

Differences in Predators of Artificial and Real Songbird Nests: Evidence of Bias in Artificial Nest Studies

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Abstract: *In the past two decades, many researchers have used artificial nests to measure relative rates of nest predation. Recent comparisons show that real and artificial nests may not be depredated at the same rates, but no one has examined the mechanisms underlying these patterns. We determined differences in predator-specific predation rates of real and artificial nests. We used video cameras to monitor artificial nests baited with quail and plasticine eggs and Field Sparrow (*Spizella pusilla*) and Indigo Bunting (*Passerina cyanea*) nests in field habitats in central Missouri (U.S.A.). Although daily predation estimates (all predators pooled) were similar between artificial and real nests, predators differed substantially in their depredation of artificial versus real nests. Snakes were the major predator at real nests, and raccoons (*Procyon lotor*) were the major predator at artificial nests. We found strong support for models that distinguished predation between two or among three predator groups and between artificial and real nests. There was no snake predation of artificial nests, and the odds of predation of artificial nests was 115–551% (95% confidence interval) and 2–154% of the odds of predation of real nests by mammals and birds, respectively. Artificial nests with plasticine eggs could not be used reliably to identify predators. In several cases plasticine eggs were marked by mice, and raccoons were recorded on video removing the quail egg. Because biases for artificial nests were positive for some predators and negative for other predators (and could be compensating), and potentially existed for all predator groups, conclusions based on artificial nest studies should be suspect even when there is evidence that overall predation rates are similar among real and artificial nests.*

Key Words: artificial nests, Field Sparrows, Indigo Buntings, nest predation, predators, raccoons, snakes, songbirds

Diferencias entre Nidos Artificiales y Reales de Aves Canoras: Evidencia de Sesgos en Estudios de Nidos Artificiales

Resumen: *En las últimas dos décadas, muchos investigadores han utilizado nidos artificiales para medir las tasas relativas de depredación de nidos. Comparaciones recientes muestran que nidos artificiales y reales no pueden ser depredados con las mismas tasas, pero nadie ha examinado los mecanismos que subyacen en estos patrones. Determinamos diferencias en las tasas de depredación específicas en nidos reales y artificiales. Utilizamos video cámaras para monitorear nidos artificiales cebados con huevos de codorniz y de plastilina y nidos de *Spizella pusilla* y *Passerina cyanea* en hábitats de pradera en Missouri central (E.U.A.). Aunque las estimaciones de depredación diarias (todos los depredadores combinados) fueron similares en los nidos artificiales y reales, los depredadores difirieron sustancialmente en su depredación de nidos artificiales versus reales. Los principales depredadores de nidos reales fueron culebras y los principales depredadores de nidos artificiales fueron mapaches (*Procyon lotor*). Encontramos un fuerte sustento para modelos que distinguieron depredación entre dos o tres grupos de depredadores y entre nidos artificiales y reales. No hubo depredación por culebras en nidos artificiales y la probabilidad de depredación de nidos artificiales fue 115–551% (95%*

IC) y de 2-154% en nidos reales por mamíferos y aves, respectivamente. No se pudieron utilizar los nidos artificiales con huevos de plastilina confiablemente para identificar depredadores. En varios casos, los huevos de plastilina fueron marcados por ratones y se filmó a mapaches removiendo el huevo de codorniz. Debido a que los sesgos para nidos artificiales fueron positivos para algunos depredadores y negativos para otros (y podrían compensarse) y existieron potencialmente para todos los grupos de depredadores, se debe desconfiar en conclusiones basadas en estudios con nidos artificiales aun cuando haya evidencia de que las tasas generales de depredación en nidos reales y artificiales sean similares.

Palabras Clave: aves canoras, culebras, depredación de nidos, depredadores, mapaches, nidos artificiales, *Passerina cyanea*, *Spizella pusilla*

Introduction

In recent decades, artificial nests have become a popular tool for measuring aspects of nest predation, which is the largest source of mortality in birds (Ricklefs 1969). Interest in nest predation and use of artificial nests to measure it have attracted additional interest because of population declines in some North American birds, especially grassland and shrubland birds (Askins et al. 1990; Askins 2000). Artificial nests offer intriguing possibilities for nest-predation studies because they are amenable to manipulation, can be used in designed experiments, and are available in large enough quantities to permit statistical inference (Major & Kendal 1996).

It remains unclear, however, whether artificial nests and real nests are subject to the same predators and factors that influence predation. Researchers examining the eggs used in artificial nests have found that certain nest predators, particularly snakes, may not take eggs, at least in experimental settings (Marini & Melo 1998). Others have found that different egg types used in artificial nests may be subject to different rates of predation or disturbance (Yahner & Mahan 1996; Lindell 2000) and that the quail eggs (*Coturnix japonica*) often used in artificial nests are too large for smaller mammalian predators (Roper 1992; Haskell 1995; Maier & DeGraaf 2000). Comparisons of predation of artificial nests and active bird nests at the same sites show different levels of predation between the two types, with artificial nests typically experiencing the higher rates (Reitsma 1992; Wilson et al. 1998; King et al. 1999; Burke et al. 2004), although some have shown that artificial nests experience lower predation (Roper 1992; Davison & Bollinger 2000).

The message from these studies is often that results from artificial nest experiments should be interpreted with caution. Although this advice is worthwhile, we still do not know why predation of artificial nests does not reflect predation of real nests. Furthermore, because researchers usually do not know the identity of predators, we do not know whether differences in predation between artificial and real nests vary among predators.

We evaluated the hypothesis that predation differs at real and artificial nests. We used video-monitoring equipment to identify predators at both nest types. Specifically, we evaluated support for our hypothesis that dif-

ferences in predation between real and artificial nests would vary among predators. The predator community at real nests at our old-field study sites has been well documented through video monitoring in two previous studies (Thompson et al. 1999; Thompson & Burhans 2003), but no researchers we know of have used video recorders to monitor artificial nests. In addition to comparing predation at both nest types, we compared predator identification by video monitoring with identification from tooth and claw marks on plasticine eggs, which have been used to identify predators in many artificial nest studies (reviewed in Major & Kendal 1996).

Methods

Study Site

In two earlier studies (Thompson et al. 1999; Thompson & Burhans 2003), we used a miniature video system to identify nest predators in old fields and forests. We located bird nests in field and forest habitats distributed throughout the 920-ha Thomas S. Baskett Wildlife Research and Education Center (38°45'N, 92°12'W) near Ashland, Missouri (U.S.A.). The old fields were 2.4–15.4 ha in size, and forest formed the matrix of the study area. Approximately 60% of the area was mature, oak- (*Quercus* spp.) dominated forest, 16% sapling- to pole-size red cedar (*Juniperus virginiana* L.) and hardwoods, and 8% old fields. The surrounding landscape was approximately 43% forest, and the balance was pasture and dispersed rural housing (E.R.T., unpublished data).

Real Nests

Habitats were searched on 1- to 5-day intervals during 25 April to 30 July in the years 1997–2000, and nests were located by systematic searching of potential nest sites and for behavioral cues from adult birds. We marked nest locations with plastic flagging placed at least 3 m from the nest. We studied Field Sparrows (*Spizella pusilla*) and Indigo Buntings (*Passerina cyanea*) in the field habitat because they were the most abundant nesting species.

We visited nests daily to check their status and to change videotapes. We approached nests and viewed

their contents at the maximum distance possible to determine status and were careful not to leave "dead-end trails" leading to the nest. We confirmed nest fate by viewing videotapes from the last observation day. Video systems consisted of a miniature video camera, a time-lapse video recorder in a weatherproof case (Fuhrman Diversified, Seabrook, Texas), and a 12-V, deep-cycle marine battery. The video camera and six infrared light-emitting diodes were contained in a camera housing of $32 \times 32 \times 60$ mm. The 950-nm infrared light was not visible to vertebrates and allowed us to film in total darkness. The camera housing was on an articulating arm and connected to the video recorder and battery by an 18-m cable. The camera housing and articulating arm were covered by a sleeve made from green camouflage material. The video recorder filmed six frames per second, about one-quarter the speed of standard VHS video, which allowed us to record for 24 hours on standard T120 VHS videotape.

We attached each camera and articulating arm to a wooden stake made from a small dead branch found at the field site. We placed the stake 0.5–1.0 m from the nest and extended the arm so the camera housing was approximately 50 cm from the nest. The camera was located close to the nest to provide adequate infrared illumination at night. We positioned the camera to get the clearest view of the nest, without altering nest concealment, and as low as possible to be inconspicuous and to avoid creating a potential perch site. The video recorder and battery were placed 10–18 m from the nest. We changed the videotape daily and replaced the battery with a fully charged battery every 2–3 days.

We used 12 camera systems to monitor up to 12 nests simultaneously (including artificial nests). We monitored nests with cameras until a nest was entirely depredated, fledged, or abandoned, after which we moved the camera set-up to another nest. Videotapes from the day of a predation event or suspected fledging date were viewed in the lab to confirm the fate of the nest and to identify predators. We placed video cameras at nests after the laying period to minimize nest abandonment caused by disturbance. To further reduce abandonment, starting in 1999 we placed cameras 8–10 m from nests and moved them 2–3 m closer daily until they were 0.5–1.0 m from the nest. We assumed that nests were abandoned in response to cameras if they were abandoned shortly after camera placement and if there was no other stimulus that could have caused abandonment, such as parasitism by Brown-headed Cowbird (*Molothrus ater*).

Artificial Nests

In 2000 and 2001 we placed artificial nests in the same four field sites that comprised the main study sites where real nests were monitored. We placed 10 artificial nests at a time in a field at randomly selected distances along the perimeter of the field (but at least 50 m apart) and

at randomly selected distances from the edge of the field. The distance from the edge of the field was randomly selected from a list of actual observed distances to edge for real Indigo Bunting and Field Sparrow nests. We observed nests daily until they were depredated or until 2 weeks passed. We simultaneously monitored nests at two sites and rotated trials among the four sites.

We used standard tools common to many artificial nest studies (Major & Kendal 1996): artificial nests made of wicker and baited with quail eggs (*Coturnix japonica*). In addition to quail eggs, we baited each nest with a plasticine egg. We used plaster molds made from real quail eggs to make plasticine eggs, which were tied to the artificial nests with a short length of monofilament to deter removal by predators. We placed artificial nests in the nest plant species used by Field Sparrows and Indigo Buntings and within the range of nest heights commonly used by these species, which overlap substantially (0.25–1.25 m; Burhans 1997; Burhans & Thompson 1998).

We used the same protocol for monitoring and placing video cameras at artificial nests and real nests, except we placed the camera within 1 m of the artificial nest on the first day. We monitored a maximum of 12 artificial nests at a time, usually 6 at each of the two sites that were simultaneously monitored. When a nest was depredated, we usually moved the camera to another nest at the same site.

Due to logistical constraints and the limited number of camera set-ups, we deployed cameras mostly on artificial nests in 2000 and exclusively in 2001 and compared these to real nests monitored from 1997 to 2000. Because this design potentially confounds nest-type effects with year effects, we conducted a preliminary analysis of rates of predation by snakes versus birds and mammals with data on real nests from 1997 to 2000. We found no effect of year, and the importance of predators did not vary greatly among years (likelihood-ratio test comparing model with and without year, $\chi^2_6 = 5.1$, $p = 0.531$; see description of general logit models below), so we assumed that our comparisons across years were acceptable. Real and artificial nests were monitored for the same period within each year (10 May–8 August) to minimize the confounding of seasonal effects with nest-type effects.

Analysis

We calculated daily predation of artificial nests and real nests (Field Sparrows and Indigo Buntings combined) for all sources of predation combined. We used the methods of Mayfield (1961, 1975) and Johnson (1979) to calculate daily predation and recommendations by Johnson (1979) and Manolis et al. (2000) for calculating exposure days.

We used an information-theoretic approach to determine support for models representing alternative hypotheses concerning the effect of nest type and differences among predators. We used multinomial logistic regression (Proc Logistic, SAS version 8.02) to model

Table 1. Numbers of predators identified depredating real and artificial songbird nests in field habitats in Missouri, 1997–2001.

Predator	Nest type	
	real	artificial
Black rat snake (<i>Elaphe obsoleta</i>)	18	0
Prairie kingsnake (<i>Lampropeltis calligaster</i>)	6	0
Blue racer (<i>Coluber constrictor</i>)	6	0
Speckled kingsnake (<i>Lampropeltis getulus holbrooki</i>)	1	0
<i>Thamnophis</i> spp.	1	0
Unidentified snake	2	0
Opossum (<i>Didelphis virginiana</i>)	0	1
Raccoon (<i>Procyon lotor</i>)	4	16
<i>Peromyscus</i> spp.	2	6
Long-tailed weasel (<i>Mustela frenata</i>)	1	0
Fox squirrel (<i>Sciurus niger</i>)	1	0
Unidentified mammal	1	0
Barn Owl (<i>Tyto alba</i>)	1	0
Broad-wing Hawk (<i>Buteo platypterus</i>)	2	0
Unidentified raptor	0	0
American Crow (<i>Corvus brachyrhynchos</i>)	5	27
Brown-headed Cowbird (<i>Molothrus ater</i>)	1	0
Total	52	50

the outcome of each daily nest observation. We used the counting process approach (Hosmer & Lemeshow 2000) and analyzed the fate of each daily interval between nest checks, so the exposure period was constant for each observation in the analysis. We compared models that included depredation by different numbers of predator groups for the response variable, one to four predator groups or not depredated (Table 2), by constraining parameters for the covariates in the model to have the same values for the predation categories that were considered "pooled" in reduced models. Models also varied with the inclusion or exclusion of a nest type (real vs. artificial; Table 2) as a covariate.

We performed a likelihood-ratio test comparing the global model (five predation categories with nest type as a covariate) to a null model with two predation categories (depredated, not depredated) and no covariates as an assessment of goodness of fit (Hosmer & Lemeshow 1999; Table 2). Upon confirming that the global model fit the data, we proceeded with model selection to find the best (most parsimonious) model (Burnham & Anderson 2002). We calculated Akaike's information criteria (AIC), Δ AIC, and Akaike weights (w) to identify the best models (Burnham & Anderson 2002). The model with the smallest AIC is the best approximating model for the data. Akaike weights represent the likelihood of a given model, and evidence ratios can be constructed as the ratio of weights for the two models being compared (Burnham & Anderson 2002). We report parameter estimates and odds ratios for a subset of the candidate models that had substantial support.

We also compared predator identification between video and plasticine egg methods for the subset of artificial nests that were monitored by video. We identified marks on plasticine eggs by comparing them to marks we made in plasticine with museum specimens of potential predators. We used a simple cross-tabulation to compare predators identified from marks on plasticine eggs and those identified from videotape.

Results

Predation of Artificial versus Real Nests

We monitored 79 Field Sparrow nests for 657 days, 42 Indigo Bunting nests for 378 days, and 154 artificial nests for 1192 observation days with video cameras. Including predation events in which predators were not identified, there were 41, 14, and 87 predation events on Field Sparrow, Indigo Bunting, and artificial nests, respectively, monitored by video cameras. Some of these included predation events in which the nest ultimately fledged one or more host young. We identified predators (to class, genus, or species) on videotape at 50 artificial nests and 52 real nests (Table 1).

In the first 3 weeks of the study in 2000, one or more American Crows (*Corvus brachyrhynchos*) were responsible for an unusually high frequency of depredations at both real and artificial nests (Table 1). In many cases, crows took all of the video-monitored nests at a given site within a day of camera placement. We trapped and removed a single crow and crow predation stopped. Because we considered this crow predation anomalous, we included only the first observed crow predation of an artificial and real nest in the remaining analyses.

In 1152 exposure days we observed 60 depredated artificial nests, and in 1027 exposure days we observed 49 depredated real nests. Daily nest predation was 0.055 (0.041–0.069; 95% confidence interval [CI]) and 0.042 (0.030–0.053) for artificial and real nests, respectively.

Multinomial logistic regression requires at least one event (predation) for each combination of response category (predation categories) and independent variable (nest type). We observed no snake predation of artificial nests, so we fabricated one daily nest interval of an artificial nest with a snake predation event to allow us to estimate all candidate models. Estimates based on the fabricated data point are clearly identified. The only bird predation of an artificial nest was the crow predation described above.

The likelihood-ratio test indicated the global, multinomial logistic-regression model fit the data ($\chi^2_7 = 98.7$, $p < 0.001$), so we proceeded with model selection. The results of model selection supported our hypothesis that predator-specific predation rates differed between real and artificial nests (Table 2). The model with three

Table 2. Multinomial-logistic models representing alternative hypotheses concerning differences in songbird nest predation between real and artificial nests and among different groups of predators in field habitats in Missouri, 1997–2001.^a

Model	–2(L)	K	AIC	ΔAIC	w
3 predation categories ^b = $\beta_0 + \beta_1(\text{nest type})$	685.442	4	693.442	0.000	1.000
4 predation categories ^c = $\beta_0 + \beta_1(\text{nest type})$	711.079	6	723.079	29.637	0.000
3 predation categories = β_0	730.423	2	734.423	102.655	0.000
5 predation categories ^d = $\beta_0 + \beta_1(\text{nest type})$	750.436	8	766.436	134.668	0.000
4 predation categories = β_0	763.229	3	769.229	137.461	0.000
5 predation categories = β_0	803.547	4	811.547	179.7791	0.000
2 predation categories ^e = β_0	890.097	1	892.097	198.6552	0.000
2 predation categories = $\beta_0 + \beta_1(\text{nest type})$	889.885	2	893.885	200.443	0.000

^aModels are ranked from best to worst based on Akaike's information criteria (AIC), delta (ΔAIC), and Akaike weights (w); AIC is based on $-2 \times \log \text{likelihood (L)}$ and the number of parameters in the model (K).

^bResponse variable categories were depredated by (1) snakes and (2) birds and mammals and (3) not depredated.

^cResponse variable categories were depredated by (1) snakes, (2) birds, and (3) mammals and (4) not depredated.

^dResponse variable categories were depredated by (1) snakes, (2) birds, (3) raccoons, and (4) other mammals and (5) not depredated.

^eResponse variable categories were depredated and not depredated.

predation categories (depredated by snake, by bird or mammal, or not depredated) and nest type had overwhelming support, indicating that predation differed among predators and between real and artificial nests (Table 2). Odds ratios indicated that the odds of snake predation of artificial nests were only 0.4–19.4% (95% CI) of the odds of snake predation of real nests. (Actually they were infinitely lower because there was no snake predation of artificial nests and we fabricated one event to run the model; Table 3.) The odds ratio for predation of artificial versus real nests by birds and mammals was not greatly different than 1, suggesting a minimal difference between nest types (Table 3). The second-best model was based on four predation categories and distinguished predation by snakes, mammals, and birds (Table 2). This model had less support than the best-supported model, but odds ratios indicated potentially meaningful patterns. The pattern for snake predation was the same as in the first model. However, the odds of mammal predation of artificial nests were

115–551% of the odds of mammal predation of real nests, and the odds of bird predation of artificial nests were 2–154% of the odds of bird predation of real nests (Table 3). The second model indicated potential biases for artificial nests in different directions for birds and mammals that were obscured when birds and mammals were pooled in the first model. Therefore, we chose to estimate predation rates by predation category and nest type with the second model (Fig. 1).

Plasticine Egg versus Video Identification

Based on video evidence, we were unable to identify or misidentified 42 predators from marks on plasticine eggs (Table 4). Crows marked plasticine eggs in 1 of 27 video events, and raccoons (*Procyon lotor*) marked plasticine eggs in 2 of 16 video events. In three cases, mice (*Peromyscus* spp.) marked plasticine eggs but videotape showed that raccoons removed the quail eggs from those

Table 3. Parameter estimates for the two best-supported multinomial logistic-regression models predicting the probability of predation of artificial and real nests by snakes or birds and mammals in field habitats in Missouri, 1997–2001.

Parameter	Response category*	Estimate	Odds ratio (95% CI)
Model with three response categories			
intercept	snake	–5.181	—
intercept	bird or mammal	–4.073	—
nest type (artificial vs. real)	snake	–1.816	0.026 (0.004–0.194)
nest type (artificial vs. real)	bird or mammal	0.254	1.661 (0.841–3.279)
Model with four response categories			
intercept	snake	–5.181	—
intercept	mammal	–4.337	—
intercept	bird	–6.139	—
nest type (artificial vs. real)	snake	–1.816	0.026 (0.004–0.194)
nest type (artificial vs. real)	mammal	0.475	2.586 (1.151–5.508)
nest type (artificial vs. real)	bird	–0.857	0.180 (0.021–1.542)

*Reference category for all models was “not depredated.”

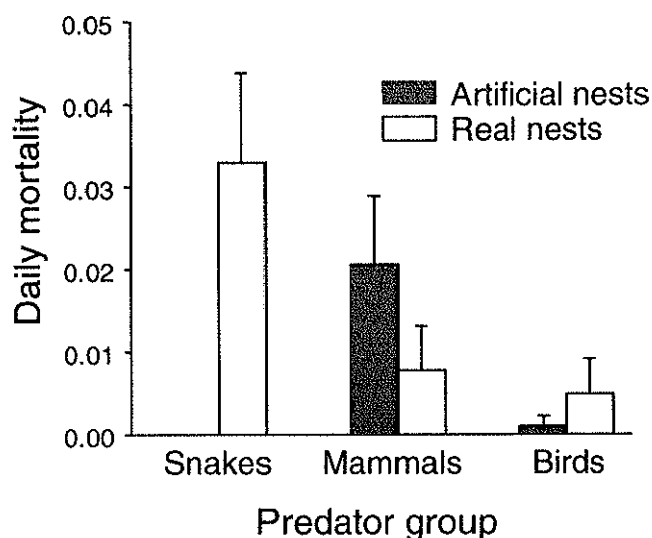


Figure 1. Differences in daily predation of real and artificial songbird nests by different predator groups in field habitats in Missouri, 1997–2001. Estimates were calculated from a multinomial logistic-regression model with four response categories: depredated by snake, mammal, or bird or not depredated.

nests. In all five cases where mice were identified as predators based on evidence of both plasticine eggs and videotape, quail eggs remained in the nest. In one of these events there was a small hole in the quail egg. Quail eggs disappeared at one of five nests where the video system failed. We identified mice based on marks on plasticine eggs at three of four nests where the video system was operating, but no predator was recorded on tape.

Discussion

Even though daily predation estimates (all predators pooled) did not differ greatly between artificial and real nests, predators differed substantially between them.

Snakes were the major predator at real nests and raccoons the major predator at artificial nests. We chose to draw primary inference from the second-best model even though, based on AIC, the first model had stronger support (Table 2). Odds ratios for the second model indicated that the odds of predation of artificial nest by mammals were higher and that those by birds were lower than the odds of predation of real nests. When predation by birds and mammals was pooled in the first model, however, these effects were compensating, and the model was not perceived to have poorer fit and in fact had a lower (better) AIC value than the second model. Therefore, we believe that the first model was not biologically appropriate, and we draw inference from the second-best supported model (which still had much more support than all remaining models). Among all models with multiple predator groups (three, four, and five predation classes), the model with nest type had much more support than the model without nest type, and models with multiple predator groups had more support than the model with just two predation classes (depredated and not depredated; Table 2). These model-selection results provide strong support for our hypothesis that artificial nests provide biased estimates of predation that differ by predator group.

The odds ratios for the multinomial logistic-regression models provide a direct estimate of the level of bias. For example, snake predation of artificial nests was nonexistent, and the odds of mammal predation were 115–551% of the odds of mammal predation at real nests (four-category model; Table 3; Fig. 1). Bird predation tended to be lower at artificial nests (18% of the odds of predation of real nests), but the CI bracketed 100% (2–154%; Table 3).

Other researchers comparing artificial and real nests have inferred that potential biases exist with artificial nests (Wilson et al. 1998; Davison & Bollinger 2000; Zanette 2002; Burke et al. 2004), but because they did not directly identify predators at both nest types, they could only speculate about processes underlying these apparent biases. King et al. (1999) reported higher predation on artificial nests and, among three hypotheses based on

Table 4. Cross-tabulation of predator identifications (ID) from marks on plasticine eggs versus video monitoring of artificial nests in field habitats in Missouri, 1997–2001.

Egg identification	Video identification					
	<i>crow</i>	<i>opposum</i>	<i>Peromyscus</i>	<i>raccoon</i>	<i>unknown^a</i>	<i>failure^b</i>
American Crow	1	0	0	0	1	0
Opossum	0	0	0	0	1	0
Peromyscus	0	0	5	3	4	5
Raccoon	0	0	0	2	1	3
Unknown ^c	26	1	1	11	14	9

^aPredator not identified because of obstruction or light.

^bCamera or battery failed during interval in which predation occurred.

^cNo prints on plasticine egg or plasticine egg was missing.

odor, concealment, and nest defense, concluded that the absence of nest defense at artificial nests was the most likely explanation. We compared artificial nests to both egg and nestling stages of real nests. Arguably, to be more relevant, artificial nest studies could limit inferences to only the egg stage. Data from the real nests in our study and previous ones (Thompson et al. 1999; Thompson & Burhans 2003), however, indicate that snakes are the dominant predator during both stages in fields, and their importance tends to increase later in the nestling stage. Given the reduction in sample size (number of depredation events) that would occur if we excluded the nestling stage, we think our approach was justified and relevant.

As far as we know, only Buler and Hamilton (2000) have also used cameras to document predators at both real and artificial nests. Unfortunately, their cameras did not capture predators at real nests. Field assistants, however, observed both snakes and corvids depredating real nests in several instances, whereas corvids were responsible for 90% of depredations at their artificial nests. Davison and Bollinger (2000) believe that snakes were the principal predators at their grassland sites and found that predation at artificial nests made of wicker was lower than at real nests. However, they also found that predation at artificial nests constructed with grass was similar to that at real nests. Davison and Bollinger (2000) also noted that studies in forested habitat have found greater predation at artificial nests (Reitsma 1992; Wilson et al. 1998), whereas artificial nests in grassland studies experience lower rates of predation than real nests. They speculate that this may be due to snakes being important nest predators in grassland habitats but not consuming eggs at artificial nests.

Although crows depredated many of our nests in 2000, this appeared to be an unusual event because we had not documented them before in any of 61 videotaped predation events (Thompson et al. 1999; Thompson & Burhans 2003). We consider this an anomaly attributable to the intelligence of corvids, their discovery of our video monitoring equipment, and their ability to use a search image (Yahner & Wright 1985). Other researchers have cautioned against checking nests in the presence of corvids because they may learn to find nests based on human activity (Yahner & Wright 1985; Buler & Hamilton 2000 and references therein). Buler and Hamilton (2000) similarly found that once crows found an artificial nest, they "trap-lined" all nests in the plot within a few hours.

Several recent studies indicate that artificial nests with quail eggs may not experience the same predation as real nests, at least in part because most mice and possibly other small mammals may not be able to take quail eggs (Haskell 1995; Maier & DeGraff 2000). Conversely, other studies indicate that size of eggs has little influence on predation or that small mammals can at least occasionally break or eat larger eggs (Craig 1998; Lewis & Montevocchi 1999). We never observed a mouse removing a quail egg, but in four instances where plasticine eggs

were marked by mice, we did not see the predator that removed the quail egg on videotape. These instances and others in which we were unable to observe a predator even though we had videotape were usually caused by less than ideal camera placement, resulting in poor illumination of the nest at night or vegetation blocking the view of the nest. In three instances, we could have wrongly concluded that mice had removed quail eggs based on results from plasticine eggs because videotape showed that raccoons actually removed quail eggs. Had we used only the results from plasticine eggs, we might have concluded that mice were responsible for 17 depredations. Unfortunately, for 9 of the latter events we were unable to identify a predator on camera. The frequency of marks by mice on plasticine eggs may be due to the apparent attraction of mice to plasticine (Rangen et al. 2000). Maier and DeGraff (2001) suggest that mice may nibble plasticine to gather olfactory information but would not necessarily depredate nest contents. Buler and Hamilton (2000) documented 35 mouse visits to artificial nests based on cameras and evidence at the nest but found only 8 depredations on quail eggs by small-mouthed mammals. They did not use plasticine eggs in their study. Our results show that mice may frequently visit artificial nests but either do not easily penetrate quail eggs (DeGraaf & Maier 1996) or are simply attracted to plasticine (Rangen et al. 2000).

Video-camera studies are constrained by the expense of equipment and labor. We could have included other factors in the study design or models, such as year, nest stage, or bird species. The trade-off, however, is that the number of depredation events in any particular response category gets smaller with additional parameters, making it harder to fit models and to detect effects. We believe we reached the best compromise and adequately justified it given the uniqueness of the data.

We provided direct evidence that artificial nests provide biased estimates of nest predation and that these biases are predator-specific. Because biases were both positive and negative, depending on predator group, and they existed for potentially all predator groups (snakes, mammals, and possibly birds), conclusions from artificial nest studies are suspect even when there is evidence that overall predation rates are similar among real and artificial nests. Daily nest predation can appear similar between artificial and real nests because biases in different directions can compensate for each other when different predator groups are pooled, but very different processes may affect nest fate at each nest type. If predator abundance varies among habitats, landscapes, or experimental treatments, the effects of abundance and bias will be hopelessly confounded. Furthermore, artificial nests with plasticine eggs or sign at real nests (Thompson & Burhans 2003) cannot be reliably used to identify predators at nests. Although it is not without problems and occasional failures, we believe that video monitoring is a reliable method by which to identify predators at nests.

Acknowledgments

We thank the many field assistants who gathered information for this study, including T. Hinkleman, C. Rittenhouse, D. Robinson, H. Heitz, K. McGee, S. Ernst, and J. Voss. R. DeGraaf, D. King, D. Dearborn, and anonymous reviewers provided comments that greatly improved the manuscript. The U.S. Forest Service North Central Research Station funded this study, and The University of Missouri provided study sites at the Thomas S. Basket Wildlife Research and Education Center.

Literature Cited

- Askins, R. A. 2000. Restoring North America's songbirds. Yale University Press, New Haven, Connecticut.
- Askins, R. A., J. E. Lynch, and R. Greenberg. 1990. Population declines in migratory birds in eastern North America. *Current Ornithology* 7:1-57.
- Buler, J. J., and R. B. Hamilton. 2000. Predation of natural and artificial nests in southern pine forest. *Auk* 117:739-747.
- Burhans, D. E. 1997. Habitat and microhabitat features associated with cowbird parasitism in two forest edge cowbird hosts. *Condor* 99:866-872.
- Burhans, D. E., and E. R. Thompson III. 1998. Effects of time and nest-site characteristics on concealment of songbird nests. *Condor* 100:663-672.
- Burke, D. M., K. Elliott, L. Moore, W. Dunford, E. Nol, J. Phillips, S. Holmes, and K. Freemark. 2004. Patterns of nest predation on artificial and natural nests in forests. *Conservation Biology* 18:381-388.
- Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Springer-Verlag, New York.
- Craig, D. P. 1998. Chipmunks use leverage to eat oversized eggs: support for the use of quail eggs in artificial nest studies. *Auk* 115:486-489.
- Davison, W. B., and E. Bollinger. 2000. Predation rates on real and artificial nests of grassland birds. *Auk* 117:147-153.
- DeGraaf, R. M., and T. J. Maier. 1996. Effect of egg size on predation by white-footed mice. *Wilson Bulletin* 108:535-539.
- Haskell, D. G. 1995. Forest fragmentation and nest predation: are experiments with Japanese Quail eggs misleading? *Auk* 112:767-770.
- Hosmer, D. W., and S. Lemeshow. 1999. Applied logistic regression. Wiley, New York.
- Hosmer, D. W., and S. Lemeshow. 2000. Applied survival analysis. Wiley, New York.
- Johnson, D. H. 1979. Estimating nest success: the Mayfield method and an alternative. *Auk* 96:651-661.
- King, D. I., R. M. De Graef, C. R. Griffin, and T. J. Maier. 1999. Do predation rates on artificial nests accurately reflect predation rates on natural nests? *Journal of Field Ornithology* 70:257-262.
- Lewis, K. P., and W. A. Montevicchi. 1999. Predation on different-sized quail eggs in an artificial-nest study in western Newfoundland. *Canadian Journal Zoology* 77:1170-1173.
- Lindell, C. 2000. Egg type influences predation rates in artificial nest experiment. *Journal Field Ornithology* 71:16-21.
- Maier, T. J., and R. M. DeGraaf. 2000. Predation on Japanese Quail vs. House Sparrow eggs in artificial nests: small eggs reveal small predators. *Condor* 102:325-332.
- Maier, T. J., and R. M. DeGraaf. 2001. Differences in depredation by small predators limit the use of plasticine and Zebra Finch eggs in artificial-nest studies. *Condor* 103:180-183.
- Major, R. E., and C. E. Kendal. 1996. The contribution of artificial nest experiments to understanding avian reproductive success: a review of methods and conclusions. *Ibis* 138:298-307.
- Manolis, J. C., D. E. Anderson, and E. J. Cuthbert. 2000. Uncertain nest fates in songbird studies and variation in Mayfield estimation. *Auk* 117:615-626.
- Marini, M. A., and C. Melo. 1998. Predators of quail eggs, and the evidence of the remains: implications for nest predation studies. *Condor* 100:395-399.
- Mayfield, H. 1961. Nesting success calculated from exposure. *Wilson Bulletin* 73:255-261.
- Mayfield, H. 1975. Suggestions for calculating nest success. *Wilson Bulletin* 87:456-466.
- Rangen, S. A., R. G. Clark, and K. A. Hobson. 2000. Visual and olfactory attributes of artificial nests. *Auk* 117:136-146.
- Reitsma, L. 1992. Is nest predation density dependent? A test using artificial nests. *Canadian Journal of Zoology* 70:2498-2500.
- Ricklefs, R. E. 1969. An analysis of nesting mortality in birds. *Smithsonian Contributions to Zoology* 9:1-48.
- Roper, J. J. 1992. Nest predation experiments with quail eggs: too much to swallow? *Oikos* 65:528-530.
- SAS Institute. Version 8.02. Cary, North Carolina.
- Thompson, F. R., III, W. Dijk, and D. E. Burhans. 1999. Video Identification of predators at songbird nests in old fields. *Auk* 116:259-264.
- Thompson, F. R., III, and D. E. Burhans. 2003. Predation of songbird nests differs by predator and between forest and field habitats. *Journal Wildlife Management* 66:240-249.
- Wilson, G. R., M. C. Brittingham, and L. J. Goodrich. 1998. How well do artificial nests estimate success of real nests? *Condor* 100:357-364.
- Yahner, R. H., and A. L. Wright. 1985. Depredation on artificial ground nests: effects of edge and plot age. *Journal of Wildlife Management* 49:508-513.
- Yahner, R. H., and C. G. Mahan. 1996. Effects of egg type on depredation of artificial ground nests. *Wilson Bulletin* 108:129-136.
- Zanette, L. 2002. What do artificial nests tell us about nest predation? *Biological Conservation* 103:323-329.

