

HYBRIDIZATION IN MEADOWLARKS

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INTRODUCTION

THE BREEDING RANGE of the polytypic Eastern Meadowlark (*Sturnella magna*) extends throughout eastern North America westward to Ontario, Nebraska, Texas, and Arizona, and southward through Middle and South America as far as northern Brazil. The monotypic Western Meadowlark (*Sturnella neglecta*)¹ breeds only in western North America eastward to the Great Lakes region, Missouri, and Texas, and southward on the Mexican plateau to northern Jalisco. Studies of the comparative morphology, behavior, and ecology of these sibling species suggest that they are virtually, if not completely, isolated reproductively throughout a rather narrow zone of sympatry that extends from Jalisco northeastward to the Great Lakes region (Lanyon, 1953a, 1953b, 1956a, 1956b, 1957, 1962). A differential habitat preference reduces the number of interspecific contacts within this zone of sympatry but constitutes only a partial isolating mechanism. In localities where the two forms occur together, the males maintain mutually exclusive territories. The continued separation of these species in areas of coexistence appears to rest primarily on the ability of the females to discriminate males of their own kind and secondarily on the interspecific aspect of the territorial behavior of the males. Slight morphological differences may contribute toward the maintenance of the pairing bond but are not believed to play an important role in species recognition at time of pair formation. The vocalizations of the two species have been shown to be consistently distinct throughout the area of sympatry, and it has been postulated that female meadowlarks normally pair only with males having vocalizations characteristic of their respective species.

At the time of my review of this problem in 1957, I concluded that it would be presumptuous to eliminate unconditionally the possibility of hybridization in wild populations. George Saunders' success in producing a hybrid between *S. neglecta* and *S. magna hoopesi* in captivity in 1933 (*in litt.*, 1948) suggested that certain populations of these

species might be genetically compatible. Furthermore, my own field observations of an attempted mixed mating and of an aborted mixed pairing indicated a potential for interbreeding under appropriate environmental conditions. With allowance for the possibility of occasional hybridization among meadowlarks, how might one proceed to demonstrate this? Would a single specimen of a hybrid between these sibling species be recognizable?

The specific identification of single specimens of *Sturnella* can be effected without difficulty on the basis of conventional color comparisons with series of specimens of comparable age, sex, and plumage condition. The extent of yellow on the cheek and the general coloration of the crown and back are useful specific characters when determined carefully and with full knowledge of the range of intraspecific variation for each. Extensive overlap in all mensural characters and in the amount of white in the rectrices precludes the use of these characters for identifying all but the "extreme" specimens.

Identification of a hybrid *Sturnella* is quite another matter. Quantitative evaluations of hybrid recombinations of the characters of unlike parental forms have been made successfully in a number of avian genera. This "hybrid index" approach is most useful when (1) the parental phenotypes are markedly distinct; (2) when the differences in the parental phenotypes are not transgressed by geographical variation within one or both of the "pure" populations; and (3) when the hybrid recombinations are phenotypically expressed in such a way that they can be "scored" along a quantitative gradient with some degree of objectivity. A recent attempt to apply this approach to *Sturnella* (Szijj, 1963) has failed, in my opinion, for none of these qualifications can be satisfied when one examines the nature of phenotypic expression in meadowlarks. Szijj used four characters as the basis for his hybrid index: (1) pattern of dark markings on the central rectrices; (2) pattern of dark markings on feathers of the dorsal tract; (3) size and shape of dark markings on the upper sides; and (4) extent of yellow color on the cheek. Extensive intraspecific

¹ A poorly differentiated northwestern race, *S. n. confluenta*, is recognized by some authorities.

variation within both species precludes the use of the first three of these characters in this type of analysis. It is possible, for example, to find specimens of *magna* from Connecticut that would be "scored" as "pure" *neglecta* with respect to all three of these characters. Only one of Szijj's characters, i.e., the extent of yellow color on the cheek, is a valid specific character. But unfortunately it cannot be "scored" along a graded series as required in this type of analysis, because of the limited degree of specific distinction and the difficulty inherent in measuring this character objectively.

In view of the great similarities in the phenotypes of the two species of meadowlarks, I doubted very much that a hybrid specimen could be recognized as such without some prior knowledge of how the parental characters might be recombined. The key to the relationships of these sibling species, it seemed to me, rested on field studies of their interactions on a common breeding ground, observations of mixed pairing, and aviary studies of the morphology and behavior of individual hybrids of known parentage. Above all, there seemed to be an obvious need for careful documentation of the morphology of any individuals suspected of being hybrids on the basis of such field evidence. Subsequently this opportunity was afforded to me and the documentation of the first generation of hybrids resulting from the crossing in the wild of a male *S. neglecta* with a female *S. m. magna*¹ forms the substance of the present report. The number of hybrids involved is regrettably small, a fact that precludes any meaningful discussion of the genetic control of the observed phenotypes. It is also lamentable that we have no data on the reciprocal cross or on populations of *magna* other than the nominate race.

METHODS

Hybrid individuals were compared with their parents and with series of *S. neglecta* and *S. m. magna* in the collections of the American Museum of Natural History, with respect to plumage coloration and mensural

characteristics. Linear measurements, in millimeters, were taken as follows: wing, flattened; "tarsus," with calipers, taken as the diagonal distance from the depression at the rear of the joint between the tibiotarsus and the tarsometatarsus to the distal edge of the most distal undivided scute on the front of the junction of the tarsometatarsus with the bases of the third and fourth digits; tail, with calipers, from the point of insertion of the medial rectrices to the tip of the longest rectrix. 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 onto the cheek region, the apterium extending posteriorly from the mandibular ramus was readily delineated by wetting the feathers on each side with alcohol. Data were accumulated with regard to the extent of yellow coloration, dorsad to this apterium. The extent of white in rectrices 3 through 6 (numbered from the center) was determined by measuring, in millimeters, that portion of the rachis of each rectrix not bordered by pigmentation in either the inner or the outer vane. By expressing the "extent of white in the rectrices" as a percentage of the tail length, we could circumvent sexual dimorphism in tail length and thus facilitate direct comparison of this character in both sexes. Three to four different measurements for each character were available for most of the hybrid individuals and for the parent birds maintained in captivity over a period of three years, representing different basic (definitive) plumages in the case of "wing," "tail," and "extent of white in the rectrices." No analysis was made of the juvenal plumages of the hybrids. Additional morphological characters considered were the general coloration of the crown, that of the back, that of the throat, and that of the breast.

In the diagramming of statistical analyses, 1.3 times the standard deviation has been plotted on each side of the mean (forming a solid rectangle). Thus, when two samples are compared, non-overlap 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.

¹ The northernmost subspecies, which breeds from southern Canada south to central Oklahoma, northern Tennessee, and southern Virginia.

Field recordings of vocalizations were made with a Magnemite recorder (in 1962 only) operated at 15 inches per second, a Uher 4000 Report operated at 7.5 inches per second, a preamplifier, and an Altec 660B microphone mounted in a 24-inch parabolic reflector. No preamplifier or reflector was used for the recording of captive birds. Representative vocal patterns were then selected for analysis with a sound spectrograph, with the use of the narrow band-pass filter.

Close-up photographs of the cheek coloration were made with a Kodak Startech camera equipped with a 1 to 1 accessory lens system, Ektachrome X film, an 82A filter, and M3B flash bulbs. Colored photographs of the upper parts were made with Kodachrome II daylight film and a strobe-flash unit.

The housing and maintenance of captive meadowlarks are discussed in some detail in the text.

ACKNOWLEDGMENTS

Field studies of meadowlarks breeding at the periphery of their ranges were made possible by the valuable assistance of a number of persons familiar with local distributions. Among those to whom I am especially grateful for information on the histories of

peripheral colonies are Mr. James Beatty (Ohio), Dr. Russell Mumford (Indiana), Mr. Oscar Bryens (Michigan), Mr. Aloysius Kaszynski (Illinois), Dr. Harrison Tordoff (Kansas), Miss Doris Gates (Nebraska), and Mr. Kenneth Krumm (South Dakota).

For the opportunity to study a hybrid meadowlark from Quebec, I am indebted to Mr. Raymond Cayouette, Curator of Birds, and Dr. J. A. Brassard, Director, of the Quebec Zoological Garden.

The splendid cooperation of Mr. Geoffrey Carleton, Miss Regina Roberts, Mrs. Alice Jones, Mr. Otis Waterman, and members of the Ralph T. Waterman Bird Club enabled me to find and obtain a mixed pair of meadowlarks and their hybrid young on the William L. Layton farm in Dutchess County, New York. To Mrs. Layton I am grateful for courtesies extended during this phase of the study. Mr. Frank Gill provided valuable assistance with the actual procurement of these birds and their transport to aviaries on Long Island. My wife, Vernia, and Mr. William Hutchins, Jr., Station Manager of the Kalbfleisch Field Research Station of the American Museum of Natural History, have shared with me the responsibility for maintaining meadowlarks in captivity.

HYBRIDIZATION AT THE RANGE PERIPHERY

IN VIEW OF MY PERSONAL EXPERIENCE with the independence of these species throughout the greater part of their zone of sympatry and of reports of isolated birds and of "pioneering" colonies at the edge of this sympatric zone, it seemed likely that hybridization, if it occurs at all, might take place at the periphery of the sympatric zone where a greatly imbalanced ratio of the two species might conceivably lead to a mixed pairing. Peripheral colonies of Eastern Meadowlarks were subsequently visited in Kansas, Nebraska, and South Dakota, and reports of "pioneering" colonies and isolated singing males of Western Meadowlarks were investigated in northern Indiana and Ohio, and southern Michigan. In all these localities the distributional pattern was found to be the same, with a small number of the peripheral species maintaining territories and surrounded by a "sea" of individuals of the other species. In all instances in which it could be determined that the peripheral males were actually paired, the females were identified as also belonging to the peripheral species. This remarkable ability of males to attract and pair with appropriate mates at the range periphery further attests to the effectiveness of the isolating mechanisms that operate to keep these sibling species apart. The only convincing evidence of meadowlark hybridization that has come to my attention has involved peripheral localities in Oklahoma, Quebec, Ontario, and New York.

Sutton and Dickson (1965) collected a mixed pair (male *neglecta* × female *magna*) and their hybrid young in Cleveland County, central Oklahoma, on May 29, 1965. We have no data on the phenotypic expression of the definitive plumage of these hybrids, for the fledgling young, along with the adults, were preserved as study skins. The reader is referred to the note by Sutton and Dickson for further details of this record of hybridization in Oklahoma.

QUEBEC

The province of Quebec, Canada, lies well outside the range of the Western Meadowlark and can only barely be included within

the recent northeastward range extension of the species (Lanyon, 1956a). An isolated, singing male was observed in Temiscaming County (the most southwestern county in the province) in 1952. The first successful attempt, to my knowledge, to hand-raise a young meadowlark suspected of being a hybrid from a mixed pairing in the wild was made at the Zoological Garden in Quebec, Canada, in 1957.¹ A territorial male, identified as *neglecta* by its pale coloration and its primary song, was discovered by Benoit Asselin on June 2, 1957, near Giffard (a suburb of Quebec City). A nest with three young was found on July 31, within the territory of this male, and the female in attendance was thought to be an Eastern Meadowlark by virtue of its darker coloration and call notes. Both adult birds were observed carrying food and were noticeably disturbed when two of the young were banded. The third young was taken to be hand-raised at the Zoological Garden in Quebec where it thrived nicely under the expert care of the Curator of Birds, Mr. Raymond Cayouette.

In January, 1959, this presumed hybrid meadowlark was shipped by air to the American Museum of Natural History in New York City, and later transferred to the Kalbfleisch Field Research Station of the American Museum on Long Island. The results of the subsequent analysis of the morphology and behavior of this bird, confirming its alleged hybrid status, are presented elsewhere in this report where the bird is referred to as the "Quebec hybrid."

ONTARIO

The eastern Ontario population of the Western Meadowlark represents the spearhead of the well-documented northeast extension of the range of this species (Lanyon, 1956a). Isolated, singing *neglecta* males were reported from eastern Ontario as early as 1936 (Saunders, 1937) and 1937 (Dale, 1941), but the species is not reported to have bred

¹ The one young produced by George Saunders in an interspecific cross of captive individuals of *S. neglecta* and *S. magna hoopesi* in 1933 was "killed by one of the adults when it was only one day old" (*in litt.*, 1948).

successfully until the late 1940's, when a nest was discovered near Hamilton (*vide* Fred Hall, *in litt.*, 1953). In 1959, L. J. Szijj discovered a mixed pair of meadowlarks near Springford, Ontario, in an area where the western species occurs only in isolated pairs or as single birds, surrounded and vastly outnumbered by the eastern species (personal communication). In four years of intensive search in areas of Ontario where both species were known to occur, Szijj found nine nests belonging to five mixed pairs. Most of these mixed pairs consisted of a male *magna* with one or two *neglecta* females. Because of his difficulty in hand-raising nestlings of mixed parentage, Szijj suggested (1963) that hybridization in the Ontario region must be "incidental" and that the few mixed pairs were having limited breeding success because of the "reduced viability of the F₁ hybrids."

NEW YORK

Isolated, singing Western Meadowlarks have been reported sporadically along the south shore of Lake Ontario since 1948 (Klonick, 1951), and there is some evidence that at least one properly mated pair of *neglecta* may have raised a brood of young in this region in 1957 (Miller, 1958).

On June 13, 1962, Regina Roberts discovered a male Western Meadowlark singing on the William L. Layton farm near the village of Bangall in Dutchess County, southeastern New York. Subsequently a number of local observers determined that the bird was territorial, and one of them, Alice Jones, was able to locate a nest with young on June 23 (Jones, 1963). On June 26, Frank Gill and I visited the locality, made observations of the behavior of the male and its mate, and obtained sound recordings of their vocalizations. The male appeared to have primary songs and call notes typical of *neglecta*, but its mate rendered the characteristic chatter and "dzert" notes of *magna*. These field identifications were confirmed subsequently. At no time during our eight hours of continuous observation did we observe any other meadowlark within the territory of this male *neglecta*, though *magna* males could be heard on neighboring farms. The female made a number of visits to the nest, carrying food for the nestlings. During these visits by the female,

the male rendered songs and calls from a telephone wire less than 50 feet from the nest site, or dropped into grass nearer the nest. On occasion the male carried food in its bill for several minutes at a time, but we could not be certain whether it actually visited the nest during our period of observation. The five hybrid young were judged to be about nine days old and hence capable of fledging, which suggested, by extrapolation, that the eggs must have hatched about June 18 and that the female probably began nest construction about May 27.

Several considerations led to my decision to trap the adults and take the hybrid young to be hand-reared. It was imperative that the morphology of the adult birds be examined in the hand and their identity established without question. By taking them alive, we would not only accomplish this objective but also could make further attempts at hybridization in captivity. The prospects for determining the phenotypes of the hybrids after maturity and for comparing them with those of the parent birds were especially promising. Likewise, the potential for documenting the development of vocalizations and the fertility of these hybrids was infinitely greater under controlled conditions of an aviary than in the wild. The *neglecta* male was trapped with the aid of a live, hand-reared, decoy meadowlark and of a playback of its own primary songs. The *magna* female was bow-netted at the nest. On June 26, 1962, the two adults and the five nestlings were placed in aviaries at the Kalbfleisch Field Research Station of the American Museum of Natural History, at Huntington, New York. These individuals are hereinafter referred to as the "New York adults" and the "New York hybrids."

The preliminary identification of the New York adults, based on field observations, was quickly confirmed by a closer examination of their morphology and a more objective analysis of their vocalizations. In the three years that the adult male (Y-YX)¹ has been maintained in our aviaries, it has not differed at any season, in typical coloration and plumage patterns, from a large museum series of *neglecta* males of comparable feather wear.

¹ Each captive meadowlark is identified individually on the basis of symbols referring to the bands placed on its legs.

Most convincing among the plumage characters were the generally pallid and grayish coloration of the crown and back (pl. 1, fig. 1) and the presence of an extensive area of yellow on the cheek (pl. 8, fig. 1). Also well outside the range of variation for *magna* males was the limited extent of white in the rectrices of this male (text fig. 1).

The mensural character that provides the greatest degree of separation between these sibling species is the ratio of wing length to length of tarsus. Here again, this character places the New York male well outside the range of variation in my museum series of *magna* males (text fig. 2). Measurements of this male (Y-YX) are presented in table 1, in which they can be compared with those of the museum series of *S. neglecta* and *S. m. magna*.

All three call notes that are characteristic of the Western Meadowlark (Lanyon, 1957, 1962) have been recorded from the New York male, and at no time has this male been heard to render any other calls. The most distinctive of these are illustrated spectrographically in plate 2, figures 1 and 4. During the first summer (1962) in our aviaries it was established that this male had a repertoire of six primary song patterns, and this has been confirmed by intensive observations during three subsequent years. My previous studies (1957) disclosed that the size of the primary song repertoire, as well as the actual patterns of the songs themselves, was specifically distinct for each of these sibling species. Males of *neglecta* usually have six to nine song patterns which remain fixed year after year, whereas *magna* males have many times that number of different patterns in their song repertoires. For example, I have spectrographic evidence that a male *magna* in Huntington, New

York, delivered 26 basically distinct song patterns in a period of 30 minutes. During subsequent recording sessions throughout the following two days, 22 additional new patterns were obtained from this same male, bringing the minimum size of its song repertoire to 48 distinct patterns.

Each of the six song patterns of Y-YX had the terminal phase of complex elements, involving a broad frequency spectrum, that is characteristic of *neglecta* (pl. 3, figs. 1-6; and see Lanyon, 1957, 1962). Some of these song patterns were so familiar to me, as the result of my field work within the main range of *neglecta*, that I had no difficulty in rather closely matching patterns of Y-YX with patterns rendered by *neglecta* males in Wisconsin and other north-central states (pl. 3, figs. 7, 8).

The female (G-GX) of this mixed pair of New York adults was typically *magna* with respect to plumage coloration, including the intense melanic pigmentation and the lack of yellow on the cheek (pls. 1 and 8). The great amount of white in the rectrices places it well outside the range of variation known for *neglecta* females (text figs. 1 and 3). Likewise, the ratio of wing length to length of tarsus for this bird is smaller than the extreme for *neglecta* females (text fig. 2). Measurements of this adult female (G-GX) are presented in table 2, where they can be compared with those of large series of *S. neglecta* and *S. m. magna*. The call notes of this female consisted of the species-specific "dert" and chatter (Lanyon, 1957), and these calls were recorded on numerous occasions during three years of captivity (pl. 2, figs. 7 and 9). No other calls have been heard.

HYBRIDIZATION OF CAPTIVE MEADOWLARKS

I HAVE MAINTAINED hand-reared and wild-caught meadowlarks of both species in aviaries for the past 12 years. During this period, numerous attempts have been made to induce breeding of appropriately paired birds as well as of mixed pairs, but none of these efforts has been successful. Adjustment in diet and the size and nature of the enclosures appeared not to be the limiting factors. The opportunity to work with the mixed pair from New York under captive conditions seemed especially promising because of the previous mating and nesting experience that they were known to have shared.

When the New York adults were first brought to the Kalbfleisch Field Research Station, both birds were placed in a flight pen that measured 30 feet by 8 feet by 8 feet and was situated adjacent to similar pens containing other meadowlarks. Two-thirds of this enclosure (160 square feet) was essentially out-of-doors, except for a plastic roof, and there was a lush growth of grasses and herbaceous vegetation within this "open" section (pl. 4, fig. 3). The diet consisted of a staple mixture of several ingredients, ground up and presented in pellet form: turkey starter mash, horse meat, hard-boiled egg with shell, raw carrot, "dried flies" (commercial preparation of assorted aquatic invertebrates), oystershell, and wheat germ. This staple mix was supplemented with mealworm larvae, a vitamin and mineral preparation, and insects that occurred naturally in the sod floor or that flew into the aviary. Both birds adapted quickly to confinement, as evidenced by the male's renditions of its primary song patterns at full intensity and the female's responsive call notes. There was, however, no resumption of breeding activity during that summer.

At the beginning of the breeding season in 1963 these two birds were once again placed together in the aviary described above. After a two-month period, during which time the *magna* female (G-GX) showed no reproductive behavior, the *neglecta* male (Y-YX) was "paired" with a hand-reared *neglecta* female (W-WX) that had been taken from a nest in California in 1959. These birds likewise failed to breed.

In March, 1964, and again in April, 1965, Y-YX was placed in a larger aviary situated within one of the sections of the Kalbfleisch Field Research Station that is maintained as permanent grassland. This aviary, which measured 8 feet in height, enclosed 580 square feet of natural sod, providing what appeared to be an optimal nesting substrate for meadowlarks (pl. 4, fig. 1). This male established song perches, from which it rendered its complete repertoire of six primary song patterns as well as its flight song. After a two-week period, to permit the male to establish "territory," G-GX (the female *magna* with which it had mated in the wild) was introduced into the enclosure. During the ensuing two months, frequent observations from a blind at one end of the aviary (pl. 4, fig. 1) revealed repeated attempts at mounting by the male but no successful copulations, and there was no indication of nest-building activity by the female. In June, 1964, the hand-reared *neglecta* female (W-WX) from California was placed in the same enclosure with the New York adults. Meadowlarks are frequently polygynous, and there was the possibility that the presence of an additional female might stimulate breeding. Such was not the case, however, and the factors inhibiting breeding in captive meadowlarks remain the subject of current and future studies.

MORPHOLOGY OF HYBRIDS

THE QUEBEC HYBRID (—X; see p. 8 for a discussion of its origin) proved to be a male. It has been housed in a flight pen measuring 30 feet by 8 feet by 8 feet and has received the same diet that was given to the New York adults, as described above. An analysis of its morphology is included with the following analysis of the sibling hybrids from New York, for it was produced by the same cross, i.e., a male *neglecta* with a female nominate *magna*. Unfortunately we do not have exact phenotypic data on the parents of the Quebec hybrid.

The five New York hybrids (see pp. 9 and 10 for a discussion of their origin) were at first fed on a diet of bits of lean beef and hard-boiled egg, sometimes rolled in wheat germ and a multivitamin preparation, supplemented with small mealworm larvae. Begin-

ning at about three weeks of age (pl. 4, fig. 2), they were gradually shifted over to the same diet that was provided for the adult birds.

I have found that the most critical phase in hand-raising young meadowlarks is that period between fledging (at about nine or 10 days of age) and the time that they are capable of feeding themselves (at about four weeks of age). If one is successful in bringing the young birds through this phase, the chances are excellent that they will do well in captivity. Normally we are successful in bringing through but one or two of any given brood, presumably the hardiest individuals. Knowing this past record, I was truly surprised when we were able to bring *all five* of the young hybrids through this critical period. Our success in this venture appears to counter Szijj's claim (1963) for reduced via-

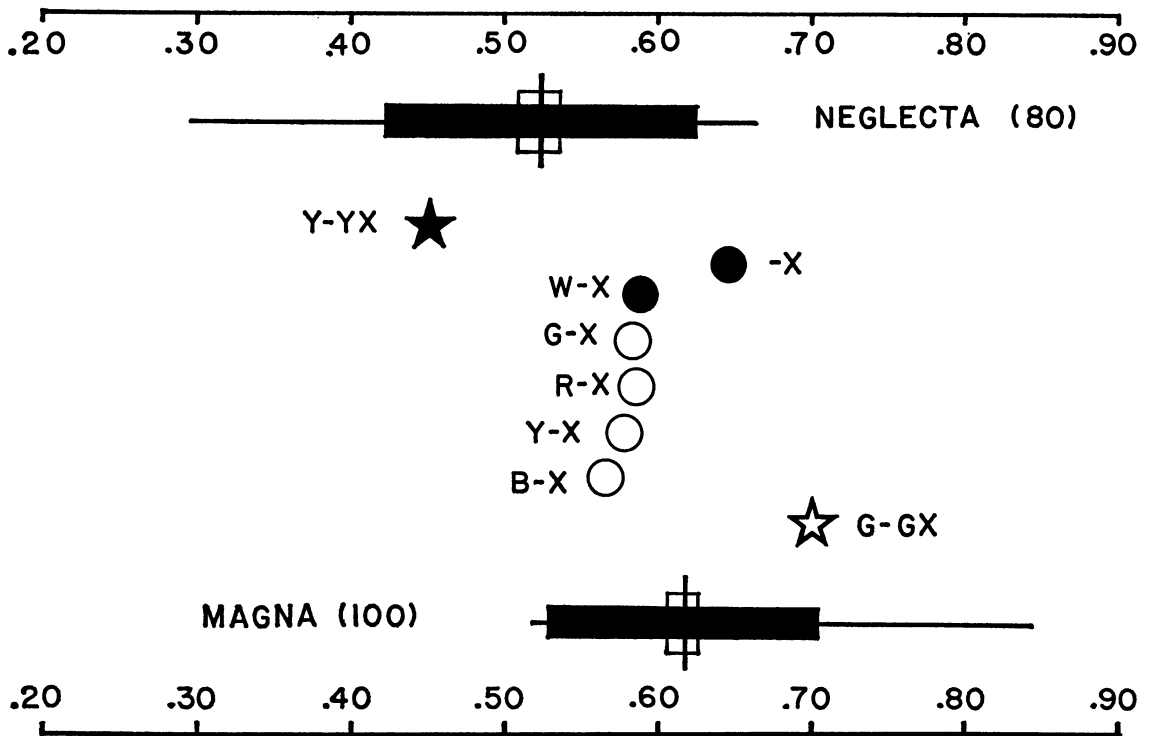


FIG. 1. Extent of white in the inner web of the fourth rectrix of each of the hybrids and of each of the New York adults, as compared with statistical analyses of this character in museum series of *S. neglecta* and of *S. m. magna*, determined by the measurement, in millimeters, of that portion of the rachis not bordered by pigmentation and expressed as a percentage of tail length.

Symbols: Stars, New York adults; circles, hybrids; solid figures, males; open figures, females.

TABLE 1
MEASUREMENTS (IN MILLIMETERS) OF MALE MEADOWLARKS AND HYBRIDS

	N	Range	Mean, S.E.	S.D.	C.V.
Wing					
<i>S. neglecta</i>	40	119-133	125.90 ± 0.52	3.29	2.61
New York adult (Y-YX)	4		129.0		
New York hybrid (W-X)	3		124.7		
Quebec hybrid (—X)	4		127.3		
<i>S. m. magna</i>	50	117-131	122.78 ± 0.47	3.33	2.71
Tail					
<i>S. neglecta</i>	40	69-83	76.17 ± 0.57	3.61	4.74
New York adult (Y-YX)	4		78.8		
New York hybrid (W-X)	3		76.3		
Quebec hybrid (—X)	4		76.3		
<i>S. m. magna</i>	50	73-86	79.08 ± 0.43	3.03	3.83
Tarsus					
<i>S. neglecta</i>	40	36-42	39.65 ± 0.22	1.42	3.58
New York adult (Y-YX)	4		39.5		
New York hybrid (W-X)	3		41.4		
Quebec hybrid (—X)	4		41.4		
<i>S. m. magna</i>	50	38-47	42.52 ± 0.24	1.73	4.07
Wing/tarsus ratio					
<i>S. neglecta</i>	40	2.90-3.43	3.17 ± 0.017	0.11	3.44
New York adult (Y-YX)	4		3.27		
New York hybrid (W-X)	3		3.01		
Quebec hybrid (—X)	4		3.07		
<i>S. m. magna</i>	50	2.64-3.08	2.88 ± 0.013	0.09	3.12
Extent of white					
Rectrix 6, inner web					
<i>S. neglecta</i>	40	41-55	47.35 ± 0.56	3.53	7.46
New York adult (Y-YX)	4		46.5		
New York hybrid (W-X)	3		45.7		
Quebec hybrid (—X)	4		49.8		
<i>S. m. magna</i>	50	42-60	48.84 ± 0.53	3.75	7.68
Rectrix 5, inner web					
<i>S. neglecta</i>	40	37-54	45.82 ± 0.57	3.62	7.90
New York adult (Y-YX)	4		44.0		
New York hybrid (W-X)	3		47.3		
Quebec hybrid (—X)	4		49.8		
<i>S. m. magna</i>	50	43-60	49.38 ± 0.47	3.33	6.74
Rectrix 4, inner web					
<i>S. neglecta</i>	40	22-48	39.32 ± 0.78	4.94	12.56
New York adult (Y-YX)	4		35.5		
New York hybrid (W-X)	3		45.0		
Quebec hybrid (—X)	4		49.3		
<i>S. m. magna</i>	50	37-56	47.16 ± 0.58	4.07	8.63
Rectrix 3, inner web					
<i>S. neglecta</i>	40	0-28	4.50 ^a		
New York adult (Y-YX)	4		0.0		
New York hybrid (W-X)	3		29.6		
Quebec hybrid (—X)	4		34.0		
<i>S. m. magna</i>	50	0-48	33.86 ^a		

^a No S.D. or S. E. calculated because of skewed distribution.

TABLE 2
MEASUREMENTS (IN MILLIMETERS) OF FEMALE MEADOWLARKS AND HYBRIDS

	N	Range	Mean, S.E.	S.D.	C.V.
Wing					
<i>S. neglecta</i>	40	109-118	113.72 ± 0.36	2.26	1.99
New York hybrid (R-X)	3		109.3		
New York hybrid (G-X)	3		109.6		
New York hybrid (Y-X)	1		106.0		
New York hybrid (B-X)	1		110.0		
New York adult (G-GX)	4		112.5		
<i>S. m. magna</i>	50	105-115	110.32 ± 0.36	2.57	2.33
Tail					
<i>S. neglecta</i>	40	63-74	67.80 ± 0.35	2.22	3.27
New York hybrid (R-X)	3		66.0		
New York hybrid (G-X)	3		66.3		
New York hybrid (Y-X)	1		64.0		
New York hybrid (B-X)	1		68.0		
New York adult (G-GX)	4		66.8		
<i>S. m. magna</i>	50	62-75	68.56 ± 0.48	3.38	4.93
Tarsus					
<i>S. neglecta</i>	40	35-40	37.15 ± 0.17	1.05	2.83
New York hybrid (R-X)	3		40.2		
New York hybrid (G-X)	3		39.1		
New York hybrid (Y-X)	1		36.8		
New York hybrid (B-X)	1		39.2		
New York adult (G-GX)	4		41.8		
<i>S. m. magna</i>	50	36-42	39.40 ± 0.19	1.37	3.48
Wing/tarsus ratio					
<i>S. neglecta</i>	40	2.85-3.28	3.06 ± 0.016	0.10	3.27
New York hybrid (R-X)	3		2.72		
New York hybrid (G-X)	3		2.81		
New York hybrid (Y-X)	1		2.88		
New York hybrid (B-X)	1		2.80		
New York adult (G-GX)	4		2.70		
<i>S. m. magna</i>	50	2.55-3.03	2.80 ± 0.013	0.09	3.21
Extent of white					
Rectrix 6, inner web					
<i>S. neglecta</i>	40	38-47	42.12 ± 0.36	2.25	5.34
New York hybrid (R-X)	3		39.0		
New York hybrid (G-X)	3		38.3		
New York hybrid (Y-X)	1		38.0		
New York hybrid (B-X)	1		40.0		
New York adult (G-GX)	4		45.0		
<i>S. m. magna</i>	50	38-57	44.56 ± 0.59	4.14	9.29
Rectrix 5, inner web					
<i>S. neglecta</i>	40	36-48	41.02 ± 0.44	2.76	6.73
New York hybrid (R-X)	3		40.0		
New York hybrid (G-X)	3		39.0		
New York hybrid (Y-X)	1		39.0		
New York hybrid (B-X)	1		43.0		
New York adult (G-GX)	4		47.0		
<i>S. m. magna</i>	50	38-57	45.22 ± 0.57	4.02	8.89
Rectrix 4, inner web					
<i>S. neglecta</i>	40	25-45	35.77 ± 0.71	4.49	12.55
New York hybrid (R-X)	3		38.6		



1



2



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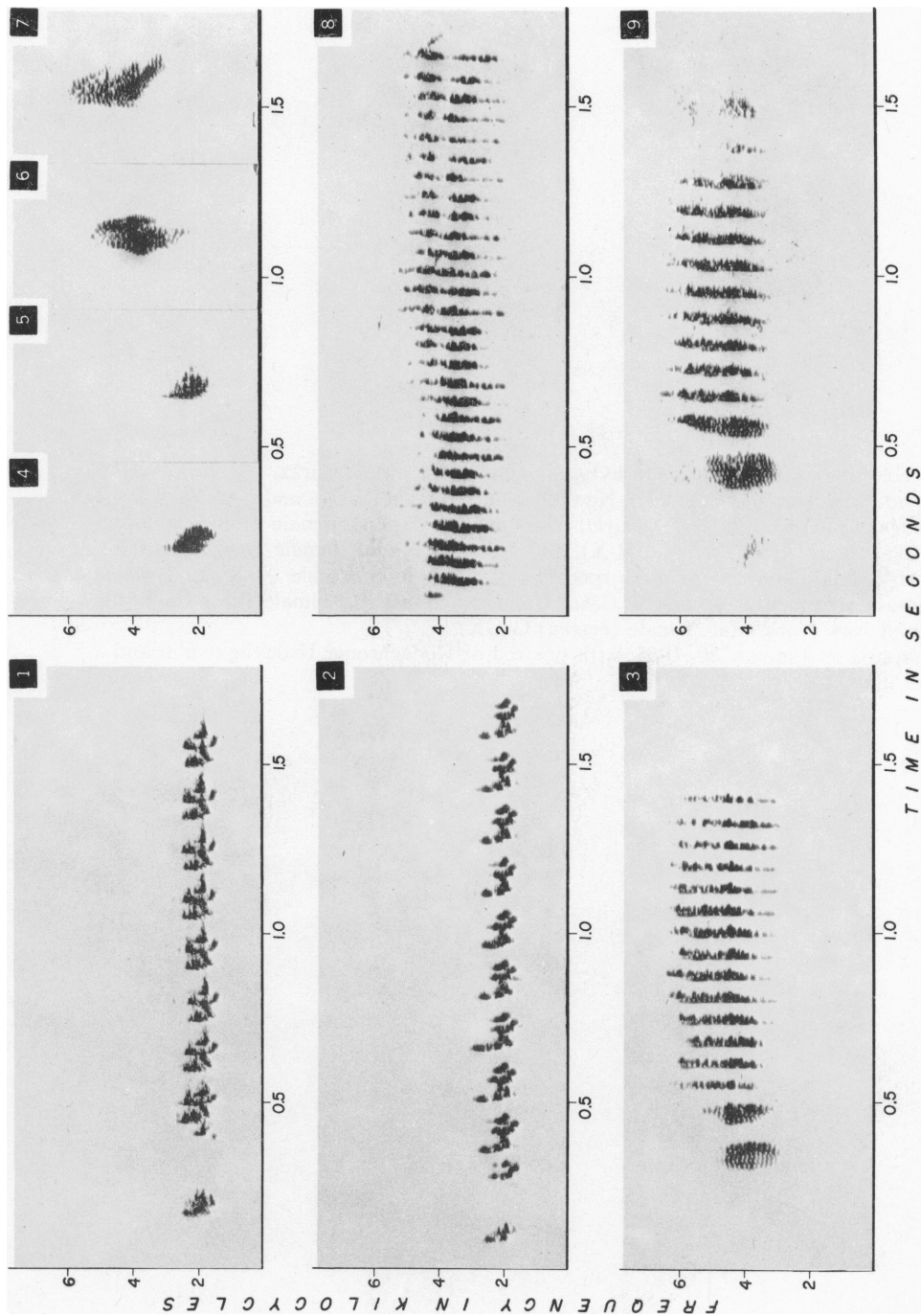


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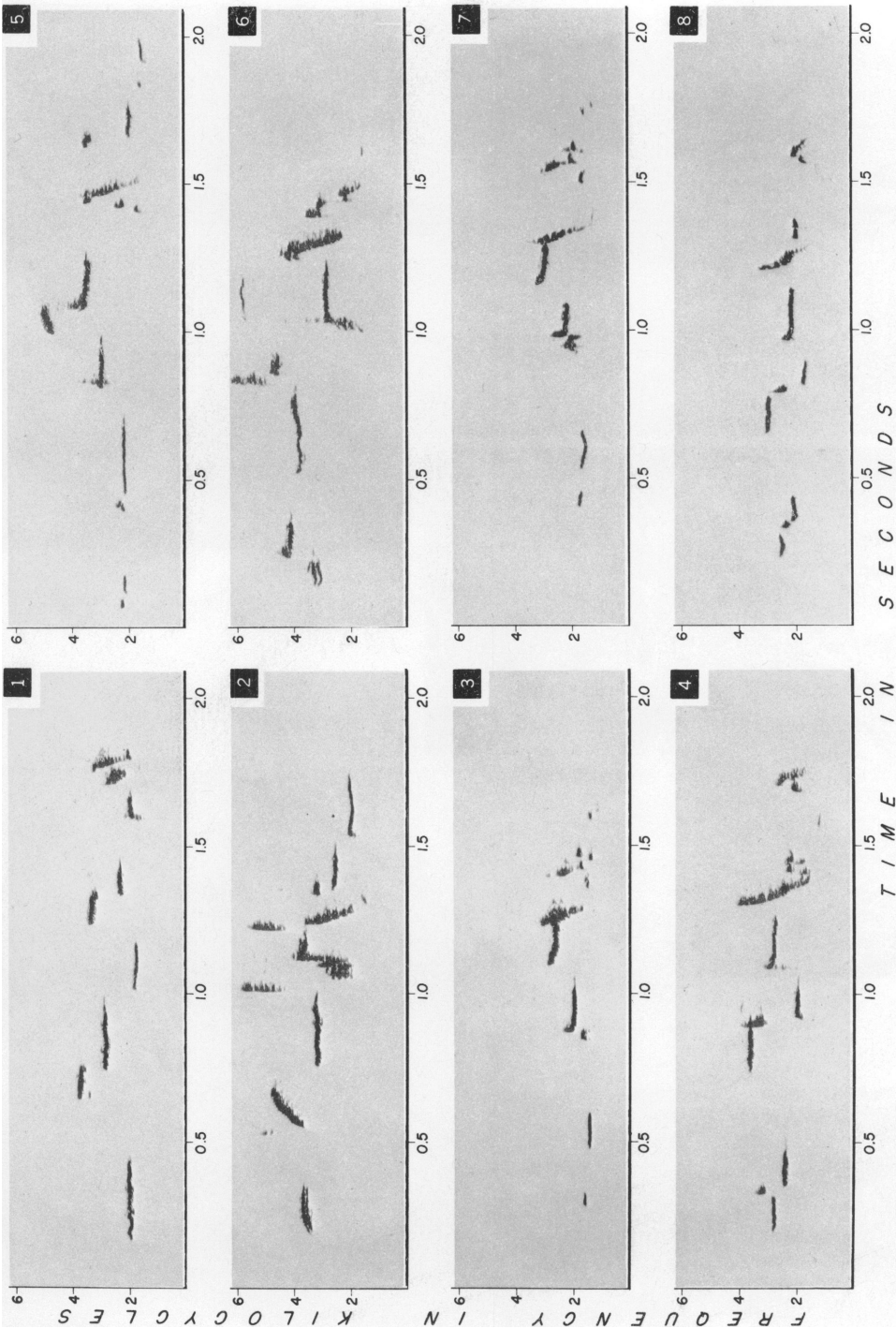
PLATE 1

General coloration of upper parts of hybrids and of other meadowlarks. 1. *Left to right:* New York adult male (*neglecta*; Y-YX), New York hybrid male (W-X), and New York adult female (*magna*; G-GX). 2. *Left to right:* Hand-reared *neglecta* female from California (W-WX), New York hybrid female (R-X), and New York adult female (*magna*; G-GX). 3. *Left to right:* Male *neglecta* (museum specimen), Quebec hybrid male (—X), and *magna* male (museum specimen). 4. *Left to right:* Hand-reared *neglecta* female from California (W-WX) and New York adult female (*magna*; G-GX)

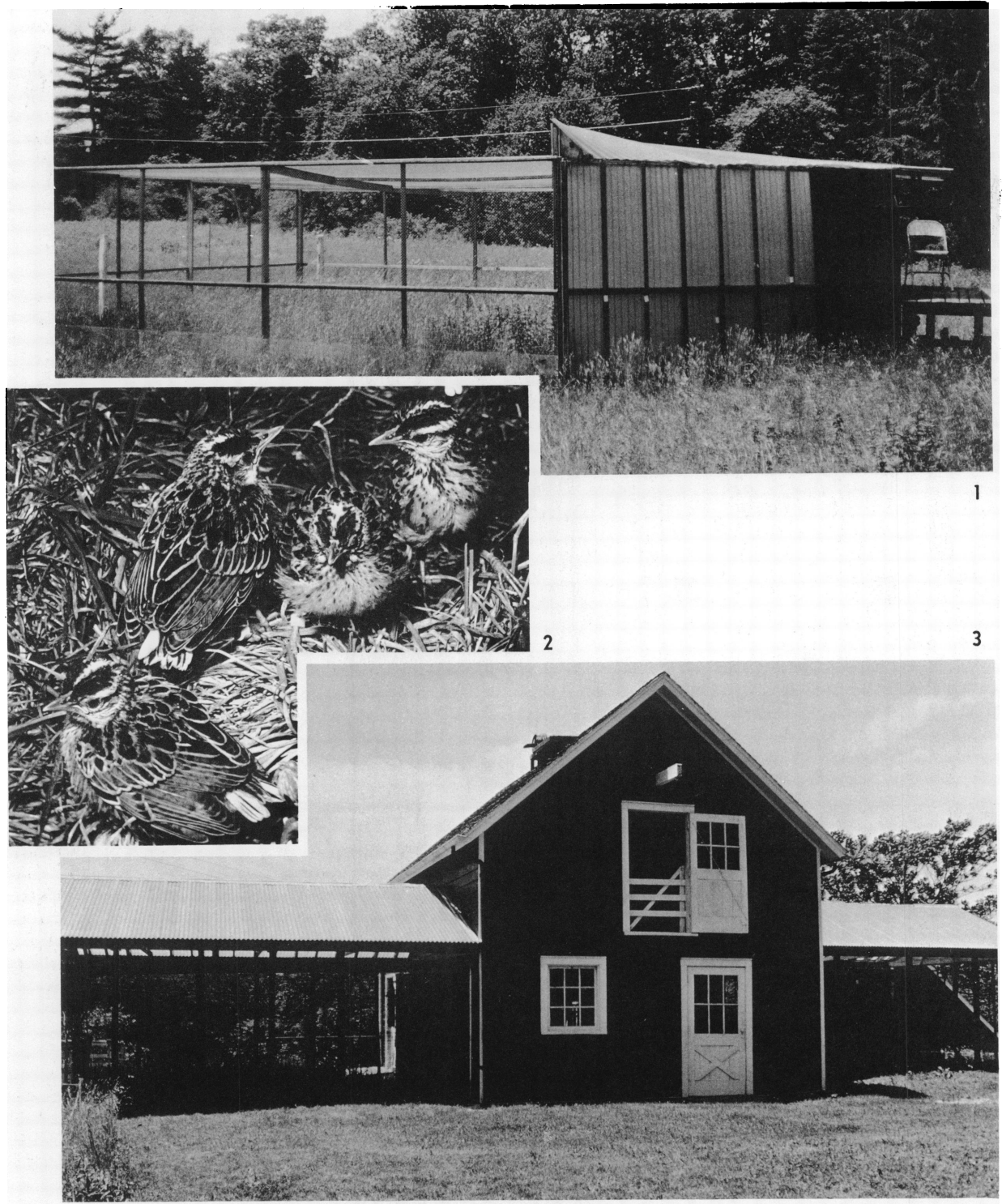
Photographed on January 30, 1965, with one roll of Kodachrome II daylight film and a strobe-flash unit



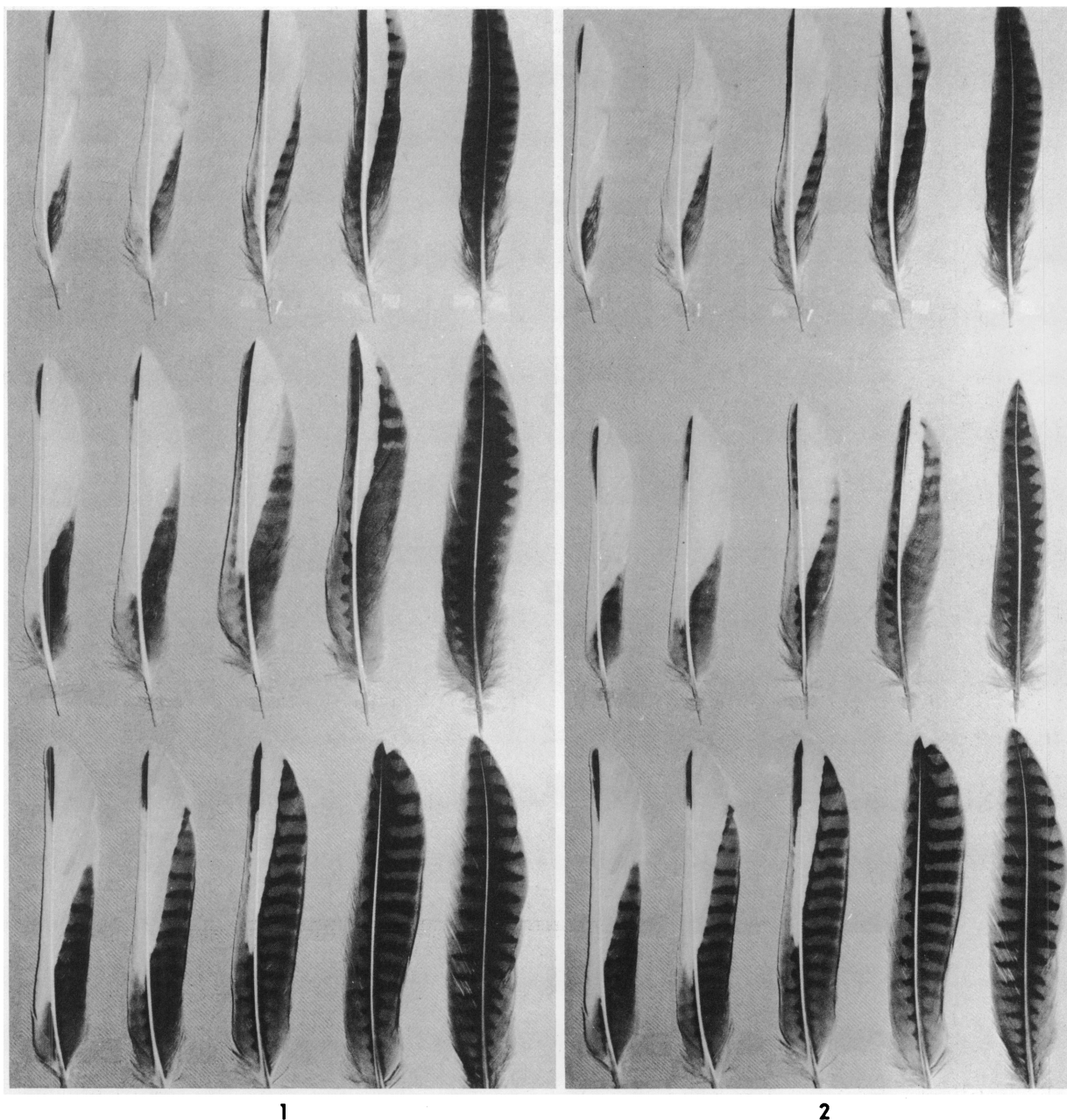
Sound spectrograms of call notes of the New York adults compared with spectrograms of their respective species. 1. Roll of the New York adult male (*neglecta*; Y-YX). 2. Roll of a *neglecta* male from Wisconsin. 3. Chatter of a *magna* female from Huntington, New York. 4. "Chupp" of the New York adult (*neglecta*; Y-YX). 5. "Chupp" of a *neglecta* male from Wisconsin. 6. "Dzert" of a *magna* female from Huntington, New York. 7. "Dzert" of the New York adult female (*magna*; G-GX). 8. Rattle of a *neglecta* female from Wisconsin. 9. Chatter of the New York adult female (*magna*; G-GX).



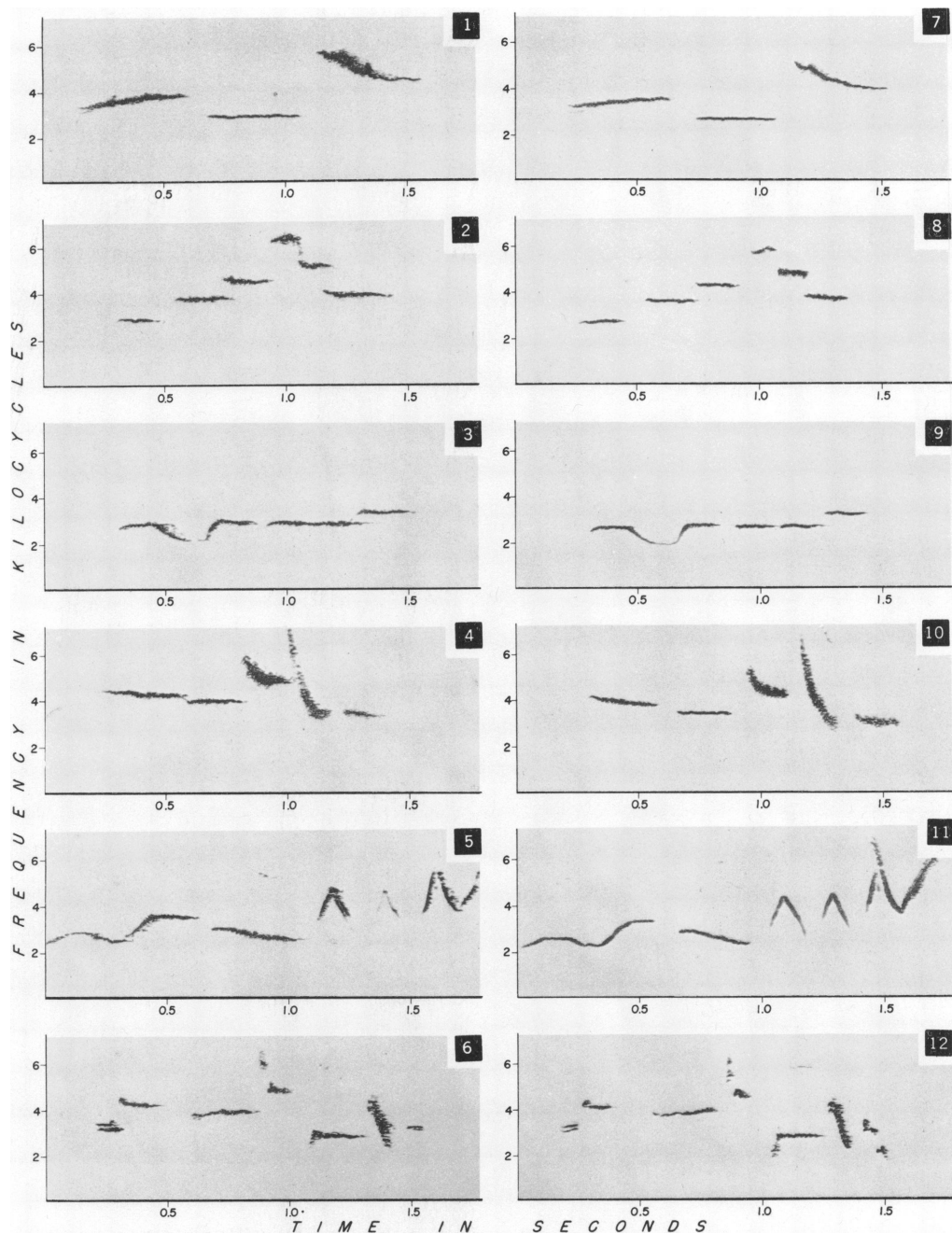
Sound spectrograms of the six patterns that constitute the entire repertoire of primary song of the New York adult male, Y-YX (1-6). Two of these patterns (3 and 4) are similar to two recorded from *neglecta* males in Wisconsin in 1952 (7 and 8)



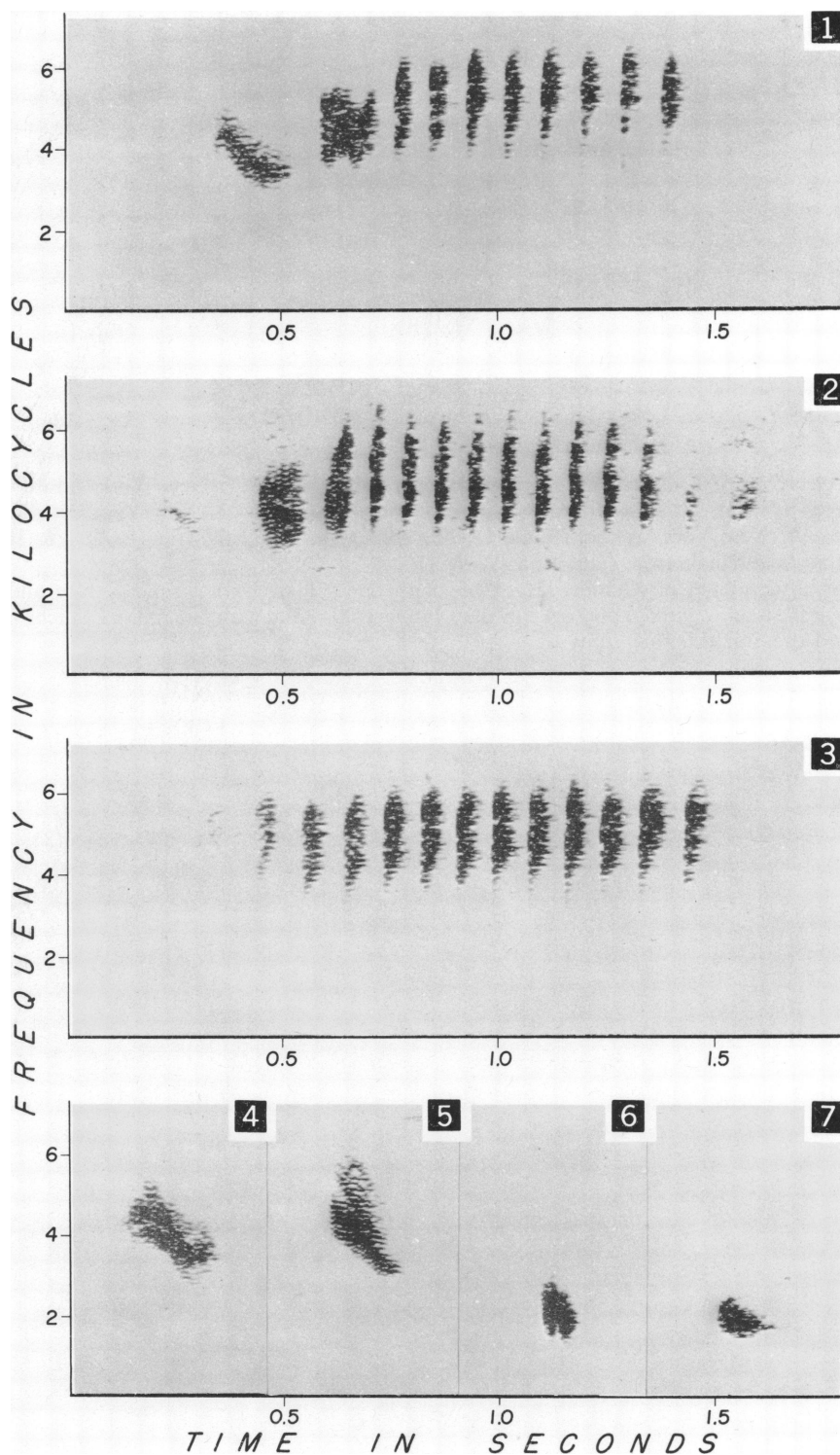
1. Field enclosure in which attempts were made to induce subsequent breeding by the New York adults at the Kalbfleisch Field Research Station. 2. The New York hybrids in the aviary, taken on July 8, 1962 (21 days of age). 3. Aviaries in which the hybrids and other meadowlarks were housed at the Kalbfleisch Field Research Station



Intermediacy of the New York hybrids between the two New York adults with respect to extent of white in rectrices 6 through 2. 1. *Top row*: Set of rectrices removed from the New York adult female (*magna*; G-GX). *Middle row*: Set of rectrices removed from the New York hybrid male (W-X). *Bottom row*: Set of rectrices removed from the New York adult male (*neglecta*; Y-YX). 2. *Top row*: Same as in 1. *Middle row*: Set of rectrices removed from one of the New York hybrid females (G-X). *Bottom row*: Same as in 1. Rectrices removed and photographed on October 21, 1962



1-6. Sound spectrograms of six different primary song patterns of the New York hybrid male (W-X), which were developed as imitations of songs rendered by the Quebec hybrid (—X) and by the New York adult male (Y-YX). 7-11. Imitated song patterns of the Quebec hybrid (—X). 12. Imitated song pattern of the New York adult male (Y-YX)



Sound spectrograms of call notes of the hybrids and of the New York adults. 1, 3. Chatters of the New York hybrid male (W-X). 2. Chatter of the New York adult female (*magna*; G-GX). 4. "Dzert" call of the New York hybrid male (W-X). 5. "Dzert" call of the New York adult female (*magna*; G-GX). 6. "Chupp" call of the New York adult male (*neglecta*; Y-YX). 7. "Chupp" call of the Quebec hybrid (—X)

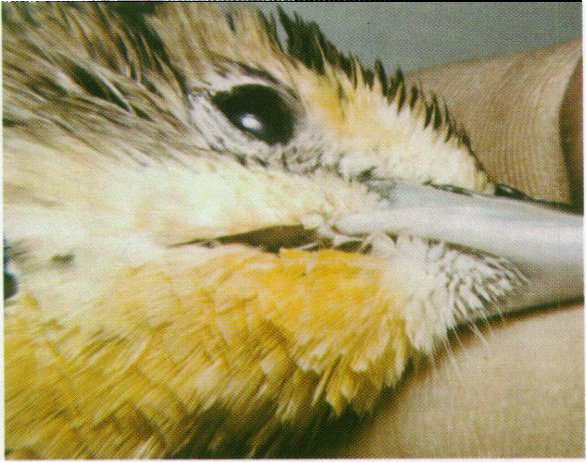
PLATE 8

Cheek coloration of hybrids and of other meadowlarks. 1. New York adult male (*neglecta*; Y-YX). 2. New York adult female (*magna*; G-GX). 3. New York hybrid male (W-X). 4. New York hybrid female (R-X). 5. Quebec hybrid male (—X). 6. Hand-reared *neglecta* female from California (W-WX)

1-4 photographed on October 21, 1965, with one roll of Ektachrome X film and the Startech flash unit; 5 and 6 photographed on January 30, 1965, with one roll of Ektachrome X film and the Startech flash unit



1



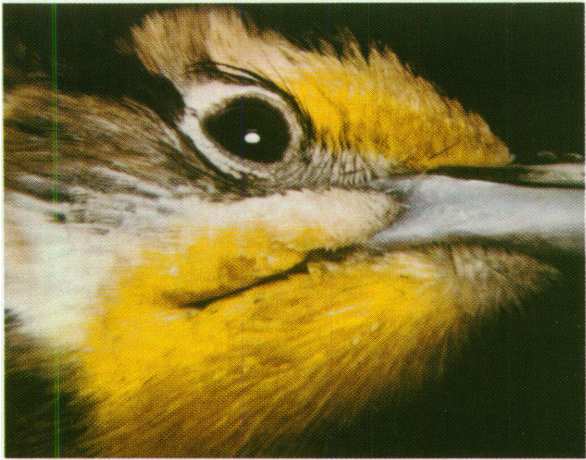
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6

TABLE 2—(Continued)

	N	Range	Mean, S.E.	S.D.	C.V.
Extent of white (continued)					
New York hybrid (G-X)	3		38.7		
New York hybrid (Y-X)	1		38.0		
New York hybrid (B-X)	1		41.0		
New York adult (G-GX)	4		46.8		
<i>S. m. magna</i>	50	35-59	43.56 ± 0.65	4.57	10.49
Rectrix 3, inner web					
<i>S. neglecta</i>	40	0-33	6.53 ^a		
New York hybrid (R-X)	3		34.3		
New York hybrid (G-X)	3		25.3		
New York hybrid (Y-X)	1		38.0		
New York hybrid (B-X)	1		41.0		
New York adult (G-GX)	3		44.3		
<i>S. m. magna</i>	50	0-47	34.64 ^a		

^a No S.D. or S.E. calculated because of skewed distribution.

bility of young hybrid meadowlarks and stresses the imperative need for adequate field data to substantiate such statements. After the five New York hybrids had completed their first prebasic (postjuvenile) molt, in October, 1962, it became possible to sex them by wing length: one male (W-X), 124 mm.; and four females (G-X, R-X, B-X, Y-X), 106, 108, 110, and 110 mm., respectively. This imbalanced sex ratio is probably not unusual. Most of our hand-raised birds that have survived through their first prebasic molt have been females. Furthermore, an unbalanced sex ratio in the nest appears to be reflected in the polygynous behavior of the adults and the large numbers of females on any breeding ground (Lanyon, 1957).

Two of the four female hybrids (B-X and Y-X) met with accidental deaths in March, 1963, but not until after an analysis had been made of the first basic plumage of all the hybrids, in comparison with the parental types. The remaining three hybrids from New York (W-X, G-X, and R-X) and the Quebec hybrid (—X) are in excellent health at this writing.

Measurements of the five New York hybrids and the Quebec hybrid are presented in tables 1 and 2, where they can be compared with those of the two New York adults and with series of museum specimens of *S. neglecta* and *S. m. magna*. The means for the captive birds were derived from measurements taken

of several different plumages over a period of three years. There are no mensural characters that exhibit complete specific separation between *S. neglecta* and *S. m. magna*. Since the longer-winged *neglecta* has the shorter tarsus, the ratio of wing length to length of tarsus is more useful than either of these characters applied separately. All five of the New York hybrids were intermediate between their parents with respect to this character (text fig. 2).

I have discussed the usefulness of the extent of white in the rectrices as a diagnostic character for distinguishing between certain populations of these species, but have warned against its use in differentiating between *neglecta* and nominate *magna* because of extensive character overlap (Lanyon, 1962). Only in the case of those individuals reflecting an "extreme" condition, as with both of the New York adults (Y-YX and G-GX), can the extent of white in the tail be a useful species-diagnostic character (text figs. 1 and 3). It is of interest, from the standpoint of the phenotypic expression of this character in first-generation hybrids, to compare the extent of white in the rectrices of a brood of hybrids with that of the known parents (table 3). The inner webs of the fourth and third rectrices provide the greatest degree of specific separation between *neglecta* and nominate *magna* (tables 1 and 2), and a statistical analysis of the extent of white in these

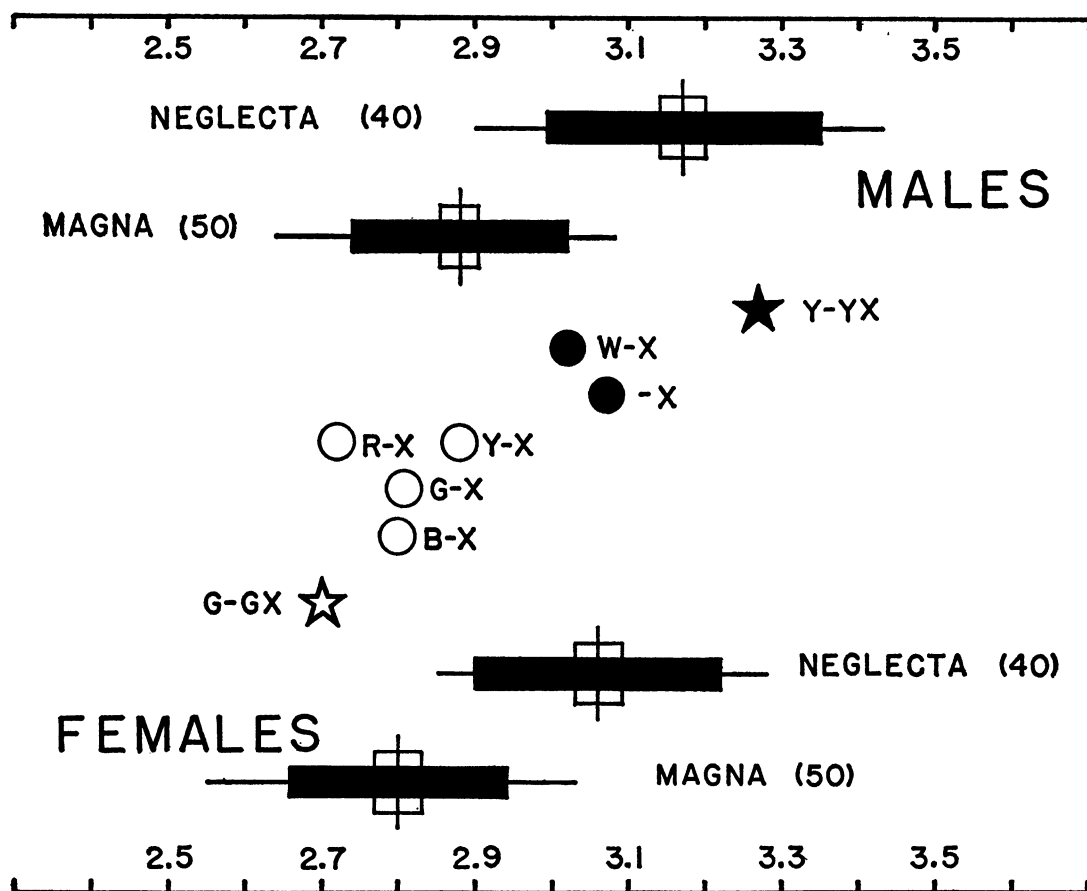


FIG. 2. Ratio of length of wing to length of tarsus for the hybrids and the New York adults, as compared with statistical analyses of this character in museum series of *S. neglecta* and of *S. m. magna*.

Symbols: Stars, New York adults; circles, hybrids; solid figures, males; open figures, females.

TABLE 3
EXTENT OF WHITE IN RECTRICES OF NEW YORK HYBRIDS OF KNOWN PARENTAGE,
EXPRESSED AS PERCENTAGE OF TAIL LENGTH

	Rectrix 6		Rectrix 5		Rectrix 4		Rectrix 3	
	Outer	Inner	Outer	Inner	Outer	Inner	Outer	Inner
Adult ♂ (Y-YX)	0.448	0.590	0.444	0.558	0.317	0.451	0	0
Hybrid ♂ (W-X)	0.537	0.599	0.547	0.620	0.433	0.590	0.223	0.388
Hybrid ♀ (R-X)	0.424	0.591	0.444	0.606	0.308	0.585	0	0.579
Hybrid ♀ (G-X)	0.377	0.578	0.427	0.588	0.321	0.584	0	0.382
Hybrid ♀ (Y-X)	0.469	0.594	0.438	0.591	0.391	0.578	0.188	0.500
Hybrid ♀ (B-X)	0.382	0.588	0.353	0.652	0.235	0.565	0	0.471
Average of hybrids	0.438	0.590	0.442	0.611	0.338	0.580	0.082	0.464
Adult ♀ (G-GX)	0.599	0.674	0.623	0.704	0.499	0.701	0	0.663

areas has been graphed in text figures 1 and 3. These figures illustrate the intermediacy of the New York hybrids with respect to their parents and also to samples of museum specimens. This hybrid intermediacy with respect to extent of white in the rectrices can also be appreciated in plate 5, which compares the rectrices of the New York adults with the first basic rectrices of their male hybrid (W-X) and of one of their female hybrids (G-X).

When museum series of fresh-plumaged *neglecta* and nominate *magna* are compared, one can readily identify the *neglecta* specimens, regardless of sex, by their less intense melanin pigmentation. This contrast between the grayer, more pallid *neglecta* and the browner, darker *magna* is most evident on the crown and back and can be appreciated in plate 1, figure 4. Coloration of the upper parts of both sexes of the New York hybrids was conspicuously darker and browner than that of the *neglecta* parent and indistinguishable

from that of the *magna* parent (pl. 1, figs. 1 and 2). The Quebec hybrid is as dark as or darker than specimens of nominate *magna* of comparable condition of feather wear (pl. 1, fig. 3).

Nominate *magna* is also characterized by a more intense carotenoid pigmentation than *neglecta*, i.e., the yellow of the under parts of both sexes is richer and slightly more orange, as illustrated in plate 8, figures 1 and 5. Here again, the New York hybrids and the Quebec hybrid were indistinguishable from nominate *magna* and more richly colored than *neglecta* (pl. 8).

The extent to which the yellow of the throat extends onto the cheek region is a reliable sexually dimorphic character for distinguishing between these forms. Males of *neglecta* have a prominent area of yellow on the cheek, extending for 2 mm. or more above the apterium which extends posteriorly from the mandibular ramus, whereas *magna* males

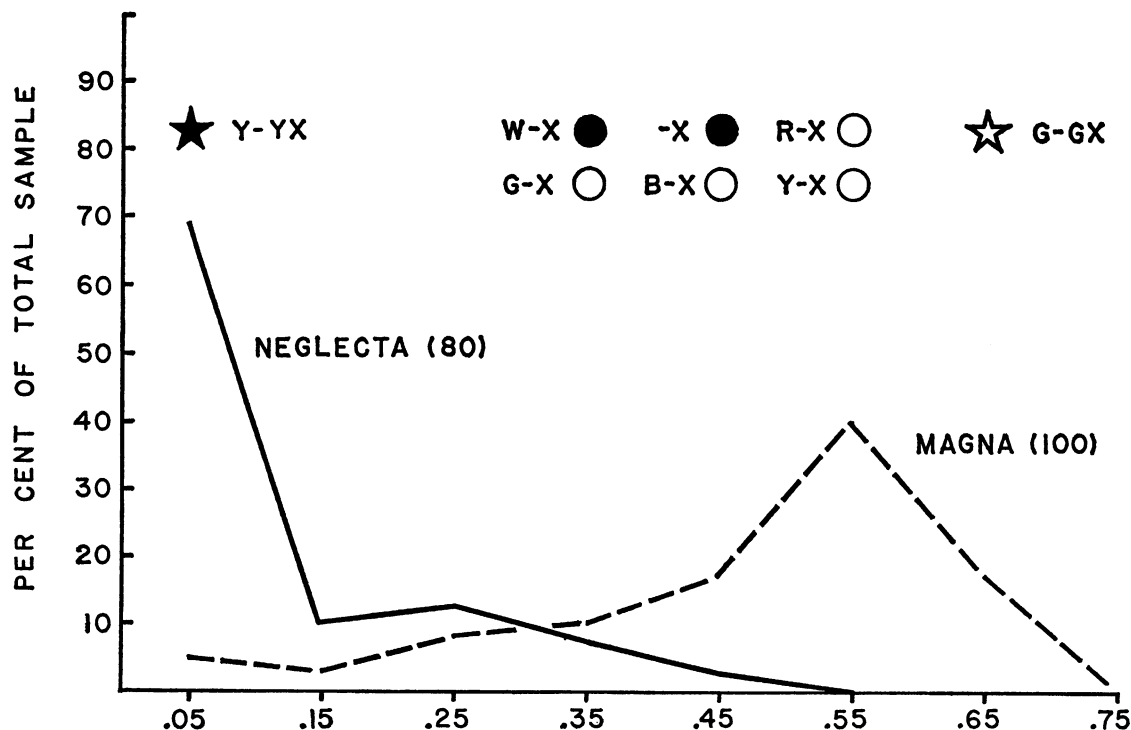


FIG. 3. Extent of white in the inner web of the third rectrix of each of the hybrids and of each of the New York adults, as compared with the distribution of this character in museum series of *S. neglecta* and of *S. m. magna*, determined by the measurement, in millimeters, of that portion of the rachis not bordered by pigmentation and expressed as a percentage of tail length.

Symbols: Stars, New York adults; circles, hybrids; solid figures, males; open figures, females.

(all populations within the United States and Canada) have no yellow feathers dorsad to this apterium or, at most, a fringe of yellow involving up to a dozen feathers and extending no more than 1 mm. above this apterium. Female *neglecta* always have some yellow on the cheek, though less extensively than do the males. In the museum series examined, none of the *magna* females had yellow feathers above this apterium, and frequently the yellow of the throat even failed to include all the feathers along the lower fringe of the apterium. The male hybrid from New York (W-X) exhibits a prominent patch of yellow on the cheek which extends about 2 mm. above the apterium, as illustrated in plate 8, figure 3. This is conspicuously less yellow

than in the case of the *neglecta* parent (Y-YX) in which the yellow extends for a distance of 5 mm. above the apteryal line (pl. 8, fig. 1) but is conspicuously more extensive than in any specimen of nominate *magna* that I have examined. The male Quebec hybrid also has a very prominent yellow cheek patch (pl. 8, fig. 5). The four hybrid females from New York are only barely distinguishable from the *magna* parent (G-GX) on the basis of cheek coloration, by virtue of a trace of yellow along the dorsal edge of the apterium, involving no more than six feathers in each bird (pl. 8, fig. 4). The *magna* parent (G-GX) has no yellow above the apterium (pl. 8, fig. 2).

VOCALIZATIONS OF HYBRIDS

MY PREVIOUS STUDIES (1957, 1960) showed the importance of exposure to experienced individuals for the full development of primary song patterns in young male meadowlarks. There is no evidence that an offspring's primary song patterns *per se* are determined by the genotype of the male parent. Which song patterns a particular young male develops is determined by those patterns it hears from the time it is about four weeks of age (when it becomes independent of the parents) until it is about six months old. Individuals experimentally isolated from such tutors during this critical learning period demonstrated this predilection to develop patterns through learning by acquiring the song motifs that they heard from species other than *Sturnella* (meadowlarks) in their sound environment.

SIZE OF REPERTOIRE OF PRIMARY SONG PATTERNS

In view of this information regarding the ontogeny of primary song, the actual song patterns developed by the Quebec hybrid (—X) and by the male New York hybrid (W—X) were of little consequence in reflecting their parentage. The results in both cases merely reinforced our current concept of ontogeny, as briefly outlined above. Of considerable significance, however, was the *number* of primary songs that each of these hybrid males developed. Repertoire size had been found to be specifically distinct in these sibling species, with *neglecta* males having only six to nine song patterns and *magna* males capable of rendering 50 or more different patterns.

The Quebec hybrid (—X) has 11 primary song patterns in its repertoire—almost certainly showing a capacity for variability greater than that of its male parent, though we have no data on that point, unfortunately. The derivation of these 11 patterns is obscure, for we have no objective data on the sound environment to which this male was exposed during its critical learning period at the Quebec Zoological Garden.

Fifteen different primary song patterns have been recorded from the male New York

hybrid (W—X), as contrasted with the (Y—YX) repertoire of six patterns of its male parent. In this instance, since the sound environment during the critical learning period was well known, it is possible to trace the origin of most of this hybrid's primary song patterns. Eight of the 15 songs were developed through imitation of songs rendered by the Quebec hybrid (—X) in an adjacent pen (pl. 6, figs. 1–5). One song consists in part of a good imitation of the song of a Black-capped Chickadee (*Parus atricapillus*), also maintained in an adjacent pen. Another song appears to have had the alarm note of the Redwinged Blackbird (*Agelaius phoeniceus*) as its model, and this species was common in the vicinity of the meadowlark aviaries. Only one of the 15 songs in this hybrid's repertoire was developed through imitation of its male parent (pl. 6, figs. 6 and 12). The remaining four songs are of unknown origin, though they consist primarily of gently sloping, rather pure whistles and have some of the quality of the primary song of Eastern Meadowlarks. Individuals of the latter species occasionally may be heard in the vicinity of the aviaries but do not breed within a radius of one-half mile.

FREQUENCY OF PRIMARY SONG

In addition to the size of primary-song repertoire, the two species of meadowlarks have been found to differ with respect to the frequency (pitch) of their songs. The Western Meadowlark characteristically sings at frequencies about 1.5 kilocycles lower than those at which the eastern species renders its songs (Lanyon, 1957). The possibility of a genetic influence upon the normal frequency response of the sound-producing apparatus of meadowlarks was suggested by an experiment conducted in the Wisconsin study, in which a young male Eastern Meadowlark was hand-reared in a field enclosure where it was exposed primarily to the songs of Western Meadowlarks. Among the large number of primary song patterns that this experimental bird developed were imitations of nine Western Meadowlark songs. All the imitations, though remarkably similar in pattern, were

TABLE 4
FREQUENCY (IN KILOCYCLES) OF PRIMARY SONGS OF HYBRID MALES, COMPARED
WITH THAT CHARACTERISTIC FOR EACH SPECIES

	No. of Different Patterns Analyzed	Average Lowest Frequency	Average Highest Frequency	Extremes of Frequency	Frequency Range
<i>S. m. magna</i> ^a	44	3.0	6.2	2.5-7.7	5.2
New York hybrid (W-X)	15	2.7	6.2	1.8-7.7	5.9
Quebec hybrid (-X)	11	2.4	5.6	1.7-7.2	5.5
<i>S. neglecta</i> , New York adult (Y-YX)	6	1.4	4.8	1.2-6.3	5.1

^a Male recorded on territory 0.5 mile from Kalbfleisch Field Research Station on June 8-10, 1965.

rendered at frequencies higher than those of the songs copied (Lanyon, 1957).

A comparison of the lowest and highest frequencies in the songs of the Quebec hybrid (-X) and of the New York hybrid (W-X) with a similar analysis of the songs of the male parent (Y-YX) and of a nominate *magna* male is presented in table 4. Both hybrid males exhibit a greater range of frequencies in their primary songs than would be expected from males of either species. The songs of the New York hybrid (W-X) are significantly higher in frequency than those of its *neglecta* parent (Y-YX), and the same is almost certainly true of the Quebec hybrid, though we lack the data to confirm this point. In the case of the single song pattern of W-X developed through imitation of a song of the Western parent, the most noticeable difference in the spectrograms of these songs (pl. 6, figs. 6 and 12) is in the lowest frequencies constituting the terminal phase. The lowest frequency in the pattern of Y-YX, the *neglecta* parent, is 1.5 kilocycles, whereas the lowest frequency in the pattern of W-X is only 2.3 kilocycles.

CALL NOTES

The development of species-characteristic call notes in these two species is much less influenced by the sound environment than is the case with their primary song patterns. My experiments in Wisconsin and subsequently in California and Arizona have indicated that young meadowlarks isolated from experienced individuals of their own kind from the age of nine days (time of fledging) are capable of developing their own

species-characteristic call notes. The latter generally first appear during the fourth week of age. No one as yet has successfully raised meadowlarks from the egg to rule out the possible influence of parental calls during the nestling stage. Some insight into this aspect of call-note development was obtained from an experiment in which eggs were exchanged (Lanyon, 1957). Three captive *neglecta* females, hatched and reared in the field by adult *magna* until they were nine days old, developed the "chupp" call note of their own species. However, the *magna* nest in this experiment was situated within a quarter of a mile of *neglecta* territories, and we cannot entirely eliminate the possibility of exposure to adult *neglecta* calls during the nestling period. The development of call notes in hybrid meadowlarks that have been raised by their parents during the nestling period, though of considerably greater significance than the primary song patterns developed under the same circumstances, still leaves us with some unanswered questions regarding the relative importance of genotypic control and learning from adults that call in the vicinity of the nest. We have a further complication in interpreting these results in that negative evidence is not conclusive in such instances. Hand-raised females call only infrequently in captivity, presumably because they lack the appropriate stimulus situations provided by courtship and the rearing and defense of young.

The male New York hybrid (W-X) has been heard to give two types of call notes during the three years that it has been under observation. These are the "dzert" and the

chatter call that are characteristic of *magna*, and spectrographic analysis shows them in fact to be indistinguishable from the same calls rendered by the female *magna* parent, G-GX (pl. 7). One of the female hybrids (R-X) is known to have given the "dzert" call when alarmed, but it is likely that a courtship situation will be required before we can detect the presence of the *magna* chatter in the repertoire of the females.

It is tempting to interpret the call-note performance of W-X, the male New York hybrid, as evidence of a nestling's imitation of the calls it hears most frequently while in the nest. The female parent, in this case a *magna* (G-GX), is the more attentive sex during this period, and it frequently renders call notes (both "dzerts" and chatters) in the vicinity of the nest, particularly when it is disturbed by an intruder or predator. One might also propose an alternative hypothesis, solely on the basis of the data from W-X, that the ontogeny of call notes is genetically sex-linked, which would result in the development by the young bird of call notes like those of the female parent, regardless of its sound environ-

ment. But attractive as these explanations may be when applied to W-X, neither can account for the call notes that have been recorded from the Quebec hybrid, —X, which also represents the first generation produced from the crossing of a *neglecta* male with a nominate *magna* female. The only call notes that have been heard from —X have been a "chupp" and an alarm whistle. The whistles recorded from —X appear to be closer in frequency to those characteristic of *neglecta*, centering on about 2.0 kilocycles. The "chupp" call rendered by —X has all the characteristics of the species-specific "chupp" of *neglecta* (pl. 7). In summary, we have two hybrid males, both produced from the crossing of a *neglecta* male with a nominate *magna* female, that render distinctly different call notes: in the one case, comparable to those of the *magna* parent, and, in the other case, comparable to those of the *neglecta* parent. Observations of the ontogeny of call notes in additional hybrids, reared from the egg in acoustical chambers, are needed to rectify this apparent enigma.

DISCUSSION OF THE IDENTIFICATION OF HYBRIDS

WHEN I SCORED the New York hybrids and the Quebec hybrid according to Szijj's (1963) hybrid index, both weighted and unweighted, all six birds were misclassified, i.e., they fell within the range of variation assigned to Eastern Meadowlarks rather than within the "approximate range of the actual hybrid morphology." This is not surprising, in view of the fact that (1) three of the four morphological characters used in this index are directly influenced by the intensity of melanin pigmentation, and that (2) it has been demonstrated in the present study that the first-generation hybrids of this particular cross are indistinguishable from the *magna* parent with respect to the over-all intensity of melanin pigmentation. The results of the present study make it clear that hybrid meadowlarks can be identified with accuracy and authority only on the basis of a prior knowledge of the phenotypic recombination of specific characters in hybrids of known parentage, rather than by applying a hybrid index.

It might be expedient, at this point, to summarize the data accumulated in this study for the identification of first-generation hybrids produced by the crossing of a *neglecta* male with a nominate *magna* female.

The fallacy of using primary song patterns *per se* as an indication of hybridization in meadowlarks was revealed in my publication of 1957. An occasional male meadowlark may have a bivalent repertoire of primary song, not as a result of mixed parentage but because of the particular aberrant conditions prevalent during its critical learning period—perhaps a more continuous and proximate exposure to singing males of the opposite species. However, the *number* of different primary song patterns in the vocal repertoire shows some promise as a clue for the field identification of hybrid males. Such males must be individually marked (by bands, or other means) and must have their song repertoire carefully and objectively documented, preferably by sound recordings and spectrographic analysis, over a period of several days. Any male having more than 10 but fewer than 20 primary song patterns in its

repertoire is suspect, in view of the data presented here. There is no evidence, at present, to support the use of call notes for the field identification of hybrids. At best, then, voice can be used only as a tentative indication of hybridization in males for which the complete repertoire of primary songs is known. Positive identification should be withheld until a morphological examination has been made.

Morphologically, the first generation of hybrids of this cross are phenotypically indistinguishable from the *magna* parent with respect to those characters that are dependent on the intensity of melanin and carotenoid pigmentation, including the coloration of the crown, that of the back, that of the throat, and that of the breast. It should be noted that these particular characters show little, if any, sexual dimorphism in meadowlarks. With respect to the sexually dimorphic characters, i.e., cheek color and all mensural characters, these hybrids are phenotypically intermediate between the parental types. But cheek color is the only one of this group of characters in which there is no overlap of *neglecta* and nominate *magna*; the mensural characters, including wing to tarsus ratio and extent of white in the rectrices, are useless as indices of hybridization except for the elimination of "extreme" specimens.

According to these data, then, males of the first generation of hybrids produced from the crossing of a *neglecta* male with a nominate *magna* female can be recognized by the concordance of a prominent yellow area on the cheek with an over-all dark plumage coloration. In these specimens the yellow of the throat can be expected to extend onto the cheek for nearly 2 mm. or more, dorsad to the apterium that extends posteriorly from the mandibular ramus, and involve more than a dozen feathers. Separation of these hybrid males from males of nominate *magna*, which they most closely resemble, depends entirely on the careful and objective determination of this cheek character. Caution should be exercised, for (1) fresh-plumaged specimens of *magna* will normally have the white cheek feathers tipped with *buff* (not yellow, as on

the throat), and (2) males of nominate *magna*, even in the Atlantic coastal states, frequently have a fringe of yellow feathers (fewer than a dozen) that extend up to 1 mm. dorsad to the mandibular apterium, as described above. The available evidence indicates that all hybrid males from this cross should be identifiable.

Identification of the females of the first generation of hybrids resulting from this cross depends on the same concordance of characters that is used for the males, but it is questionable that all such females can, in fact, be recognized as hybrids. Each of the four hybrid females in this study had a trace of yellow along the dorsal edge of the mandibular apterium, involving no more than six feathers, whereas their *magna* parent had no

extension of yellow onto the cheek. But, until additional evidence becomes available on the limits of variation of this character in females, this separation between hybrids and "pure" *magna* is too tenuous for use with any degree of confidence.

This study has yielded no data that would aid in the identification of specimens resulting from backcrosses and from the interbreeding of first-generation hybrids. Austin doubts the fertility of meadowlark hybrids and has predicted (1957) that "if hybrid offspring between *magna* and *neglecta* are ever reared successfully in captivity they will prove only partially if at all fertile." Efforts to breed the New York hybrids and to backcross them with their parents, unsuccessful to date, will be continued.

SUMMARY

PREVIOUS STUDIES of the comparative biology of the Eastern Meadowlark (*Sturnella magna*) and the Western Meadowlark (*S. neglecta*) have revealed that these sibling species are virtually, if not completely, isolated throughout a rather narrow zone of sympatry from central Mexico to the Great Lakes region of the United States. A case of hybridization of the two species in New York is fully substantiated by the capture of both adults and their hybrid offspring, and by the subsequent analysis of the morphology and vocalizations of the captive birds. Another hybrid, from Quebec, was also raised in captivity and is included in this analysis. A total of six hybrids are reported on here, all of which represent the first generation of hybrids produced by crossings in the wild of *neglecta* males with nominate *magna* females. No data are currently available on the reciprocal cross or on populations of *magna* other than the nominate race. Attempts to breed and to hybridize these captive individuals have failed.

Morphologically, the first generation of hybrids of this particular cross are phenotypically indistinguishable from the *magna* parent with respect to those characters that depend

on the intensity of melanic and carotenoid pigmentation, but are intermediate between the parental types with respect to the sexually dimorphic characters, including cheek color and mensural characteristics. Mensural characters are useless as indices of hybridization except for the elimination of "extreme" specimens. All hybrid males from this cross should be identifiable by the concordance of a prominent yellow area on the cheek with an over-all dark plumage coloration. The same characters must be used for females, but with considerably less confidence.

The size of the repertoire of primary song patterns shows some promise as a clue for the field identification of hybrid males, but the actual patterns of primary song are meaningless for this purpose. Conflicting evidence on the call notes of hybrids necessitates further experimentation in this area and, at present, precludes their use for the identification of hybrids in the field.

The results of this study make it clear that hybrid meadowlarks can be identified with accuracy and authority only on the basis of a prior knowledge of the phenotypic recombinations of specific characters in hybrids of known parentage.

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