EXPERIMENTAL ANALYSIS OF NEST PREDATION IN AN OLD-FIELD HABITAT

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ABSTRACT.—Experimental nests, each containing two Japanese Quail eggs, were systematically distributed in 10 ha of old-field habitat near Oxford, Ohio, to analyze the effect of human visits, vegetation type, concealment, and normal parental nesting behavior on the likelihood that predators will discover open nests. Each week for 12 weeks, 20 varying nest sites were selected and used. From 4 May to 26 July 1975 we exposed these nests for 6 days apiece in 240 locations. We made daily visits to 10 nests each week, none to the other 10. Seasonal rates of predation of experimental nests followed the pattern observed for natural nests in other old-fields. Daily visits did not affect the likelihood that predators would discover experimental nests. Well concealed experimental nests were no less likely to suffer predation than poorly concealed ones. Type of vegetation chosen for the experimental nest site was not related to predation rate. Comparison of survival of natural and experimental nests revealed no significant differences in numbers succumbing to predators or in the duration of survival of nests preyed upon. These experimental results indicate that visits to nests by investigators do not appear to affect success or failure. *Received 2 June 1976, accepted 10 December 1976.*

THE nest success of most birds that breed in some old-field habitats in the eastern United States is quite low, averaging only about 20%. Here nest success varies seasonally, with low success in May and early June followed by higher success in late June, July, and August. Predation of nest contents causes most losses (Nolan 1963, Ricklefs 1969, Thompson and Nolan 1973).

The great pressure of nest predation on open-nesting altricial birds is generally thought to be responsible for the evolution of their short incubation and nestling periods (Lack 1968: 172; Ricklefs 1969: 41–42; Welty 1975: 329). The demonstrable effect of nest predation on reproductive success and its inferred effect as a selective evolutionary force lead one to ask what factors determine whether a nest will succeed or fail.

The investigator's trips to studied nests could conceivably increase, or even decrease, the likelihood that they would be found by a predator (Stoddard 1931, Earl 1950, Willis 1973, Mayfield 1975, Picozzi 1975), a possibility that must be investigated before the importance of other factors can be evaluated properly. Beyond this possible observer effect, the many suggestions that have been advanced to explain how predators find nests can be grouped into four general categories: (1) Predators are attracted by parental activity (Skutch 1949); (2) predators are attracted by the cries of begging young (Skutch 1949, Young 1963, Perrins 1965); (3) predators respond to olfactory cues emanating from nest, parents, eggs, or young (Henry 1969, Willis 1973, Lill 1974); and (4) predators locate nests visually (Lill 1974). The problem of evaluating these possibilities is complicated by the fact that nest predators include mammals, snakes, and birds, each of which could be using different cues or combinations of cues. To date, most studies investigating cues used by predators have involved ground-nesting birds, particularly waterfowl, gulls, and gallinaceous species, which seem especially vulnerable to mammalian and avian predators (Earl 1950, Hammond and Foreward 1956, Keith 1961, Matschke 1965, Evans and Wolfe

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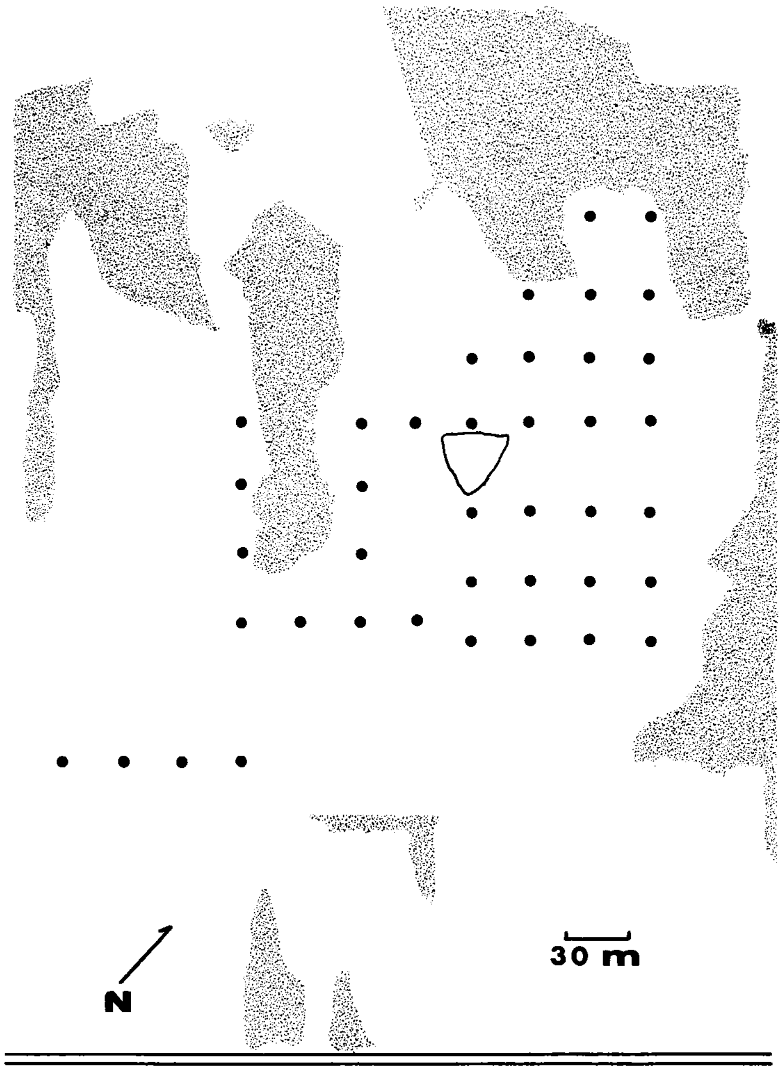

Fig. 1. Bachelor Estate study area and location of points used to determine placement of experimental nests. Shaded areas are woods.

1967, Tinbergen 1968, Henry 1969, Klimstra and Roseberry 1975, and Picozzi 1975). In old-field habitats, where open-nesting birds are exposed to an assortment of nest predators that includes snakes as well as birds and small mammals (Nolan 1963, Thompson and Nolan 1973), little is known about the effects on nest success of either observer activity or the role of the aforementioned cues. The experiment herein reported was designed to investigate some of these questions.

STUDY AREA AND METHODS

We performed the experiment from May through July 1975 at Miami University's field station on the Bachelor Estate approximately 2 km west of Oxford, Butler County, Ohio. The 10-ha tract (Fig. 1) consisted of a group of contiguous upland agricultural fields abandoned for varying lengths of time. Osage orange (*Maclura pomifera*), multiflora rose (*Rubrus* sp.), and red cedar (*Juniperus virginianus*) are among the most common woody species; goldenrod (*Solidago* spp.) and asters (*Aster* spp.) are the dominant forbs.

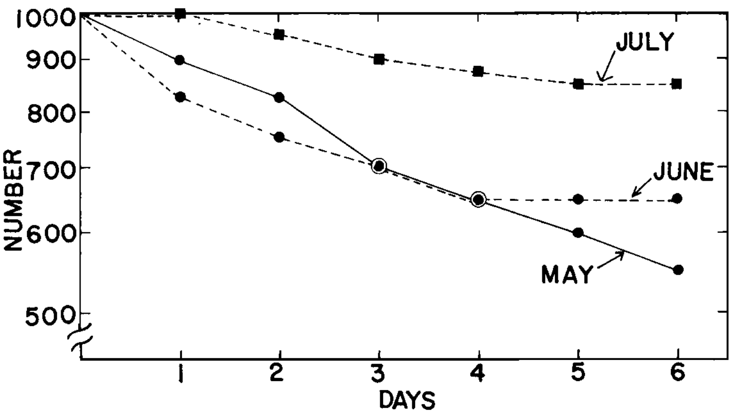

Fig. 2. Survivorship curves of visited experimental nests, according to month, assuming an initial cohort of 1,000 nests.

The most abundant breeding birds are the Cardinal (*Cardinalis cardinalis*), Mourning Dove (*Zenaida macroura*), Field Sparrow (*Spizella pusilla*), Yellow-breasted Chat (*Icteria virens*), Red-winged Blackbird (*Agelaius phoeniceus*), American Goldfinch (*Carduelis tristis*), Song Sparrow (*Melospiza melodia*), and American Robin (*Turdus migratorius*).

We placed abandoned nests of American Robins, Cardinals, and Field Sparrows, each containing eggs of the Japanese Quail (*Coturnix coturnix*), in nest sites typically used by the aforementioned species. Twenty such experimental nests were set out on the Sunday of each of 12 weeks, beginning on 4 May 1975, and from these 20 were selected 10 by lot to visit daily. These 10 we inspected in the late afternoons or early evenings but did not visit the remaining 10 nests until Saturday. On that day, after their 6 days of exposure to predators, we collected and removed from the study area any eggs that remained in the 20 nests. On Sunday we moved all nests to different locations, added fresh quail eggs, and repeated the procedure. Thus during the 12 weeks we placed experimental nests at 240 different locations.

As the nests deteriorated through wear, we replaced them with fresh ones. Quail eggs, which we obtained from a laboratory colony, were either fresh or had been refrigerated for a period not exceeding 6 weeks before being used.

Dispersion of experimental nests within the 10 ha was achieved by first establishing 40 evenly spaced points over the tract (Fig. 1), then using alternate points for placement of each week's 20 nests. Actual locations of nests in relation to each point were determined by selecting two numbers between 0 and 18 from a table of random numbers. These numbers dictated the distance in paces and compass direction from the point (even, north and east; odd, south and west) that each nest was to be placed. We then put the

TABLE 1. The outcome of visited and unvisited experimental nests, according to month

	Preyed upon								
	Failed[a]		Disturbed[b]		Successful		Destroyed by weather		
Month	N	%	N	%	N	%	N	%	Total
May									
Visited nests	13	33	7	17	20	50	0	0	40
Unvisited nests	10	25	2	5	27	68	1	2	40
June									
Visited nests	10	25	4	10	26	65	0	0	40
Unvisited nests	7	18	4	10	25	62	4	10	40
July									
Visited nests	5	12	1	2	33	84	1	2	40
Unvisited nests	5	12	5	12	28	71	2	5	40
Total	50	21	23	10	159	66	8	3	240

[a] Failed = two eggs missing after 6 days.
[b] Disturbed = one egg missing after 6 days.

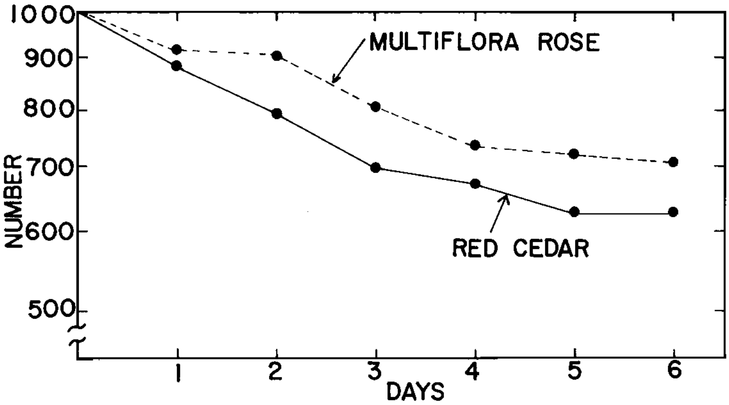

Fig. 3. Survivorship curves of visited experimental nests in multiflora rose and red cedar; data from all months pooled.

nest in the nearest site that appeared suitable. This insured even dispersion of nests throughout the study area each week.

Experimental nests were placed in sites that we think closely resembled nest sites of Cardinals, chats, Mourning Doves, and Field Sparrows. Most frequently selected sites were in multiflora rose, red cedar, and on the ground at the base of small cedars and saplings. After placing each elevated nest in position, the junior author estimated its degree of concealment to the human eye. Nests were ranked as concealed (rank = 2), intermediate (1), or exposed (0) from each of three perspectives, viz., above, below, and to the sides. Rankings of the three positions were summed to give concealment ratings for all elevated nests. Completely concealed nests were rated as 6, totally exposed nests as 0.

On finding an experimental nest with one or both eggs missing, we examined the nest and ground below to determine if wind had dumped the contents. If so, the nest is excluded from all analyses. All other nests that lacked eggs are classified as preyed upon (Nolan 1963, Thompson and Nolan 1973), since it is unlikely that Brown-headed Cowbirds (*Molothrus ater*) took any of the missing eggs (Thompson and Gottfried 1976).

While the experiment was being performed, we also followed the nest success of birds breeding on the study area. All natural nests were visited daily and the eggs in each were handled in the same way as in the experimental nests. To calculate success of these natural nests, we used only those found before the last egg of the clutch was laid. Although this decreases our sample of natural nests, it eliminates the bias toward success that comes from including nests found at different stages of the nesting cycle (Mayfield 1961; 1975; Nolan 1963). Of the 30 natural nests studied, 10 each were found in May, June, and July.

The following subsamples and terms are defined for analytical purposes: (1) For comparisons of visited vs. unvisited and experimental vs. natural nests, nests that lost one egg (disturbed) or both eggs (failed) are pooled as having been taken by a predator. (2) For comparisons of durations of survival of nests and for construction of survivorship curves both disturbed and failed nests are used; when nests failed but eggs disappeared on different days, we calculated failure as occurring on the date the first egg disappeared. The figure used for the time of failure was 0.5 days before the day the failure was discovered.

RESULTS

Seasonal predation trends.—Predation of experimental nests was highest in May (41%) and declined through June (33%) and July (21%). Although the monthly survivorship curves of the visited experimental nests differ greatly, the approximately straight lines obtained for May and July indicate a constant rate of predation throughout the 6 days of exposure (Fig. 2). Visited June nests, however, suffered no losses after their third day of exposure. The mean length of survival of experimental nests suffering predation did differ significantly between months (May $\bar{x} = 2.5$ days, June $\bar{x} = 1.6$ days, July $\bar{x} = 2.7$ days; Kruskal-Wallis test, $H = 124.25$, $P < 0.05$).

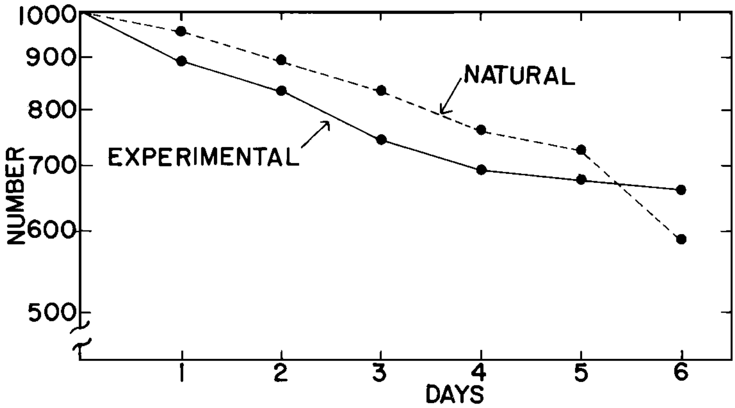

Fig. 4. Survivorship curves of visited experimental and natural nests; data from all months pooled.

Effect of observer visits.—To determine whether observer activity affected the chance that a predator would take the eggs, data on predation of visited nests are compared with those for unvisited experimental nests (Table 1). There were no differences either for the season as a whole (adjusted χ^2 test, $\chi^2 = 0.34, P > 0.05$) or for any month (May $\chi^2 = 2.28$, $P > 0.05$; June $\chi^2 = 0.03$, $P > 0.05$; July $\chi^2 = 0.81, P > 0.05$). Thus daily visits to nests did not significantly increase predation rates.

Effect of concealment and site.—Concealment ratings of 68 elevated nests taken by predators did not differ significantly from ratings of 137 successful elevated nests (successful median = 3.0, unsucessful median = 3.0; Mann-Whitney *U*-test, $U = 3926$, $P > 0.05$). Furthermore, the length of survival of 26 visited elevated nests that lost both eggs was not correlated with their concealment ratings (Kendall's tau = 0.12, $P > 0.05$).

The numbers of experimental nests taken by predators in multiflora rose and red cedars did not differ significantly for the season ($\chi^2 = 1.89$, $P > 0.05$) or for any month (May $\chi^2 = 1.64$, $P > 0.05$; June $\chi^2 = 1.06$, $P > 0.05$; July $\chi^2 = 0.01$, $P > 0.05$) (Table 2). Nor did duration of survival of visited nests that were taken differ significantly between multiflora rose and red cedar nests (cedar median = 1.5 days; multiflora rose median = 2.5 days; $U = 149.5$, $P > 0.05$). Inspection of survivorship curves of nests in the two substrates suggests that the failure rate was constant and therefore independent of the duration of exposure (Fig. 3).

Numbers of elevated and ground experimental nests preyed upon were not significantly different ($\chi^2 = 1.41, P > 0.05$). Duration of survival of ground and elevated experimental nests suffering predation cannot be compared because of the small sample size of visited ground nests.

Comparison between experimental and natural nests.—To approach the problem of whether nest failure is related to parental activity, visited experimental nests (no parental activity) and visited natural nests (parental activity) are compared. Because of the 6 day period of our experiments, only the first 6 days after discovery of the natural nests are considered. Twelve of 30 natural nests (40%) and 40 of 119 experimental nests (34%) were taken; this difference is not statistically significant ($\chi^2 = 0.19$, $P > 0.05$). Similarily, the duration of survival of experimental nests preyed upon (median = 2.5 days) and of natural nests (median = 2.5 days) did not

TABLE 2. The outcome of experimental nests in relation to nest site. Visited and unvisited nests are pooled

	Preyed upon								
	Failed		Disturbed		Successful		Destroyed by weather		
Month	N	%	N	%	N	%	N	%	Total
May									
Elevated nests									
Multiflora rose	7	22	4	12	20	63	1	3	32
Cedar	14	42	3	9	16	49	0	0	33
Other[a]	1	50	0	0	1	50	0	0	2
Ground nests	1	8	2	16	10	76	0	0	13
June									
Elevated nests									
Multiflora rose	5	14	5	14	24	64	3	8	37
Cedar	10	36	2	7	15	54	1	3	28
Other[a]	1	17	0	0	5	83	0	0	6
Ground nests	0	0	1	11	8	89	0	0	9
July									
Elevated nests									
Multiflora rose	6	16	3	8	26	68	3	8	38
Cedar	3	9	3	9	26	82	0	0	32
Other[a]	1	20	0	0	4	80	0	0	5
Ground nests	1	20	0	0	4	80	0	0	5
Totals									
Elevated nests									
Multiflora rose	18	17	12	11	70	65	7	7	107
Cedar	27	29	8	9	57	61	1	1	93
Other[a]	3	23	0	0	10	77	0	0	13
Ground nests	2	7	3	11	22	82	0	0	27

[a] Other includes blackberry (*Rubus* sp.), hawthorn (*Crataegus* sp.), honeysuckle (*Lonicera* sp.), etc.

differ significantly ($U = 312.0$, $P > 0.05$). The survivorship curves of both visited experimental and of natural nests suggest that likelihood of failure was independent of duration of exposure (Fig. 4).

DISCUSSION AND CONCLUSIONS

Predation of the experimental nests follows the pattern observed for natural nests in other old-field habitats (Nolan 1963, Thompson and Nolan 1973) as well as for natural nests found on the Bachelor Estate (Fig. 4, Thompson and Gottfried unpubl. data). Although we estimate that our placement of experimental nests approximately doubled the density of nests on the study area, we saw no evidence that this attracted unusual numbers of predators. Since circumstances of disappearance of eggs from both natural and experimental nests were indistinguishable, we think that conclusions derived from the use of experimental nests can be applied to natural nests.

Observer activity.—No statistically significant differences were found in any comparison of visited and unvisited nests. Only in May was there an appreciable, but still statistically insignificant, difference in proportions of visited and unvisited nests that failed. Both Stoddard (1931: 195) and Klimstra and Roseberry (1975: 31), who studied the ground-nesting Bobwhite (*Colinus virginianus*) in habitat similar to ours, found no evidence that nest visits by observers affected the chance that a nest would be destroyed by a predator. Roseberry and Klimstra (1970: 258) reached the same conclusion after visits to Eastern Meadowlark (*Sturnella magna*) nests, and Willis' (1973) elegant indirect observations on visited and unvisited nests of Bicolored Antbirds (*Gymnopithys bicolor*) in tropical rainforest also revealed no differences.

In old fields, mammals, birds, and snakes are predators of eggs and nestlings. Nolan (1963, unpubl. data), Thompson and Nolan (1973), and Thompson (unpubl. data) have observed several species of snakes, Blue Jays (*Cyanocitta cristata*), and eastern chipmunks (*Tamias striatus*) take eggs and young from nests in Indiana and Georgia old fields. We saw few chipmunks on the Bachelor Estate. However, black rat snakes (*Elaphe obsoleta*), other snakes, and Blue Jays were abundant and probably were responsible for most egg losses. These predators, unlike larger mammals, take only contents and leave the nest intact (Nolan 1963, Thompson and Nolan 1973), which was the condition of the large majority of our natural and experimental nests suffering predation.

Of the potential predators, mammals are the most likely to find nests by noting human activity or by following trails (Earl 1950, Willis 1973). However, Stoddard (1931: 195) makes an important point about predators' using human activity to find nests, ". . . [where] the whole terrain is daily crisscrossed by the trails of people going about their work afield . . . there would be no conceivable gain for any creature to follow out these countless trails." Blue Jays also might use cues left by humans (cf. Picozzi 1975), but in our opinion snakes would be less likely to do so. As most predators on our nests probably were snakes and, perhaps, Blue Jays, the lack of difference between visited and unvisited nests is not unexpected.

Two features of the design of our experiment should be kept in mind when considering the results. First, each experimental nest was exposed to predators for only 6 days, to avoid spoilage of the eggs. Daily visits over longer periods might increase the likelihood of their discovery. If this were true, however, one would expect natural nests to experience higher daily failure rates after 6 days and, probably, an increase in daily failure rates during the first 6 days; neither of these expectations was fulfilled (see also Mayfield 1975, Thompson and Nolan 1973, Willis 1973). Second, we went to each unvisited nest once, of course, to set it in place. One visit might attract predators just as readily as many visits. But this seems likely to be true only of mammalian predators using scent trails, and we think that it is not applicable to old-field habitats and can be ignored.

Why are some nests preyed upon?—Elimination of questions of the potential effect of observer visits clarifies consideration of other factors that contribute to discovery of nests by predators. Despite the obvious selective value that predator-avoidance adaptations must have for open-nesting birds facing heavy predation, remarkably little attention has been given to such adaptive responses. Use of experimental nests is ideal for such investigations, as one can have large sample sizes and can easily manipulate nest site characteristics.

An obvious hypothesis is that poorly concealed nests are more easily found by predators than are well concealed nests. Nice (1937: 93–94) and Nolan (1977) reported that nests of Song Sparrows and Prairie Warblers (*Dendroica discolor*), respectively, rated by them as poorly concealed were indeed more easily found by predators, but Roseberry and Klimstra (1970: 246) found no relationship between concealment and nest success in Eastern Meadowlarks. Dwernychuk and Boag (1972), using a visual rating system, found no relationship between egg loss and concealment in natural duck nests, but did find an inverse relationship in artificial nests. Cryptically colored eggs of Black-headed Gulls (*Larus ridibundus*) survived significantly longer than exposed or white eggs (Tinbergen et al. 1967). Our results provide no evidence that better concealed nests (to the human observer) suffer less predation: Concealment ratings of preyed upon and successful experimental nests are not significantly different, nor is the duration of survival of nests suffering predation correlated with concealment rating. This was unexpected and may be due, of course, to the crudeness of the visual rating system and analysis. If, however, the results are correct, they suggest that predators do not find nests by simple visual searches, but rather employ subtler means.

Absence of differences in predation of nests in red cedar and multiflora rose was unexpected. Based on past experience in other old-field habitats, we anticipated that few natural nests would be built in red cedars during June and July, when deciduous plants provide adequate nesting cover. If predators focus searching activities on vegetation types in which nests are most frequent, nests in red cedar would be less likely to be taken than those in multiflora rose during June and July. That no difference occurred may have been the result of selection of nest sites in red cedar throughout June and July by Mourning Doves and, unexpectedly, Cardinals and Field Sparrows. Natural nests were probably sufficiently numerous in both coniferous and deciduous sites all summer to keep predators searching in both.

The suggestion that predators find nests by being attracted to parental activity appears to be widely accepted (Skutch 1949, Hammond and Foreward 1956, Willis 1973), although Ricklefs (1969: 6) pointed out that his survey of the literature on nest success produced little evidence to support the hypothesis. Neither did our results support it. Experimental nests suffered approximately the same loss as natural nests built and attended by parents. Of course, our experimental nests may have been more poorly concealed than natural nests, and deficient concealment may have offset the attraction of parental activity to natural nests. However, although we did not give concealment ratings to natural nests, it seems unlikely that experimental nests were regularly more poorly concealed than natural nests. Furthermore, the demonstrated lack of correlation between concealment and survival of experimental nests suggests that concealment may not strongly affect nest success.

The design of this experiment does not allow further investigation of possible cues that predators use to find nests. More experimental work in old-field habitats is needed to examine the roles played by concealment, olfaction, and nest site in determining nest success.

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