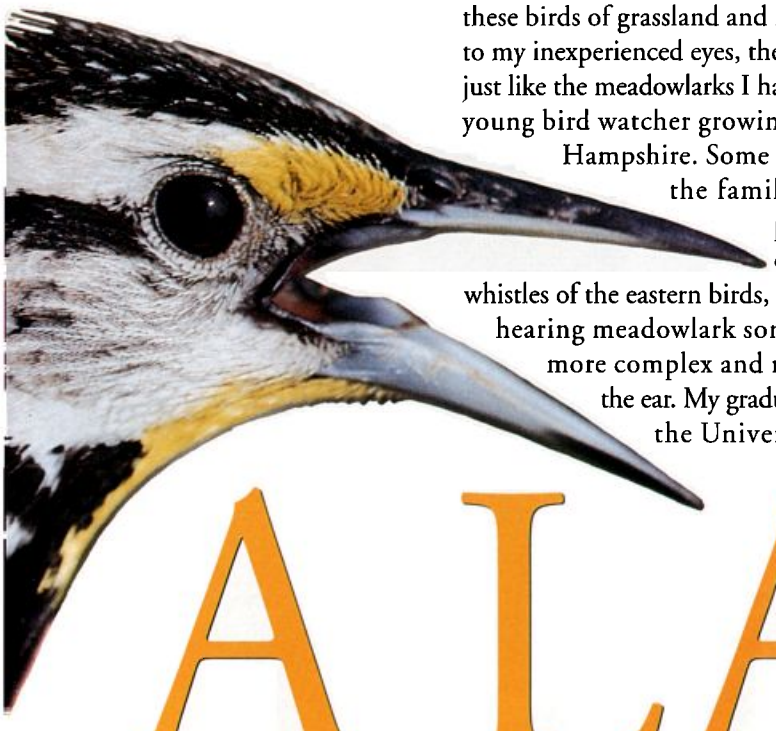

A LARK

HOW A DOCTORAL CANDIDATE FOUND A DISSERTATION, AND 26 YEARS OF

Wisconsin was the furthest west I had ever been, but the birds were not all that different from those I knew back east, as an undergraduate at Cornell. I soon discovered there was something strange about the meadowlarks I was seeing—or, more accurately, hearing —near Madison. Wisconsin's dairy farms are an ideal environment for these birds of grassland and meadow and, to my inexperienced eyes, the birds looked just like the meadowlarks I had known as a young bird watcher growing up in New Hampshire. Some of them sang the familiar series of plaintive, down-slurred whistles of the eastern birds, but I was also hearing meadowlark songs that were more complex and melodious to the ear. My graduate advisor at the University of Wisconsin, John T. Emlen, Jr., identified them as Western Meadowlarks (*Sturnella neglecta*), presumably a different species from Eastern Meadowlarks (*Sturnella magna*), although he admitted there was some controversy on that academic point. John suggested this might be a good research project for me, one that he "had placed on the back burner, so to speak," waiting for "just the right grad student to come along." I soon realized this was another way of saying he had been unable to convince any of his previous students to accept this classic example of a high risk dissertation topic!

Eastern Meadowlark (above) and Western Meadowlark (right) provided years of research for the author.

Like most professional ornithologists, I started out as a bird watcher, and admit to a more than casual preoccupation with my daily and annual lists of birds observed. To be able to discriminate between the difficult species was the obvious key to building a large list. This may account for my early fascination with the cryptic or sibling species of birds—those that look so very much alike in the field that you wonder how they are able to tell one another apart (species recognition). What behavioral or morphological mechanisms operate to prevent one species from interbreeding with another (isolating mechanisms)? These subconscious concerns may explain the naive readiness with which I accepted my advisor's suggestion. Regardless of the reason, it was a decision that would profoundly influence my life for the next 26 years.

The scientific literature raised more questions than answers, the usual dilemma facing a beginning doctoral candidate. John James Audubon's revelation that there were meadowlarks west of the Mississippi similar in appearance but differing in voice from the familiar eastern birds touched off a wave of controversy among ornithologists. Spencer F. Baird, John Cassin, J. A. Allen, and Elliot Coues were influential in arguing that the two kinds of meadowlarks belonged to a single species. The latter reported with an air of finality: ". . .the case of *Sturnella magna neglecta* is settled and explained: *magna* shades directly into *neglecta*. . .The change is imperceptibly effected." The authoritative first Check-List of the American Ornithologists' Union concurred in 1886. Robert Ridgway and Witmer Stone led the opposition, and Coues later offered a curious reversal of his earlier position: "I have never seen a specimen of *neglecta* that could not be distinguished from *magna*: under which circumstances I do not follow the A.O.U. in reducing neglecta to a subspecies of magna." In 1908 the A.O.U. recognized the two mead-

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owlarks as distinct species. Continuing reports from the field of individual meadowlarks singing the "wrong song," "hybrid song," or singing both kinds of songs, nurtured an undercurrent of thought that the two kinds of meadowlarks might be interbreeding, and museum curators were having difficulty identifying certain specimens of meadowlarks in their collections.

A doctoral dissertation, whose main thrust was an intensive study of color-banded individuals of both kinds of meadowlarks on a common breeding ground, appeared to offer a logical starting point in solving this problem in evolutionary biology. I spent four years (1952-1955) studying the comparative behavior and ecology of meadowlarks in Wisconsin and other northcentral states, with the focal point being the birds breeding on 100 acres of permanent pasture located in the prairie-forest ecotone near Madison. Though the eastern form was present in this region prior to 1900, the western form did not become well established as a breeding bird until the late 1920's. Presumably the two forms were isolated during the last glacial advance and remained effectively isolated until the agricultural frontier reached the prairies of the northcentral states, permitting a secondary contact in a relatively narrow zone of sympatry and a test of the effectiveness of any isolating mechanisms developed.

I had little difficulty in identifying the meadowlarks observed on my study area, for I found their vocal repertoires to be very different. With the aid of technologically advanced sound recording and analytical equipment just beginning to be used by biologists at the time (high quality reel-to-reel, battery-operated tape recorders, and the sound spectrograph), I was able make a more detailed and objective analysis of these vocalizations than had been possible previously. The two forms were easily identified by call notes rendered when an intruder entered the territory, and that accompanied most forms of posturing in territorial and courtship behavior. Their songs were very different, and consistently so wherever I traveled throughout the northcentral states. Western songs are lower in frequency and more heterogeneous, having two distinct phases: an initial phase of a series of pure whistles, varying from one to six in number, and a terminal phase of one to five more complex elements, each with energy over a range of 1.5 kilohertz and within a brief period of 0.05 second. Eastern songs are higher in frequency and more homogeneous, consisting of a series of clear, whistled notes that are often slurred together and that drop in frequency.

OR TWO

WORK WITH EASTERN AND WESTERN MEADOWLARKS. BY WESLEY E. LANYON

Because of the presence of the complex elements in the terminal phase, it was easy for me to characterize each Western song by assigning to it an appropriate phrase of words. Some of these, often shared by several males, I knew as "I am a meadowlark," "Phoebe, call the bird whip-poor-will," and "Gee, see me, crazy bird." No doubt there is something very Freudian about this technique, but it did make it possible for me to remember the song types from one year to the next and to determine with great accuracy that each Western male has a repertoire of six to nine different song patterns. One color-banded male was singing the same nine song patterns in 1955 as were recorded from him in 1953.

A Western decoy was just as effective in attracting and capturing an Eastern male (below) as another Western male.

I was unable to apply this technique to Eastern songs, however, due to the homogeneity of the plaintive, down-slurred whistles and the seemingly infinite variety of combinations of these elements in the repertoire of each male. I once made a recording of a color-banded Eastern male that lasted for over an hour. Subsequent laboratory analysis revealed that the recording contained over 100 different song patterns and that the male had not once repeated the same song pattern during that time period.

Once I had become proficient in identifying meadowlarks by voice, it became clear the two forms were not randomly distributed, but clumped according to preferred habitat. Wherever I traveled in the northcentral states, I found Easterns in greater numbers in river bottoms and the more poorly drained grasslands, while Westerns preferred the uplands and better-drained, prairie-type grasslands. I could see this same difference, though on a smaller scale, among the birds breeding on my 100 acre study area, with a difference of only 70 feet between the highest and lowest elevations. When I plotted the location of meadowlark nests found over the four year period, most Western nests were concentrated on higher ground, while Eastern nests were more numerous on lower ground. Might not this difference in ecology play a role in keeping these forms from interbreeding throughout the zone of sympatry? Of course it could only be a partial isolating mechanism, for wherever habitats merge the two forms come into contact, as illustrated on my study area.

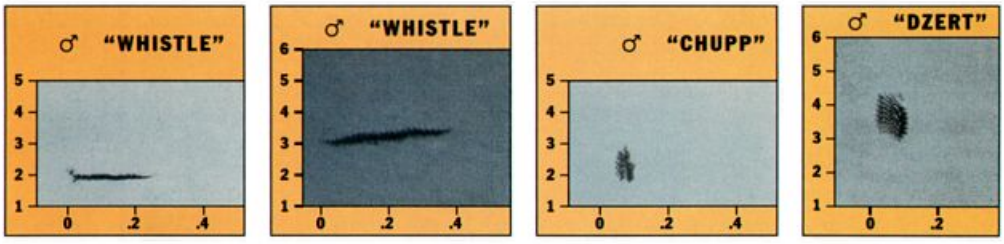
PHOTOGRAPH WESLEY E LANYON

Meadowlarks have territories established and maintained solely by the males, for mating, gathering food, and rearing young, and that are vigorously defended against intruding meadowlarks. The first surprise in this study came with the realization that the two kinds of meadowlarks were defending territories that did not overlap, *i.e.* their territories were mutually exclusive. I determined this from the behavior of males at the territorial boundaries; an Eastern male would defend his territory against a neighboring Western male with the same intensity and the same behavioral posturing that he would use against another Eastern male. It was also apparent from my experience with the use of hand-reared meadowlarks as live decoys for trapping territorial males (in order to color-band them). A Western decoy was just as effective in attracting and capturing an Eastern male as another Western male. These findings were startling and provocative. At least with respect to territorial behavior, the males of the two kinds of meadowlarks were behaving as though they belonged to the same species!

Notwithstanding this lack of discrimination by the males, I had no evidence of interbreeding between Eastern and Western Meadowlarks on my study area, based on observations of over 100 male-female pair bonds over the four year period. Eastern males always paired with Eastern females, and Western males with Western females. This forced the conclusion that the integrity of the two species, the assurance of reproductive isolation, must rely on the discriminatory ability of the females at time of pair formation. But how would this work?

The females normally arrive several weeks after the males establish territories. The difference in preferred habitat would increase the probability of appropriate pairing, assuming that females exhibit the same preferences as prospective mates. I had no way of demonstrating that, however, and knew that could be only a partial isolating mechanism at best. There had to be something else operating. Subtle differences in plumage coloration and pattern permitted me to identify individuals

captured for banding, but there was no reason to believe that females would be any better than males at utilizing these as clues to species recognition. I theorized that the females must be responding to behavioral differences between the males, and the only behavioral differences I was able to detect, after hours of observation from my blinds, were the differences in vocalizations. My working hypothesis, then, was that the females were responding to an appropriate set of male vocalizations as the primary basis for species discrimination at time of pair formation.



Sound spectrograms aided the author in his studies of call notes and primary songs. Here are comparisons between the whistle of Western (left) and Eastern (right) males, and the typical "chupp" of Western and "dzert" of Eastern males.

Given the increasing importance of vocalizations in this study, I decided it would be prudent to investigate the development of meadowlark call notes and song. What role might learning play in their ontogeny, and to what extent would they develop in isolation from other meadowlarks? Behind every successful graduate student there surely must be an understanding, talented, and cooperative spouse, and I was no exception. My wife, Vickie, and I began hand-rearing meadowlarks in 1952, sharing our mobile home with them during the last three years that we were in Madison. And we continued to maintain meadowlarks in captivity for the next 22 years, in Arizona, Ohio, and finally in New York. These hand-reared birds were valuable as live decoys, for the decoy trap proved to be the most effective and efficient means of capturing birds to color-band and mark for quick identification in the field. They were equally valuable in providing exceptional opportunities for studying, close-up and personal, the ontogeny of meadowlark behavior. In Madison, most of our captive birds were isolated from other meadowlarks from the time they would normally have fledged or slightly earlier. In New York we improved our technique and our meadowlarks were reared from the egg stage.

From these unique studies we learned that young meadowlarks reared in isolation from other meadowlarks from the egg stage are able to develop their own species-specific call notes, and these calls are given under the same circumstances known to elicit these calls from wild birds. In one field experiment in Wisconsin, three Western females raised from the egg by foster Eastern parents and then maintained in our laboratory in isolation from other meadowlarks, developed their own species-specific call notes.

meadowlarks did not develop their characteristic songs unless exposed to these songs during a critical learning period from about one month to nine months. If deprived of hearing meadowlark songs during this receptive period, they will learn the songs of other species that serve as tutors. Since our mobile home was located on the wooded edge of a marsh, void of meadowlarks, none of our young birds developed songs of their own species, but instead learned the songs of Red-winged Blackbirds (*Agelaius phoeniceus*), Eastern Wood-Pewees (*Contopus virens*), Northern Orioles (*Icterus galbula*), and Common Yellowthroats (*Geothlypis trichas*). A young Western male was raised in our mobile home for his first two months, and then placed in a field enclosure on my study area for the following two months, exposed to songs of both Eastern and Western males. Thereafter this bird was in isolation until its first spring, by which time it had developed a bivalent repertoire of song: a group of two Red-winged Blackbird songs (learned while in our mobile home at the edge of the marsh), and a larger group of seven songs that were imitations of familiar song patterns sung by Western males on my study area. In an equally critical field experiment, an Eastern male was reared in a field enclosure during its first five months in a locality on my study area where it was exposed primarily to songs of Western males. It could hear songs less regularly from more distant Eastern males on ter-

"... the only behavioral differences I was able to detect, after countless hours of observation from my blinds, were the differences in vocalizations."

ritory, as well as songs from migrants of both species in the early fall. This young Eastern developed a bivalent repertoire of song: one large group of song patterns with characteristics of Eastern song (13 different Eastern songs were recorded from this individual within a half-hour period), and a second group of nine Western-like songs that corresponded to familiar Western song patterns on the study area. These field experiments revealed two important aspects of development of meadowlark song: (1) though there is no innate basis for the patterns of these songs, as revealed by spectrographic analysis, young males do have an inherited capacity for acquiring a repertoire size characteristic of their species; and (2) young males under certain atypical circumstances in their learning environment may develop bivalent repertoires that include song patterns of the opposite species or song patterns of both species. I was now in the enviable position of being able to reevaluate those accounts in the scientific literature of meadowlarks singing the "wrong song, "hybrid song," or "bivalent repertoires" of song. It was now clear that rather than being evidence for hybridization, the usual interpretation, these individual meadowlarks were merely victims of atypical environmental conditions during their critical learning period. Subsequently two remarkable natural experiments supported this hypothesis. I had a perfectly normal looking Eastern male on territory; he had his species-specific call notes and was able to maintain pair bonds with five perfectly normal Eastern females over a two year period. But this male had a bivalent repertoire of song, as did my experimental bird in the field enclosure. One group of song patterns, probably more than 10 in number, were typically Eastern, while a second group consisted of five typically Western songs. Years later a colleague sent me a recording that he personally had made of a bivalent song repertoire of an Eastern Meadowlark. At times this bird sounded like a typical Eastern, but at other times he sang excellent imitations of Northern Cardinal (*Cardinalis cardinalis*). Certainly there was no reason to invoke an explanation involving hybridization, but imagine the impact such a bird must have had on any bird watcher unfortunate enough to encounter it.

Having demonstrated the innate nature of the call notes of meadowlarks, compared with the obvious role of learning in the development of song, I decided to alter my earlier working hypothesis. I questioned the continued integrity of these species could depend solely upon the females' preference for an acquired behavior; and considered it more likely the females are responding to the species-specific call notes of the males.

I had found

Tower blind used on Wisconsin study area. An electric fence discouraged curious cattle.

no evidence of interbreeding on a common breeding ground in southern Wisconsin. Yet, George Saunders' success in producing a hybrid meadowlark in captivity (in 1933; later killed by one of the parents) suggested that certain populations of these species might be genetically compatible. Furthermore, my own field observations of an attempted mixed mating on my study area and of an aborted mixed pairing in central Illinois indicated a potential for interbreeding under appropriate environmental conditions. Conceivably there might be a greater probability of this occurring at the range periphery where one of the species was a fairly recent immigrant and present only in isolated, pioneering colonies, where a male might have difficulty in finding a mate of his own species. As noted earlier, the Western Meadowlark was a relative newcomer to the northcentral states early in this century. By the time of my field work in Wisconsin, the species was a common breeding bird throughout much of Wisconsin and northern Illinois, and was present in isolated breeding colonies in Michigan, northern Indiana and Ohio, and southern Ontario. The isolated and widely scattered Western Meadowlarks at the periphery of this northeastward range extension were likely candidates for such a scenario, and these thoughts provoked residual questions left unanswered by my Wisconsin field work. Are the two kinds of meadowlarks capable of interbreeding, if given no other choice? And just for the sake of argument, if interbreeding were to occur, would the hybrids be fertile?

In 1962, 12 years after I joined the curatorial staff at the American Museum of Natural History, an historic event in Dutchess County, New York, was to dictate my research program for the next 16 years. A singing male Western Meadowlark was reported, obviously far out of its normal range. I had no difficulty in locating the bird by its typical songs and call notes, and determined that it was paired with an Eastern female (with typical Eastern call notes). Lady luck was certainly with me, for I located their nest with five hybrid young!

I trapped the Western male with the use of a live decoy, and a bow-net at the nest secured the Eastern female as she approached her nestlings with food. The entire family was transported to the Museum's field station on Long Island, where the hybrid young were hand-reared to maturity. Now I had the answer to the first question raised by the Wisconsin study: The two species are capable of interbreeding, though apparently rarely in nature and only under unusual circumstances.

This unique, fully documented record of hybridization in nature gave me the incentive I needed to launch the next phase of my research—a long term program of breeding aviary birds in order to answer the ultimate question: Are the hybrids fertile? The difficulties inherent in this kind of research, and the time required to amass adequate samples, have precluded its use with birds, with the exception of those working on some game species. Earlier attempts to breed my captive birds had failed, presumably because the aviaries were too small and offered inadequate nesting substrate. Ultimately I resorted to aviaries located in a grassland habitat at the Museum's field station that provided 60 square meters of natural sod per breeding pair and ample unobstructed space to permit aerial components of courtship. My breeding stock consisted of seven birds from California, New York, and New Jersey. Whenever possible hybrids were paired with mates known to have bred successfully to maximize the significance of the performance of the hybrids. Fertility of eggs was established by candling after a minimum of four days of incubation, when the embryos and air sacs are clearly visible. Mixed pairings between Easterns and Westerns were as readily achieved as pure pairings, and it was now clear that the two species will interbreed freely given no other choice.

Aviaries used for captive breeding of meadowlarks at the American Museum of Natural History's Long Island field station.

Some of the eggs produced in the field pens were artificially incubated in the laboratory to continue our studies of the development of vocalizations and other behavior. While development of meadowlark song requires learning from tutors, no tutoring is required for the normal development of other aspects of meadowlark biology, including nest

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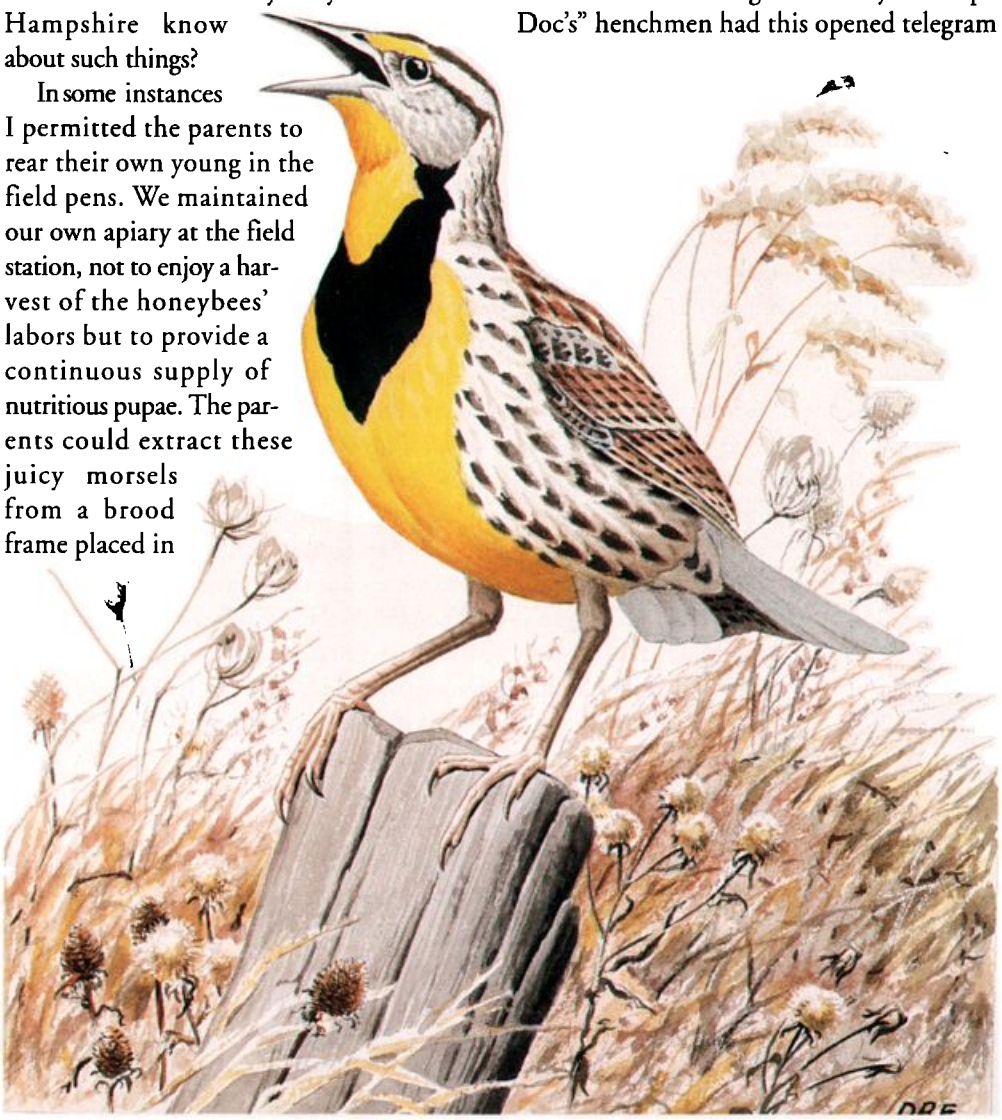
"While development of meadowlark song requires learning from tutors, no tutoring is required for the normal development of other aspects of meadowlark biology..."

building and the rearing of young. One 10-month-old female meadowlark, isolated from other birds since four days prior to hatching, was placed in a field pen with an experienced male in breeding condition. She mated, built a typical domed nest in the pen's natural sod, laid and incubated her eggs, and successfully reared her young as though she had been performing these tasks for years. I showed a film of these extraordinary findings to a meeting of the American Ornithologists' Union, normally a rather staid gathering, and was surprised at one point in my talk when the audience broke out in an unanticipated bout of laughter. Somewhat later a sympathetic colleague, aware of my innocence, explained. As the film progressed, I had expressed amazement and wonder that this female could have performed so ably and naturally, "even though she had been on grass for only three weeks." What does a country boy from New Hampshire know about such things?

In some instances I permitted the parents to rear their own young in the field pens. We maintained our own apiary at the field station, not to enjoy a harvest of the honeybees' labors but to provide a continuous supply of nutritious pupae. The parents could extract these juicy morsels from a brood frame placed in the aviary and feed them to their nestlings as a supplement to the staple soft bill mix available at all times.

Here I digress to relate an incident that occurred four years after the capture of the male Western Meadowlark in Dutchess County. This proven breeder had an important role in our captive breeding program and was an invaluable voucher specimen for the unique record of hybridization in nature. At the time I was busy with other research in Haiti. Those were the days of "Papa Doc" Duvalier's iron-fisted rule, the consequences of which I experienced on several occasions when requesting and receiving interviews with various bureaucrats. Imagine my astonishment and considerable concern upon receiving a telegram from my wife: "Western Escaped. *Stop.* Searching Neighborhood. *Stop.* Please Advise Procedure for Recapture." There was no telling how many of "Papa Doc's" henchmen had this opened telegram



WATERCOLOR DON R ECKELBERRY

pass over their desks. I surmised that it was too late to do anything constructive about this crisis from Haiti, and resigned myself to the loss of this extremely valuable bird. I learned later that Vickie needed no advice. She and the children spent two weeks driving up and down the roads of Long Island, looking for this bird and answering the queries of curious spectators with the somewhat incongruous and inadequate "We're listening for a Western Meadowlark." After many tears and uncontrolled sobbing, they heard the bird on a dairy farm just a few miles from the field station. They had seen me operate a live-decoy trap on many occasions in Wisconsin and knew exactly what had to be done. An hour later, the Western Meadowlark was back in its aviary, doing penance and receiving grateful absolution from my good wife!

Our 12 years of breeding meadowlarks in captivity produced 44 clutches (158 eggs). By placing two meadowlarks in field pens, if all went well, I may have four or five young in a couple of months. If not, there was always next year! Then I wait another year to find out whether they are fertile or not. This kind of research is unprecedented in ornithology.

The end result of these time consuming efforts is that the eggs produced from mixed pairings (*i.e.* Western x Eastern) had a fertility of 90 percent, not significantly different from the 87 percent fertility of eggs produced from pure matings. We now know that on the rare occasions when these two species do have an opportunity to interbreed, such as at the range periphery, their eggs will be fertile, as was the case with the Dutchess County birds.

When the hybrids were given an opportunity to breed, only 10 percent of their eggs were fertile. Actually it was only one hybrid female that was responsible for the fertile eggs; the others produced infertile eggs. All eggs resulting from pairing the one surviving backcross hybrid were infertile. Indicative of the infertility of the hybrids is the performance of three siblings produced in 1975 from a mixed pairing of a male Eastern and a female Western. The three hybrids, two males and a female, did not breed at age one, although paired with experienced mates. In 1977 the female hybrid was paired with a male Western that had bred successfully the previous year. Her clutch of four eggs proved infertile on the eighth day of incubation, while the Western male demonstrated his continued fertility by breeding successfully the following year. One of the male hybrids was paired in 1977 with an experienced female Western, and she laid a clutch of four eggs determined to be infertile after six days of normal incubation. Also in 1977, the second male hybrid was paired with a 2-year-old female Eastern, who laid a clutch of three eggs that proved to be infertile after 10 days of incubation. This female laid fertile eggs the following year in a mixed pairing with a male Western. The causal factors for the hybrid sterility are as yet unknown, but apply to hybrids of both sexes and to hybrids resulting from both categories of mixed pairings.

FERTILITY OF EGGS PRODUCED BY CAPTIVE EASTERN (E) AND WESTERN (W) MEADOWLARKS

Category of pairing	No. of fertile/infertile eggs in complete clutches	Total number of fertile/infertile eggs	% Fertility
PURE PAIRINGS			
Western	4/0, 3/0, 3/0, 3/0, 2/0,	17/2	0.89
Eastern	2/2	3/1	0.75
All pure pairings	3/1	20/3	0.87
MIXED PAIRINGS (MALE x FEMALE)			
Eastern x Western	5/0, 5/0, 4/0, 4/0, 4/0, 4/0, 3/0, 2/0, 2/0	33/0	1.00
Western x Eastern	4/0, 4/0, 4/0, 3/1, 3/0, 3/1, 0/4	22/6	0.79
All mixed pairings		55/6	0.90
PAIRING OF HYBRIDS (MALE x FEMALE)			
F1WE x E	0/4, 0/3, 0/2, 0/2,	0/11	0
F1WE x W	0/4,	0/4	0
F1EW x E	0/3,	0/3	0
F1WE x W	0/4,	0/4	0
W x F1WE	0/4, 4/0,	4/4	0.50
W x F1EW	0/4, 0/4, 0/3,	0/11	0
E x F1WE	0/3, 3/0,	3/3	0.50
E x F1EW	0/4, 0/3,	0/7	0
F1WE x F1WE	0/4, 0/4, 0/4	0/12	0
Backcross hybrid x W	0/5	0/5	0
Backcross hybrid x E	0/3	0/3	0
All Pairings of hybrids		7/67	0.10

Captive breeding of both meadowlarks led to important conclusions. Years after his original inquiry, the author knew that the two kinds of meadowlarks behaved like any good species in nature—reproductively isolated, except in rare instances.

Loss of fertility in the hybrids is not accompanied by an obvious reduction in viability, for the captive hybrids appeared to be as healthy and vigorous as other captives. Nevertheless the results suggest that hybrid meadowlarks are going to be at a disadvantage in nature and be selected against. At last I had the answer to the ultimate question raised 23 years earlier in my field work in Wisconsin—the two kinds of meadowlarks are behaving as perfectly good species in nature—reproductively isolated, except for rare instances such as at the range periphery, where an occasional mixed pairing may occur. But when this happens, the chances of the eggs being fertile are poor. Occasional interbreeding between these good species is an evolutionary dead end!

Wesley E. Lanyon is the Lamont Curator of Birds Emeritus of the American Museum of Natural History.