In the immediate foreground is a territory of *Pezites defilippii*. In the background are the fence and the low scattered trees used as singing perches by the male of *Pezites militaris* that was collected (see text).

collected (see above) occupied a territory just north of that of the male Greater Red-breasted Meadowlark that I obtained. To the west other pairs of P. defilippii occupied the entire field up to the fence. None was seen to perch on the fence or on any of the scattered bushes and small trees between the road and the fence. Indeed, no individuals of P. defilippii were noted in the disturbed grassland along the road south of the fence. The singing males of defilippii rendered primary songs (see below) from the ground and from perches in grass up to about 40 centimeters in height. They seemed to avoid singing from the highest blades of grass; hence they were usually partly obscured by grass as they sang. The most common song emitted by these birds was rendered in flight. Females of the pairs could be found by means of these flight

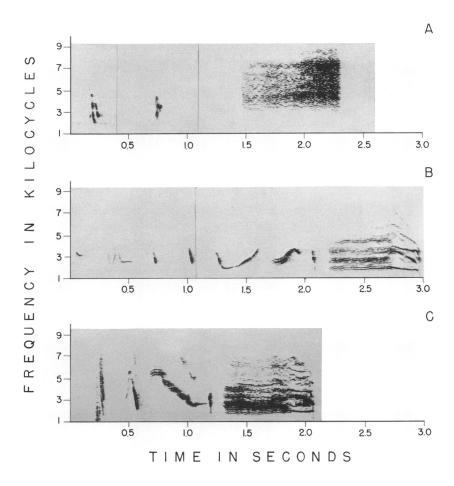


FIG. 9. Sound spectrograms of various vocalizations of red-breasted meadowlarks. A. From left to right, a "peet" call of *Pezites m. militaris*, a "peet" call of *P. defilippii*, and the "zheet" call of *P. defilippii*. B. A typical primary song type I of *P. militaris*. C. A typical primary song type II of *P. militaris*.

displays, for the males often centered the flight over the female. Encounters between males were not uncommon. I saw several chases involving two males; once a bird flew at another male in flight and actually pecked it as he drove it away.

Wetmore (1926, pp. 373-375) had previously taken both species at Lake Epiquén, near Carhué, western Buenos Aires Province, on December 16, 1920. Although he did not note their nesting in the grasslands by this lake, the date suggests the possibility that both nest there.

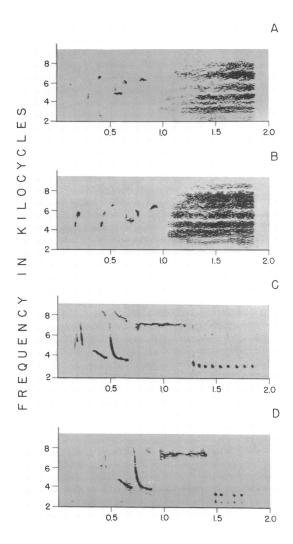


Fig. 10. Sound spectrograms of songs of *Pezites defilippii*. A, B. Primary songs. C, D. Secondary (flight) songs.

VOCALIZATIONS

Recordings of various vocalizations of four or five different males of *Pezites defilippii* were obtained on December 4 at 23 kilometers west of Bahía Blanca. The vocalizations of two males of *P. m. militaris* were

recorded at 21 kilometers west of Médanos (about 45 kilometers west of the above-mentioned locality) on December 3. All recordings were made with a Uher 4000 Report L tape recorder, operated at 7.5 inches per second, and a Uher M-514 microphone mounted in a 24-inch parabolic reflector. The narrow band-pass filter of a sound spectrograph was used for the analysis of representative recorded vocalizations (figs. 9, 10).

Vocalizations of the red-breasted meadowlarks were recorded during a brief period; hence these recordings probably reflect only a small portion of their total vocal repertoires. For example, the closely related yellow-breasted meadowlarks (Sturnella magna and S. neglecta) of North America have a varied repertoire, including several to many primary songs and calls (Lanyon, 1966). The vocalizations discussed herein do, however, show certain differences between the two red-breasted meadowlarks.

CALLS

Calls heard in the field include the "peet" call note (fig. 9) of both species and the "zheet" call note of *Pezites defilippii* (fig. 9). The "peet" call is a double note of slightly higher (about 1 kilocycle higher) frequency in *P. defilippii*. There is an upward-trending element, and an inverted V-shaped element at frequencies between 1.8 and 5.0 kilocycles, in both species. The "peet" call of *P. militaris* is of greater intensity and longer duration (about 0.12 second compared to 0.05 to 0.07 second in *P. defilippii*) than the compressed call of *P. defilippii*, but their calls are otherwise similar. I heard about 200 such calls of two males and two females of *P. militaris*, and about 100 calls of perhaps 10 males and several females of *P. defilippii*.

The "peet" calls seem to be the functional equivalent of the "chupp" and "dzert" calls, respectively, of the Western Meadowlark (Sturnella neglecta) and the Eastern Meadowlark (S. magna), but they structurally resemble more closely the "weet" note of those species, and especially their "location notes" (Lanyon, 1957). In fact, a very rapid, compressed location note of the type figured by Lanyon (1957, fig. 25B) for S. neglecta would be a close match for the "peet" call of the two species of Pezites. It is noteworthy that the Sturnella location notes are rendered only by juvenile birds (Lanyon, 1957, p. 48), whereas the physically similar but apparently functionally different note of Pezites is given by adults.

The "zheet" call of Pezites defilippii, which may be likened to the

"chatter" call of Sturnella magna (Lanyon, 1957, pp. 12-13), comprises a variable number of similar elements at a frequency of 2.5 to 9.0 kilocycles, with the greatest intensity between 3.0 and 8.0 kilocycles. The duration of the call is from 0.8 to 1.0 second. I heard this call no more than a half dozen times. I could not determine the situations in which this call is given, nor could I determine whether it occurs in P. militaris. It forms, however, the terminal portion of the primary song of P. defilippii, and a very similar group of elements comprises the terminal portion of both types of primary songs delivered by P. militaris (see below). As noted above, there are similarities between the "zheet" call of P. defilippii and the "chatter" call of Sturnella magna, and also the "rattle" call of S. neglecta, the "chupp" call of that species, and the "dzert" call of S. magna (Lanyon, 1957, figs. 7-9). The "chatter" call of S. magna would be identical with the "zheet" call of P. defilippii if it were shortened slightly, and delivered more rapidly (with less time between individual elements) and at a somewhat higher frequency.

Songs of Pezites militaris

I heard two distinctive primary songs of Greater Red-breasted Meadowlarks. Several hundred such songs were heard, mainly emitted by two males on December 3, but similar songs were heard on December 4 from at least one male of *P. militaris* in the field where this species occurred in sympatry with *P. defilippii*. The songs were delivered by males singing from high perches above the level of the grass (see above). Although both types of song were usually given separately, they were several times combined into a "double" song.

Song Type I (fig. 9): Songs of this type are longer than those of song type II, averaging 2.3 seconds. They are variable in length (from 2.15 to 2.90 seconds) apparently depending upon the number of introductory elements given. The frequency of the song is between 1.5 and 9.0 kilocycles; the introductory notes are all between 1.5 and 4.5 kilocycles, and only the terminal portion, which is almost identical with the "zheet" call note (see above) of *Pezites defilippii*, spans the entire range of frequencies from 1.5 kilocycles to 9.0 kilocycles. The terminal portion is most intense at from 2 to 5 kilocycles, and it differs from the "zheet" note of *P. defilippii* in having a slight terminal drop. The terminal portions of song type I and of song type II are identical. The introductory elements of song type I are five to eight in number, including: (a) several simple, whistled elements, all of 0.1 second or less in duration; (b) a characteristic down-curving then up-curving whistle of

about 0.4 second in duration, and at from 2 to 4 kilocycles in frequency; (c) a characteristic, upward-slurred whistle of about 0.25 second in duration and at from 2.5 to 4.0 kilocycles; and (d) a weak, and perhaps sometimes omitted, down-up-down whistle about 0.2 second in duration at from 2 to 3 kilocycles. The longest songs have elements rendered in this order: a-a-d-a-a-b-c-a-terminal portion. All songs of this type have the terminal portion preceded by elements "b," "c," and "a," in that order. These are almost invariably preceded by two "a" elements. It is possible that element "d" is regularly included, but that it is too weak to be heard, or recorded, in songs delivered at a substantial distance from the observer.

Song Type II (fig. 9): Songs of this type are shorter than those of song type I, averaging 1.75 seconds in duration (from 1.6 to 1.9 seconds). They contain fewer elements, namely, a terminal portion identical with that of song type I, preceded by only three or four elements. The introductory elements terminate in a single note of element "a" (as they do in song type I; see above). This element is preceded by two types of elements, each involving a greater frequency range than that found in any introductory element of song type I. These elements are: (1) element "e," one or two inverted-V-shaped, whistled notes of 0.10 to 0.15 second in duration, with frequencies between 1 and 7 kilocycles, and most intense on the terminal, downward phase; (2) element "f," a single, long (0.4 to 0.5 second), intense, downward-slurred whistle at frequencies from 6 kilocycles to 2 kilocycles. The latter element precedes the "a" element that is followed by the terminal portion of the song.

Double Song: Several double songs were heard, and one was recorded on December 3. As noted above, this song comprises connected song types I and II, in that order. The recorded double song was 4.8 seconds in duration and contained a complete song of song type I, followed in 0.19 second by a song of type II that lacked only an initial element "e" (see discussion of song type II above). The interval between the two song types was less than that separating most elements of song type I and nearly as brief as the intervals among elements of song type II.

The occurrence of other songs, the functions of the songs described above and any others that may occur in *Pezites militaris*, and their variation still remain to be documented. Lanyon (personal communication) has noted certain songs of the northwestern Argentine *P. militaris catamarcanus* that are different from the songs of *P. m. militaris* described herein. Likewise the occurrence of flight songs in *P. militaris militaris*

remains to be demonstrated. Lanyon (personal communication) reports an instance of such a flight song in *P. m. catamarcanus*. Until the variation in songs of *P. militaris* is investigated, the significance of song differences between *P. militaris* and *P. defilippii* cannot be fully appreciated.

Songs of Pezites defilippii

Two distinctive songs of *Pezites defilippii* were heard and recorded. These include a single type of primary song and one type of secondary song (this terminology follows that of Lister, 1953, as utilized in studies of *Sturnella* by Lanyon, 1957).

PRIMARY SONG (FIG. 10): The one primary song frequently delivered by presumed males of Pezites defilippii on December 4 was heard from individuals perched on low or moderately tall stalks of grass, or on the ground, in contrast to the delivery of the primary songs (i.e., song type I, song type II, and double song) of P. militaris discussed above. Approximately 150 such songs were heard from at least eight males. The primary song varies in duration from 1.7 to 2.0 seconds and comprises a terminal portion preceded by five or six introductory notes. The terminal portion is identical with the "zheet" note described above. The introductory notes include: (1) two or three preliminary notes (each containing two or three elements, or two or three weakly connected points of high intensity) of increasing frequency starting at 4.2 to 4.5 kilocycles and concluding from 0.05 to 0.15 second later at a frequency of about 5.6 kilocycles (when there are two points of high intensity) or at about 6.7 kilocycles (when there are three points of high intensity); (2) these are followed by a 0.06- to 0.08-second note of high intensity delivered at about 5.0 kilocycles and apparently containing a weak, rapid initial element of slightly higher (5.5 kilocycles) frequency; (3) there is next a strong, rapid (duration 0.02 to 0.04 second) note delivered at 6.1 kilocycles and then descending to as low as 5.5 kilocycles; and (4) a strong note at a constant frequency of from 6.1 to as much as 6.3 kilocycles for about 0.1 second. With the exception of the number of preliminary notes (item 1 above), these notes were characteristic of all primary songs that I heard. The final introductory note (item 4 above) is followed in about 0.1 second by the terminal portion of the song. The introductory notes appear to bear no marked resemblance to those of the various primary songs of P. militaris that I heard.

Secondary Song (fig. 10): The flight song of *Pezites defilippii* was delivered more frequently than were primary songs on December 4. I

heard hundreds of these songs over the course of three hours. One or another of the dozen or so males that I saw in that time was usually singing, so these songs were heard almost constantly. This entirely different song is composed of three parts: an introductory series of four short notes of varying frequency lasting about 0.5 second; an intermediate, continuous note at a frequency of about 7 kilocycles lasting 0.4 to 0.5 second; and a terminal series of from five to nine elements delivered at the same frequency (between 3.0 and 3.5 kilocycles) and lasting from 0.3 to 0.6 second. There is less than a 0.1-second interval among the three parts, and the entire song is 1.5 to 1.8 seconds in duration, depending on the number of elements in the terminal part of the song. The initial, introductory element is a very weak, inverted-Vshaped note, rising and falling in 0.02 to 0.03 second within a frequency range of 5.0 to 6.5 kilocycles, which is immediately followed by a somewhat stronger, very rapid (0.02 second), down-sloping note going from a frequency of 7.8 to 5.3 kilocycles. After a short pause there is a descending note of greater intensity going from 5.0 to 4.0 kilocycles in from 0.15 to 0.17 second. This note is followed immediately by a very sharply descending note of great intensity, dropping from 8 or 9 kilocycles down to 3.8 kilocycles in about 0.2 second. I also recorded an abbreviated flight song that lacked the third (terminal) part of the full flight song. This song contained all the elements of the introductory and intermediate parts of a normal song, and its duration (1.1 second) was also normal.

The primary song of Pezites defilippii that I discuss probably functions as do those of P. militaris; the nature of this function remains to be demonstrated. The secondary song of P. defilippii has no equivalent in the songs I noted for *P. militaris*, but Lanyon (personal communication) informs me that at least one flight song of P. militaris catamarcanus was heard (but not recorded) on his recent trip to Tucumán, Argentina. Hudson (1920, p. 129) noted that the flight song of P. defilippii does not seem to occur in P. militaris. Wetmore (1926, p. 375; and his field notes, which I have seen) commented on the flight songs of P. defilippii, which were not noted in P. m. militaris at a possible site of their sympatric breeding at Carhué, western Buenos Aires Province, during December, 1920. Functionally, the flight song of P. defilippii appeared related to courtship in those instances in which I noted it. I often detected a female on the ground in the vicinity of the highest point of the display flights of the males, during which the flight songs were delivered. I am not certain whether females were always situated below such displaying, singing males, for it was difficult to discern the birds on

TABLE 1

A Comparison of Some Measurements (in Millimeters) of Male Meadowlarks $^{\alpha}$

Bill

Form (N)	Wing Length	Tail Length	Bill Length (Nostril)	Bill Length (Culmen)	Bill Depth	Bill Width	Wing Tail	Tarsal Length	Middle Toe
Pezites defilippii (20)	118-127	73.4-81.8	18.0-22.0	18.0-22.0 24.1-28.7	9.1-9.9	6.8-7.5	6.8-7.5 0.60-0.67	28.0-33.6	19 4-22 9
Pezites defilippii ⁶	124	79.1	22.2	30.1	9.4	6.9	0.64	30.5	22.1
Pezites m. militaris ⁶	122	93.4	21.6	30.2	10.7	7.7	0.77	33.8	23.6
Pezutes m. militaris (24)	115-129	85.8-98.3	19.7–26.6	28.3-36.4	9.8 - 11.5	7.0-8.2	7.0-8.2 0.72-0.80	31.6-37.4	22.0-25.8
Fezites m. falklandicus (4)	130-135	95.0 - 101.0	24.0 - 33.2	32.5 - 42.4	10.8 - 11.0	7.6–8.6	7.6-8.6 0.72-0.74	35.9-37.1	25.9-28.0
Pezites m. catamarcanus (4)	126-131	93.0-100.7	23.2 - 25.4	32.3 - 34.1	(11.2)	7.5-8.2	0.73-0.77	35.1-36.0	24 6-25 6
Pezites m. bellicosa (15)	107-121	64.8-77.3	17.6-20.2	24.8-28.7	9.8-11.2	6.9–8.1	0.60-0.68	34.9–38.5	24.5-27.5
Leistes m. militaris (20)	94 - 102	59.9 - 68.1	14.3-16.4	20.5-23.0	8.5-9.7	6.5 - 7.2	0.62-0.69	30.2-33.0	19 9-22 6
Leistes m. superciliaris (23)	95-107	56.4-68.0	11.2-14.1	18.0-20.4	8.8-10.1	6.7-7.4	6.7-7.4 0.55-0.66	29.2–32.4	18.9–21.8
a Males are in comparable (mon)		7	=						
the chord hill and hill width was measured as	umage, exce	ept for very si	mall samples	, in which ev	ery male w	as utilized	. The wing	length was	neasured as
in the middle toe was measured at the center of the nostrils, and the middle toe was measured without including the claw.	ere measur	ed at the cen	ter of the no	strils, and th	e middle to	e was me	asured with	nout includir	ig the claw.
These are the sympatric males from west of Bahia Blanca, discussed in the text.	n west of B	ahia Blanca,	discussed in	the text.					

the ground amid the grass. Flight songs have been noted (Lanyon, 1957, pp. 22-23) less frequently in *Sturnella magna* and, especially, in *S. neglecta*, but they have not been recorded and analyzed. Although the flight songs of these species of *Sturnella* have been called "courtship" songs (Tullsen, 1911), Lanyon (1957, p. 23) considered them as manifestations of "intense excitement."

Although further investigations are necessary to determine the variation and function of the various vocalizations of *Pezites militaris* and *P. defilippii*, it is evident that their differences in primary and secondary songs approach the level of difference of that existing between the song of *Sturnella magna* and that of *S. neglecta*. The lack of similarity between introductory notes of the primary songs of the two species of *Pezites* is particularly noteworthy. Equally significant are the differences in utilization of song perches and the occurrence of many flight songs of *P. defilippii* coincidental with the absence (or infrequency) of such songs in sympatric *P. m. militaris*. Whether, and how, these relate to reproductive isolation of the two species remain to be determined.

MORPHOLOGY OF PEZITES DEFILIPPII AND PEZITES MILITARIS MILITARIS

Various forms of meadowlarks are compared mensurally in table 1, which also contains measurements of the two males that I collected. Compared with males of *Pezites militaris militaris*, those of *P. defilippii* exhibit a similar wing length, a considerably shorter tail, a shorter, narrower, and shallower (less deep) bill, shorter toes, and shorter, thinner legs. The males taken in sympatry fall within the range of variation of their respective species, except that the male Lesser Redbreasted Meadowlark has a longer bill (culmen) than other males of that species that I have examined. The long tail of *Pezites militaris* (except *P. m. bellicosa*; see below) sets this species apart from other meadowlarks, including forms currently placed in the genus *Leistes*. The functional significance of its longer tail is unknown, but it is interesting that it is *P. defilippii*, rather than *P. militaris*, that resembles other meadowlarks in this feature.

Comparably plumaged males of the Lesser Red-breasted Meadowlark are blacker dorsally (on the crown, sides of the neck, back, wings, and tail) and on the sides, flanks, and abdomen, than males of *Pezites m. militaris*. The former has, in addition to blacker coloration of these regions, a greater distribution of black in the feather bases, and narrower brown tips of these feathers. Thus, the two forms are most alike

in fresh plumage when the maximum amount of brown is evident. Subsequent wear reduces the brown tips, exposing ever more black in both species, but especially in the more narrowly tipped feathers of defilippii. This effect is enhanced by a fading of the brown in the tips of the feathers, for, whereas the narrower brown edges of defilippii are rapidly lost, exposing more black, the broader brown feather tips of militaris remain, fade, and gradually become pale. Thus, males of these red-breasted meadowlarks exhibit their greatest difference in worn, breeding plumage. It is possible (likely?) that the differences between the males of militaris and those of defilippii help the females to discriminate between them.

The red ventral color of *Pezites defilippii* averages redder than that of the pinker *P. m. militaris*. This difference is strongly evident in the two specimens I obtained, and, indeed, was a useful supplemental field character for their identification. The same color difference is found in the red of the lower malar region, the loral portion of the superciliary stripe, the shoulder (= true "wrist"), and the leading edge of the wing of males.

The tail of males of *Pezites m. militaris* is usually more heavily barred than that of *P. defilippii*. The upper tail coverts are barred in both forms, whereas the under tail coverts are barred in the former and solidly black with a white tip in *defilippii*.

As noted above, the under wing coverts of these two meadowlarks differ, and this difference constitutes a diagnostic field character. This area is white in *Pezites m. militaris*, but black in *P. defilippii*.

The wings of *Pezites defilippii*, which average about as long as those of *P. m. militaris*, are more pointed. The outer (ninth) primary of *P. defilippii* tends to be as long as, or longer than, the adjacent several primaries, primary 5 is usually shorter, and primary 4 is much shorter. In contrast, primaries 9 and 5 of *P. militaris* are subequal, and both tend to approach primaries 6–8 closely in length; primary 4 is but moderately shorter than primaries 9 and 5. The primaries of *P. defilippii* also tend to be more sharply pointed and narrower (more falcate) than the primaries of *P. militaris*.

The legs and feet of *P. defilippii* are thinner and less massive than those of *P. m. militaris*. This difference is greater than that suggested by the data for tarsal length and the length of the middle toe (table 1).

Likewise, the difference between bills of the two species is more disparate than the data (table 1) suggest, particularly when the equally long bills of the two males that I collected are compared. The bill of Pezites defilippii is thinner and proportionally longer and less deep and

wide than that of *P. m. militaris*. The latter has, especially, a more massive (broader, more flattened) culmen. Although the contents of the stomachs of the two males collected provide very meager data (see above), the bill difference between the two species would assume greater significance if *P. defilippii* proves to be more insectivorous than is *P. m. militaris*.

As I mention above, the females of these forms are more similar than are the males. Despite their similarity, they exhibit to a lesser extent the differences found between males. Dorsally (crown, hind neck, back, wing coverts) and on the sides, flanks, and abdomen, feathers of females of Pezites defilippii have broader black bases and centers than those of P. m. militaris, and these feathers in the latter have broader pale brown and white edges and tips. Because fresh-plumaged females of both forms have brown-edged feathers, the females are much more alike in fresh than in worn plumage. The effects of wear and fading render females less similar, just as in the case of the males. Thus, worn females of P. m. militaris are paler brown than worn females of P. defilippii.

These external morphological differences, in contrast to such differences between *Sturnella magna* and *S. neglecta* (Lanyon, 1957, 1966), are sufficiently great to permit species recognition. Whether or not they actually function in this manner remains to be demonstrated.

THE TAXONOMY OF MEADOWLARKS

The study of the interaction between *Pezites defilippii* and *P. m. militaris* suggested the need for a reappraisal of the relationships of the largely allopatric forms included within *Pezites* (see fig. 1), and between this "genus" and other meadowlarks. Indeed, the relationships within *Pezites* can be appreciated only within a framework of understanding of relationships within the entire group.

I preface consideration of these relationships with the generalization that I believe the meadowlark line of blackbirds comprised of Leistes, Pezites, and Sturnella to be monophyletic, and that existing species more or less form a morphological cline from the more Agelaius-like Leistes group through Pezites to Sturnella. I intend to imply not that any existing species is ancestral to any other one, but only that some of them resemble ancestral forms in various stages along the meadowlark phyletic line. Beecher's (1951) consideration of jaw muscles of these meadowlarks focused on their "gaping" trait, rather than on their relationships. His figure 8 shows Leistes, Pezites, and Sturnella as derived from an Agelaius-like ancestor, while he commented (1951, p. 424) on the free lacrimal bone of Pezites and Sturnella (it is fused in other blackbirds). The Leistes-Pezites-

Sturnella progression was noted by Ridgway (1902, p. 172), who stated, "Sturnella [is related] to Troupialis [= Pezites], and this, through Leistes, obviously [leads] to the Agelaiine type." I believe the morphological similarity of these species (including features of the plumage, bill structure, and body proportion) is sufficiently great, and involves such minor details, as to indicate close relationship, rather than the effects of parallel evolution. Let us briefly consider the species of meadowlarks.

Leistes militaris

Figure 11

This species comprises two disjunct forms or groups of populations: the northern militaris group of northern Amazonian Brazil, the Guianas, Colombia, Venezuela, Panama, and northeastern Peru; and the southern superciliaris group of central and southern Brazil and southeastern Peru south to Uruguay and northern Argentina. Some mensural characters of the two groups (males only) are contained in table 1. Both forms are similarly colored, resembling species of Pezites, except that the males are blacker, the females are browner, and their bills are smaller. Freshplumaged males are browner than worn males of Pezites defilippii and P. (militaris) bellicosa. Both forms of Leistes occupy grassy edges of marshes and wet savannas or pampas (E. Eisenmann, personal communication, concerning militaris in Panama; and personal observation of superciliaris in Argentina). In this respect, as well as in some plumage features and elements of songs (fide W. E. Lanyon, and personal observation), Leistes is similar to marsh blackbirds of the genus Agelaius. They differ from Agelaius in their stockier body and somewhat heavier, more finchlike bills. The militaris and superciliaris groups are somewhat different in body size, militaris being the larger (except for birds from Trinidad and from Panama; the latter area is occupied by a tiny form which is probably racially separable). The superciliaris group has white superciliary stripes, lacking in males of the militaris group. What is more important in terms of the possible biological interaction between them, superciliaris has a shorter, stubbier bill (which, incidentally, is very similar to that of the Bobolink, Dolichonyx oryzivorous, females of which closely resemble females of Leistes). Indeed, there is a morphological progression of bills from the short, heavy bill of superciliaris, through the longer bill of militaris, to the longer but yet heavy bill of Pezites (militaris) bellicosa; their bills appear identical in features other than dimensions. In view of the bill difference between Pezites defilippii and P. militaris it seems prudent to consider Leistes militaris and L. superciliaris as separate species, comprising a superspecies, pending study of their possible interaction in Brazil (e.g.,

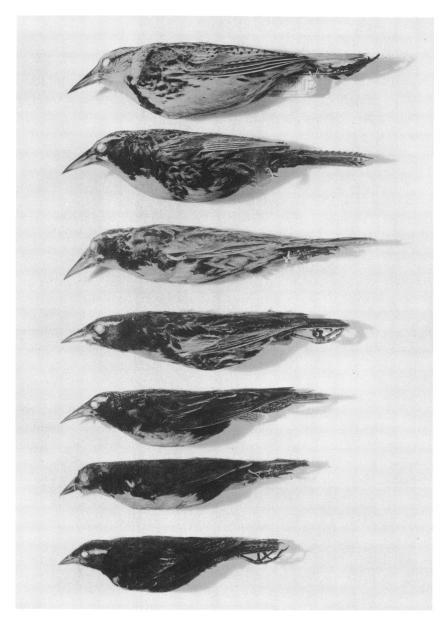


Fig. 11. Males in breeding plumage of the various species of meadowlarks comprising the genus Sturnella (see text). Top to bottom: Sturnella magna (the quite similar S. neglecta is not illustrated), S. loyca loyca, S. loyca catamarcanus, S. bellicosa, S. defilippii, S. militaris, and S. superciliaris.

the Maranhao population may comprise a peculiar subspecies of *militaris*, or a hybrid population as a result of interbreeding with *superciliaris*). Thus, the "genus" *Leistes* is comprised of but a single superspecies.

Pezites militaris and Pezites defilippii

Figure 11

The morphology and interaction of these species are considered above. In the course of investigating their morphology, I also studied the variation among presently recognized races of *Pezites militaris*. There are four completely allopatric subspecies. Pezites m. falklandicus (see map, fig. 1) of the Falkland Islands is a large, long-tailed form tending to have a spatulate-tipped bill, somewhat reminiscent of that of another icterid, Amblyramphus holosericeus. It otherwise closely resembles P. m. militaris. The latter is a clinally variable (birds of the southern populations have longer wings and tails), long-tailed form that occupies the region from central Chile and central Argentina to Tierra del Fuego. This form has a long, moderately heavy bill. The most weakly characterized race is P. m. catamarcanus, a browner, pale version of P. m. militaris, occupying the Andean foothills of northwestern Argentina (field study is necessary to determine whether or not this race is in contact with P. m. militaris in San Juan or Mendoza, Argentina, during the breeding season). The strongly differentiated P. m. bellicosa occupies the western Andes and coastal region of Ecuador, Peru, and the northern edge of Chile. This race differs markedly from other races of P. militaris in having a short tail, as do the other species of meadowlarks (table 1), in its shorter, proportionally heavier bill, and, especially, in its very heavy, Sturnella-like legs and feet. This form seems to be included within P. militaris on the basis of its white under wing coverts. However, it resembles Leistes militaris and Pezites defilippii in as many ways as it resembles P. militaris, and it has unique features not found in other species of Leistes and Pezites. Its resemblances to L. militaris and P. defilippii include its quite black plumage (worn males are very like those of P. defilippii), its redder under parts, its short tail and general size, and its short bill. It is unique among species of Leistes and Pezites, and bears resemblance to Sturnella, in its very white flanks and abdomen (in contrast to its blacker dorsal coloration, it is whiter ventrally, thus differing from P. defilippii), its generally white, rather than brown or black, leg feathering, and its proportionally large legs. I think that bellicosa is fully as distinct (perhaps more so) than P. defilippii and that it constitutes a species separate from P. militaris. Pezites defilippii is peculiar among species of Pezites in having a thinner bill, black under wing lining (as in Leistes), and thin legs. I consider the "genus" *Pezites* to comprise a superspecies, containing the species *P. militaris*, *P. defilippi*, and *P. bellicosa*, although the last-named may ultimately prove too strongly differentiated for inclusion within this superspecies.

Taken as a group, the three species of Pezites are morphologically intermediate between Leistes and Sturnella. Within the group, however, there is no strong morphological progression. Rather, the species exhibit various combinations of features, the only unique one of which appears to be the development of a long, heavy bill as is found in P. militaris. Comparison of the three species discloses that P. defilippi is least like Sturnella and most like Leistes; however, P. bellicosa also exhibits strong resemblance to species of Leistes. The Sturnella-like features most pronounced in P. bellicosa and P. militaris are their heavier legs, longer bills (militaris), white under wing coverts, and browner, more patterned dorsal plumage. Pezites defilippii tends toward Leistes superciliaris (and Agelaius) in its shallower, narrower bill, its black under wing coverts, and its thin legs and weaker feet. It is intermediate between P. militaris and species of Leistes in its blacker plumage, shared to a degree by P. bellicosa. Wetmore (1926, p. 374) has noted a resemblance in the habits of P. defilippii to Leistes superciliaris: indeed, he considered the habits of the former more like those of the latter than like those of P. militaris. Pezites bellicosa is similar to species of *Leistes* in its short, heavy bill and tends toward them, rather than toward P. militaris, in its quite black coloration. Long-billed variant females of Leistes militaris are very like those of P. bellicosa. However, P. bellicosa is more Sturnella-like than is P. militaris in leg and foot structure, and in its whiter posterior under parts and leg feathering. These tendencies are best accounted for by the close relationship of the species of Leistes, Pezites, and Sturnella. Vocalizations are also suggestive of this relationship, for the songs of P. militaris militaris and P. defilippii resemble those of Sturnella magna and S. neglecta in certain respects, and those of species of Leistes (and even Agelaius) in other respects (see above). Hudson (1920, p. 121) described the flight song and the associated display of males of Leistes superciliaris; these seem very like those I have described for Pezites defilippii. Species of Leistes, Pezites, and Sturnella build a ground nest that is characteristically domed or semidomed, with a side entrance (see Johnson, 1967, pp. 237-238, for P. bellicosa and P. militaris; Herklots, 1961, p. 250, for such nests in Leistes militaris; and Hudson, 1920, p. 129, on the similarity of the nest and eggs of P. defilippii and P. militaris). The eggs of these species are generally similar in having a white to bluish, gray, or buff background, with blotches to fine spots of various colors from black and violet through brown and red. Infraspecific

variation in egg color is great; I have seen variant eggs of Sturnella magna that are very like the finely speckled eggs of Leistes militaris, as well as many that are like those of Pezites militaris.

Sturnella magna and Sturnella neglecta

Figure 11

These species are so similar that I have not illustrated both. Various northern South American populations assigned to Sturnella magna remain to be studied, and their relationships elucidated. When all the forms currently included in these two species are considered, it is evident that these meadowlarks are highly specialized, with a highly patterned plumage, heavy, large legs, and a broad, long bill (resembling that of Pezites militaris). The songs of these species (Lanyon, 1957) appear to be the most specialized of meadowlark songs, and the least like those of species of Agelaius. As S. magna and S. neglecta have geographically complementary ranges, and a narrow (probably increasing) area of sympatry, I regard them as constituting an "emergent" superspecies. Their resemblance to species of Pezites and Leistes would be even more apparent if their breasts, throats, and anterior superciliary stripes were red, rather than yellow. The rather simple genetic and chemical change making possible a shift from red to yellow (or vice versa) is demonstrated by the occurrence of such differences between interbreeding forms of woodpeckers (Colaptes; Short, 1965), tanagers (Ramphocelus; Sibley, 1958), and bulbuls (Pycnonotus; Sibley and Short, 1959), as well as by similar red to yellow color replacement in the related marsh blackbirds (Agelaius).

The presence of red at the bases of the black loral feathers of some individuals of both Leistes militaris and L. superciliaris, called to my attention by Miss Penny Short, suggests the evolution of these species from an ancestor that had a full superciliary stripe with a red anterior (loral) portion. Such a condition exists elsewhere in the Icteridae only among the other species of meadowlarks, which have the loral portion of the superciliary red (Pezites) or yellow (Sturnella). This supports the relationship of Leistes to the meadowlarks, and suggests that Leistes, evolved from a form with a more meadowlark-like pattern on the head, is close to the evolutionary line leading from Agelaius to Pezites and Sturnella. (An intriguing alternative would be the evolution of Agelaius from ancestral Leistes-Pezites stock, with extant species of Leistes convergent on Agelaius.)

I have elsewhere (Short, 1967, pp. 11-12) discussed the generic concept. Briefly, I consider that most avian genera should contain some species that are sympatric. It is through an evaluation of morphological

and other differences between related species that have reached or passed the final stage of the speciation process (sympatric coexistence) that the taxonomist can avoid use at the generic level of characters properly employed only at the species level. Also, the generic level must not be set close to the species level by the treatment of "species" differences among species of a superspecies as the "norm" for differences among the species comprising a genus. It is obvious that no species outside a superspecies (which, after all, is comprised of forms that are in the final stages of speciation) can be so closely related to member species of a superspecies as those members are to one another. Hence the use of differences among species of a superspecies as criteria for consideration of other possibly congeneric species is not valid; it virtually precludes the inclusion of other species in the same genus, and is therefore tantamount to equating the superspecies with the genus.

Species constituting the presently recognized genera Leistes, Pezites, and Sturnella have in each case differentiated about to the level of superspecies. I believe that the differences among these genera, as presently constituted, are at the level of differences among species of a single genus. We have indications (interactions of Sturnella magna and S. neglecta, and Pezites militaris and P. defilippii) that the species of these "genera" have in each case not fully completed speciation. Indeed, to find "good" biological species of meadowlarks that have completed speciation we must go outside each "genus." For example, Leistes militaris is sympatric with Sturnella magna in northern South America, and Leistes superciliaris is sympatric with Pezites defilippii in Brazil and Argentina. When it becomes evident that "generic" differences are of the valence necessary for sympatry within a group, these differences are appropriately used at the level of species, and such "genera" are probably not valid. I believe that differences among species of Leistes, Pezites, and Sturnella are those one would expect to find among related species and groups of species within a single genus. Indeed, I believe that the meadowlarks are more closely interrelated than are the species within the more diverse, related genus Agelaius (compare, e.g., Agelaius phoeniceus, itself highly variable, with A. cyanopus, A. ruficapillus, A. thilius, and A. forbesi). Hence I consider the monophyletic meadowlark line leading from Agelaius to Sturnella as representing a single genus, Sturnella Vieillot. The relationships within the genus are best rendered by utilizing Amadon's (1966) system to indicate superspecies, as follows:

Sturnella [militaris] superciliaris (Bonaparte), Southern Marsh Meadowlark Sturnella [militaris] militaris (Linnaeus), Northern Marsh Meadowlark Sturnella [loyca] bellicosa Filippi, White-thighed Meadowlark

Sturnella [loyca] defilippii (Bonaparte), Pampas Meadowlark Sturnella [loyca] loyca (Molina), Long-tailed Meadowlark Sturnella [magna] magna (Linnaeus), Eastern Meadowlark Sturnella [magna] neglecta Audubon, Western Meadowlark

The merger of Leistes and Pezites into Sturnella unfortunately necessitates changing the specific name of Pezites militaris (Linnaeus), 1771, to Sturnella loyca (Molina), 1782, as Leistes militaris (Linnaeus), 1758, has priority over it; the latter thus retains the specific name militaris, becoming Sturnella militaris (Linnaeus). This change in names is less traumatic than might be supposed, because it has always been confusing to have two more or less similar blackbirds with the same specific name.

I suggest possible vernacular names for these meadowlarks because I think that the present names (de Schauensee, 1967) must be suitably modified to include the two additional species that I recognize. Also, use of "meadowlark" in all these names is suggestive of the relationship of these species.

DIAGNOSIS OF THE GENUS STURNELLA

Small to medium-sized icterids; terrestrial, grassland, and marsh-edge species. Bill variable, from short and conical (finchlike), like that of species of Agelaius (phoeniceus) and of Dolichonyx, to longer and narrower, although invariably with moderate to strong culmen; in some cases flattened, "spatulate" (S. magna, S. neglecta, S. loyca falklandicus). Wings moderately short to long; primaries 5-8 or 6-8 sinuated on outer web; tertial feathers elongate, longer than innermost secondaries (as in Dolichonyx). Tail moderate to long (S. loyca only), with elongate upper and lower tail coverts (as in Dolichonyx). Legs moderately strong to strong (S. neglecta, S. magna, S. bellicosa); toes long, hallux as long as or longer than lateral toes. Sexual dimorphism strongly developed (S. militaris, S. superciliaris) to weakly developed (S. magna, S. neglecta). Plumage a mixture of browns, black, white and yellow, or red. Anterior under parts of males, and of females of most species, yellow or red; sides of throat black and tending to spread across (S. loyca), or fully spreading across, (S. neglecta, S. magna) the breast. Abdomen black, buff, or white with some evidence of streaking; females of sexually dimorphic species streaked below, especially laterally, on buffy to white background, in many cases with some red on breast. Dorsal pattern from predominantly brown (S. neglecta, S. magna; females of S. militaris, S. superciliaris) to mainly black (worn males of S. militaris, S. superciliaris, S. bellicosa, S. defilippii). Tails and tail coverts, and in many cases secondaries, showing weak to strong barring, distinctly separating browner-plumaged forms of Sturnella from females of Dolichonyx and Agelaius; white occurring in outer rectrices of some species (S. neglecta, S. magna, S. loyca falklandicus). Head with central white crown stripe (in many cases obscured) and white superciliary stripes (except males of S. militaris). Anterior (loral) portion of superciliary stripe yellow or red in males of all species; even males of S. militaris, which lacks superciliary stripes, show red at bases of loreal feathers (majority of random specimens examined; lacking in some). All species exhibiting red or yellow at leading edge of wing; red or yellow occurring also as "shoulder" patch in males (and to a lesser degree in females) of S. defilippii, S. bellicosa, S. loyca, S. militaris, and S. superciliaris. Under wing coverts black (in three species) or white (S. neglecta, S. magna, S. bellicosa, and S. loyca). Nest on or very close to ground and partly or completely domed; eggs whitish, with variable reddish to purplish brown markings.

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SUMMARY

The red-breasted meadowlarks *Pezites militaris* and *P. defilippii* come into contact during the breeding season in southern Buenos Aires Province, Argentina. They behave as separate species, with moderate morphological differences and differences in various vocalizations, some of which probably function in species discrimination.

A comparison of the morphology of these two species led to an investigation of the taxonomy of all the meadowlarks. Each of the genera Leistes, Pezites, and Sturnella is considered as comprising a single superspecies. Leistes superciliaris is considered a species, as is Pezites bellicosa. The close relationship among the meadowlarks, their monophyly, and the morphological progression they represent warrant considering all meadowlarks as congeneric. Sturnella Vieillot becomes the generic name for the group, necessitating a change in the name of Pezites militaris to

Sturnella loyca, because Leistes militaris has priority and becomes Sturnella militaris.

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