FIELD SPARROW REPRODUCTIVE SUCCESS AND NESTING ECOLOGY

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ABSTRACT.—Field Sparrow reproductive success and nesting ecology were studied in central Illinois on a tract composed of grassland, shrub-grassland, and shrub-woodland. Egg and nest successes were 11.2% and 10.2% respectively. Major causes of nest failure included: predation, primarily by snakes (76% of all active nests), nest desertion following brood parasitism by the Brown-headed Cowbird (7%), and nest desertion from unknown causes (7%). Eleven percent of the nests were parasitized; most (63%) were deserted as a result. Nests with young received heavier predation than nests with eggs. Early nests were placed predominantly in standing grass litter, but as the breeding season advanced forbs, trees, and shrubs became the most frequently used nesting substrates. Mean nest height increased as the season advanced.

The frequency of desertion (from unknown causes), cowbird parasitism, snake predation, and successful fledging was not significantly different among nests placed in the major vegetation types, although mammalian predation did differ significantly. Nest height did not influence nesting outcome significantly. Nest vulnerability to snake predation was independent of relative nest concealment. Desertion (nonparasitized nests) and snake predation were distributed uniformly among nests throughout the study area, but nests preyed upon by mammals were somewhat clumped, and cowbirds parasitized nests within or near the shrub-woodland. The occurrence of snake predation was proportional to the number of nests. Predation intensity was not related to brood size. Nesting success increased slightly as the season advanced. The incidence of snake predation was negatively correlated with maximum daily relative humidity, but unrelated to other weather measurements.—*Department of Ecology, Ethology, and Evolution, University of Illinois, Champaign, Illinois 61820. Present address: Department of Animal Ecology, Iowa State University, Ames, Iowa 50011.* Accepted 28 June 1976.

DESPITE the proliferation of statistics on reproductive success in ornithological literature, few studies attempt in-depth analyses of factors influencing the nesting outcome. The Field Sparrow (*Spizella pusilla*), a species common to old fields in eastern United States, provides such an example. The breeding biology of this species has been well documented (Walkinshaw 1936, 1939, 1945, 1968; Crooks 1948; Crooks and Hendrickson 1953; Sutton 1960; Best 1977; and others), but the factors influencing its nesting success have yet to be scrutinized. The persistent renesting of the Field Sparrow over a long breeding season, concomitant with the intense predation pressure observed in the present study, afforded an excellent opportunity to quantify and evaluate variables influencing nesting outcome.

STUDY AREA AND METHODS

The 23.6-ha study area was in Allerton Park, near Monticello, Illinois. Approximately 8.5 ha of shrub-woodland occupied its periphery (Fig. 1), with tree heights reaching 15 m. The central region consisted of 9.0 ha of shrub-grassland (tree and shrub heights all under 8 m) and 6.1 ha of grassland. The major plant species in the three vegetation types are described in Best (1974b).

In 1971 I visited the study area on 72 days between 25 April and 24 August, more frequently after May; I made 133 visits in 1972 from 9 April to 15 September. During each visit I recorded the status of each nest. Time spent at active nests was minimized to avoid attracting predators. Most nests were located by watching females during nest building. Additional nests were found while walking through territories or by closely watching pairs known to be actively nesting. Nest locations were recorded on a grid map of the study area. Adult and nestling Field Sparrows were individually marked with leg bands.

The following were recorded after nest abandonment: nest height, vegetation providing nest support and cover, relative nest concealment at and below nest level, and degree of disturbance to the nest and surrounding vegetation after nest predation.
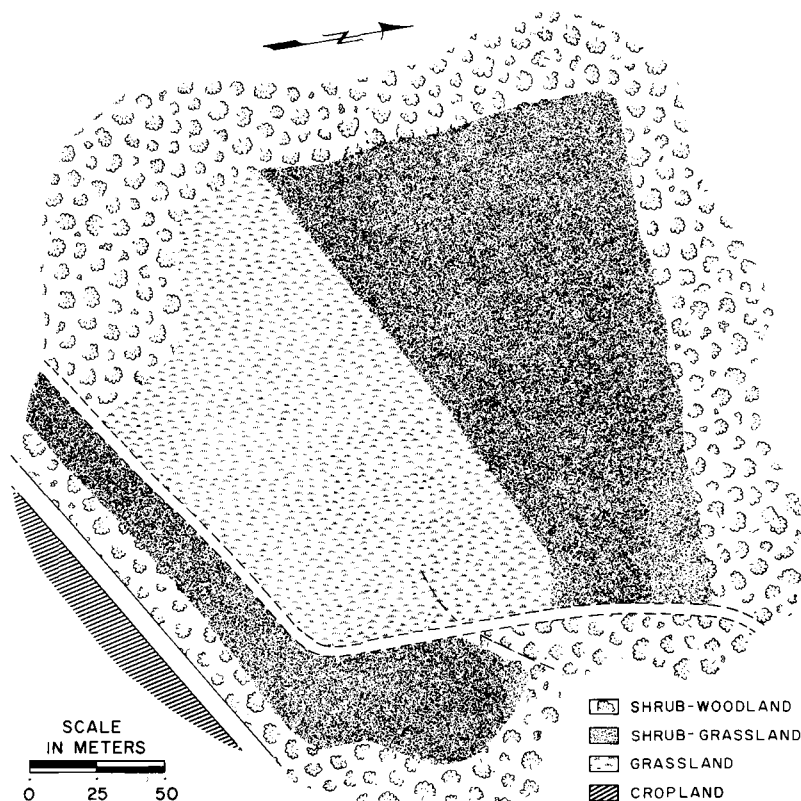
Statistical significance was set at $P \leq 0.05$.

Fig. 1. The study area showing the major vegetation types.

SCALE
IN METERS

0   25   50

SHRUB-WOODLAND
SHRUB-GRASSLAND
GRASSLAND
CROPLAND

RESULTS AND DISCUSSION

A general discussion of this species' breeding biology is presented in Best 1974b.

BREEDING SUCCESS

Nest predators.—Snakes were the principal predators on my study area, predominantly blue racers (*Coluber constrictor*), and to a much lesser extent prairie king-snakes (*Lampropeltis calligaster*), based on the frequency with which these species were encountered on the area and at nest sites. Sutton (1960) also suspected blue racers of destroying many eggs and young. The massasauga (*Sistrurus catenatus*) and the plains garter snake (*Thamnophis radix*) were also seen occasionally. Racoons (*Procyon lotor*), gray foxes (*Urocyon cinereoargenteus*), red foxes (*Vulpes fulva*), and opossums (*Didelphis marsupialis*), as well as domestic cats and dogs were among potential mammalian predators frequenting the study area. Avian predators did not threaten nesting efforts significantly (see also Nolan 1963). Although Blue Jays (*Cyanocitta cristata*) were common and have been blamed for nest losses (Walkinshaw 1968, Fretwell 1972), I never saw any near Field Sparrow nests or evoking alarm in nesting adults.

All predation on my study area was attributed either to larger mammals or snakes. Nests preyed upon by mammals were tilted, or more often, partially or entirely torn

TABLE 1

NEST SUCCESS DATA FOR THE 1971 AND 1972 BREEDING SEASONS

Outcome	1971		1972		1971 and 1972 combined	
	No. of nests	% of total	No. of nests	% of total	No. of nests	% of total
Deserted during egg-laying or incubation	4	6.8	6	6.8	10	6.8
Parasitized by Brown-headed Cowbirds	4 (2)[1]	6.8 (3.4)	12 (8)	13.6 (9.1)	16 (10)	10.9 (6.8)
Predation by snakes or mammals	46	78.0	66	75.0	112	76.2
Successfully fledged young	7	11.9	8	9.1	15	10.2
Juveniles surviving 1 month after fledging	4	6.8	5	5.7	9	6.1
Total	59	—	88	—	147	—

[1] Nests deserted following brood parasitism.

from the original position. The surrounding vegetation was matted down to varying extents. Indications of predation by smaller mammals, such as partial removal of nest contents (Walkinshaw 1968), egg shell fragments in the nest vicinity, or minor disturbance to the nest bowl, were rare. In contrast to mammalian predators, snakes did not disturb the surrounding vegetation or nests, except for an occasional circular hole in the bottom of the nest. The rationale for ascribing this predation to snakes was threefold. First, snakes, mainly blue racers, were frequently encountered on the study tract without actively searching for them. Second, I witnessed two incidents of blue racer predation on nestling Field Sparrows (Best 1974a), and saw a blue racer and prairie kingsnake at two other nests from which the young had been removed. Third, in many cases nest contents disappeared during the day, eliminating the possibility of nocturnal predators.

Nesting success.—The outcome was known of 403 Field Sparrow eggs laid during the two breeding seasons. Eight eggs (2%) failed to hatch, probably from infertility or incomplete embryonic development. Desertion from unknown causes during egg-laying and incubation resulted in a loss of 16 eggs (4%); 19 eggs (5%) were lost during egg-laying and incubation because of brood parasitism by the Brown-headed Cowbird (*Molothrus ater*), either through removal by the cowbird or nest desertion after parasitism. Snake predators removed 193 eggs (48%), almost all during incubation, and mammals removed 30 eggs (7%) during incubation. Only 137 (34.0%) of the original 403 eggs hatched successfully. Snakes took 74 nestlings (18% of the total eggs laid) from nests, and mammals removed 16 (4%). Two other nestlings (<1%) were lost; one died in the nest—probably a premature hatchling; and the other, with a broken leg, accidently fell from the nest. Only 45 (11.2%) of the 403 eggs produced fledglings.

Nest success is summarized in Table 1. Of 147 nests in which eggs were laid, 18 (12%) were lost during egg-laying, 82 (56%) during incubation, 32 (22%) during the nestling period, and 15 (10%) successfully fledged young. The similarity in percentages between years suggests that factors affecting nesting outcome were consistent from year to year. Percentage differences, particularly brood parasitism, probably resulted largely from collecting less complete nesting success data early in the 1971 breeding season.

The similarity of egg success and nest success (11% versus 10%) indicates minimal partial brood mortality. Such mortality factors include: failure of eggs to hatch, egg removal by brood parasites, partial predation on nest contents, and starvation. Partial predation was rare, and no nestling starvation was evident (Best 1977). Most nesting failure resulted from loss of the entire nest contents (nest desertion and predation). Adult mortality, also a cause of nesting failure, occurred only once, when a mammalian predator (probably a house cat) killed an adult female and three nestlings in the nest (see also Walkinshaw 1968).

My estimates of nesting success are conservative; the actual values are slightly lower than those herein reported. No nest fledging young escaped attention, as adults with nestlings or new fledglings were easily recognized by their behavior. Thus any unlocated nests were unsuccessful. Despite this conservative bias, nesting success of the Field Sparrow on my study area was far below that observed by others (Walkinshaw 1945, Crooks 1948, Batts 1958, Nolan 1963, Fretwell 1968). The low nesting success on my study area is also well below that expected for other passerine species (see Nice 1957, Ricklefs 1969).

Nest desertion and cowbird parasitism.—In addition to nest desertion following brood parasitism, other nests were abandoned for unknown reasons during nest construction, egg-laying, and incubation (Best 1974b). Nests with young were never deserted. Apparently factors causing desertion affect mainly early stages of the nesting period, or adults develop stronger nest tenacity as the nesting cycle progresses (Ricklefs 1969).

Only 11% of the nests on the study area were parasitized by cowbirds. Others have reported more intense brood parasitism on Field Sparrow nests (Hicks 1934, Norris 1947, Berger 1951, Crooks and Hendrickson 1953, Walkinshaw 1968). Most nests were parasitized during egg-laying, although twice cowbird eggs were deposited during incubation. The cowbird did not always remove a host egg from the parasitized nest. Of the 16 nests parasitized, 10 (63%) were deserted. Similarly Walkinshaw (1968) reported 55% nest desertion following parasitism, and Friedmann (1963) noted that Field Sparrows will "frequently" desert their nests when parasitized.

Nests were parasitized from 9 May to 10 July (see also Crooks and Hendrickson 1953). As the breeding season of the Field Sparrow extended through August (Best 1974b), late summer nesting efforts were free of cowbird parasitism.

Multiple parasitisms were more frequent early in the breeding season. The average numbers of cowbird eggs deposited per parasitized nest for May, June, and July were 1.8, 1.3, and 1.0 respectively. Three cowbird eggs were deposited in one May nest, other nests were parasitized either once or twice. In all but one nest in which more than one cowbird egg was deposited, the nest was deserted after the first egg was laid. Crooks and Hendrickson (1953) and Walkinshaw (1968) have also reported multiple parasitisms.

Temporal distribution of mortality.—Nest predation was minimal during egg-laying prior to the start of incubation (Table 2, see also Willis 1973). This is reasonable, as activity at the nest site is low during this period. Predation during the incubation period was highly variable. No mortality occurred the 5th day into incubation, but was exceptionally high the day preceding and the day following. The cause of this variation is not known. Predation was lower late in the incubation period (see also Holcomb 1972, Willis 1973). Holcomb (1972) suggested that reduced egg mortality late in the incubation period may result from adults behaving differ-
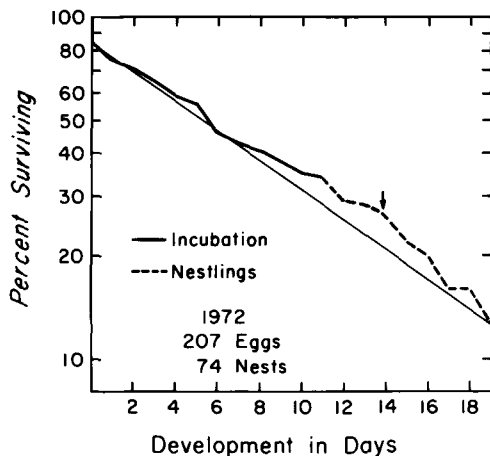
Fig. 2. Survival of Field Sparrow eggs and nestlings. Includes only nests where the exact number of eggs laid was known and the day of egg or nestling disappearance was definite. Eggs failing to hatch were not included. The straight line represents a constant rate of mortality and the arrow indicates the point of inflection in the survival curve.

ently during this interval, thus attracting less attention. Crooks and Hendrickson (1953) reported male Field Sparrows occasionally feeding their mates on the nest, more often early in incubation than near hatching time. Such behavioral changes could affect egg mortality. Also, predators probably found the most easily discoverable nests early in the incubation period (Willis 1973).

Predation during the nestling stage was less variable. No predation occurred the first day of hatching or 7 days into the nestling period. Nestlings usually fledged on the 8th day. Transition from the incubation to nestling stage may involve behavioral shifts that could reduce vulnerability to predation, although Robertson (1972) reported increased mortality during hatching in the Red-winged Blackbird (*Agelaius phoeniceus*).

Although nesting outcome data were less complete in 1971, no predation was observed on the 5th day into incubation or the first day of hatching, indicating consistency from year to year and suggesting some unknown biologically significant factor(s) reducing susceptibility to predation.

The distribution of nesting failure was also analyzed by constructing a survival curve (Fig. 2). The curve is plotted from the start of incubation because embryonic development begins at that time; 10% of the eggs were lost during egg-laying before incubation began. The mortality rate remained fairly constant during the incubation

TABLE 2

DISTRIBUTION OF NEST PREDATION THROUGHOUT THE NESTING CYCLE[1]

	Day												Total nests
	0[2]	1	2	3	4	5	6	7	8	9	10	11	
Egg-laying		1	2										3
Incubation[3]	5	5	3	3	7		7	2	2	1	2	1	38
Nestlings		3	1	2	3	1	2		2				14

[1] Includes only 1972 nests for which the day of nest predation was definite (55 nests).
[2] Day "0" represents the day incubation was begun or the day the first nestlings hatched.
[3] Incubation was assumed to begin the day before the last egg was laid unless observed otherwise (see Walkinshaw 1968).
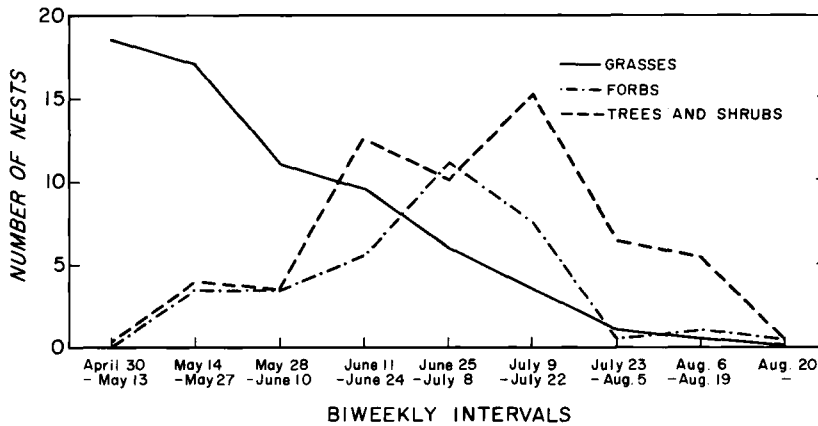
Fig. 3. Seasonal distribution of nest placement in the three vegetation types. Nests were placed within biweekly intervals using the date construction was completed.

and nestling periods, with a slight increase 3 days after hatching (point of inflection). Of the original 207 eggs, only 8 juveniles remained 25 days after hatching, representing 4% survival (or 3%, considering all 257 eggs laid in 1972; see restrictions in Fig. 2). Crooks and Hendrickson (1953) reported 10 juveniles surviving until fall from 45 eggs laid (22%).

I calculated the average daily mortality rate (m) using the formula $m = - (\log_e P)/t$ where P is the proportion of the nests or individuals surviving any given portion (t) of the nest period (Ricklefs 1969). Eggs were considered present in nests during a 13-day period (2 days laying and 11 days incubation) and the nestlings for 8 days. The daily mortality rate of nests was 8.8% during laying and incubation and 14.3% during the nestling period. The corresponding mortality rates for eggs and young were 8.3% and 13.4%, respectively. Mortality during egg-laying and incubation included factors other than predation, whereas predators were responsible for all but two nestling losses. Consequently differences in mortality rates from predation during these two periods are greater than the percentages indicate. Both snake and mammalian predation were more intense during the nestling period.

The presence of young and increased frequency of visits to the nest during the nestling period apparently attract the attention of predators (Skutch 1949). In the Field Sparrow the mortality rate increased 3 days after hatching (Fig. 2). Reduction in brooding time and increase in feeding frequency as nestlings grow older (Walkinshaw 1968) apparently reach a critical limit 3 days after hatching, attracting more predators to the nest. The limited activity and vocalization by younger nestlings may also reduce their vulnerability to predation (see Holcomb 1969, White and Woolfenden 1973).

NEST PLACEMENT

Table 3 shows the predominant plant species used for nest support (see Best 1974b for a complete list of nesting substrates). Nests were often supported by more than one plant species. Nest support in grasses consisted almost entirely of standing litter, while both dead and live black raspberry (Rubus occidentalis) briars were used. Almost all other nests were in live plants.

TABLE 3

NESTING OUTCOMES IN THE MAJOR PLANT SPECIES USED FOR NEST SUPPORT
IN 1971 AND 1972[1]

| | Nest height (cm) | | Nesting outcomes (Expressed as a percentage of the total number of nests)[2] | | | | | |
Plant species	Mean	Range	Deser-tion	Cowbird para-sitism	Snake preda-tion	Mammal preda-tion	Suc-cessful fledging	Total nests
Grasses[3]	30	9–57	9	6	70	2	13	54
Poa pratensis	15	9–23	27	0	64	0	9	11
Sorghastrum nutans	34	22–57	3	8	74	3	13	39
Forbs[3]	36	20–56	8	16	60	24	4	25
Rubus occidentalis[4]	37	20–56	11	11	61	22	6	18
Solidago altissima	23	20–25	0	100	50	50	0	2
Trees and Shrubs[3]	45	19–89	6	12	60	16	10	50
Crataegus mollis	48	27–89	0	0	67	33	0	6
Malus ioensis	38	23–66	15	15	46	15	8	13
Prunus sp.	55	27–69	0	0	50	0	50	4
Quercus imbricaria	52	19–76	0	17	67	17	0	6
Rhus glabra	62	51–76	0	0	33	67	0	3
Rosa multiflora	53	37–77	25	25	50	0	0	4
Ulmus rubra	37	20–57	0	9	82	9	9	11
Total[3]	37	9–89	8	10	64	12	10	129

[1] Only the single plant species providing the majority of the support was considered in each case. Nests supported equally by two plant species were excluded, except when calculating values for the major vegetation types, and then only when both species belonged to the same type.
[2] The percentage totals may not equal 100%, because of rounding off and overlap between cowbird parasitism and predation.
[3] These also include minor plant species used for support.
[4] Because of its growth form, this species was considered a forb.

Nest building began before the current year's vegetation had grown substantially and before foliage developed significantly on trees and shrubs. During the first 2 weeks of nesting, nests were placed almost entirely in standing grass litter (Fig. 3). As the breeding season progressed, grass litter became less important as a nesting sub-strate, while forbs and trees or shrubs increased in importance, with the latter constituting the predominant nest site toward the end of the season (see also Crooks and Hendrickson 1953, Walkinshaw 1968).

Walkinshaw (1968) attributed this transition to development of foliage. While foliation did increase the cover value of forbs and shrubs, the transition to these nest sites was not entirely synchronous with leaf development. Grass litter remained the dominant nesting substrate in early June (Fig. 3) although foliation was nearing completion. This preference persisted, despite the availability of forbs and shrubs, until the current year's growth of grass overtopped the litter. Nests were never placed entirely in life grass. Use of Kentucky bluegrass (*Poa pratensis*) litter dropped off sharply early in the season, probably because of early development of new growth. Indian grass (*Sorghastrum nutans*) grew more slowly, and nesting persisted in this species as long as isolated clumps of litter remained exposed from the new growth. The avoidance of new growth for nest sites might result from the ease with which a nest could be tipped or dislodged as the grass culms increase in height. Also, new grass culms are more flexible than dried ones from the previous season, thus decreas-ing their stability as a nesting substrate. As the Field Sparrow nest is not attached to adjacent vegetation, it is vulnerable to changes in the nesting substrate. Red-winged Blackbird nests attached to both old and rapidly growing new vegetation are some-times turned over (Holm 1973).

Field Sparrow nests were placed farther from the ground as the breeding season progressed. Of 53 nests built during May, nest height (from ground to upper rim) ranged from 9 to 48 cm and averaged 26. The average for 44 June nests was 38 cm, with a range of 23–77. Heights of 49 nests located in July ranged from 22 to 89, with a mean of 47 cm. The average for the 10 August nests was 48, ranging from 30 to 76.

The seasonal shift in nest placement, initially from predominantly grasses to a mixture of grasses, forbs, trees and shrubs, and finally to predominantly trees and shrubs represented an increase in mean nest height (Table 3). Nest height also increased within a given vegetation type and within a plant species. The average heights in Indian grass during May, June, and July were 29, 34, and 47 cm respectively. This may have been due to new growth of vegetation, which the birds avoided by placing the nest higher. Nest height in trees and shrubs also increased from May to August (see also Crooks 1948). Means for the 4 months were 27, 42, 51, and 49 cm respectively. This suggests that Field Sparrows nest progressively farther from the ground for reasons other than development of foliage or growth of herbaceous vegetation, as trees and shrubs had completed foliation by early June.

FACTORS AFFECTING NESTING OUTCOME

Plant species used for nest support.—Table 3 shows nesting outcomes in the major plant species used for nest support at nests where eggs were laid. The relationship between the three major vegetation types (grasses, forbs, and trees or shrubs) used for nest support and the nesting outcomes was tested statistically using 2 × 3 Chi-square contingency analyses, comparing nests of each outcome with all other nests. (In all 2 × n contingency analyses, expected values of one or greater were not pooled, Lewontin and Felsenstein 1965.) Frequency of desertion from unknown causes, cowbird parasitism, snake predation, and successful fledging were not significantly different among nests placed in the three types of vegetation. Mammalian predation was significantly less than expected for nests in grass litter but higher than expected for nests in forbs and trees or shrubs ($\chi^2 = 9.74$, 2 df).

Difficulty in detecting mammalian predation on nests placed in Kentucky blue-grass (many nests were low to the ground and openly exposed) may partially explain low predation in grass litter (Table 3), but foraging habits of mammalian predators are probably more important in determining variations in predation intensity. Much of the predation occurred at moderately open sites, and four incidents took place near well-used trails. A few nests surrounded by tall-grass species were destroyed by mammals, but these grass stands were never extensive. Nests in large expanses of tall grass never suffered from mammalian predators. This probably accounts for the infrequent predation on nests placed in Indian grass.

Although mammalian predation was highly variable in the major plant species used for nest support, snake predation was quite constant (Table 3).

Nest height.—Nests nearer the ground were more frequently deserted (Table 4). Cowbird parasitism varied inconsistently with nest height. According to Friedmann (1929), nest height makes little or no difference to the cowbird. Snake predation occurred at all heights, but was particularly intense on nests 16–30 cm above the ground. This may represent the height range over which snakes search for nests most actively. Predation by mammals was restricted to nests 25–60 cm high. Nests located near the ground were predominantly in grass litter, where mammalian predation was limited (Table 3). Nests higher than 60 cm may have been inaccessible. Nestlings

A COWBIRD PARASITISM   △ SUCCESSFUL FLEDGING
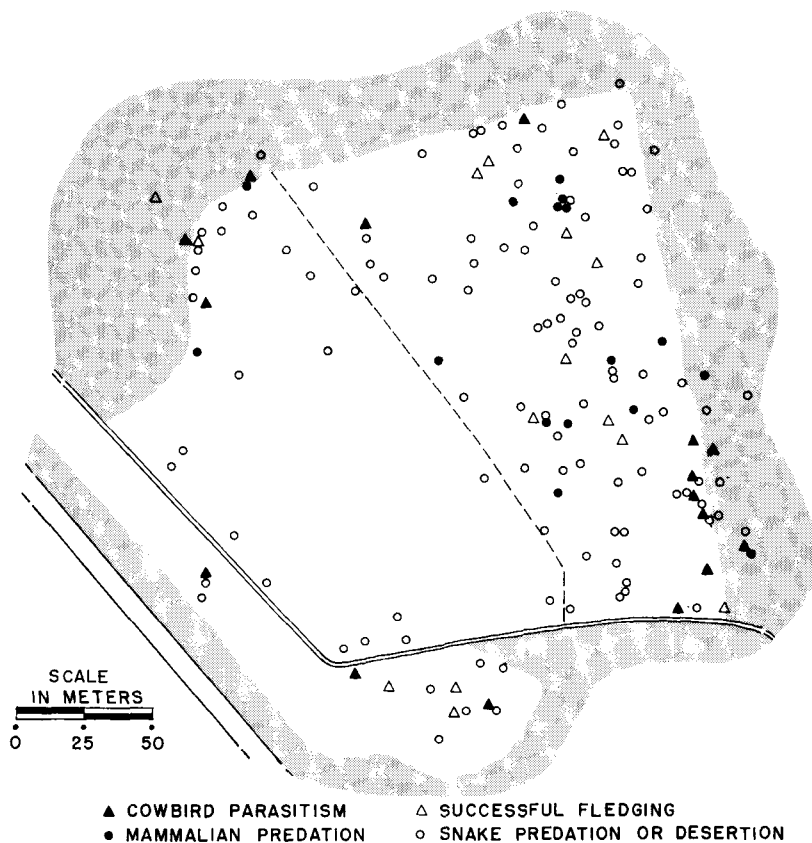**● MAMMALIAN PREDATION   ○ SNAKE PREDATION OR DESERTION**

Fig. 4. The distribution of Field Sparrow nests throughout the study area (1971 and 1972).

fledged most frequently from nests located either close to the ground or at taller heights, largely because of mammalian and snake predation patterns. None of the above relationships were statistically significant (2 × 6 Chi-square contingency analyses comparing nests of each outcome with all other nests).

Nest concealment.—The conspicuousness of each nest to snakes was estimated by classifying relative concealment at and below nest level as: poor, fair, good, or excellent. Distribution of snake predation among nest concealment classes was proportional to their frequency of occurrence ($\chi^2 = 0.98$, 3 df, $P > 0.5$), suggesting that nest cover does not influence vulnerability to snake predation significantly. Concealment above the nest was not measured, and its importance in cowbird parasitism, and possibly nest desertion, are not known. Nocturnal predation by mammals would not likely be affected by nest concealment.

Spatial distribution of nests.—Desertion (from unknown causes) and snake predation were uniformly distributed among nests throughout the study area (Fig. 4). Nests preyed upon by mammals were somewhat clumped, being largely confined to one very restricted and another more extensive region. Two additional nests destroyed by mammals were near a well-used trail. This distribution of predation may result from specific foraging patterns of mammalian predators.

Cowbirds parasitized Field Sparrow nests located either within or near the shrub-woodland (Fig. 4). The mean distance from the shrub-woodland of all
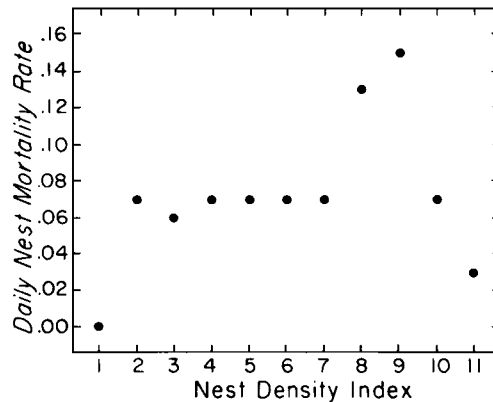
Fig. 5. The relationship between daily nest mortality resulting from snake predation and nest density.

parasitized nests was 13.4 m, with all but two located within 26 m. Berger (1951) also reported that parasitized nests in fields were generally near bordering woodlots or thickets. Brown-headed Cowbirds ordinarily find host nests by watching nest building (Friedmann 1929). The taller, denser woody vegetation within the shrub-woodland may provide better vantage points to watch Field Sparrow nest-building activities (see Crooks 1948), while reducing risk of detection, of advantage to the cowbird, as Field Sparrows chase cowbirds from their territories with vigor (Crooks and Hendrickson 1953). Another factor may influence the paucity of parasitized nests away from shrub-woodland. Norris (1947) reported that until mid-May most cowbird eggs were laid in nests of birds of field and open country, and after mid-May in nests of woodland species. All Field Sparrow nests parasitized on my study area after mid-May were within 26 m of the shrub-woodland.

Nest density.—I determined the relationship between nest density and mortality rate from predation using a modification of Mayfield's (1961) method employed by Fretwell (1972). The number of known active nests during each 24-hour period was used to index nest density. During each period nest failures from predation were also tabulated. The daily mortality rate (M) was estimated by the formula: M = (number of mortalities on days when density is d_1)/(days when density is d_1)·(d_1). The correla-

TABLE 4

NESTING OUTCOMES IN RELATION TO NEST HEIGHT[1]

Nest height (cm)	Nesting outcomes (Expressed as a percentage of the total number of nests)					Total nests
	Desertion	Cowbird parasitism[2]	Snake predation	Mammalian predation	Successful fledging	
0–15	28.6	0.0	42.8	0.0	28.6	7
16–30	2.0	10.2	79.6	6.1	10.2	49
31–45	9.3	11.1	61.1	14.8	7.4	54
46–60	7.4	14.8	51.9	22.2	3.7	27
61–75	0.0	0.0	57.1	0.0	42.9	7
76–90	0.0	33.3	66.7	0.0	0.0	3
All heights combined	6.8	10.9	64.6	11.6	10.2	147

[1] Nests deserted during construction are excluded.
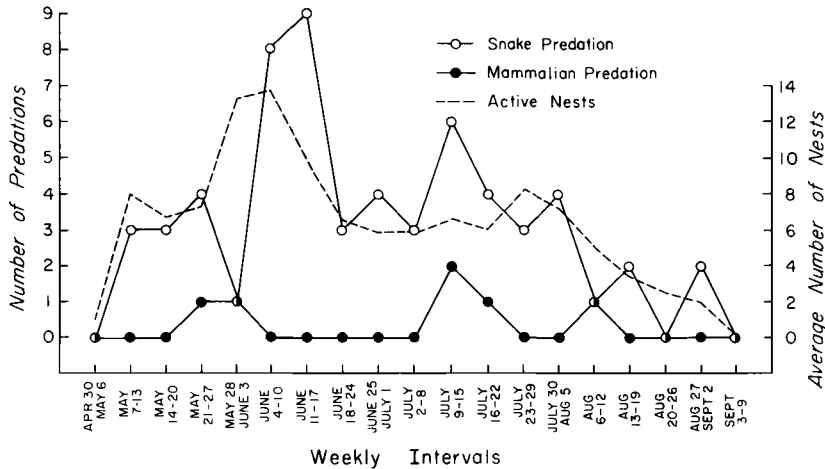[2] Some of these nests were also subjected to predation.

Fig. 6. The relationship between predation intensity and the average number of active nests.

tion between nest density indices and estimated daily mortality rates was determined by a weighted regression procedure (Steel and Torrie 1960).

Nest density during the 1972 season ranged from 1 to 16 nests for the entire study area, but the relationship between daily nest mortality estimates and the density indices was not statistically significant ($t = 0.74$, 13 df). The analysis was also conducted using only the contiguous territories in the shrub-grassland tract (nest density ranging from 1 to 11), and again considering only mortality from snake predation on these territories (Fig. 5), but the results were nonsignificant ($t = 1.52$ and 1.65, respectively, 9 df). Small sample size prevented a similar analysis with mammalian predation.

The daily mortality rate was constant over much of the range in nest density (2 through 7). Days with the highest nest densities (10 and 11) occurred consecutively and yet did not exceed the average mortality rate. The constancy in mortality rate indicates a close linear relationship between the number of nests lost to predators and nest density.

Fretwell (1972) reported a significant, positive relationship between nest mortality and nest density for the Field Sparrow. Although causes of mortality were not differentiated, he considered Blue Jays the major predators. Perhaps the response of avian predators to nest density is density-dependent, while that of snakes is density-independent.

The total number of predations per week in 1972 was compared with the average number of active nests (Fig. 6). The correlation between snake predation and nest numbers was highly significant ($r = 0.638$, 17 df), although weekly fluctuations in predation were not consistent with concurrent changes in the number of available nests, and may indicate a time lag greater than 1 week in the response of snakes to changes in nest density. Mammalian predation was apparently independent of nest density.

Brood size.—Skutch (1949) felt that snakes locate nests visually, chiefly by following movements of parent birds. He suggested that smaller broods would be less vulnerable to predation because of less frequent visits to the nest. The results of a Chi-square contingency analysis between brood size and nesting outcome (either predation or successful fledging) were nonsignificant, indicating that while feeding

activity probably attracts predators to the nest (see *Temporal distribution of mortality*, above), predation intensity is presumably independent of variation in feeding rate resulting from differential brood size (total feeding trips increased with brood size, Best 1977). Apparently the frequency of nest visits reaches a level beyond which further increases in visitation rate will not increase vulnerability to predation. Perrins (1965) reported more intense predation on larger Great Tit (*Parus major*) broods, but the range in brood size was much greater than for the Field Sparrow, and mammals were the principal predators.

Time of season.—Nesting success increased slightly as the breeding season progressed. Of 36 nests built in May where eggs were laid, 3 (8%) successfully fledged young, 1 of 19 in June (5%), 3 of 27 in July (11%), and 1 of 6 in August (17%). This increase probably resulted largely from the absence of cowbird parasitism later in the breeding season, as the proportion of nests lost to snakes during the season remained relatively constant (see Fig. 6). Reduced predation pressure later in the season has been advanced to explain seasonal increases in nesting success in other studies (Nolan 1963, Roseberry and Klimstra 1970).

Weather conditions.—Snake activity patterns are largely dependent upon weather conditions, particularly temperature (Fitch 1956, Klimstra 1958). The influence of weather on snake predation was evaluated by conducting a correlational analysis between predation and the following weather parameters, measured at 24-hour intervals: temperature (maximum and minimum), relative humidity (maximum and minimum), precipitation, and total radiation (indirect). Only maximum daily relative humidity was significantly correlated with snake predation ($r = -0.281$, $n = 103$).

The absence of temperature-dependent predation is understandable, as the activity period of blue racers spans the entire nesting season of the Field Sparrow, and they remain active up to an air temperature of 32.4°C (Fitch 1963), which was never exceeded during the entire summer. Precipitation was sufficiently sporadic to obscure any effect it may have had on predation, although Klimstra (1958) reported no correlation between total precipitation and seasonal occurrence of snakes. Klimstra also concluded that a relationship between relative humidity and snake activity "was not readily apparent." The seemingly suppressing effect of higher relative humidity on snake predation on my study area remains unexplained. Perhaps relative humidity is closely correlated with yet another variable, such as parental activity, that was not considered.

Mammalian predation showed no significant relationship to any of the weather measurements, but sample size was small.

Inclement weather was not directly responsible for nest failure or adult mortality on my study area, although Crooks and Hendrickson (1953) reported weather causing egg and nestling losses.

CONCLUDING COMMENTS

Causes of nest failure in the Field Sparrow differed both in severity and the potential for their avoidance. Brood parasitism by the Brown-headed Cowbird was spatially and temporally limited (distance from woodland vegetation and length of breeding season), providing a means of escape from this cause of nest failure. Mammalian predation was also not a serious threat to the reproductive effort. Nesting attempts successfully avoiding mammalian predation included those situated in expanses of grassland, or at other localities where foraging by mammals was probably

limited, and those located at less accessible heights. The high abundance of snakes on the study area seriously threatened the ability of the population to maintain itself. Nest placement (with the possible exception of height), concealment, and density apparently did not affect vulnerability to snake predation. The snakes seemingly searched randomly, taking nests in proportion to their abundance. Although the habitat appeared ideally suited for the Field Sparrow when compared with other studies, the birds apparently lacked behavioral mechanisms to avoid intense depredation on the reproductive effort by snakes.

Reproductive recruitment was far below that needed to maintain the population. In addition to extremely low nesting success, post-fledging losses were also high. The reproductive effort of 23 breeding pairs yielded a maximum of 8 juveniles at the end of summer in 1972. For the population to sustain its numbers, a return of 85% (including yearlings) would be necessary, much higher than could be expected. Influx from outside areas must maintain the population from year to year.

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