

INVESTIGATOR VISITATION AND PREDATION RATES ON
BIRD NESTS IN BURNED AND UNBURNED TALLGRASS
PRAIRIE IN OKLAHOMA: AN EXPERIMENTAL STUDY

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Activities of field ornithologists can influence the phenomena they observe (Lenington, 1979; Götmark, 1992). In studies of nest success, which require repeated visits to active nests (Mayfield, 1961, 1975), predators following investigators or investigator spoor to nests could lead to biased estimates for nest survival and predation rates (MacInnes and Misra, 1972; Bowen et al., 1976). Investigator visitation may have no effect on rates of nest loss in some habitats or for some species (e.g., Gottfried and Thompson, 1978; Götmark et al., 1990), but because habitat structure and distribution and type of predators can vary among study sites, it is prudent to perform preliminary tests before assuming that rates of predation on nests are unaffected by human disturbance during any particular study of nest success.

In recent years, investigators have performed controlled studies on environmental factors that can affect rates of nest success, through widespread use of artificial nests (e.g., Gottfried and Thompson, 1978; Janzen, 1978; Loiselle and Hoppes, 1983; Wilcove, 1985; Martin, 1987; Sieving, 1992). Although rates of nest loss obtained from most of these experiments cannot be directly extended to real nests, they can, nevertheless, provide some idea about the kinds of cues predators use to locate nests, and help identify habitats where nests may be more vulnerable to predation.

We conducted two sets of artificial nest experiments as part of a larger study of nesting success of breeding birds in native tallgrass prairie. In particular, we wished to determine (1) whether the frequency of our visits to nests biased rate of nest loss to a significant extent, and (2) if the pattern varied between burned and unburned grasslands. We discuss patterns detected by our experiments and identify reasons for caution in interpretation and application to natural nests. To the best of our knowledge, information of this kind from extensive tracts of tallgrass prairie is limited to Bowen et al. (1976; but see also Mankin and Warner, 1992).

Our field experiments were conducted in northeastern Oklahoma. During 14–27 July 1992, three lines of artificial nests were placed on a private ranch about 5 km SE of Bartlesville, Washington Co.; the ranch had been burned in early April and was being grazed by cattle at the time of the experiment. Concurrently, three lines of artificial nests were placed on The Nature Conservancy's Tallgrass Prairie Preserve, about 24 km N of Pawhuska, Osage Co.; this area had been unburned and ungrazed for the previous two years. During 7–12 June 1993, six lines of artificial nests were placed on the Tallgrass Prairie Preserve. Three lines were in sites unburned for three years (lines 2 and 3 in Table 1 were in the same site each year) and three lines were in sites burned in April; all sites experienced about three weeks of grazing in May. At all sites where cattle grazing occurred, stock densities were moderate for tallgrass prairie (usually <3.0 individuals/ha). All lines in both experiments were placed in relatively homogeneous grassland without obvious habitat edges, although two lines in 1992 and one line in 1993 crossed drainages. In none of these cases was there a correlation between predation rate and proximity to a drainage. No two lines were closer than 1 km. Use of three lines within each land treatment during each experiment decreased the likelihood of bias from habitat patchiness and the non-uniform distribution of predators. For logistical reasons, initial placement of lines varied by three days between land treatments in 1992, and four days in 1993.

Artificial nests were commercial canary wicker nest cups (10 cm wide by 6 cm deep), each containing three quail (*Coturnix coturnix*) eggs. Eggs were kept refrigerated prior to use and inspected at the time they were placed in nests to insure that none were cracked or dented; all eggs used were spotted or mottled to some degree.

Lines of artificial nests consisted of ten stations of paired ground nests, for a total of 20 nests per line. Stations were about 30 m apart, with one nest placed 10 m perpendicular to the axis of the

TABLE 1—Total number of visited and control nests depredated from each of three lines in two land treatments in tallgrass prairie, Oklahoma (see text for further description of land treatments). Each line initially contained 20 nests, divided equally between visited and control groups.

	1992		1993	
	Visited	Control	Visited	Control
Burned				
Line 1	1 ¹	1 ¹	2	2
Line 2	3 ²	0 ³	1	1
Line 3	5 ¹	3 ¹	1	2
Unburned				
Line 1	2	2	4	6
Line 2	1	3	3	3
Line 3	3 ¹	4	10	7

¹ One nest trampled by cattle during experiment.

² Two nests trampled by cattle during experiment.

³ Four nests trampled by cattle during experiment.

line on either side of the station marker (a small flag or wooden survey stake). Only a minimal effort was made to simulate natural nest sites, so most artificial nests were more exposed than natural ones. No two artificial nests were closer than 20 m. All nests were left in place for two weeks to simulate natural incubation periods of ground-nesting passerines at our sites, and were subjected to one of two treatments. Half of the nests on each line ("visited nests"), all on the same side of the station markers, were checked every three or four days for a total of four visits after initial placement. This frequency of visitation matched that of natural nests monitored concurrent with our experiments. The other half of the nests ("control nests") were not revisited until retrieved two weeks after placement.

Artificial nests were considered depredated if at least one egg was destroyed or removed. Length of nest survival for visited nests was 14 days if undisturbed, or the number of days from initial exposure to the mid-point between the day a nest was found depredated and the previous check day. Daily probabilities of nest survival on visited artificial nests were calculated according to Mayfield (1961, 1975) as $1 - (\text{number of destroyed nests} \div \text{total nest-exposure days})$; 95% confidence limits follow Johnson's (1979) method.

Vegetation near lines on the ranch was dominated by switchgrass (*Panicum virgatum*), little bluestem (*Schizachyrium scoparium*), Indian grass

(*Sorghastrum nutans*), southern ragweed (*Ambrosia bidentata*), and big bluestem (*Andropogon gerardii*). Dominant vegetation on the Tallgrass Prairie Preserve was switchgrass, big bluestem, Indian grass, and rough dropseed (*Sporobolus asper*). Measurement of maximum vegetation height was taken at 20 random points on 16.3-ha study plots monitored for grassland bird nesting activity during each breeding season. Vegetation measurements were collected during 21–30 July in 1992 and 25 May–8 June in 1993. At each point, height of the tallest vegetation within a 1-m radius circle was recorded. In 1992, three plots on the ranch yielded 60 points from burned prairie and six plots on the Tallgrass Prairie Preserve yielded 119 points (one point inadvertently skipped) from unburned prairie. In 1993, three plots on the Tallgrass Prairie Preserve yielded 60 points from burned prairie and six plots yielded 120 points from unburned prairie. Statistical procedures follow Sokal and Rohlf (1981).

Although substantial variability in predation rates existed between lines within land treatments (e.g., burned areas in 1992 and unburned areas in 1993; Table 1), there is no a priori reason to assume results from any single line were most representative of average conditions. Therefore, results from all lines within a treatment were pooled for each year.

In 1992, 34.6% of visited nests and 16.7% of control nests were depredated in burned grassland ($G = 2.136$, $d.f. = 1$, $P > 0.2$); in unburned grassland, 20.7% of visited and 30.0% of control nests were depredated ($G = 0.678$, $d.f. = 1$, $P > 0.4$). Nests trampled by cattle (Table 1) were not included in those comparisons, but loss of nests to trampling may have influenced the P value in the burn treatment because of reduced sample sizes. In 1993, 13.3% of visited nests in burned grassland and 16.7% of control nests were depredated ($G = 0.132$, $d.f. = 1$, $P > 0.5$), whereas 56.7% of visited and 53.3% of control nests in unburned grassland were depredated ($G = 0.068$, $d.f. = 1$, $P > 0.5$).

Cumulative frequencies of nest loss for visited nests varied between treatments and years (Fig. 1). In 1992, seven (77.8%) of nine depredated nests in the burn treatment and five (83.3%) of six depredated nests in the unburned treatment were lost by the second nest check (day 8). In contrast, respective treatment values of nest loss in 1993 were zero (0.0%) of four nests and nine (52.9%) of 17 nests by the second check (day 7).

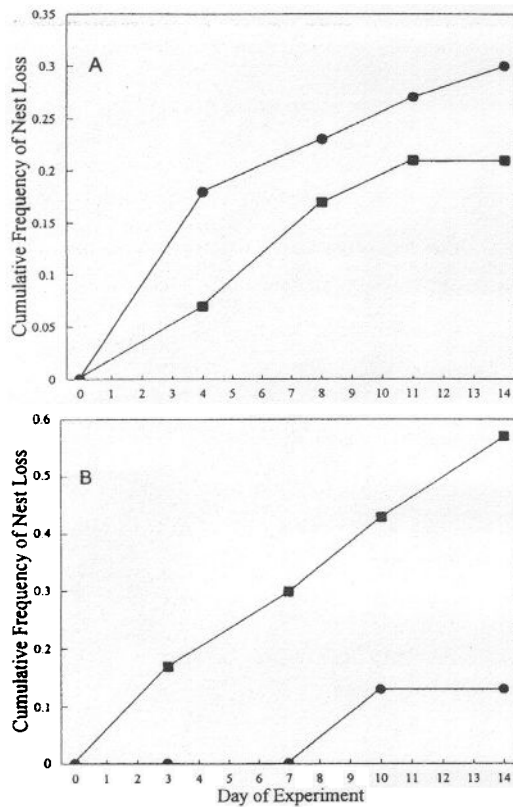


FIG. 1.—Cumulative frequency of nest loss in tall-grass prairie, Oklahoma for visited artificial nests in 1992 (A) and 1993 (B). Circles are values from burned treatments and squares are values from unburned treatments.

Length of survival of visited nests was nearly equal between treatments in 1992 (burned $\bar{X} = 11.1$ d, $n = 26$; unburned $\bar{X} = 12.2$ d, $n = 29$; Wilcoxon Rank Sum test on medians, $z = -0.90$, $P = 0.367$), but differed significantly in 1993 (burned $\bar{X} = 13.3$ d, $n = 30$; unburned $\bar{X} = 9.7$ d, $n = 30$; $z = -3.03$, $P = 0.002$).

Total nest loss, with visited and control nests pooled from all lines, differed little between treatments in 1992 ($G = 0.004$, $df = 1$, $P > 0.9$), but artificial nests in the unburned areas experienced much greater predation than in burned areas in 1993 ($G = 22.084$, $df = 1$, $P \ll 0.001$). Daily probability of survival ($\pm 95\%$ confidence limits) was greater for visited artificial nests in unburned than burned grassland in 1992 (0.981 ± 0.015 versus 0.958 ± 0.023 , respectively; $P < 0.01$). The pattern was reversed in 1993, with greater probability of survival for visited artificial

nests in burned grassland (0.990 ± 0.010 versus 0.942 ± 0.027 for unburned grassland; $P < 0.01$). These daily survival probabilities are for all destroyed artificial nests, including those trampled by cattle in 1992. When trampled visited nests were deleted from the 1992 experiment, there was still a significant difference in daily survival for artificial nests in unburned and burned grassland (0.983 ± 0.014 and 0.969 ± 0.020 , respectively; $P < 0.01$).

Maximum height of grassland vegetation at the time of our experiments was greater in the unburned treatments in both years. However, the difference was slight in July 1992 (burned = 90.6 ± 25.7 cm, $n = 60$; unburned = 96.7 ± 19.8 cm, $n = 119$; $t = 1.613$, $P > 0.1$) whereas height in unburned sites was double that in the burned sites in June 1993 (burned = 34.4 ± 10.4 cm, $n = 60$; unburned = 68.0 ± 15.7 cm, $n = 120$; $t = 17.108$, $P \ll 0.001$). Maximum height was highly correlated ($r = 0.9$, $P < 0.001$) with an index of vegetation density in the first 0.5 m of above-ground vegetation (Hendricks and Reinking, unpubl. data), indicating that vegetation was both denser and taller on unburned sites, thereby providing more overhead cover to ground nests.

Visiting artificial nests every three or four days had little apparent influence on vulnerability to predation on our study sites (Table 1), a result consistent with other experimental studies in old-field and grassland habitats (Bowen et al., 1976; Gottfried and Thompson, 1978; Mankin and Warner, 1992). We conclude that predators are probably not following our spoor to natural ground nests to any significant extent, at least during the incubation phase of nesting.

Daily survival probabilities for our artificial nests often exceeded values for natural nests of Dickcissels (*Spiza americana*), Grasshopper Sparrows (*Ammodramus saviarum*) and Eastern Meadowlarks (*Sturnella magna*) by 0.2 to 10.8% on our study plots (Hendricks and Reinking, unpubl. data). Several factors could contribute to the disparity. First, no adult birds incubated our artificial nests, so cues used by predators to locate those nests were unrelated to parental behavior of birds (see Bowen and Simon, 1990). Second, because artificial nests were only crude mimics of natural nests, predators may have failed to recognize them as sources of food rewards (Martin, 1987). Third, quail eggs are larger than eggs of ground-nesting passerines on our study plots and may have been too large for some

predators to handle (Roper, 1992), leading to underestimates of predation rates. In 1992 we found several unbroken quail eggs in nests or on the ground nearby that had been gnawed by mice, most likely *Microtus ochrogaster*. Conversely, absence of adult birds may have encouraged some predators usually denied access to nests. In 1993, 13 eggs in 10 nests were punctured (holes up to 12 mm diameter) in a manner attributable to Eastern Meadowlarks (Picman, 1992). We suspect that most birds could defend nests against mice and meadowlarks, but it remains undetermined to what extent these two species destroy natural nests in tallgrass prairie. Fourth, density of nests in our experiments (20 in 1.32 ha) probably exceeded natural conditions for tallgrass prairie. However, predator search patterns for natural nests may not have been adjusted to this unnatural situation (e.g., Anglestam, 1986). Other experimental studies have failed to detect a relationship between nest density and predation rate (Reitsma, 1992), and predation on natural nests also appears to be density-independent in tallgrass prairie, at least for Dickcissels (Zimmerman, 1984). Fifth, our experiments were conducted during a small segment of the breeding season; differences in survival probabilities between artificial and natural nests may relate to seasonal variation in vulnerability.

Susceptibility to nest predation differed between burned and unburned prairie grassland for artificial nests, but the pattern was unaffected by investigator visitation in either treatment (Table 1). Artificial nest survival was slightly better on unburned treatments in 1992 and significantly better on burned treatments in 1993 (Table 1, Fig. 1). Inconsistencies in experimental results could relate to weaknesses in our experimental design. For example, experiments were conducted in different months during the two years, and burned treatments where artificial nests were placed experienced different grazing impacts. Both of these variables probably affected our results to some extent. Even the unburned treatments were not directly comparable between years. One of three lines of artificial nests had to be moved to a new location in 1993, and all 1993 unburned sites had undergone an additional year without burning. Nevertheless, daily survival probabilities declined in 1993 for artificial nests in unburned treatments, consistent with a positive relationship between frequency of burning and nest survival for several passerine species breeding in

tallgrass prairies in Minnesota (Johnson and Temple, 1990). This result suggests that certain patterns of nest predation on natural nests may be detected by use of artificial substitutes. However, general patterns of nest survival may not be uniform among species using the same suite of habitats (Hendricks and Reinking, unpubl. data), so caution is required when extrapolating results from nest-survival experiments to natural nests.

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LITERATURE CITED

- ANGELSTAM, P. 1986. Predation on ground-nesting birds' nests in relation to predator densities and habitat edge. *Oikos*, 47:365-373.
- BOWEN, D. E., AND M. P. SIMON. 1990. Greater Prairie Chickens attract predators to their nests. *Trans. Kansas Acad. Sci.*, 93:3-7.
- BOWEN, D. E., R. J. ROBEL, AND P. G. WATT. 1976. Habitat and investigators influence artificial ground nest losses: Kansas. *Trans. Kansas Acad. Sci.*, 79: 141-147.
- GÖTMARK, F. 1992. The effects of investigator disturbance on nesting birds. *Curr. Ornithol.*, 9:63-104.
- GÖTMARK, F., R. NEERGAARD, AND M. ÅHLUND. 1990. Predation of artificial and real Arctic Loon nests in Sweden. *J. Wildl. Mgmt.*, 54:429-432.
- GOTTFRIED, B. M., AND C. F. THOMPSON. 1978. Experimental analysis of nest predation in an old-field habitat. *Auk*, 95:304-312.
- JANZEN, D. H. 1978. Predation intensity on eggs on the ground in two Costa Rican forests. *Amer. Midland Nat.*, 100:467-470.
- JOHNSON, D. H. 1979. Estimating nest success: the Mayfield method and an alternative. *Auk*, 96:651-661.
- JOHNSON, R. G., AND S. A. TEMPLE. 1990. Nest predation and brood parasitism of tallgrass prairie birds. *J. Wildl. Mgmt.*, 54:106-111.
- LENINGTON, S. 1979. Predators and blackbirds: the

- "Uncertainty Principle" in field biology. *Auk*, 96: 190-192.
- LOISELLE, B. A., AND W. G. HOPPE. 1983. Nest predation in insular and mainland lowland rain-forest in Panama. *Condor*, 85:93-95.
- MACINNIS, C. D., AND R. K. MISRA. 1972. Predation on Canada Goose nests at McConnell River, Northwest Territories. *J. Wildl. Mgmt.*, 36:414-422.
- MANKIN, P. C., AND R. E. WARNER. 1992. Vulnerability of ground nests to predation on an agricultural habitat island in east-central Illinois. *Amer. Midland Nat.*, 128:281-291.
- MARTIN, T. E. 1987. Artificial nest experiments: effects of nest appearance and type of predator. *Condor*, 89:925-928.
- MAYFIELD, H. 1961. Nesting success calculated from exposure. *Wilson Bull.*, 73:255-261.
- . 1975. Suggestions for calculating nest success. *Wilson Bull.*, 87:456-466.
- PICMAN, J. 1992. Egg destruction by Eastern Meadowlarks. *Wilson Bull.*, 104:520-525.
- REITSMA, L. 1992. Is nest predation density dependent? A test using artificial nests. *Canadian J. Zool.*, 70:2498-2500.
- ROPER, J. J. 1992. Nest predation experiments with quail eggs: too much to swallow? *Oikos*, 65:528-530.
- SIEVING, K. E. 1992. Nest predation and differential insular extinction among selected forest birds of central Panama. *Ecology*, 73:2310-2328.
- SOKAL, R. R., AND F. J. ROHLF. 1981. *Biometry*. W. H. Freeman and Co., San Francisco, California.
- WILCOVE, D. S. 1985. Nest predation in forest tracts and the decline of migratory songbirds. *Ecology*, 66:1211-1214.
- ZIMMERMAN, J. L. 1984. Nest predation and its relationship to habitat and nest density in Dickcissels. *Condor*, 86:68-72.