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YAHNER, R. H., AND C. A. DELONG. 1992. Avian predation and parasitism on artificial nests and eggs in two fragmented landscapes. Wilson Bull. 104:162–168.

PREDATION ON ARTIFICIAL NESTS IN LARGE FOREST BLOCKS

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Abstract: Neotropical migrant birds are declining within many forest communities in North America and concern exists regarding the impact of forest fragmentation on their breeding success, particularly with respect to nest predation. We studied predation on artificial ground nests in large forest blocks to provide information for comparison with forest fragments and to determine the importance of predator community and vegetation. From May through August 1991, we distributed 320 artificial ground nests over 8 4-ha study plots and measured 12 vegetational variables at these nests. We used remote-triggered cameras to identify predators. Nest predation rates varied from 5 to 40% among study plots. Vertical vegetational density, horizontal log density, and percent herbaceous, rock, soil, and litter cover were different ($P < 0.05$) between successful and unsuccessful nests. A diverse predator community, including small mammals, is responsible for loss of artificial nests and predation rates are not solely a function of forest size.

J. WILDL. MANAGE. 58(2):254–260

Nest predation is the major factor reducing breeding success of open-nesting passerine birds (Ricklefs 1969, Martin 1991). High predation rates may cause fluctuations in bird populations (Angelstam 1986, Sherry and Holmes 1991). The decrease of Neotropical migrants that breed within forest interior habitats of the eastern United States has been attributed to increased nest predation rates as a consequence of forest fragmentation (Wilcove 1985, Terborgh 1989, Askins et al. 1990).

Some artificial nest studies have demonstrated that nest predation rates increase with a decrease in forest area (Wilcove 1985, Small and Hunter 1988). High rates of nest predation in forest fragments are usually attributed to a few predator species, such as raccoon (*Procyon lotor*), gray fox (*Urocyon cinereoargenteus*), sciurids, and corvids, that show increased densities along forest edges (Gates and Gysel 1978, Yahner and Wright 1985, Ratti and Reese 1988). However, techniques used to identify predators often were not successful (Wilcove 1985) or predator identity was speculated (Rearden 1951, Yahner and Wright 1985, Angelstam 1986). Recently, more refined techniques for identifying nest predators, such as trip cameras, have been developed (Martin 1987, Picman 1988, Reitsma et al. 1990).

Foliage and spatial vegetational densities also influence nest predation by affecting nest concealment and hinderance of predator movement (Martin 1991). Studies of artificial nest predation in forest fragments have not assessed the importance of vegetation (Wilcove 1985, Yahner and Scott 1988). Few studies have attempted to identify predators and the influence of vegetation on predation rates (Boag et al. 1983, Reitsma et al. 1990).

Prior to studying the impact of forest area on nest predation, it is necessary to understand how vegetational features and predator composition influence nest predation in large forest blocks, the natural breeding habitats of interior forest bird species. Our objective was to determine the intensity of predation on artificial ground nests, quantify the importance of understory vegetation relative to nest predation, and identify nest predators associated with large forest blocks.

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STUDY AREA

We established 8 plots: 3 plots were located on the Conservation and Research Center (CRC), a 1,200-ha research facility located 2 km southeast of Front Royal, Virginia; and 5 plots were located in the northern sector of the Shenandoah National Park (SNP), Virginia. The 8 plots were randomly selected from 24 potential sites within a 40-km radius of CRC. Potential sites met several criteria: they had similar overstory composition and were ≥1 km apart in large (CRC, 400 ha; SNP, 77,900 ha), mature (>40 yrs) forests on federal lands. All sites were >200 m from a large (>1 ha) forest opening and had not experienced significant dieback due to insect defoliation.

We placed eggs within plots, as opposed to a transect, to minimize linear placement of eggs and allow the location of all eggs within a plot to be described by the same vegetational measurements taken for the forest stand. Each plot consisted of a 4-ha grid of 100 stations. Each station was 20 m apart and marked with a 30-cm, white, plastic pipe. Four plots with 3-m-high wire fences, constructed during winter 1991, excluded white-tailed deer (*Odocoileus virginianus*). The mesh size was 19 × 16 cm for the lower 1.5 m.

Red oak (*Quercus rubra*), white oak (*Q. alba*), tulip poplar (*Liriodendron tulpifera*), hickory (*Carya* spp.), black locust (*Robinia pseudoacacia*), and white ash (*Fraxinus americana*) dominated forest overstories (Gleason and Cronquist 1963). Common understory shrubs were spicebush (*Lindera benzoin*), dogwood (*Cornus florida*), hackberry (*Celtis occidentalis*), and hawthorn (*Crateagus* spp.).

METHODS

Field Procedure

To determine predation rates we placed 10 artificial ground nests on 2 plots each week from May through August 1991. We tested each of these plots 4 times, with ≥3 weeks between

trials. We tested 2 plots each week due to limited numbers of remote-triggered cameras. Nest sites were ≥60 m apart at randomly selected stations. No station was used as a nest site twice. We constructed ground nests within 5 m of a station by forming depressions in the ground or in leaf litter close to a shrub, log, or trunk. We lined nests with leaves, moss, dry grass, and other organic materials found in the vicinity. We placed 2 fresh northern bobwhite (*Colinus virginianus*) eggs in each nest. At the end of each 7-day trial we removed the eggs. We chose this 7-day period to avoid attracting predators to putrid eggs (McDonald et al. 1994) and to allow comparison with previous artificial nest predation studies (Wilcove 1985, Yahner and Scott 1988). We handled eggs and nest materials with vinyl rubber gloves. A nest was considered unsuccessful when ≥1 egg was destroyed or removed.

Each week from June through August 1991, we monitored 8 of the 10 nests on each plot with remote-triggered, 35-mm cameras to identify nest predators. The camera system had an infrared light beam and was activated by sudden changes in the heat profile of the monitored area (Rappole et al. 1986). An automatic flash enabled identification of nocturnal as well as diurnal predators. Cameras were equipped with automatic film advance, and each picture was stamped with day-hour-minute. We mounted cameras to trees within 1.5–5.0 m of the nest and focused them on the nest. We considered a nest detected when it was either unsuccessful or ≥1 picture of a nest predator was obtained. We considered species photographed at nests predators when they destroyed a nest or were previously reported to prey on bird eggs.

To test the impact of cameras and fences on predation rates, we established control plots 40 m from 2 fenced and 2 unfenced plots. We tested control plots at the same time as their corresponding study plots, using the same protocol, except no cameras monitored nests.

To examine the rate at which predators triggered camera systems without the presence of nests, we set up 10 cameras without nests on 4 study plots for 7 days in April 1991. Two plots were fenced and 2 unfenced. We mounted cameras to trees at randomly selected stations and set the cameras to their maximum monitoring range of approximately 25 m to increase triggering by passing animals.

We measured vegetational variables at 199 nests of which 62 were unsuccessful. We deter-

mined foliage density at 2 heights (0.0–0.5 and 0.5–1.0 m) by counting the squares (10 × 5 cm) that were covered by foliage on a 0.25-m² board (Nudds 1977). We obtained these counts for the 4 cardinal compass directions at a distance of 5 m. We added the 4 foliage cover values for each height and used them as an index (Cover I and II) of foliage density.

To assess spatial densities of trees, shrubs, and logs, we used a point-centered quarter method (Mueller-Dombois and Ellenberg 1974). We established 4 quadrants around the nest site and determined the distance from the nest to the closest tree, shrub, and log in each quadrant. We averaged the 4 values and used it as an index for the variable's density at each nest site. We counted the number of woody stems within 1 m² of the nest and estimated percent ground cover for 6 variables (woody stems, herbaceous, logs, rocks, soil, and leaf litter).

Analyses

The number of predated and nonpredated nests was compared for each month and each site, using Chi-square and Tukey tests (Meyers and Grossen 1974). We compared the number of detected and undetected nests for each site, using Chi-square tests. The number of predated and nonpredated nests, for nests with and without cameras, was compared using Chi-square analysis. To obtain information about the distribution of predator species over the landscape, we used the ratio of mean to variance in the number of pictures per study plot: $D = s^2/\bar{x}$ (Pianka 1974). For randomly distributed predators this coefficient equals unity. Distribution coefficients greater than unity indicate clumped distributions, and those less than unity reflect dispersion of predators over plots.

Analyses examining the effect of vegetation on predation rates included a test for normal distribution and homogeneity of variances before employing 2-tailed t-tests and analysis of variance. The mean values for all vegetational variables were compared for predated and nonpredated nests. Percent cover data were arcsine transformed to meet assumptions of normal distribution prior to analyses.

RESULTS

Predation Rates

Predators detected 114 (35.6%) nests and destroyed or removed eggs at 63 (19.7%) nests. Predation did not change over time (pairwise

Table 1.   Number of detected (predator photographed but eggs not destroyed) and destroyed artificial nests set up for 7 days on study plots in large (>300 ha) forest blocks, Virginia, 1991. Predation rates for control plots in parentheses.

Study plots[a]	No. of nests	No. of detected nests	No. of predated nests	Predation rate
A	40	14	5	12.5 (35.0)
B	40	17	13	32.5 (15.0)
C	40	7	2	5.0
D	40	13	3	7.5
E	40	14	5	12.5 (20.0)
F	40	17	12	30.0 (20.0)
G	40	18	16	40.0
H	40	14	7	17.5
Total	320	114	63	19.7

[a] Study plots A through D were fenced in winter 1990–91.

comparisons between months; $n = 32$, 28 df, HSD = 1.68, $P > 0.05$), and the number of unsuccessful nests from May through August was pooled by plot. Predation rates ranged from 5.0 to 40.0% among plots and were different among plots ($n = 320$, $\chi^2 = 29.23$, 7 df, $P < 0.001$) (Table 1). Detection rates among study plots ranged from 17.5 to 45.0% (Table 1), but were not different ($n = 320$, $\chi^2 = 9.10$, 7 df, $P = 0.245$) (Table 1). Detection rates were correlated with predation rates ($n = 8$, $r_s = 0.855$, $P = 0.007$).

Predation was lower on one fenced study plot and higher at the other fenced study plot than on their corresponding control plots (A: $n = 80$, $\chi^2 = 5.60$, 1 df, $P = 0.018$; B: $n = 80$, $\chi^2 = 3.38$, 1 df, $P = 0.066$) (Table 1). Because large predators such as black bear (*Ursus americanus*) and bobcat (*Lynx rufus*) were photographed on fenced plots (Table 3) and thus not obstructed by fences, differences in predation rates may not be attributed to fences.

Cameras did not affect predation rates. There were no differences in predation rates between the 2 unfenced study plots with cameras and their corresponding control plots without cameras (E: $n = 70$, $\chi^2 = 0.73$, 1 df, $P = 0.393$; F: $n = 80$, $\chi^2 = 1.07$, 1 df, $P = 0.302$) (Table 1).

Predator Identification

Cameras were present at 52 of 63 destroyed nests and identified predators at 35 nests. Striped skunk (*Mephitis mephitis*) and raccoon were the most important predators, having destroyed 15 and 12 nests, respectively (Table 2). Of the 35 camera nests that provided identification of predators, 18 (51%) were visited subsequently by ≤5 species. In 5 cases photographs did not

Table 2.   Number of artificial nests, destroyed or detected (includes predator photographed when eggs were not destroyed; in parentheses), by predators at 8 study plots in large (>300 ha) forest blocks, Virginia, 1991; n = 40 nests/plot.

Species	Study plots[a]							
	A	B	C	D	E	F	G	H
Raccoon	2 (6)	0	0 (1)	0 (2)	1 (2)	8 (10)	0 (1)	1 (1)
Striped skunk	0	7 (7)	0	0 (1)	0	0 (1)	8 (8)	0
White-footed mouse	0	2 (4)	0 (1)	0 (3)	0	0 (2)	0	0 (1)
Gray squirrel	0 (4)	1 (1)	0 (1)	0	0 (2)	0	0	0 (2)
Black bear	0	0	0	0	0	0	1 (1)	0 (1)
Bobcat	0	0	0	0	0 (1)	0 (1)	0	0
Virginia opossum[b]	0	0	0	0 (1)	0 (1)	0	0	0
Gray fox	0	0	0	0	0	0	0	1 (2)
Eastern chipmunk[b]	0	0	0	0	0 (1)	0	0	0
Domestic cat	0	0	0	0	0 (1)	0	0	0
Unknown mammal	0 (1)	0 (1)	0	0	0 (1)	0	0 (1)	0
American crow[b]	0	0	0	0	0	0	0	1 (1)
Blue jay[b]	0 (1)	0	0	0	0	0	0	0
Unknown bird	1 (1)	0	0	0 (2)	0 (1)	0	1 (2)	0 (1)

[a] Study plots A through D were fenced in 1990–91.

[b] Scientific names for opossum (*Didelphis virginiana*), eastern chipmunk (*T. striatus*), American crow (*Corvus brachyrhynchos*), and blue jay (*Cyanocitta cristata*) not in text.

enable us to determine which predators actually ate or removed eggs. These nests were first detected by 1 raccoon, 3 striped skunks, and 1 gray fox; we concluded that these predators removed eggs.

We obtained 241 predator pictures at detected nests (Table 3). The number of pictures was higher than the number of detected or destroyed nests because predators did not always destroy nests after detection and 43% of all detected nests were visited by 2–5 species.

Most predators were photographed investigating nests. The mean number of predators per 100 camera hours detected at nests with cameras ($\bar{x}$ = 0.83, SD = 0.46) was higher than the mean number of predators per 100 camera hours detected at cameras ($\bar{x}$ = 0.12, SD = 0.11) in April 1991 (F = 8.57, 1 df, P = 0.015).

The majority of predators occurred in clumped distributions, with highest values for striped skunk and raccoon (Table 3). Striped skunk were responsible for much of the predation at plots B and G, whereas raccoon caused most of the predation on plot F.

Vegetational Effects

There were differences between successful and unsuccessful nests for 6 variables (Table 4). When compared with unsuccessful nests, foliage density (Cover I and II) and herbaceous ground cover were high at successful nests, while log density, rock, and soil ground cover were low at successful nests.

DISCUSSION

High nest predation rates within small (<100 ha) forest blocks versus large forest blocks are often attributed to a higher abundance of nest

Table 3.   Number of pictures for predator species at artificial nest plots (A–D fenced, E–H unfenced) in large (>300 ha) forest blocks, Virginia, 1991.

Species[a]	Study plots								D[b]
	A	B	C	D	E	F	G	H	
Raccoon	13	1	2	1	14	40	2	2	16.30
Striped skunk	0	25	0	1	0	1	29	0	19.20
White-footed mouse	0	8	1	6	0	7	7	2	2.58
Gray squirrel	8	3	2	0	5	0	0	5	2.65
Black bear	0	4	0	0	1	0	10	1	5.92
Bobcat	0	1	0	2	1	0	0	0	1.00
Opossum	0	0	0	1	1	1	4	0	1.84
Gray fox	0	0	0	0	0	0	0	5	2.62
Eastern chipmunk	1	0	0	0	1	0	0	0	0.87

[a] One each of the following were photographed: domestic cat, long-tailed weasel (*Mustela frenata*), American crow, and blue jay.

[b] Distribution coefficients were calculated by $D = s^2/\bar{x}$ (Pianka 1974).

Table 4. Vegetation measurements at successful and unsuccessful artificial nests in large (>300 ha) forest blocks, Virginia, 1991.

Vegetational variable	Successful nests n = 137		Unsuccessful nests n = 62		
	$\bar{x}$	SE	$\bar{x}$	SE	*t*-value[a]
Cover I[b]	79.94	20.20	66.24	27.20	3.96***
Cover II[b]	49.54	30.24	39.08	31.32	2.24*
Tree density[c]	3.73	1.03	3.63	1.18	0.62
Shrub density[c]	4.44	3.58	4.69	3.37	−0.46
Log density[c]	1.39	0.89	2.00	1.42	−3.64***
Woody stems[d]	6.00	7.61	4.15	6.31	1.75
Woody stems cover[e]	0.33	0.28	0.28	0.20	1.18
Herbaceous cover[e]	0.56	0.38	0.45	0.31	2.08*
Log cover[e]	0.23	0.17	0.26	0.15	−1.31
Rock cover[e]	0.21	0.16	0.29	0.19	−3.01**
Soil cover[e]	0.10	0.01	0.13	0.13	−2.01*
Litter cover[e]	0.67	0.30	0.73	0.24	−1.55

[a] Values generated by a 2-tailed *t*-test with 197 df; *$P = 0.05$, **$P = 0.01$, ***$P = 0.001$.

[b] No. of squares on coverboard that contained vegetation at 0.0–0.5 (Cover I) and 0.5–1.0 m (Cover II) aboveground.

[c] Distance (m) from nest to nearest feature for 4 quadrants around nest.

[d] No. within m².

[e] % cover within m².

predators such as raccoon or corvids (Wilcove 1985, Ratti and Reese 1988, Yahner and Scott 1988). The effect of these edge-adapted predators in large forests is considered to be minimal and therefore nest predation rates were generally assumed to be low in these habitats (Gates and Gysel 1978, Wilcove 1985, Yahner and Scott 1988).

We observed predation rates in large (>300 ha) forest blocks that are above those described for large forest blocks in previous artificial nest studies (Wilcove 1985, 9%; Small and Hunter 1988, 3–9%; Yahner and Scott 1988, 9%). Nest predation rates within forest habitats are not solely determined by forest size but also by predator species, density, and composition (Reitsma et al. 1990), as well as vegetational characteristics (Bowman and Harris 1980, Martin 1991). In this study, the clumped distribution of striped skunk and raccoon resulted in high predation rates at 3 plots. Nest success may depend on placement relative to predator distribution (Boag et al. 1983, Reitsma et al. 1990).

Many investigators have attempted to identify nest predators. Identification techniques used included determination of predator sign characters (Rearden 1951), trackboards (Wilcove 1985, Angelstam 1986), fluorescent pigments (McDonald et al. 1994), and trip cameras (Martin 1987, Picman 1988, Reitsma et al. 1990). Our results differ from these studies in composition of the nest predator community, the high number of predator species, and because

nests were frequently detected by >1 predator species.

Former studies, even those that used cameras, did not report sequences of predators at nests (Wilcove 1985, Angelstam 1986, Martin 1987, Picman 1988). Single species were identified as nest predators in these studies, but we suspect these techniques may be selective, with results biased toward large or medium-sized predators.

Raccoon and striped skunk were the most important nest predators in our study, indicating that these edge-habitat species may be as important in large forest blocks as they are in forest fragments. Although small rodents, such as deer mice (*Peromyscus maniculatus*), have been identified as nest predators (Maxson and Oring 1978, Boag et al. 1983, Reitsma et al. 1990), they often have been ignored in studies on nest predation in large forest blocks (Wilcove 1985, Yahner and Wright 1985, Yahner and Scott 1988). In our study, white-footed mice (*P. leucopus*) frequently detected nests and destroyed ≥2 of them. Nevertheless, egg loss relative to detection was low for white-footed mice and gray squirrels (*Sciurus carolinensis*). This may be due to the large bobwhite eggs that are less vulnerable to predation by small predators than are passerine eggs (Reitsma et al. 1990). Given the high number of nests detected by white-footed mice and gray squirrels, these species may be important nest predators on small passerines.

Using cameras, we found a more diverse nest

predator community (13 species) than described in other studies (Henry 1969, Wilcove 1985, Reitsma et al. 1990; 6–9 species). Predation on artificial nests in this study did not depend on a few important species but on the community of predators. Therefore, removal of specific predator species, as practiced in marsh and forest habitats (Chesness et al. 1968, Duebbert and Lokemoen 1980, Reitsma et al. 1990), may temporarily reduce predation, but would soon be compensated for by other species.

High foliage and spatial vegetational densities reduce nest predation in woodlands (Martin 1991). Bowman and Harris (1980) demonstrated that increased densities of trees and shrubs decreased predation efficiency of raccoon. Our results also suggest that there is an effect of foliage density on artificial nest predation. Nest predation was correlated with several vegetational variables at the microhabitat level (i.e., nest). Except for log density, however, we did not find differences in spatial vegetational density (e.g., tree or shrub density) between successful and unsuccessful nests. The preferred use of logs as pathways by small mammals (Barnum et al. 1992) may result in higher activity in areas with high log densities and thus explain the influence of this variable.

The shortcomings of using artificial nests to study nest predation have been discussed (Lennington 1979, Götmark and Åhlund 1986, Martin 1987, Stooras 1988, Reitsma et al. 1990). Artificial nests differ in many ways from natural nests (e.g., appearance, nest location, obstructive identification techniques, human scent at the nest, egg size, absence of adult birds). Although the accuracy of artificial nests in measuring predation on real nests is uncertain (Martin 1987, Yahner and Voytko 1989), they permit controlled experiments with sophisticated identification techniques and large sample sizes.

We took precautions to minimize the negative impacts of our methods. However, many nests were detected by predators but not destroyed. Cameras did not affect predation rates, but timid species may have been discouraged from destroying nests by egg size or unnatural appearance of the nests. Cameras enabled us to determine these potential predators and to quantify their potential impact on the nest predation rate (i.e., by creating a nest detection rate). We believe that detection rates may be a more accurate measurement for actual nest predation. However, focus should be placed on us-

ing real nests to test the role of vegetation and predator distribution in determining predation on ground nests. Results from artificial nest studies should be used to develop hypotheses about predation on natural nests.

MANAGEMENT IMPLICATIONS

Predation rates may not be solely determined by forest size. Large forest blocks can have high nest predation rates and need to be managed to increase their suitability as breeding grounds for migratory songbirds.

The relationship between vegetation and predation on artificial ground nests in this study suggests that management decisions (e.g., selective logging, gypsy moth control, and regulation of white-tailed deer populations) that affect understory vegetation also will affect migratory bird populations (DeGraaf et al. 1991, McShea and Rappole 1992). Because of the compensatory effects that are to be expected in a diverse predator community, we feel that removal of predators is not an appropriate tool to reduce predation rates and manage forest habitats for migratory birds.

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