

THE NESTING ECOLOGY AND REPRODUCTIVE PERFORMANCE OF THE EASTERN MEADOWLARK

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THIS paper reports on a study of 450 nests of the Eastern Meadowlark (*Sturnella magna*) near Carbondale, Illinois from 1960 to 1967. Data were collected in conjunction with long-term field studies of the Bobwhite (*Colinus virginianus*) conducted jointly by the Illinois Natural History Survey, Urbana and the Cooperative Wildlife Research Laboratory of Southern Illinois University.

Despite the abundance of meadowlarks, their wide-spread distribution, and membership in a relatively well-studied family (Icteridae), the nesting habits and breeding biology of the species have received surprisingly little attention. This probably reflects the difficulties involved in finding large numbers of these well-concealed nests. Nice's (1957) classic review of the nesting success of 17 open-nesting, altricial species contains no reference to meadowlarks; nor does Davis' (1955) list of studies on clutch size of 53 species of birds. Saunders (1932) gave breeding dates, nesting success, and clutch size of Eastern Meadowlarks near Ithaca, New York. Lanyon (1957) reported on nest success and clutch size of both Eastern Meadowlark and Western Meadowlark (*Sturnella neglecta*) near Madison, Wisconsin, and Johnston (1964) noted breeding season and clutch size of both species for Kansas. Sample sizes reflected by these studies ranged from 16 to 62 nests. Data presented by Gross (*in Bent*, 1958) represent largely the contribution of Saunders (1932). In addition to these studies, numerous accounts of a few nests are reported in the literature but the small sample size, lack of certain details, and variation in observational and reporting techniques make them of limited value.

STUDY AREAS AND METHODS

Studies were conducted primarily on the Carbondale Bobwhite Quail Research Area, a 1450-acre tract of privately-owned farms located 6 miles northeast of Carbondale in Jackson and Williamson Counties, Illinois. The topography is gently rolling and soils are of low productivity. Meadowlark nesting habitat is mainly represented by permanent pastures and hayfields which occupy some 27 per cent of the area; approximately 31 per cent of the acreage is planted yearly to corn and soybeans, 10 per cent is woods and 20 per cent is idle or fallow land. One 50.5-acre pasture (40 acres of nesting cover) on the west border of the Research Area, hereafter referred to as Bigler's pasture, served as a focal point for studies during the latter phase of the project. Some nests were also located on University-owned farmland just south and west of the main campus of Southern Illinois University in Jackson County.

Nest searching methods were identical to those employed in finding Bobwhite nests. Walking abreast, at intervals of 4 feet and with the aid of walking sticks, crews of four

to eight men systematically searched all cover. From 1960 to 1963, the entire Carbondale Research Area, excluding woodlots and intertilled cropland, was searched at least twice; in 1964, selected portions of this area were hunted and in 1965, one field on the Research Area (Bigler's pasture) and selected fields on the University property were hunted. In 1966 and 1967 a limited amount of nest hunting was conducted on the University property.

From 1960 to 1963, nest hunting was begun around 20 May and terminated 10 September; in 1964 hunting was conducted during the periods of 10-19 June and 13-25 August. In 1965, fields were searched from 10-19 May and 16-25 June. All fields searched were covered at least twice except during 1965, 1966, and 1967 when portions of the University properties were hunted only once.

When found, each nest was marked; active nests were revisited every 3-4 days until final outcome was established. When nests were no longer active, fate, approximate date of egg laying, number of eggs, plant materials in the nest, degree of overhead cover and concealment, direction of nest entrance and slope, and drainage at the nest site were recorded.

THE NEST

Construction.—Actual nest construction was not witnessed during the study; this activity has been described by Saunders (1932:178-180). He believed that only the female participated in nest building, which normally took from 3 to 5 days, even though numerous earlier workers had credited both sexes. Lanyon (1957) found that earlier nests took from 6 to 8 days to complete but later nests were built in as few as 4 days.

Nests were virtually always in a slight bowl-like depression. This bowl, normally from 1 to 3 inches deep and 4 to 4½ inches in diameter, was apparently scraped out by the bird prior to nest construction but on occasion, deeper natural depressions such as hoofprints of cattle or horses were used. As described in detail by Saunders (1932:180-181), a typical meadowlark nest consists of (1) an inner subspherical shell composed of a shallow bowl of finely woven grass stems on which the eggs are laid and a thin subspherical superstructure of coarser stems placed between the shell and the ground and (2) an outer covering of coarse grass or other material bent over the shell to form a canopy.

Most nests found during our study conformed to the above type, however, there were numerous exceptions. Form and degree of construction seemed at least partially dependent upon time of nesting season and type of cover in the immediate area. Some nests were large structures with thick sides and heavy, complete roofs closely resembling those of the Bobwhite while others lacked both sides and top, consisting only of the inner subspherical shell of fine stems with some coarser plant material beneath it. The most common nest type was intermediate between these extremes; it consisted of a complete subspherical structure, often tilted at a 20° to 30° angle with the back of the nest built up to form a partial canopy. Of 220 used nests, 17.3 per cent lacked a canopy;

44.5 per cent had a partial canopy; and 38.2 per cent had a full canopy. Occasionally, nests were located so as to use the natural canopy provided by lodged grasses.

The time of nesting clearly influenced nest architecture. Of those nests built prior to 26 May, 21.0 per cent lacked a canopy, 53.2 per cent had a partial canopy, and 25.8 per cent had a full canopy. Of those built after 26 May, only 12.1 per cent lacked a roof, 36.4 per cent had a partial roof, and 51.5 per cent had a full canopy. This increase in the construction of elaborate nests possibly reflected seasonal enrichment of the vegetation. Interestingly, Lanyon (1957) found that early nests generally took from 2 to 4 days longer to complete than later nests yet our data showed the former to be generally less elaborate than the latter.

Several writers (Gross *in* Bent, 1958; Saunders, 1932; Lanyon, 1957; and Thoms, 1924) reported nests with obvious trails, and even covered passageways or tunnels, leading to them through the vegetation. The presence of such covered passageways was not observed during our study although in a few instances, rather obvious runways were noted leading to the entrance of the nest.

Building materials.—As noted by Saunders (1932) and circumstantially confirmed during our study, the female tended not to use plants present at the nest site for the inner lining of the nest but almost always brought this material from a considerable distance. On our study areas, the material most commonly used for the inner subspherical shell was the fine-stemmed, grass-like rush *Juncus tenuis*. This plant was seldom found growing at the nest site. Of 853 plant occurrences in 406 nests, grasses and grass-like forms (*Juncus* and fine-stemmed legumes) accounted for 823 or 96.5 per cent (Table 1). In all, 32 individual plant species were identified in 406 nests. *Juncus*, whose use was limited almost exclusively to the inner lining, occurred in 63.3 per cent of the nests. Fine stems of bluegrass or lespedeza were most often used as substitutes for *Juncus* in the nest lining. Meadow fescue at times was found in the canopy but mainly was used in the subspherical superstructure. When fescue was not available, other coarse-stemmed species such as timothy, orchard grass, wheat, and rye were used. Of the nests examined, 81.6 per cent were constructed of more than one species of plant with 56.7 per cent containing two and 21.4 per cent containing three; five different species were the most found in any one nest.

Concealment and drainage.—Nests were rated on the basis of concealment to the human eye, a factor influenced by the amount and type of vegetation in which the nest was situated and to a lesser extent the presence or absence of a nest canopy. Of 377 nests, 19.1 per cent were judged to have excellent concealment. These were difficult to see even when the location was known within

TABLE 1
PLANT MATERIALS USED IN THE CONSTRUCTION OF 406 MEADOWLARK NESTS

Species	Frequency of occurrence	
	Number	Per cent
Rush (<i>Juncus</i> spp., mostly <i>tenuis</i>)	257	63.3
Cheat (<i>Bromus secalinus</i>)	168	41.4
Meadow fescue (<i>Festuca elatior</i>)	95	23.4
Bluegrass (<i>Poa compressa</i> and <i>pratensis</i>)	77	19.0
Common and Korean lespedeza (<i>Lespedeza striata</i> and <i>stipulacea</i>)	46	11.3
Panic grasses (<i>Panicum</i> spp.)	30	7.4
Common tickle grass (<i>Agrostis hyemalis</i>)	27	6.7
Small wild barley (<i>Hordeum pusillum</i>)	24	5.9
Paspalums (<i>Paspalum</i> spp.)	18	4.4
Red clover (<i>Trifolium pratense</i>)	17	4.2
Timothy (<i>Phleum pratense</i>)	15	3.7
Orchard grass (<i>Dactylis glomerata</i>)	14	3.4
Foxtail grasses (<i>Setaria</i> spp.)	10	2.5
Crabgrasses (<i>Digitaria</i> spp.)	9	2.2
Wheat (<i>Triticum aestivum</i>)	8	2.0
Slender fescue (<i>Festuca octoflora</i>)	6	1.5
Corn (<i>Zea mays</i>)	4	1.0
Broomsedge (<i>Andropogon virginicus</i>)	4	1.0
Lance-leaved ragweed (<i>Ambrosia bidentata</i>)	4	1.0
Redtop (<i>Agrostis alba</i>)	4	1.0
Plantains (<i>Plantago</i> spp.)	3	0.7
Low hop-clover (<i>Trifolium procumbens</i>)	3	0.7
Oak (leaves) (<i>Quercus</i> spp.)	2	0.5
Rye (<i>Secale cereale</i>)	2	0.5
Yarrow (<i>Achillea millefolium</i>)	1	0.2
Alsike clover (<i>Trifolium hybridum</i>)	1	0.2
Elm (leaves) (<i>Ulmus</i> sp.)	1	0.2
Sedge (<i>Carex</i> sp.)	1	0.2
Rough buttonweed (<i>Diodia teres</i>)	1	0.2
Dropseed (<i>Sporobolus</i> sp.)	1	0.2

a square yard or so; often, they became visible only after the vegetation was parted directly over them. A rating of good was given to 47.8 per cent of the nests; these were visible from above without intense searching. Ratings of fair and poor were given to 28.9 per cent and 4.2 per cent, respectively; the latter classification applied to nests visible from several yards away. Nice (1964) found a positive correlation between nest success of the Song Sparrow (*Melospiza melodia*) and degree of nest concealment; but, no such relationship was evident from our data.

TABLE 2
ORIENTATION OF MEADOWLARK NESTS IN SOUTH-CENTRAL WISCONSIN
AND SOUTHERN ILLINOIS

Direction Nest Facing	Wisconsin ¹		Illinois ²	
	Number	Per cent	Number	Per cent
North	19	14.5	49	14.0
Northeast	23	17.6	74	21.2
East	36	27.5	48	13.7
Southeast	13	9.9	39	11.1
South	11	8.4	33	9.5
Southwest	5	3.8	39	11.1
West	5	3.8	29	8.3
Northwest	19	14.5	39	11.1
Totals	131	100.0	350	100.0

¹ Calculated from Lanyon (1957, Table 8, p. 42).

² Our study.

When nesting in areas of gently rolling or moderately hilly terrain, meadowlarks showed a definite affinity to slopes as opposed to flat crests or valleys. Of 412 nest sites, drainage was considered excellent for 37.1 per cent and good for 45.2 per cent. These represented nests which would not be expected to flood or wash out except possibly under torrential conditions. Only 12.4 per cent and 5.3 per cent of the nest sites were classified as having fair or poor drainage, respectively. The latter type included nests which could be flooded by surface runoff during moderate to heavy rain showers.

Orientation.—Earlier workers have noted that orientation of meadowlark nests appears to be non-random. In northern Illinois, Sandborn and Goelitz (1915) found eight nests of *S. magna*, all of which had entrances facing south. Saunders (1932), from observations of 29 *S. magna* nests in New York, concluded that orientation might be in any direction but suggested a possible correlation with the location of male song perches. Lanyon (1957:42), reporting on 131 nests of *S. magna* and *S. neglecta* in Wisconsin, found nests to face predominantly to the north and east. He found no relationship with position of the nest within the territory or with location of male song perches but stated: "The effect of the prevailing winds, particularly during rain or sleet storms, is to depress the vegetation toward the north and east, thus encouraging the same orientation in nidification."

As shown in Table 2, Lanyon's (1957) data showed 59.6 per cent of 131 nests faced north, northeast, or east with east the modal direction. In our study, 48.9 per cent of 350 nests faced in one of these three directions with

northeast being the modal direction; a chi square test showed this orientation pattern not to be due to chance ($P < 0.001$). Interestingly, 48.7 per cent of 915 Bobwhite nests located over a 15-year period in the same general area also faced either north, northeast, or east (Klimstra, unpublished data). Seemingly then, the factor or factors responsible for this non-random orientation similarly affect both the Bobwhite and the meadowlark. As in Wisconsin (Lanyon, 1957), nests on our study areas also tended to face away from prevailing winds. Records (unpublished data, Murdale Airport, Carbondale) from 1954 through 1963 indicated that during the period of 1 April through 21 July, winds blew toward the north and north-northeast 33 per cent of the time and field observations confirmed that vegetation, especially grasses, tended to be lodged in those directions.

Nest orientation also seemed related to the direction of slope upon which the nest was located. Hann (1937) noted that 31 of 36 (86 per cent) Ovenbird (*Seiurus aurocapillus*) nests faced down the slope at some angle although he found no affinity for any one particular direction. In our study, 47.6 per cent of the nests faced down slope at some angle while only 29.8 per cent faced up the slope ($P < 0.001$). This tendency to face nests down slopes does not entirely explain the non-random orientation as 44.7 per cent of those nests built on slopes other than north, northeast, or east faced in one of these three directions ($P < 0.05$).

Unused nests.—Saunders (1932) observed that females commonly began and worked on several nests before one site was completed. In our study, 126 of 388 (32.5 per cent) nests were thought not to have been used. Some of these were only partially built but others were indistinguishable from active nests with respect to construction. Regarding degree of construction, 32.0 per cent of the unused nests had no canopy and only 18.0 per cent had full canopies as compared to 17.3 per cent and 38.2 per cent, respectively, for used nests.

Saunders (1932) believed that the partial building of several nests occurs just prior to the female attaining the sexual and physiological stage necessary for intensive nest building. Our data tend to support this in that unused nests were much more common during early stages of the breeding season. While in most instances it was impossible to determine the date of commencement of these unused nests, for those in which dating was possible, virtually all were begun before 12 May.

THE BREEDING SEASON

The beginning and duration of a species' nesting season are important to overall reproductive performance. They determine the climatic conditions, or range of conditions, the young must cope with, and whether sufficient time is

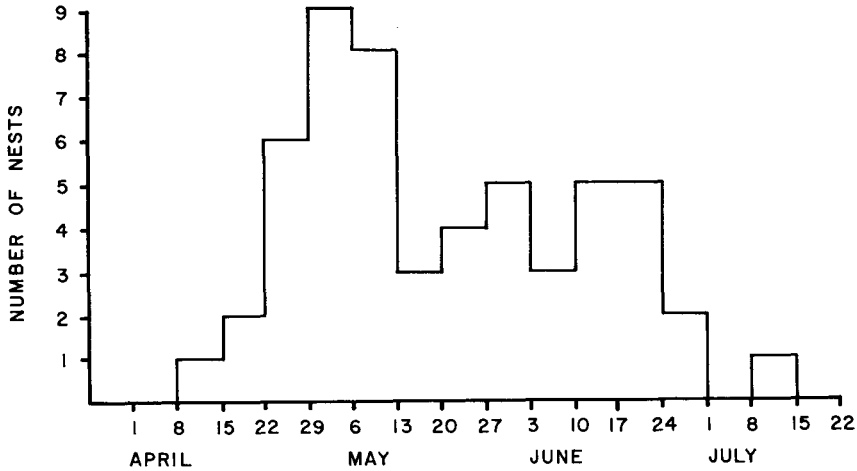


FIG. 1. Initial egg laying dates for 54 Eastern Meadowlark nests, 1965.

available to the adults for raising more than one brood or renesting after nest failure.

Our study did not attempt to correlate beginning of nesting with environmental factors, and, as the start of nest hunting efforts was not uniform from year to year, we were unable to determine whether yearly variations in nesting time occurred. It has been established that meadowlarks breed later in the northern parts of their range (Saunders, 1932; Gross *in Bent*, 1958; Lanyon, 1957; Johnston, 1964). At approximately 38° latitude (southern Illinois, Kansas, Virginia), meadowlarks apparently begin laying around 10–15 April, end around 15–22 July, with peak activity from 29 April–5 May. At 42–43° latitude (Massachusetts, New York, Wisconsin) earliest laying is from about 23 April–5 May, latest from 4–15 July, with heaviest laying around 13 May.

Our study provided estimated dates of initial egg laying for 129 nests. Dates were calculated by backdating from the particular event (laying, incubating, brooding) in progress when the nest was discovered. Unfortunately, nest searching efforts during the first four years of the study were begun in late May or early June; consequently, many of the nests found were too old to permit estimation of egg-laying dates. Those nests which were dated (75) during these years cannot be used to analyze the entire nesting season as they mostly represent mid- to late-season efforts. In 1965, nest searching was begun in early May, and the 54 nests dated during that year were representative of the entire breeding season. The earliest recorded date of egg laying was 14 April with most eggs being laid during the period of 22 April to 12 May, the

modal period being from 29 April to 5 May (Fig. 1). Dates of initial egg laying recorded during 1960–1964, while not reflecting early nesting, can be combined with those from 1965 to analyze the latter portions of the breeding season. It is apparent that on our study areas, meadowlark nesting is virtually completed by 7 July as only 3 (2.3 per cent) of 129 nests were begun after this date. The latest recorded nest was begun on 23 July and hatched on 8 August 1962.

No obvious peak for second brood nests is evident (Fig. 1), yet we suspect that most second brood nests were not begun until the middle of May or later. Theoretically, if second brood nests were begun shortly after fledging of the first brood, a second nesting peak should have been evident about 30 days after the first peak. However, as over $\frac{2}{3}$ of all nests failed at varying times after their commencement, renesting following these failures would tend to be staggered in time, thus smoothing out the nesting curve by overlapping and obscuring second brood nesting peaks.

NESTING IN RELATION TO LAND-USE TYPES

All land-use types on the Carbondale Research Area except intertilled cropland and woods were searched for nests from 1960 through 1963; only selected fields were hunted during 1964–1967. Acreage figures used in the calculation of nest densities per land-use type (Table 3) were obtained by multiplying the acreage of each tract by the number of years it was searched. Data from random, non-systematic hunting, i.e. coverage not designed to find all nests in a particular area, were not included in these calculations. A total of 435 nest locations were recorded, however, only 307 nests that contained eggs will be considered here; there appeared to be no major differences in proportions of unused nests among the various types of nesting cover.

Saunders (1932) noted that while grasslands and pastures support larger meadowlark populations than other habitats, the birds commonly nest in a wide variety of cover-types. Data from our study indicates that the preferred nesting habitat is pasture, followed in order by hayfields, soilbank fields, winter wheat fields, idle, and fallow areas (Table 3). In all these areas, however, the presence of dead grass stems at ground level and the absence of woody vegetation or numerous shrubs in the immediate vicinity appeared to be a prerequisite for nesting utilization. Height of cover at 204 nest sites ranged from 2 to 30 inches and averaged 14.9; 66.6 per cent of all nests were built in cover 10 to 20 inches high. The fact that nests are sometimes built in rather deep bowls or natural depressions often permitted utilization of areas with little cover; one nest was found in the mowed fairway of a golf course.

Pastures.—Condition and composition of pastureland on the study area

TABLE 3
MEADOWLARK NEST DENSITY IN RELATION TO LAND-USE TYPES

Land-use type	Acreage searched for nests	Nests found ¹	Nests per 100 acres
Pasture			
grazed	879	120	13.7
ungrazed ²	80	80	100.0
Total	959	200	20.9
Hayfield			
alfalfa	120	5	4.2
red clover	222	35	15.8
mixed grasses ³	62	11	17.7
Total	404	51	12.6
Soilbank (grasses)	487	25	5.1
Winter wheat ⁴	83	4	4.8
Idle	558	21	3.8
Fallow	298	6	2.0
Totals	2,789	307	11.0

¹ Used nests only.

² First and second year subsequent to removal of cattle.

³ Predominantly meadow fescue, orchard grass, timothy, bluegrass, and cheat.

⁴ Two built prior to cutting of wheat, two built in wheat stubble.

varied greatly. There was opportunity to compare utilization among lightly grazed to severely overgrazed pastures and one field left ungrazed for 2 years. Also compared were pastures receiving similar grazing pressure but composed of entirely different floral communities.

In all, 200 nests were found on 959 acres of pasture (20.9 nests per 100 acres). This, the heaviest utilization of any land-use type, mainly reflected the extremely high number of nests (80) found on one 40-acre pasture during 2 years that it was ungrazed. Nesting utilization of grazed pastures (13.7 per 100 acres) was only slightly greater than hayfields (Table 3).

We found an inverse relationship between intensity of grazing and utilization by nesting meadowlarks. An example is offered by one 40-acre field containing approximately 60 per cent meadow fescue, 35 per cent Korean lespe-deza, 5 per cent orchard grass, and no herbs and shrubs. During 1961, 1962, and 1963, the heavy grazing of this field by cattle maintained the vegetation at a height of about 1 to 3 inches and left only a few scattered clumps of fescue 12 or more inches in height. During these years, three, two, and three nests with eggs, respectively, were found. In 1964, grazing was less intense, resulting in a more abundant and uniform distribution of fescue clumps

and leaving patches of Korean lespedeza up to 5 inches in height. Eleven nests with eggs (19 including unused nests) were found that year, nearly all of which had been built in patches of lespedeza or at the base of isolated clumps of fescue. The most striking example of the effects of grazing on nest establishment was evident in Bigler's pasture. Herbaceous vegetation in this field consisted mainly of meadow fescue, cheat, lance-leaved ragweed, Korean and common lespedezas, and panic grasses; many other species were also represented. During 1960, the field was heavily grazed and three nests were found; in 1961 it was severely overgrazed and no nests were found. In 1962, grazing was heavy but less than the previous years and 13 nests were built in the field. In the spring of 1963, the pasture was renovated, manure spread, and Kentucky bluegrass seeded on about $\frac{2}{3}$ of the field and meadow fescue on $\frac{1}{3}$; 12 nests were found that season. In 1964 and 1965, the field was not grazed and exhibited large areas of dead and lodged stems of bluegrass and vigorous stands of fescue. During these years, 41 and 39 nests with eggs, respectively, were found. Considering both used and unused nests, this field yielded a total of 129 nests in 2 years, a far higher density than was recorded on any other plot during the entire study.

Hayfields.—As shown in Table 3, hayfields ranked second to pastures as favored nesting sites with an average density of 12.6 nests per 100 acres. Alfalfa (*Medicago sativa*) fields were least preferred (4.2 per 100 acres); red clover fields yielded 15.8 nests per 100 acres. Nesting was heaviest in a mixed-grass hayfield (mainly orchard grass, meadow fescue, timothy, bluegrass, and cheat) which averaged 17.7 nests per 100 acres over a 2-year period.

Alfalfa fields, especially good stands, seemingly lacked sufficient grassy cover at ground level to provide acceptable nesting habitat. This was also apparent in most red clover fields, but portions of these fields were sparse enough to allow the invasion of grasses thus providing some nesting cover. Red clover appeared in 17 nests (Table 1); it was, however, always used in conjunction with other, more finely-stemmed species. Alfalfa stems were not found in any nest.

Soilbank and wheat fields.—In 1959, five fields on the Research Area totalling 155 acres were placed in the Federal Soil Bank Program; this acreage was reduced to 135 by 1961. Under provisions of this program, fields were taken out of cultivation and seeded to grasses; mowing was permitted but fields could not be pastured or used for hay. Meadowlark utilization of these areas was not great; overall density averaged 5.1 nests per 100 acres. Once established, four of the plots displayed dense, uniform stands of meadow fescue with some orchard grass and Korean lespedeza; few nesting birds used them. The remaining field, 33 acres of gently sloping land, apparently re-

ceived a poor initial seeding and remained rather weedy throughout the period of study. During the last 2 years fescue, while retaining good stands in the lower moist areas, virtually disappeared from the dryer slopes and ridges and was replaced by a variety of invading species, especially common lespedeza, panic grasses, and rough buttonweed. During these two years, this field comprised only 13.5 per cent of the total soilbank acreage searched but yielded 40.0 per cent of the nests found.

Wheat fields, showing a density of 4.8 nests per 100 acres, seemingly did not provide good nesting habitat; this probably reflected a general lack of grasses and fine-stemmed legumes necessary for nest construction. Two of four nests in wheat were built after fields had been harvested.

Idle and fallow areas.—Although 558 acres of idle and 298 acres of fallow land (uncultivated for 1 or 2 years) were searched during the study, only 27 used nests were discovered in these habitats (Table 3). This represents a nest density of 3.8 and 2.0 per 100 acres, respectively, the lowest encountered in all types of cover.

Fallow fields were thought to be little used because of an absence of sufficient grassy cover. In this region, most areas left uncultivated are initially invaded by such species as common and Korean lespedeza, plantains (*Plantago* spp.), wild lettuce (*Lactuca* spp.), lance-leaved ragweed, cocklebur (*Xanthium* spp.), and foxtails (*Setaria* spp.). Cheat, panic grasses, and crabgrass are early invading grasses, but the amount of dead stems suitable for good nesting material is generally lacking during the year or two subsequent to fallowing.

Most idle areas searched were at least 6 years or older and were characterized by numerous woody shrubs, small trees, and patches of briar (*Rubus* spp.), intermixed with a variety of herbaceous plants and such grasses as cheat, broomsedge, and bluegrass. In many instances, the ground cover with growing grasses and dead and lodged stems looked ideal for nesting cover; however, the presence of numerous herbs and small woody species apparently precluded extensive use by meadowlarks. Those areas which received moderate use were recently idle fields which contained little or no woody cover, yet provided a better ground cover of grasses than did fallowed areas.

CLUTCH-SIZE

As pointed out by Davis (1955), published clutch-size data usually refer to the number of eggs found in nests presumed to contain complete clutches. In practice, the investigator can rarely be certain that the eggs present represent a complete clutch, i.e. the number of eggs laid in an uninterrupted series. In our study, egg counts of presumably complete clutches were available from 101 nests. Included in this sample were nests discovered while eggs were be-

TABLE 4
SEASONAL VARIATION IN THE CLUTCH-SIZE OF MEADOWLARKS

Date first egg laid	Number of eggs					Mean	Standard Deviation
	2	3	4	5	6		
14 April-5 May	0	1	1	6	1	4.78	0.79
6 May-2 June	0	5	11	18	0	4.38	0.74
3 June-30 June	2	12	26	13	0	3.94	0.80
1 July-23 July	0	3	0	2	0	3.80	0.98
Totals	2	21	38	39	1	4.16	0.83

ing deposited and subsequently observed to be incubated, and nests discovered during incubation. Conceivably, this latter group could have included some nests from which one or more eggs had been removed prior to incubation; however, observations from this study and those from a study of over 1,000 Bobwhite nests (Klimstra, unpublished data) clearly suggest that in virtually all instances of nest disturbance by predators, enough eggs (usually all) are affected to make the disturbance easily detectable. Nests found subsequent to destruction or abandonment were excluded from clutch-size calculations, as were nests containing young because of the possibility that unhatched eggs had been removed from the nest by parent birds.

The mean number of eggs found in 101 complete clutches was 4.16 ± 0.08 . Clutches varied from two to six (Table 4). As explained previously, our sample contained a disproportionately large number of mid- and late-season nests, and, as shown in Table 4, clutch-size tended to decrease as the nesting season progressed. Thus, it seems justified to assume that the mean clutch-size derived may be somewhat low. During 1965, approximately 60 per cent of all nests were started prior to 27 May and 40 per cent after that date; data from all years showed a mean clutch-size of 4.36 for the earlier period and 4.03 for the latter. Using these figures, a prorated mean clutch-size of 4.23 is obtained.

The average number of eggs per nests in our study proved considerably lower than previously reported for the Eastern Meadowlark. Lanyon (1957), from 38 nests in Wisconsin, reported a mean clutch-size of 4.81 ± 0.16 with a range of 2-6. From Saunders' (1932:197) New York data, a mean clutch-size of 4.57 ± 0.15 was calculated for 23 nests. Gross (*in Bent*, 1958) stated that Eastern Meadowlark clutches vary from 3 to 7 with sets of 5 most common and sets of 4 more usual in second brood nests. He also noted that clutches tended to be smaller in the southern part of the nesting range while Saunders (1932) found that clutches in central Oklahoma averaged smaller

than those from New York. Our data, indicating smaller clutches than those reported from Wisconsin and New York, would seem to support this. Johnston (1964), however, found a mean of 5.2 eggs (range 4–7) for 26 nests in Kansas which is approximately the same latitude as southern Illinois.

Davis (1955) cited numerous studies demonstrating that clutch-size in most species of birds decreases as the nesting season progresses; renesting apparently produces fewer eggs than initial nesting. Such seasonal decline in size of meadowlark clutches has been noted also by Johnston (1964), Saunders (1932), Gross (*in Bent*, 1958), and Lanyon (1957). The latter author found a seasonal decline in the size of Western Meadowlark clutches but data for the eastern species from the same area failed to demonstrate this. We were unable to differentiate among first and second brood nests and renesting efforts, but our data (Table 4) clearly show a seasonal decline in the number of eggs laid. Average clutch sizes recorded for the periods 14 April–5 May, 6 May–2 June, 3 June–30 June, and 1 July–23 July were 4.78, 4.38, 3.94, and 3.80, respectively.

Size of eggs.—According to Bendire (1895), 201 Eastern Meadowlark eggs in the United States National Museum averaged 27.75 mm by 20.35 mm. The largest egg was 30.78 by 22.61 mm while the smallest was 21.59 by 18.29 mm. Reed (1965) stated that egg size for this species was 27.94 by 20.32 mm but gave no range or sample size. From our study areas, mean length of 17 eggs from 9 nests was 27.97 ± 0.44 mm (range 23.54–30.62) and mean width was 20.69 ± 0.29 mm (range 18.40–23.76).

NESTING SUCCESS AND LOSSES

Determination of nest fate.—Lack (1954) believed the problems of accurately estimating nesting success have not always been appreciated. Mayfield (1960 and 1961) contended that the sampling procedure used in some past nesting studies resulted in overestimating the percentage of successful nests and eggs. Nolan (1963:306) summarized Mayfield's argument:

“Briefly, the error consisted of calculating success from the fates of all nests found while still in use, regardless of the fact that, in many, development had already advanced into the incubation or nestling stages when the nests were discovered. Nests that had failed before they were found were usually disregarded. Such calculations thus overlooked both the success already attained by some nests (and the commensurately reduced risks ahead) and the losses already incurred by other nests. This kind of sampling . . . tended toward bias by selecting nests already partly successful and then measuring success during that subsequent fraction of their histories in which they were under scrutiny by the investigator. . . .

“To avoid this error, a study of observed nest success could be based on nests found at or before the moment the first egg is laid. (Alternatively, it would be theoretically possible for the observer to rely on nests found at any stage of development either if his

coverage of his study area were efficient enough to lead to the discovery of all nests while they were still in use by the birds, or if he could find, recognize, and include in his computations nests that had already failed.)”

Our calculations of nesting success are based upon the assumption that Nolan's second contingency was satisfied, that is, all nests, regardless of whether active or terminated, were found (or had equal chance of being found) and recognized.

Determination of the fate of nests no longer in use did present certain problems. It is extremely unlikely that an investigator can actually witness the culmination of the nesting process, even if the nest is kept under observation throughout the active period. Thus, determination of fate must be based generally upon evidence at the nest site. The accuracy of this is contingent not only upon the quality and quantity of the evidence but also upon the investigator's ability to correctly interpret it. Experience gained from the study of hundreds of Bobwhite nests greatly increased our ability to read “sign” at the nest site. However, because hatched meadowlark nests contain no egg fragments and because the eggs are much more fragile (apparently because they lack a strong shell membrane), the evidence at meadowlark nest sites was generally less and of poorer quality than at Bobwhite nests. Careful examination of nests known to have contained young which had fledged provided an index to the usual appearance of nests at this stage. While young are in the nest, emergence of the primary wing feathers produces an abundance of flaky, whitish material (feather sheaths) which collects in the bottom of the nest, ultimately sifting down through the lining to the bottom of the nest bowl. This was the primary criterion used to determine if a nest had contained young. Also, the interiors of nests that had contained young were generally enlarged. It is possible that predation on young could have gone undetected if the young were removed either prior or subsequent to emergence of their primaries; however, evidence from several nests indicated that removal of young by predators left signs that could be interpreted.

Nests found without eggs or fragments and showing no sign of the presence of young or previous use were classified as unused. It is possible that some nests in which eggs were removed by snakes were erroneously placed in this category; however, nest interiors in which females had laid and incubated eggs were thought distinguishable in most cases from those which had never been used. Determination of specific predators was difficult because meadowlark eggs are extremely fragile and tend to break into tiny fragments once destroyed. While making identification of specific predators difficult, this virtually assured that some egg fragments would remain in a nest destroyed by a carnivore. Nests considered destroyed by predators could, of course, have

TABLE 5
PRODUCTIVITY OF MEADOWLARK NESTING ON STUDY AREAS, SOUTHERN ILLINOIS

	Bigler's pasture	All other areas	Total
Total nests found	170	280	450
Nests of unknown fate	13	49	62
Unused nests	60	66	126
Active nests of known fate	97	165	262
Per cent hatched	23.7 (23)	45.5 (75)	37.4 (98)
Per cent fledged	17.5 (17)	38.2 (63)	30.5 (80)
Total eggs examined 577			
Per cent hatched 42.1 (243)			
Per cent fledged 33.8 (195)			

already been abandoned before destruction; but, as will be shown later, this probably occurred very infrequently.

Of 450 meadowlark nests found, the fate of 62 could not be determined and 126 were unused; these were not included in computations of productivity. Analysis of nesting success, then, was based upon observations of 262 nests of known fate. The fate of individual eggs and nestlings were based upon observations of only a portion (170) of all nests; these represented nests in which the number of eggs laid, and their ultimate fate were known with reasonable certainty.

Success of nests, eggs, and young.—Of 262 active nests, the eggs of 98 (37.4 per cent) hatched and the young of 80 (30.5 per cent) fledged (Table 5); a "hatched nest," as used here, refers to one in which at least one egg hatched and a "fledged nest" is one from which at least one nestling successfully left the nest. Hatching and fledging success of 577 eggs was 42.1 per cent and 33.8 per cent, respectively. These data indicate a somewhat lower success than previously recorded for meadowlarks and other open-nesting, altricial species. Lanyon (1957) reported a total fledging success of 34.4 per cent for 60 *S. magna* and 62 *S. neglecta* nests in Wisconsin. In a review of 35 studies of open-nesting, altricial birds (not including meadowlarks), Nice (1957) found an overall fledging success of 49.3 per cent for 7,788 nests; hatching success of 21,040 eggs was 59.8 per cent while fledging success of 21,951 eggs was 45.9 per cent.

Overall productivity (Table 5) was lowered considerably by the extremely high losses incurred on one field of the study area (Bigler's pasture). Here, only 17.5 per cent of 97 nests fledged young as compared to 38.2 per cent of

165 nests on all other portions of the study areas. Factors thought responsible for this differential success will be discussed later.

A comparison of success of nests found before and after termination is of interest in light of Mayfield's comments previously cited (Nolan, 1963:306). This comparison is useful also in determining the possible effects of human visitations to the nest. The percentages of abandoned and preyed upon nests were 2.2 per cent and 3.4 per cent lower, respectively, in nests found while active as compared to those found after termination; this strongly suggests that careful visitations to the nest did not increase the incidence of abandonment or predation. On the other hand, fledging success was 21.3 per cent higher in nests found while active. This seems mainly to reflect the fact that hayfields were hunted after mowing, thus that portion of the nest sample found after termination includes almost all the nests destroyed by mowing.

Comparative losses of nests, eggs, and young.—Nesting efforts of birds are usually described in terms of percentage of successful nests, percentage of successful eggs, or both. Nolan (1963) noted that when only nest success is calculated, a nest which hatched only one egg received the same credit as a nest in which the entire clutch hatched. He felt that while this test was a fair indicator of predation, which normally results in all eggs being lost, it gave no measure of partial failure due to infertile eggs or embryonic mortality. Kalmbach (1939:592) stated: "Estimations on the basis of eggs hatched will regularly tend to disclose a lower degree of success than that based on so-called successful nests." Nice (1957) found that for 18 studies she reviewed, the percentage of eggs which produced fledgling young was lower than the percentage of nests which produced at least one fledgling young; but, she noted that egg success could be higher if many nests containing incomplete clutches were deserted (or destroyed) and if all eggs hatched in most successful nests.

Our findings, contrary to the above, revealed that the percentage of successful eggs was higher than nests. This mainly reflected the low number of unhatched eggs in successful nests and the large number of incomplete clutches destroyed by predators.

Our data showed a significantly higher survival rate among nestlings than eggs; 42.1 per cent of all eggs laid were hatched while 80.3 per cent of all young hatched were fledged. Apparently, this is the normal situation in open-nesting, altricial birds; examination of 26 studies (Nice, 1957:306–307) showed survival to be higher among young than eggs in 20 cases, lower in 5, and the same in 1. Using 18.5 days as the average length of time eggs occupy the nest (including laying) and 11.5 days as the average period young are in the nest, total losses of eggs averaged 3.1 per cent per day while losses of young aver-

TABLE 6
CAUSES OF NEST, EGG, AND NESTLING LOSSES FOR MEADOWLARKS, SOUTHERN ILLINOIS

Factor	Nests			Eggs ¹			Young ¹		
	No.	Per cent of lost nests	Per cent of all nests	No.	Per cent of lost eggs	Per cent of all eggs	No.	Per cent of lost young	Per cent of all young
Human disturbance	3	1.7	1.1	6	1.8	1.0	0	0.0	0.0
Abandoned	11	6.0	4.2	13	3.9	2.3	0	0.0	0.0
Destroyed by									
livestock	2	1.1	0.8	4	1.2	0.7	0	0.0	0.0
Destroyed by mowing	32	17.6	12.2	64	19.1	11.1	0	0.0	0.0
Predation	134 ²	73.6	51.2	226	67.7	39.2	46	95.8	18.9
Infertile eggs	—	—	—	7	2.1	1.2	—	—	—
Embryo mortality	—	—	—	4	1.2	0.7	—	—	—
Disappeared ³	—	—	—	10	3.0	1.7	2	4.2	0.8
Totals	182	100.0	69.5	334	100.0	57.9	48	100.0	19.7

¹ Based on observation of 170 nests.

² Eighteen of these were destroyed after hatching but prior to fledging.

³ No obvious sign of disturbance and nest not completely emptied.

aged 1.7 per cent per day. These average daily losses are not comparable to Nice's figures (1964) for the Song Sparrow, for she calculated the percentage of young lost by dividing the number lost by the number of eggs laid instead of dividing (as we did) the former number by the number of eggs hatched.

Several reasons for the higher survival of nestlings on our study areas are readily apparent. Infertility and embryonic mortality naturally affect only eggs, and desertion by the female occurs much more frequently (if not exclusively) before the eggs have hatched. Losses to mowing were rather high among eggs but did not affect young, although this must surely have been a matter of chance and timing as nests in all stages would be equally susceptible to this type of destruction. Losses to predators were more equal among eggs (2.1 per cent per day) and young (1.6 per cent per day) but still 1.3 times greater for the former if the relative time each was exposed to this hazard is taken into account. It is possible that nests containing eggs are more readily found by predators (eggs are somewhat more easily seen by humans than are the young), but we have no data to substantiate this. Rather, it is probable that those nests which are most vulnerable to predation (poorly concealed or located near hunting trails) would be found and destroyed sometime during the first 18 or so days before the eggs have hatched. Conversely, if nests survive this period without being preyed upon, it probably reflects optimum cover and concealment, hence a greater likelihood of remaining undetected throughout the remainder of their use.

Causes of Nest Failures

Abandonment.—Of 262 nests with eggs, 14 were abandoned by the female; a total representing 5.3 per cent of all nests and 7.7 per cent of all nest failures (Table 6). Saunders (1932) found that, occasionally, females deserted their nestlings; this was not observed in our study as all desertions occurred before the eggs hatched. Three nests were abandoned after having been slightly damaged by research workers; to our knowledge no other desertions were caused by human interference. Incubating females readily flushed from the nest upon approach but usually flew only a few feet off the ground and alighted within 20–30 yards of the nest. Some females were flushed as many as four times during the nesting cycle without causing desertion. At one extremely open nest site (in a mowed field) the senior author observed a female flush off the nest, fly a short distance, then land and run along the ground using the broken wing ruse. Almost immediately a male, which had been perched in a small shrub about 12 yards from the nest, alighted and began running from the nest at a 30° angle from the retreating female's path. He did not feign injury but moved slowly and stayed just ahead of the observer.

In addition to the three nest abandonments caused by human interference, 11 instances of abandonment from other causes were recorded during the study; at least two and possibly more of these were evidently due to parasitism by the Brown-headed Cowbird (*Molothrus ater*). Two nests each containing two eggs thought to be those of the cowbird were found; in one, a meadowlark egg was lying undamaged just outside the nest entrance. None of these cowbird eggs hatched, having apparently not been incubated. Of the remaining nine abandoned nests, four had single eggs lying just outside the nest, three contained a single egg in the nest, one had two eggs in the nest, and one had three eggs in the nest and one outside the entrance.

Friedmann (1963) and Gross (*in Bent*, 1958) believed the Eastern Meadowlark to be an uncommon host of the Brown-headed Cowbird. Saunders (1932) in a study of over 50 nests from New York and Oklahoma found no evidence of cowbird parasitism and Terrill (1961) reported only 1 of 52 nests parasitized in southern Quebec. Other workers, however, have noted more extensive use of meadowlark nests by cowbirds. In Wisconsin, Lanyon (1957) found cowbird eggs in 9 of 41 (22 per cent) *S. neglecta* nests and 6 of 38 (16 per cent) *S. magna* nests. In Nebraska, Hergenrader (1962) reported 5 of 31 (16 per cent) *S. magna* nests parasitized. Eifrig (1915 and 1919) wrote that he "repeatedly" found meadowlark nests containing cowbird eggs in the Chicago region.

Bobwhite eggs have also been found in meadowlark nests (Lackey, 1913); however, this apparently is uncommon and does not constitute nest parasitism

(Gross *in Bent*, 1958). On 29 May 1967, a female meadowlark was flushed from a nest containing five meadowlark and three quail eggs. On 6 June, the nest contained one newly hatched meadowlark along with the remaining undisturbed eggs; on 7 June, two meadowlarks had hatched with the quail eggs still present. The nest was revisited on 13 June and while it showed no sign of damage, all young and eggs were gone; they were believed removed by a snake.

Mowing and livestock.—Gross (*in Bent*, 1958:75) wrote: “. . . it is probably safe to state that more meadowlarks [nests] are destroyed by this means [mowing] . . . than by any other.” Losses inflicted by mowing operations during our study were relatively high but did not constitute the major source of nest destruction. Thirty-two nests were destroyed in this manner, a total representing 12.2 per cent of all nests and 17.6 per cent of all nest losses (Table 6). Twenty-two of these resulted from hay cutting, 7 from pasture mowing, 1 from wheat combining, and 2 from miscellaneous mowing. Only one female was killed at the nest by a mower. Probably the tendency of birds to readily flush upon approach accounts for this low figure.

Although 120 nests were located in areas grazed by livestock, only 2 were destroyed by trampling. During a 3-year period, Lanyon (1957) found 122 nests on 100 acres of permanent pasture on which 40–50 head of cattle grazed. He reported a loss due to cattle of 15 nests or 12.3 per cent of all nests and 18.8 per cent of all nest losses.

Predation.—Losses attributed to predation during our study amounted to 51.2 per cent of the nests (73.6 per cent of nest failures) and 47.1 per cent of the eggs and young (67.7 per cent of all egg losses and 95.8 per cent of all nestling losses). This is somewhat higher than the relative and total predation reported by Lanyon (1957) in Wisconsin; he found that 36.1 per cent of all nests were preyed upon and 55.0 per cent of all nest losses were due to predation.

Because they are always located at ground level, meadowlark nests are subject to predation by a variety of animals. Gross (*in Bent*, 1958) thought that domestic dogs and cats were especially destructive to nests located in fields adjacent to farm houses. Lanyon (1957) attributed most of the predation observed on his Wisconsin study area to the red fox (*Vulpes vulpes*) and domestic dog and cat, with skunks (*Mephitis mephitis*), thirteen-lined ground squirrels (*Citellus tridecemlineatus*), and garter snakes (*Thamnophis sirtalis*) also contributing. Saunders (1932) felt that the house cat was the most serious predator although weasels (*Mustela erminea*), skunks, and dogs also preyed upon nests. He suspected meadow mice (*Microtus pennsylvanicus*) and Common Crows (*Corvus brachyrhynchos*) as occasional destroyers of eggs.

The difficulty of assigning responsibility of individual nest destruction to specific predators has already been discussed. Of the 134 instances of predation on our study area, the precise predator involved was unknown in 100 cases. Of the remaining 34, 13 were attributed to snakes, 9 to house cats, 6 to skunks, 5 to foxes or dogs, and 1 to an avian predator. These data are misleading, however, for they imply that snakes were the most serious predators, when in fact, most of the 100 unknowns were mammals of one species or another.

As previously noted, the survival rate of nests and eggs was quite low on Bigler's pasture. Here, losses to predators amounted to 72.2 per cent of all nests and 87.5 per cent of all nest failures, as compared to 38.8 per cent and 62.7 per cent, respectively, for the remainder of the area. Similarly, nesting Bobwhite also suffered unusually heavy losses in this field during the same period (Klimstra, unpublished data). From 1954 through 1965, Bobwhite nest losses to predation amounted to 35.2 per cent on all areas other than Bigler's pasture. From 1954 through 1963, on Bigler's, Bobwhite suffered a 41.8 per cent loss to predators, but during the 2 years (1964 and 1965) when the field was not grazed and meadowlark nest density was highest, predators destroyed 24 of 29 quail nests (82.8 per cent) located in the field.

No detailed surveys were made of the kinds and numbers of predators present in this area. Nevertheless, routine observations in the course of nest hunting activities clearly indicated that this particular field served as hunting territory for an unusually large number of carnivores, especially during 1964 and 1965. Ten houses were located within $\frac{1}{4}$ mile of the field; five within 100 yards. At least six dogs were known to roam the field; house cats, while seen much less frequently, also hunted the area. While not thought overly abundant, red foxes, and possibly some gray foxes (*Urocyon cinereoargenteus*), were also present as evidenced by scat and sign. A 3.8-acre pond in the center of the field also attracted raccoons (*Procyon lotor*) and opossums (*Didelphis marsupialis*). Snakes were quite common; blue racers (*Coluber constrictor*) and prairie kingsnakes (*Lampropeltis caligaster*) were noted with regularity during the nest hunts. By far the most common carnivore, however, seemed to be the striped skunk. Numerous dens were located in and around a 4-acre woodlot near the center of the field while diggings and trails were numerous throughout the area. Frequently, skunks were seen in the field in daylight; as many as three different animals were observed in one morning.

In addition to predators, there appeared to be an extremely high population of prairie voles (*Microtus ochrogaster*). Runways and grass nests seemed uniformly abundant throughout the field and numerous voles were seen as we searched the ground for nests. It is our contention that instead of acting as

buffers, these rodents actually attracted predators to the area and held them for longer periods of time by making their hunting efforts more profitable. Because the finding of stationary and concealed nests is more or less a matter of chance, the percentage of these nests found must invariably increase in direct proportion to the number of "predator-hours" spent in the field. Stoddard (1931) also felt that high populations of rodents (cotton rats, *Sigmodon hispidus*) attracted predators which, once in the area, found and destroyed quail nests.

Infertile eggs and embryonic mortality.—Data concerning unhatched eggs in successful clutches were obtained from 63 nests which were under observation before and after hatching. Of 264 eggs in these nests, 7 (2.7 per cent) failed to hatch because of infertility, 4 (1.5 per cent) because of embryonic mortality, and 10 unaccountably disappeared (possibly removed by the female). Thus, total loss from non-hatched eggs amounted to 8.0 per cent. Saunders (1932), who suspected that the production of infertile eggs might be related to old age and highly nervous temperament of the laying female, found 14 (16.5 per cent) of 85 eggs observed to be infertile. The much higher percentage of infertile eggs in his study as compared to ours cannot at present be explained.

Factors Affecting Nest Success and Losses

Degree of nest construction.—Thinly- or non-roofed nests (61.8 per cent), in which the eggs were in some measure visible from above, suffered a 57.4 per cent loss to predation and were 33.1 per cent successful as compared to a 51.2 per cent loss and 38.1 per cent success for fully roofed nests. While not statistically significant ($P = 0.30$), these data at least suggest the possibility of greater risk of predation when eggs are visible from above. A further breakdown of these data show losses from predation to have been 60.5 per cent for open nests, 56.1 per cent for partially roofed nests, and 51.2 per cent for fully roofed nests.

Collias (1964) believed that the roofed nest, which probably evolved from a type that was open above, not only made predation less likely but also afforded cooler temperatures and protection from rain. Our data relevant to protection from heat and rain are too few to warrant discussion. However, the history of one open nest suggests the hardiness of eggs and young. Five birds successfully fledged from this unroofed nest which was located in vegetation less than 6 inches high. During the period when eggs were being laid and incubated, three daily rainfalls of 1.00, 0.58, and 0.11 inches were recorded; maximum air temperatures were 95°F or above on 6 days with a high of 97°. In the 12 days during which the young occupied the nest, three rainfalls

amounted to 1.38, 0.13, and 1.17 inches; temperatures were 90° or above on 6 days with a high of 96° recorded on 2 days.

Time of season.—Lanyon (1957), working with *S. magna* and *S. neglecta* in Wisconsin, reported a nesting success of 25.6 per cent for 86 nests of both species built during May and June and a 55.5 per cent success for 36 nests built during July and August. He suggested that higher nesting success during the latter part of the breeding season possibly reflected an increase in protective cover.

Data from our study also suggested an increase in nesting success as the season progressed. For comparative purposes, the season was divided into three parts: 14 April–26 May, 27 May–16 June, and 17 June–23 July. The per cent success of nests beginning in the above respective periods were 34.2, 37.9, and 55.6, while the percentages of nests destroyed by predators were 47.4, 43.9, and 27.8. Chi square in an $r \times 2$ contingency table was used to test whether the ratios of successful to preyed upon nests varied with the time of season. The value obtained (4.35) approached significance at the 10 per cent level. Nest losses attributable to causes other than predation (abandonment, mowing, etc.) remained fairly constant throughout the three periods at 18.4, 18.2, and 16.6 per cent, respectively.

Nolan (1963), analyzing the nesting success of 11 species of passeriformes, found that nest success increased significantly as the season progressed. He dismissed weather and nest abandonment as causes and stated: “. . . the rising rate of success as summer advances must presumably be attributed to some combination of differences in the activities, diets, numbers, or species of predators.”

As discussed earlier, skunks, house cats, dogs, and snakes were thought to have been the primary destroyers of meadowlark nests during our study. While no records were kept of their seasonal abundance and activities, some patterns were apparent from general observations. It is doubtful that the hunting habits of domestic dogs and cats varied greatly during the course of the nesting season. Snakes, on the other hand, were seen with increasing frequency during May, becoming progressively more scarce in June and July. This agrees with the observations of Klimstra (1958) in Davis County, Iowa. Conversely, skunks would logically be more numerous and active later in the season. Young skunks begin to hunt with the female at about 2 months of age, that is, sometime in July. Verts (1967) noted that female skunks were afield less during pregnancy and after it up to the time the young were about 1 month old; at that time (around 7–15 June), they resumed more or less normal nightly hunting patterns. Thus, observations of predator activities (with the exception of snakes) give no indication as to why predation should

be heavier early in the nesting season. In fact, contradictory evidence is available from Bobwhite nests located on the Research Area; these nests suffer significantly heavier losses to predators as the season progresses (Klimstra, unpublished data). At present, we have no explanation for these seemingly incompatible findings; there is nothing to suggest that Bobwhites and meadowlarks do not suffer nest losses from the various predators in relatively similar proportions. The whole problem of seasonal variation in nesting success is in need of further study.

Land-use types.—As already discussed, nests located on Bigler's pasture received unusually heavy losses from predation and, as this was thought to represent a special situation, the present section will deal only with nests located on other parts of the area. Nests in hayfields had the lowest rate of success (25.7 per cent); primarily this reflected losses to mowing (62.9 per cent). Nests in idle and fallow areas showed 29.6 per cent success with 63.0 per cent being destroyed by predators. Nests in pasture and soilbank fields had a success of 42.9 per cent and 50.0 per cent, respectively, while suffering losses to predation of 42.9 per cent and 45.0 per cent, respectively. Of the four nests located in wheat fields, three (75 per cent) were successful; however, the smallness of the sample prohibits concluding that these areas were relatively safer than others. The rate of abandonment was similar for all types of areas; 2.9 per cent in hayfields, 5.7 per cent in pastures, 5.0 per cent in soilbank fields, and 3.7 per cent in idle and fallow areas.

SUMMARY

From 1960 to 1967, 450 nests of the Eastern Meadowlark were found in the vicinity of Carbondale, Illinois. All nests were located at ground level and most were in cover 10 to 20 inches high; 17.3 per cent were open from above, 44.5 per cent were partially roofed, and 38.2 per cent had full canopies. The rush *Juncus*, meadow fescue, cheat, and bluegrass were most commonly used in nest construction. Almost 49 per cent of all nests faced in a general northeasterly direction.

Earliest date of egg laying was 14 April, the latest 23 July; peak egg laying occurred from 22 April to 12 May. Pastures showed the highest nest density per 100 acres with an average of 20.9, followed by hayfields 12.6, soilbank fields 5.1, wheat fields 4.8, idle areas 3.8, and fallow fields 2.0.

Average size of 101 complete clutches was 4.16 (range 2-6); number of eggs tended to decrease as the season progressed. Overall hatching success of 262 nests was 37.4 per cent; fledging success was 30.5 per cent. Predation (51.2 per cent) and mowing (12.2 per cent) were the primary destructive agents of nests. Extremely heavy losses to predators (72.2 per cent of 97 nests) in one field was discussed in detail. There appeared to be a direct relationship between degree of nest construction (amount of overhead protection) and nest success. The percentage of successful nests also increased as the season progressed.

ACKNOWLEDGMENTS

Thanks are due to the many graduate research assistants and undergraduate workers of the Cooperative Wildlife Research Laboratory for their help in the arduous task of nest hunting. Special thanks go to Dave Rose, Richard Bartholomew, William Allen, and Max Hutchison who, at various times throughout the study, were in charge of field crews. We are indebted also to Drs. William George and Wesley E. Lanyon for reading the manuscript and offering helpful comments and criticisms. This represents a contribution from Project No. 49, Cooperative Wildlife Research Laboratory, Southern Illinois University.

LITERATURE CITED

- BENDIRE, C. E. 1895. Life histories of North American birds. U. S. Natl. Mus. Spec. Bull. 3.
- BENT, A. C. 1958. Life histories of North American blackbirds, orioles, tanagers, and allies. U. S. Natl. Mus. Bull., 211:53-80.
- COLLIAS, N. E. 1964. The evolution of nests and nest-building in birds. Amer. Zool., 4:175-190.
- DAVIS, D. E. 1955. Breeding biology of birds. In Recent studies in avian biology. A. Wolfson, (Ed.). Univ. Illinois Press, Urbana.
- EIFRIG, C. W. G. 1915. Field notes from the Chicago area. Wilson Bull., 27:417-419.
- EIFRIG, C. W. G. 1919. Notes on birds of the Chicago area and its immediate vicinity. Auk, 36:512-524.
- FRIEDMANN, H. 1963. Host relations of the parasitic cowbirds. U. S. Natl. Mus. Bull., 233.
- HANN, H. W. 1937. Life history of the Ovenbird in southern Michigan. Wilson Bull., 49:145-237.
- HERGENRADER, G. L. 1962. The incidence of nest parasitism by the Brown-headed Cowbird (*Molothrus ater*) on roadside nesting birds in Nebraska. Auk, 79:85-88.
- JOHNSTON, R. F. 1964. The breeding birds of Kansas. Univ. Kansas Publ. Mus. Nat. Hist., 12:575-655.
- KALMBACH, E. R. 1939. Nesting success: its significance in waterfowl reproduction. Trans. N. Amer. Wildl. Conf., 4:591-604.
- KLIMSTRA, W. D. 1958. Some observations on snake activities and populations. Ecology, 39:232-239.
- LACK, D. 1954. The natural regulation of animal numbers. Oxford Univ. Press, London.
- LACKEY, J. B. 1913. Notes from Mississippi. Oologist, 30:257-258.
- LANYON, W. E. 1957. The comparative biology of the meadowlarks (*Sturnella*) in Wisconsin. Publ. Nuttall Ornithol. Club, 1.
- MAYFIELD, H. 1960. The Kirtland's Warbler. Cranbrook Inst. Sci., Bull. 40.
- MAYFIELD, H. 1961. Nesting success calculated from exposure. Wilson Bull., 73:255-261.
- NICE, M. M. 1957. Nesting success in altricial birds. Auk, 74:305-321.
- NICE, M. M. 1964. Studies in the life history of the Song Sparrow. Vol. I. A population study of the Song Sparrow. Dover Publ. Inc., New York.
- NOLAN, V., JR. 1963. Reproductive success of birds in a deciduous scrub habitat. Ecology, 44:305-313.
- REED, C. A. 1965. North American birds eggs (Revised Ed.). Dover Publ. Inc., New York.

- SANDBORN, C. C., AND W. A. GOELITZ. 1915. A two year nesting record in Lake County, Ill. *Wilson Bull.*, 27:434-448.
- SAUNDERS, G. B. 1932. A taxonomic revision of the meadowlarks of the genus *Sturnella* (Vieillot) and natural history of the Eastern Meadowlark, *Sturnella magna magna* (Linnaeus). (Ph.D. thesis, Cornell Univ.).
- STODDARD, H. L. 1931. The Bobwhite Quail; its habits, preservation and increase. Chas. Scribner's Sons, New York.
- TERRILL, L. M. 1961. Cowbird hosts in southern Quebec. *Canadian Field-Naturalist*, 75:2-11.
- THOMS, C. S. 1924. The Eastern and Western meadowlarks. *Bird Lore*, 26:315-317.
- VERTS, B. J. 1967. The biology of the striped skunk. Univ. Illinois Press, Urbana.
- COOPERATIVE WILDLIFE RESEARCH LABORATORY, SOUTHERN ILLINOIS UNIVERSITY, CARBONDALE, ILLINOIS, 6 JANUARY 1968.



NEW LIFE MEMBER

Ralph W. Schreiber, a graduate student at Florida Southern University, has recently become a Life Member of the Wilson Society. Mr. Schreiber holds degrees from The College of Wooster, and The University of Maine. His major ornithological interest is the behavior-ecology of seabirds. His work on the Herring Gull was supported by a Louis Agassiz Fuertes Grant in 1966. Mr. Schreiber is a member of the AOU, the BOU, the Cooper Ornithological Society, and other scientific organizations.