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PREDATION RATES ON REAL AND ARTIFICIAL NESTS OF GRASSLAND BIRDS

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ABSTRACT.—We estimated nesting success at real and artificial nests of grassland birds to test the influence of nest type, nest position, and egg size on predation rates. We distributed wicker nests and realistic woven-grass nests baited with a clay egg and either a Northern Bobwhite (*Colinus virginianus*) egg or a House Sparrow (*Passer domesticus*) egg in four grasslands that were part of the Conservation Reserve Program in east-central Illinois. Nesting success averaged 86.5% for 12 days of exposure for artificial nests. For real nests, nesting success was markedly lower, averaging 39% over the entire nesting cycle and 59% during approximately 12 days of incubation. Wicker nests were depredated more often than woven-grass artificial nests (18% vs. 8%), and nests baited with House Sparrow eggs were depredated more often than nests baited with Northern Bobwhite eggs (22% vs. 9%). Elevated and ground nests were depredated at the same rate. Patterns of nest predation on wicker nests were markedly different from depredation patterns on real nests over time and among fields. In contrast, patterns of nest predation on realistic woven-grass nests corresponded much more closely with predation rates of real nests over time and among fields. We suggest that future artificial nest studies use nests and eggs that mimic as closely as possible the real nests and eggs of target species. Use of unrealistic artificial nests and eggs, at least in grasslands, may result in patterns of predation that do not accurately reflect those of real nests. Artificial nests of any type appear to underestimate predation rates on nests of grassland birds, possibly because of a lack of snake predation on artificial nests. Received 30 July 1998, accepted 16 June 1999.

ARTIFICIAL NESTS have been one of the most widely used means of assessing the effect of different variables on rates of nest predation (Major and Kendall 1996). However, many of these studies may be of limited use, because they assume that data from wicker baskets and quail eggs are comparable with data from real nests. In addition, few studies have used artificial nests to study nest predation in grasslands (e.g. Kulesza 1980, Burger et al. 1994, Hughes 1996, Bergin et al. 1997). Of these, only Hughes (1996) provided comparative data on real nests in this habitat.

Artificial nests typically have been designed as all-purpose nests to examine predation rates at the community scale (Langen et al. 1991, Bayne and Hobson 1997). In addition, most of the studies that used artificial nests provided no comparative data on predation rates at natural nests, and those that provided such data have produced conflicting results (Major and Kendall 1996). There are several possible expla-

nations for this lack of consensus. Predator species are seldom documented, even though several studies have shown that different predators prey upon artificial versus natural nests (Willebrand and Marcstrom 1988, MacIvor et al. 1990). Moreover, the realism of artificial nests is known to affect predation rates (Martin 1987).

In addition, the size of the eggs used in a study can affect predation rates by reducing the influence of small predators that are unable to break large eggs (Roper 1992, Haskell 1995, DeGraaf and Maier 1996). Eighty-two percent of 67 artificial nest studies reviewed by Major and Kendall (1996) used either quail eggs or chicken eggs, both of which are much larger and have thicker shells than eggs of the small passerines that researchers usually attempt to mimic.

Many researchers acknowledge that absolute rates of predation may not be the same at artificial nests and real nests, but that artificial nests should represent the relative rates or patterns of predation among different treatments, such as habitat type, patch size, or distance from edge (Sullivan and Dinsmore 1990, Bayne

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et al. 1997). This assumption is commonly accepted despite several studies that show a lack of correlation between relative predation rates on real and artificial nests (George 1987, Stooraas 1988, Reitsma et al. 1990, Roper 1992). Given the ubiquity of artificial nest studies and their influence on ecological theory and conservation efforts, it is important that the assumptions of these studies continue to be examined critically.

Our objectives were to (1) compare absolute and relative predation rates between natural nests, and realistic and unrealistic artificial nests in grasslands; (2) compare predation rates between artificial and natural domed nests on the ground and elevated open-cup nests; and (3) assess the effect of egg size on rates of predation.

METHODS

Study area.—Our research was conducted in Coles and Cumberland counties in east-central Illinois, where the topography is primarily flat on the uplands and gently rolling along drainages. Approximately 70% of the land is used to grow corn and soybeans. The average daily maximum temperature is 29°C. The average annual precipitation is 94 cm, 60% of which falls from April through September (Illinois Agricultural Experiment Station 1993).

Six fields from the Conservation Reserve Program (CRP) were selected for study in the fall of 1996. The fields ranged in size from 13 to 29 ha (\bar{x} = 24 ha) and were planted with redtop (*Agrostis alba*) and/or orchard grass (*Dactylis glomerata*) in 1989, 1992, or 1993. Three 12-day artificial nest trials were conducted between 25 May and 13 July 1997. A 12-day exposure period was selected because it is a typical incubation period for many grassland passerines. Fourteen artificial nests were placed in each field for each trial. Trial 1 ran from 25 May to 6 June, trial 2 from 11 to 23 June, and trial 3 from 1 to 13 July. One orchard grass field was dropped from the study owing to lack of nesting activity. The real and artificial nests from two redtop fields that were connected by a grassed waterway and an unmowed section of Kentucky bluegrass (*Poa pratensis*) were lumped together into one field to increase the sample size of natural nests. This resulted in 210 artificial nests being set out in four CRP fields.

Artificial nests.—Half of the artificial nests were constructed by weaving dried grass into a wire frame (12 cm outside diameter, 6 cm high, 4.5 cm deep; see Kulesza 1980, Sieving 1992) in a manner that approximated the size and appearance of a Dickcissel (*Spiza americana*) nest. The other half of the artificial nests consisted of wicker baskets of the type

used in many previous studies (e.g. Burger et al. 1994). Dimensions of the wicker nests were 10 cm wide and 5 cm deep. All nests were exposed to the weather for one week prior to being placed in fields.

Nest sites for each trial were randomly selected along existing survey transects located 100 m apart and parallel to the longest axis of the field. The placement of each nest was determined by selecting three random numbers. The first number indicated the distance along the transect, the second indicated the right-angle distance from the transect, and the third indicated the side of the transect. Wicker and grass nests were placed alternately on the ground hidden in leaves of grass (to imitate Eastern Meadowlark [*Sturnella magna*] nests) or in an elevated position 20 to 50 cm above the ground in a suitable forb or clump of grass (to imitate Dickcissel nests). Nest locations were marked with flagging tape 5 m to the north of nests.

One Northern Bobwhite (*Colinus virginianus*; hereafter "quail") egg or one House Sparrow (*Passer domesticus*; hereafter "sparrow") egg was alternately placed in each artificial nest, which also held one clay egg. This resulted in a nearly equal number of combinations of nest positions and egg types for wicker and grass nests. Different sizes of eggs were used to assess the effect of small predators that may not be able to break the shells of quail eggs (Reitsma et al. 1990, DeGraaf and Maier 1996). Tooth and bill marks in clay eggs were used to facilitate predator identification. We wore rubber gloves when distributing artificial nests to reduce human scent.

At the time of nest placement, we measured the distance of each artificial nest to a row crop, road, and wooded edge by pacing. We checked each nest after 6 and 12 days of exposure to determine its fate. Nests were considered depredated if the sparrow egg or quail egg was damaged or missing. If the clay egg had tooth marks from rodents, but the other eggs were undamaged, the nest was not counted as depredated.

Natural nests.—The success of natural nests was determined by locating and monitoring nests in each CRP field. Teams of three to four people searched for and monitored nests in each field following guidelines in Martin and Geupel (1993). We calculated daily survival rates and estimated Mayfield nesting success (Mayfield 1961, 1975) for all nests. All nests were marked with flagging tape placed 5 m to the north. The outcome of each attempt was assessed using the techniques of Best and Stauffer (1980). Nest failure was attributed to weather when nests were abandoned after a severe storm. Nests were considered abandoned from unknown causes when nest contents remained unchanged and adults were not present during two successive visits. Nest failure was attributed to Brown-headed Cowbird (*Molothrus ater*) parasitism when nests were abandoned after cowbird egg(s) were deposited, when only cowbird eggs

TABLE 1. Number of active nests, Mayfield nesting success (number of exposure days in parentheses), and daily survival rate (\pm SE) of the most common nesting species in four Conservation Reserve Program fields in east-central Illinois in 1997.

Species	<i>n</i>	Nesting success (%)	Daily survival rate
Bobolink (<i>Dolichonyx oryzivorus</i>)	20	62.0 (173)	0.983 \pm 0.003
Dickcissel (<i>Spiza americana</i>)	36	43.0 (468)	0.964 \pm 0.009
Eastern Meadowlark (<i>Sturnella magna</i>)	81	32.0 (975)	0.960 \pm 0.002
Field Sparrow (<i>Spizella pusilla</i>)	36	39.0 (333)	0.955 \pm 0.011
Grasshopper Sparrow (<i>Ammodramus savannarum</i>)	27	35.0 (212)	0.953 \pm 0.015
Red-winged Blackbird (<i>Agelaius phoeniceus</i>)	83	20.0 (845)	0.890 \pm 0.009
Overall	283	38.5 (3,005)	0.951 \pm 0.004

remained in the nest, or when only cowbird young fledged.

Statistical analyses.—The daily survival rates between real and artificial nests were statistically compared using the methods of Johnson (1979). Multi-factor contingency analysis (PROC CATMOD; SAS 1994) was used to determine if predation rates on realistic and wicker artificial nests corresponded with predation rates on real nests among fields and over time. Nest type (wicker vs. realistic), egg type (sparrow vs. quail), nest position (ground vs. elevated), field (four fields), and time period (three time periods), were used as factors in the analysis.

RESULTS

Of the 210 artificial nests set out in CRP fields, four could not be relocated. Twenty-seven of the remaining 206 artificial nests were depredated, resulting in a daily survival rate of 0.988 and a Mayfield nesting success estimate of 86.5%. Overall, 283 nests of the six most numerous species had a daily survival rate of 0.951 and 38.5% nesting success (Table 1). The Mayfield daily survival rate differed significantly ($P < 0.001$) between artificial and real nests. Wicker nests were depredated more often (18%) than were woven-grass nests (11%; $\chi^2 = 5.9$, $df = 1$, $P = 0.02$; Table 2). Nests baited

with quail eggs were depredated less often than nests baited with sparrow eggs ($\chi^2 = 4.6$, $df = 1$, $P = 0.03$). Rates of predation on ground and elevated nests were not different ($\chi^2 = 0.04$, $df = 1$, $P = 0.84$). Patterns of nest predation on wicker nests were different from those on real nests over time ($\chi^2 = 5.9$, $df = 1$, $P = 0.05$; Fig. 1) and among fields ($\chi^2 = 10.1$, $df = 1$, $P = 0.02$; Fig. 1). However, patterns of nest predation on realistic artificial nests corresponded closely with patterns of predation on real nests over time ($\chi^2 = 0.3$, $df = 1$, $P = 0.87$) and among fields ($\chi^2 = 1.6$, $df = 1$, $P = 0.65$; Fig. 1).

Clay eggs showed signs of predation in 80 of 206 artificial nests; however, the quail egg or sparrow egg was depredated in only 27 of these 80 nests. There was no relationship between the clay egg being damaged and the fate of the real egg when nests holding either a quail egg or a sparrow egg were combined ($\chi^2 = 0.33$, $df = 1$, $P = 0.56$), or when nests were separated into those with a sparrow egg ($\chi^2 = 0.001$, $df = 1$, $P = 0.98$) and those with a quail egg ($\chi^2 = 1.0$, $df = 1$, $P = 0.31$). Fifty-four of the 206 clay eggs contained tooth marks from small rodents. Of the 27 nests in which the real egg was depredated, seven clay eggs had been removed from

TABLE 2. Mayfield nesting success (number of exposure days in parentheses) and daily survival rate (\pm SE) for different categories of artificial nests.

Nest category	No. nests	Nesting success (%)	Daily survival rate
Wicker	102	82.3 (1,386)	0.984 \pm 0.004
Grass	108	88.7 (1,488)	0.995 \pm 0.003
Elevated	109	89.2 (1,068)	0.990 \pm 0.031
Ground	101	85.2 (900)	0.987 \pm 0.048
Wicker with Northern Bobwhite	48	90.4 (636)	0.991 \pm 0.006
Wicker with House Sparrow	54	78.3 (708)	0.980 \pm 0.003
Grass with Northern Bobwhite	61	92.8 (816)	0.995 \pm 0.012
Grass with House Sparrow	47	87.5 (627)	0.989 \pm 0.007
Overall	210	86.5 (2,874)	0.989 \pm 0.014

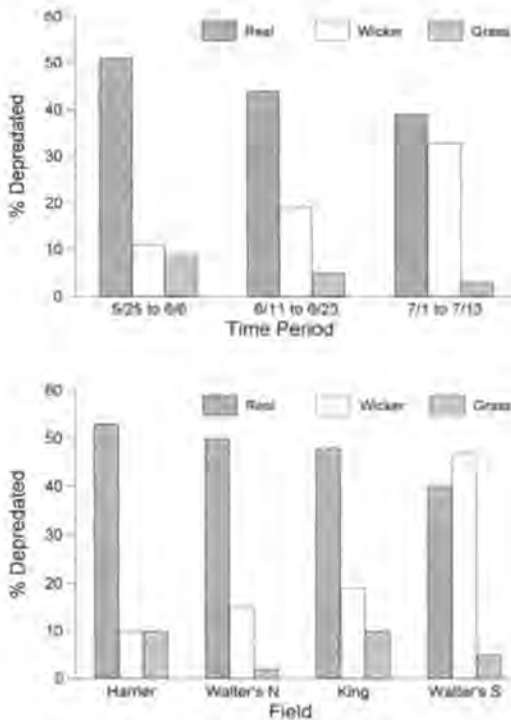


FIG. 1. Percent of real nests, artificial wicker nests, and artificial grass nests depredated in CRP fields in east-central Illinois. Comparisons are made among time periods and among fields.

the nest and could not be relocated. Nine clay eggs had small puncture marks characteristic of predation by small rodents, seven eggs had a single large puncture mark and/or parallel lines characteristic of avian predation, and four eggs had multiple medium-sized puncture marks characteristic of predation by large mammals. No relationship occurred between predator type and nest type ($\chi^2 = 0.64$, $df = 2$, $P = 0.73$), or between predator type and nest position ($\chi^2 = 0.94$, $df = 2$, $P = 0.63$).

DISCUSSION

Predation on artificial nests was significantly lower than on real nests. This is the same pattern found in Kansas CRP fields by Hughes (1996), which is the only other study that compared nesting success between real and artificial nests of grassland birds. The rate of predation on wicker nests (18%) more closely approximated that on real nests (50% over the entire nesting cycle and 34% over the incubation

period) compared with the 11% rate of predation on realistic grass nests. Most researchers acknowledge that comparisons of the absolute rate of predation between real and artificial nests are not always valid; however, these researchers often assume that artificial nests accurately represent the relative rate or pattern of predation on real nests over time, among sites, or among different types of habitat (Sullivan and Dinsmore 1990, Bayne et al. 1997). Despite more closely approximating the absolute rate of predation on real nests, patterns of predation over time and among fields for wicker nests did not correspond with those for real nests. In fact, the patterns for wicker nests were nearly opposite those for natural nests. In contrast, rates of predation on grass nests corresponded much more closely with those on real nests, both over time and among fields. This suggests that in grasslands, the realism of artificial nests is important for ensuring that patterns of predation on these nests accurately reflect patterns of predation on real nests.

For several reasons, the realism of the artificial setup (nest type and egg type) is important for studies that use artificial nests. Visually oriented predators, such as birds, may locate wicker nests more easily than real nests (George 1987, Willebrand and Marcstrom 1988, Sullivan and Dinsmore 1990). The realism of eggs used in artificial nests may be important if small predators, such as mice and shrews, are present (Maxson and Oring 1978, Roper 1992, DeGraaf and Maier 1996). The use of eggs larger than those of the target species may preclude predation by small predators (Roper 1992, Haskell 1995, DeGraaf and Maier 1996). This appears to have happened in our study, because small rodents chewed on 39% of all clay eggs, and nests baited with quail eggs were depredated less often than nests baited with sparrow eggs. The lack of parental activity at artificial nests may dramatically reduce a predator's ability to locate the nest, while at the same time allowing small predators, such as rodents, to eat eggs without being attacked by one or both parents. Also, cues given by parents (e.g. movement, sounds, and scent) may increase predation by mammals (Vickery et al. 1992), birds (Storaas 1988, Willebrand and Marcstrom 1988, MacIvor et al. 1990), and some snakes (Goodman and Goodman 1976, Hoi and Winkler 1994).

The importance of snakes as predators of bird nests in grasslands and shrublands has been well documented (Fitch 1963, Best 1978, Thompson et al. 1999). Although we cannot absolutely rule out other predators, an increasing body of evidence suggests that snakes are one of the dominant predators of nests in grasslands and shrub habitats. In addition, Thompson et al. (1999) used video cameras to document that snakes were the primary predators of bird nests in old-field habitat and that 88% of nests depredated by snakes showed no signs of disturbance other than egg removal. In contrast, 83% of the nests depredated by mammals and birds showed signs of disturbance. Given that only 10% of the 283 real nests depredated in our study showed signs of disturbance, it is likely that snakes were significant predators. Prairie kingsnakes (*Lampropeltis calligaster*), common garter snakes (*Thamnophis sirtalis*), black rat snakes (*Elaphe o. obsoleta*), and blue racers (*Coluber constrictor*) were common on our study sites. We monitored more than 20 nests where one or two young or eggs disappeared over a period of several days. The disappearance of single eggs over multiple days was observed at a Northern Mockingbird (*Mimus polyglottos*) nest, where a Texas rat snake (*Elaphe obsoleta lindheimeri*) consumed the incubating female (Joern and Jackson 1983), and at Field Sparrow (*Spizella pusilla*) and Indigo Bunting (*Passerina cyanea*) nests depredated by snakes (Thompson et al. 1999). We observed two incidents of snake predation, one in which a prairie kingsnake ate nestling Grasshopper Sparrows (*Ammodramus savannarum*), and another in which a common garter snake ate nestling Field Sparrows. The prairie kingsnake had a hatching Grasshopper Sparrow (one or two days old) in its mouth when it was discovered at the nest. Upon being disturbed, the snake dropped the nestling and disappeared. We monitored that nest over the next three days, and one nestling disappeared every day for four days until the nest was empty.

Given that snakes can be important nest predators in grasslands, understanding their role as predators of artificial nests will lead to more accurate assessments of predation on real nests. There are several reasons to question the ability of artificial nests to accurately represent snake predation. Marini and Melo (1998) showed that 22 species of snakes known to eat

bird eggs exhibited no response to quail eggs presented to them in captivity at room temperature, and an additional nine species showed no response to eggs heated to a normal incubation temperature. In addition, snakes rarely, if ever, have been documented depredating artificial nests, despite the proliferation of studies that have used cameras to monitor nests (Marini and Melo 1998).

The cues used by snakes to locate and capture their prey provide insight into why snake predation may be underestimated in artificial nest studies. Some snakes use the intensity of parental mobbing behavior to locate nests (Goodman and Goodman 1976). A combination of visual and chemical stimuli may be required to elicit a response from some snakes. Visual cues have been shown to be important for snake foraging (Czaplicki and Porter 1974, Drummond 1979), but in the absence of chemical cues it has been shown that visual stimuli from live prey do not elicit attack by newborn garter snakes (Burghardt 1966). Given the widespread occurrence of snakes and the fact that they have never been documented eating eggs in an artificial nest, it seems likely that the cold, relatively scent free, unattended eggs in artificial nests do not stimulate snakes to eat them.

Most ecological theory developed from studies that used artificial nests has been derived from forest habitats, where artificial nests often are depredated at higher rates than real nests (Reitsma 1992, Wilson et al. 1998). In contrast, predation rates on artificial nests in grasslands often are lower than those on real nests (Kulesza 1980, Hughes 1996, Bergin et al. 1997). This may be due in part to snakes not eating eggs in artificial nests.

We found that patterns of predation on artificial wicker nests did not correspond with those on real nests. The incidence of predation on wicker nests increased over time, whereas the incidence of predation on real nests decreased. Patterns of predation on our grass artificial nests accurately reflected patterns of predation on real nests, but we did not confirm whether the same species of predator had depredated real nests and grass nests. A correlation between rates of predation on real nests and grass artificial nests could reflect the general activity pattern of the entire predator assemblage (especially the "non-snake" compo-

ment). This seems to be a likely explanation, given that snakes appeared to be major predators of real nests, yet rarely (if ever) depredated an artificial nest.

Our results indicate that the relative rate of predation on wicker artificial nests does not necessarily represent the relative rate of predation on real nests. Future studies should attempt to identify predators of real and artificial nests and use artificial setups that match as closely as possible the nests and eggs of target species to reduce the biases associated with wicker nests and quail eggs. Use of artificial nests in grasslands may never be a good idea unless artificial nests can be designed to "attract" snakes as predators.

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