PREDATION OF SONGBIRD NESTS DIFFERS BY PREDATOR AND BETWEEN FIELD AND FOREST HABITATS

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Abstract: Our understanding of factors affecting nest predation and ability to mitigate high nest predation rates is hampered by a lack of information on the importance of various nest predator species in different habitats and landscapes. We identified predators of songbird nests in old-field and forest habitats in central Missouri, USA, with miniature video cameras. We used an information–theoretic approach to evaluate support for hypotheses that the importance of predator species varied among habitats and nest stage. We monitored 165 nests with cameras and 272 nests without cameras during 1997–1999, and identified predators at 61 of 74 depredated nests monitored by cameras. Model selection indicated the most support for a model with separate rates for predation by birds, mammals, and snakes in field and forest habitats. Predation by snakes was greater than predation by mammals and birds in old fields; predation by mammals (mostly raccoons [*Procyon lotor*]) was greater than by snakes and birds in forest. We found little support for the hypothesis that monitoring nests with cameras affects predation. Nests could not be assigned reliably to a predator group based on the condition of the nest. We believe that knowledge of the identity and abundance of dominant predators in a habitat or landscape is necessary to target conservation efforts to reduce nest predation or to interpret results of research on factors affecting nest success.

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Nest predation is the largest source of mortality in birds (Ricklefs 1969) and can significantly affect the demography of breeding songbird populations (Donovan et al. 1995, Brawn and Robinson 1996, Rogers et al. 1997). However, despite the acknowledged importance of nest predation and concern about apparent declines of migrant songbirds in North America (Askins et al. 1990, Askins 2000), few studies have directly identified nest predators or determined their relative importance (Thompson et al. 1999, Pietz and Granfors 2000).

Landscape and habitat-patch factors affect levels of nest predation (Marzluff and Restani 1999, Burhans et al. 2002, Thompson et al. 2002). For example, birds in fragmented forests (Donovan et al. 1995, Robinson et al. 1995) and grasslands (Johnson and Temple 1990, Winter and Faaborg 1999) can have high levels of nest predation, but in other habitats or landscapes, fragmentation may have different (or no) effects on nest predation (Tewksbury et al. 1998, Marzluff and Restani 1999). Landscape and habitat effects on nest predation may be the result of numerical or functional responses by predators, although few studies have directly tested these responses (Chalfoun et al. 2002). Some nest predators, however, have been shown to respond to landscape and habitat factors (e.g., raccoons [Bowman and Harris 1980, King et al. 1998, Dijak and Thompson 2000] and snakes [Weatherhead and Charland 1985, Durner and Gates 1993, Mullin et al. 1998])

The identity of predator species and how their importance varies with habitat and landscape factors must be known for managers and scientists to design effective conservation plans and place research on nest predation in the appropriate context (Marzluff et al. 2000, Heske et al. 2001). Until recently, the identity of nest predators was based on chance observations of isolated acts of nest predation (Best 1974, Nolan 1978, James et al. 1983), the appearance of depredated nests (Best and Stauffer 1980), or evidence from a variety of devices used at artificial nests. Plasticine eggs (Donovan et al. 1997), hair catchers (Major 1991), track plates (Angelstam 1986), and still cameras (Major 1991, Danielson et al. 1997, Hernandez et al. 1997*a*) have been used to identify predators at artificial nests. However, whether predators identified at such nests are the same as those at active songbird nests is controversial (Willebrand and Marcström 1988, Major and Kendal 1996, Wilson et al. 1998, King et al. 1999). Recently, video systems have been used to identi-

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fy nest predators (Brown et al. 1998, Thompson et al. 1999, Pietz and Granfors 2000). Due to the expense and labor required, these systems mostly have been used to identify nest predators on relatively small samples of nests.

We used miniature video cameras with infrared illumination to identify predators at songbird nests in old fields and forests and to estimate predator- and habitat-specific predation rates. We used an information–theoretic approach to determine support for our hypotheses that predation differed by predator, between field and forest habitats, and between eggs and nestlings by comparing support for models with 2–6 predation categories (not depredated and depredated by 1–5 predator groups), with and without habitat and nest stage effects. We examined support for the hypothesis that camera monitoring did not affect nest survival by comparing support for models with and without a camera effect while controlling for other sources of variation (nest stage, species, year, interval length). Because nest condition has been used to infer the identity of predator species in the past, we also presented a summary of nest conditions after predation by different predator species.

METHODS

Study Site

Our study used songbird nests in old fields and forest in 1998 and 1999, as well as nests in old fields in 1997 (Thompson et al. 1999). We located bird nests in old-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, USA. The old fields were 2.4–15.4 ha, 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*) and hardwoods, and 8% old fields. The surrounding landscape was approximately 43% forest, and the balance was pasture and dispersed rural housing (F. R. Thompson, University of Missouri, unpublished data).

Field Methods

We searched habitats on 1–5 day intervals during 1 May–30 July 1997–1999 and located nests by systematic searching of potential nest sites and behavioral cues from adult birds. Nest locations were marked with plastic flagging placed ≥3 m from the nest. We studied field sparrows (*Spizella pusilla*) and indigo buntings (*Passerina cyanea*) in the field habitat because they are the most abundant nesting species. Nest densities were lower in forest habitat, so we used nests from a variety of species that nest near the ground: indigo bunting, Kentucky warbler (*Oporornis formosus*), worm-eating warbler (*Helmitheros vermivorus*), ovenbird (*Seiurus aurocapillus*), wood thrush (*Hylocichla mustelina*), Acadian flycatcher (*Empidonax virescens*), and Louisiana waterthrush (*S. motacilla*).

We monitored nests with cameras (camera nests) and without cameras (non-camera nests). Non-camera nests were monitored every 2–3 days until fledging approached, at which time nests were monitored daily. Nests were considered successful and to have fledged young if we found the nest empty and heard nestling begging calls, or saw nestlings, parents carrying food, or parents chipping agitatedly nearby. Fates of nests in which we did not observe these activities were classified as unknown. Recorders at camera nests were visited daily to change videotapes, and nest fate was documented by the video cameras.

Video systems consisted of a miniature video camera and a time-lapse video recorder in a weatherproof case (Fuhrman Diversified, Inc., Seabrook, Texas, USA) and a 12-volt, deep-cycle marine battery. The video camera and 6 infrared light-emitting diodes were in a camera housing that measured 32 × 32 × 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 6 frames/sec, or 1/4 the speed of standard VHS video, which allowed us to record for 24 hr 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 that 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. We monitored nests with cameras until a nest was entirely depredated, fledged, or abandoned, after which we moved the camera setup to another nest. Videotapes from the day of a predation event or suspected fledging date were viewed in the lab to confirm nest fate and identify any predators.

We placed video cameras at nests after the laying period to minimize nest abandonment due to disturbance. Despite this, we had numerous abandonments, particularly at indigo bunting nests. In 1999, we tried to reduce abandonment by placing cameras 8–10 m from nests and moving 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 nests were abandoned shortly after camera placement and no other stimulus (e.g., brown-headed cowbird [*Molothrus ater*] parasitism) occurred that could have caused abandonment.

Analysis Methods

We used an information–theoretic approach to determine support for models representing alternative hypotheses concerning differences in nest predation by predator, habitat, and nest stage. We examined models with 2, 4, or 6 predation categories and with a habitat effect or habitat and nest stage effect (9 models; Table 1). By comparing support for models in which the response variable contained 2 categories (depredated, not depredated), 4 categories (depredated by bird, mammal, or snake, or not depredated), or 6 categories (depredated by passerine, raptor, raccoon, other mammal, or snake, or not depredated), we determined support for the hypotheses that predation differs among predator groups. By comparing models with and without the habitat effect, we determined support for the hypotheses that predation differed between habitats. We included nest stage in some models to control for its possible effects on predation. We used multinomial logistic regression (Proc Logistic, SAS version 8.02) to estimate the models because it allows multiple category levels for the response variable. Models with reduced numbers of predation categories essentially had the same response categories as the model with 6 predation categories, but the covariates were constrained to have the same coefficients for predation categories that were "pooled." We used the counting process approach (Hosmer and Lemeshow 1999) and analyzed the fate of each interval between nest checks, which allowed nest stage to change between intervals. We calculated Akaike's Information Criterion (AIC), ΔAIC, and Akaike weights (w) to identify the best models (Burnham and 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 2 models being compared (Burnham and Anderson 2002). Burnham and Anderson (2002) recommend assessing the goodness-of-fit of the global model in the set of candidate models. We performed a likelihood-ratio test comparing the global model to the model with no covariates as an assessment

Table 1. Multinomial logistic-regression models for effects of habitat and nest stage on predator-specific predation of songbird nests in field and forest habitats in Missouri, USA, 1997–1999 (n = 1,459). Models are ranked from best to worst based on Akaike's Information Criteria (AIC), delta (ΔAIC), and Akaike weights (w); AIC is based on –2 × log likelihood (L) and the number of parameters in the model (K).

Model	–2(L)	K	AIC	ΔAIC	w
4 predation categories[a], habitat[b]	601.43	6	613.43	0.00	0.557
4 predation categories	608.59	3	614.59	1.16	0.312
4 predation categories, habitat, stage[c]	598.31	9	616.31	2.88	0.132
6 predation categories[d], habitat	627.86	10	647.86	34.43	0.000
6 predation categories	639.32	5	649.32	35.89	0.000
6 predation categories, habitat, stage	623.47	15	653.47	40.04	0.000
2 predation categories[e]	1,218.43	1	1,220.43	607.00	0.000
2 predation categories, habitat	1,217.73	2	1,221.73	608.30	0.000
2 predation categories, habitat, stage	1,217.35	3	1,223.35	609.92	0.000

[a] Response variable categories were depredated by (1) bird, (2) mammal, (3) snake, or (4) not depredated.
[b] Field and forest habitat
[c] Egg and nestling stages
[d] Response variable categories were depredated by (1) passerine, (2) raptor, (3) raccoon, (4) other mammal, (5) snake, or (6) not depredated.
[e] Response variable categories were (1) depredated or (2) not depredated.

Table 2. Binary logistic-regression models for effects of camera, species, and nest stage on predation[a] of songbird nests in field and forest habitats in Missouri, USA, 1997–1999 (n = 2,547). Models are ranked from best to worst based on Akaike's Information Criteria (AIC), delta (ΔAIC), and Akaike weights (w); AIC is based on −2 × log likelihood (L) and the number of parameters in the model (K).

Model	−2(L)	K	AIC	ΔAIC	w
Species[b], year, interval[c]	−567.80	5	1,145.60	0.00	0.277
Year, interval	−570.05	3	1,146.10	0.50	0.216
Species, stage[d], year, interval	−567.62	6	1,147.24	1.64	0.122
Camera[e], species, year, interval	−567.69	6	1,147.38	1.79	0.114
Stage, year, interval	−569.93	4	1,147.87	2.27	0.089
Camera, year, interval	−569.94	4	1,147.88	2.29	0.088
Camera, species, stage, year, interval	−567.42	7	1,148.84	3.24	0.055
Camera, stage, year, interval	−569.75	5	1,149.50	3.91	0.039

[a] Response variable categories were not depredated or depredated.
[b] Field sparrow, indigo buntings, and forest birds.
[c] Length of interval between nest checks.
[d] Egg and nestling stages.
[e] With or without video camera.

of goodness-of-fit (Hosmer and Lemeshow 2000). We calculated odds ratios and 95% confidence intervals for parameters in the best-supported model as a measure of effect size; these estimates were conditional on that model being the best model (Burnham and Anderson 2002).

We also determined whether the data supported the hypothesis that nests monitored with cameras had different predation rates (all predators pooled) than nests monitored without cameras. We considered models based on the variables camera (camera or no-camera), nest stage (egg or nestling), year, and species (field sparrow, indigo bunting, forest birds; Table 2). We focused our discussion of these models on camera effect because the other parameters are discussed in Burhans et al. (2002). The other parameters are included in some models to control for their potential effect when interpreting the camera effect. We used the counting process approach as above. However, because interval length between nest checks varied for non-camera nests, we included the interval length as a covariate in all models to control for its effect. We performed a likelihood-ratio test and calculated odds ratios as described above.

We estimated daily predator-specific predation rates and 95% CI, based on the best-supported models, using the general approach of Mayfield (1961, 1975) and Johnson (1979) with program MICROMORT (Heisey and Fuller 1985). We report daily, predator-specific predation rates, as opposed to simple percentages of nests depredated by different predators (e.g., Thompson et al. 1999, Pietz and Granfors 2000) because this approach accounts for differences in observation days among nests and treatments. The number of observation days was estimated for each nest from the day a nest was first observed active (with eggs or chicks) to the day a nest failed or fledged. The last observation day was usually directly observed at camera-monitored nests and therefore known. We estimated the last observation day for non-camera nests as the midpoint between the last day the nest was checked and the previous visit when the nest was active. If nest fate was unknown at the last nest check, the number of observation days was the number of days to the last day the nest was known to be active. These procedures generally result in the least bias (Johnson 1979, Manolis et al. 2000). Observation days for the period before a camera was placed at a nest were counted as a non-camera nest and not included in calculations of predation rates for camera nests. Nest-success studies generally consider a nest successful if it fledges ≥1 young (Martin et al. 1997). However, to estimate predator-specific predation rates, we considered a nest depredated if video monitoring detected that ≥1 egg or chick were eaten, removed, or killed by a predator.

Nest studies have sometimes used field observation of nest condition after predation to infer the predator species (Best 1978). Because we knew the identity of predators at camera nests, we summarized observations of nest condition after predation for 5 predator groups. We placed nests in 5 categories based on field observations: undisturbed (no damage to nest); hole in nest (nests with a hole in the nest cup); tipped (nests still hanging from the nest plant but at a lower angle); torn (the lining or sides were crushed or wholly or partially removed); and removed (completely torn from the nest plant). Torn nests that

Table 3. Identities of predators videotaped depredating songbird nests in Missouri, USA, 1997–1999.

Predator	Habitat	
	Field	Forest
Black rat snake (*Elaphe obsoleta*)	18	3
Prairie kingsnake (*Lampropeltis calligaster*)	6	1
Blue racer	6	0
Speckled kingsnake (*Lampropeltis getulus holbrooki*)	1	1
Sirtalis sp.	1	0
Unidentified snake	1	0
Raccoon	4	6
Peromyscus sp.	2	0
Long-tailed weasel (*Mustela frenata*)	1	0
Fox squirrel (*Sciurus niger*)	1	0
Unidentified mammal	1	1
Barn owl (*Tyto alba*)	1	0
Broad-wing hawk (*Buteo platypterus*)	2	0
Unidentified raptor	0	1
Blue jay	0	2
Brown-headed cowbird	1	0
Total	46	15

were also tipped were classified only as "torn." No eggshells remained at any of the nest sites.

RESULTS

We monitored 165 nests, 1,500 observation days, and 74 predation events with cameras, and 272 nests, 2,022 observation days, and 79 predation events without cameras. We observed 86 predation events in 1,686 observation days for field sparrows, 33 in 1,029 for indigo buntings, and 34 in 807 for forest birds. For nests in the egg stage, we had 638 observation days with cameras and 1,421 without. For nests in the nestling stage, we had 862 observation days with cameras and 601 without.

We identified predators (to class, genus, or species) at 61 of 74 video-monitored nests that were depredated (Table 3). Eight of 61 observed predation events involved partial brood fledging. Seven partial fledging events involved snakes in which 1–3 nestlings survived; 1 was predation by a female cowbird in which 2 of 3 nestlings survived.

Video system failures occurred on 43 observation days; however, only 8 of 74 predation events were not identified due to equipment problems. The most common problem was low battery charge (28 days); other causes included moisture in the recorder case, gnawed cables, or faulty cable connections. Five predation events were not identified because the camera was knocked over, improperly aimed, or too far from the nest. In 1997 and 1998, 17 of 128 nests, (mostly indigo bunting) were abandoned in apparent response to cameras. After we modified our field methods in 1999 to move cameras close to nests over 2–3 days, only 1 indigo bunting nest was abandoned.

The likelihood-ratio test of the global model with 6 predation categories plus habitat and camera effects was significant ($\chi^2_{14} = 594$, $P < 0.001$), and we concluded that the model fit the data. Results of model selection supported our hypothesis that predation rates varied among predators and habitat (Table 1). The 3 models with 4 predation categories had overwhelming support compared to all other models, especially models with a single predation estimate. The 4 predation-category model with habitat had 1.8 times the support of the 4 predation-category model without habitat. The pattern was similar for the 6 predation-category models. We found no strong support for the effect of nest stage; nevertheless, some model selection uncertainty existed. Support for the 4 predation-category model with habitat was 4.2 times as great as support for 4 predation-category model with habitat and nest stage. The odds ratios for predation in fields versus forest were 0.53 (95% CI: 0.19 to 1.42) for predation by birds, 0.55 (95% CI: 0.12 to 2.45) for mammals, and 2.62 (95% CI: 1.01 to 6.76) for snakes, based on the 4 predation-category model with habitat. For example, predation by snakes in fields was 101–676% (mean = 262%) of predation by snakes in forest.

Based on model selection results, we estimated daily predation rates for 3-predator groups in field and forest habitats (Fig. 1). Predation by snakes was 3.6 times greater than predation by all mammals in fields, and the 95% CI for snakes did not overlap the CI for mammals or birds. The CIs for predation by birds, mammals, and snakes in

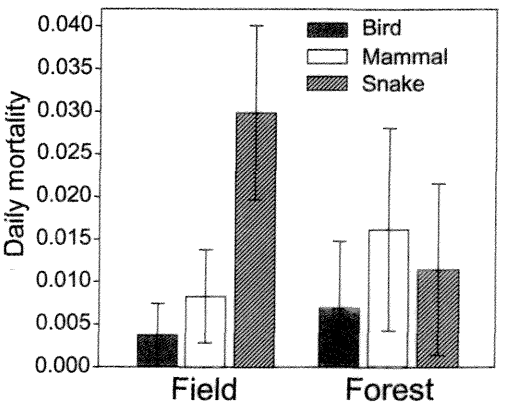

Fig. 1. Daily predation and 95% CI of songbird nests in field and forest habitats, by predator groups, in Missouri, USA, 1997–1999.

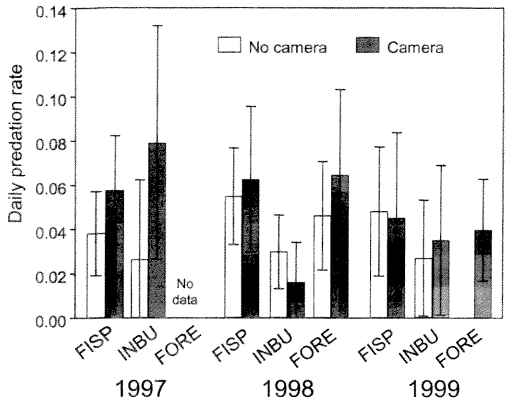

Fig. 2. Daily predation and 95% CI of field sparrow (FISP), indigo bunting (INBU), and forest songbird (FORE) songbird nests monitored with without video cameras in Missouri, USA, 1997–1999.

forest habitat overlapped. Predation by snakes in fields was 2.6 times greater than predation by snakes in forest, and predation by mammals in forest was 1.9 times greater than predation by mammals in fields, though confidence intervals overlapped for both comparisons (Fig. 1).

The likelihood-ratio test of the global model with camera, species, stage, year, and interval length was only marginally significant ($\chi^2_6 = 11.2$, $P = 0.084$), suggesting possible problems with model fit. We found no strong support for any 1 model examining the effect of cameras; the top 4 models all had weights of 0.114–0.277 (Table 2). We found stronger support for a species effect than stage or camera effects; species occurred in 3 of the top 4 models (year and interval length were in all models). The odds ratio for the nests with cameras versus nests without cameras was 0.914 (0.621–1.338) based on the model with camera, species, year, and interval length. Given the model selection uncertainty, that species and year were in all 4 of the top models, and that we were primarily interested in the effect of cameras, we estimated daily predation using the model with camera, species, year, and interval length. Confidence intervals for all estimates overlapped, and differences between camera and non-camera nests varied among species and years (Fig. 2).

Nests that were depredated by snakes and passerines (blue jays [*Cyanocitta cristata*] or cowbirds) tended to have the lowest nest disturbance overall (Fig. 3). Nests where raccoons or raptors were identified as predators were often torn, tipped, or removed entirely from the nesting substrate. A blue racer (*Coluber constrictor*) was identified as the nest predator in the only camera nest where we observed a hole in the nest; the snake emerged through the bottom of the nest cup to capture field sparrow nestlings.

DISCUSSION

We conclude that nest predation rates differed among predators and habitats at our study site. Our conclusion was supported by the results of model selection, the odds ratio for snake predation in fields versus forests, and by the estimated predation rates. We recognize that our predation estimates are somewhat imprecise, as indicated by wide CIs that often overlapped. We believe, however, that the estimates and CIs indicate biologically important differences (Fig. 1), especially since the model they are based on had strong support (Table 1).

Snakes were the dominant predator in our study, followed by raccoons and then a diversity of other predators. Studies of nest success, and especially those examining forest fragmentation effects, have speculated on the potential importance of blue jays, American crows (*Corvus brachyrhynchos*), raccoons, skunks (*Mephitis* spp.), opossums (*Didelphis virginiana*), and other medium-sized mammals as nest predators (Wilcove 1985, Small and Hunter 1988, Gates and Gysel 1978). While we detected some of these predators, none were as important as snakes in field

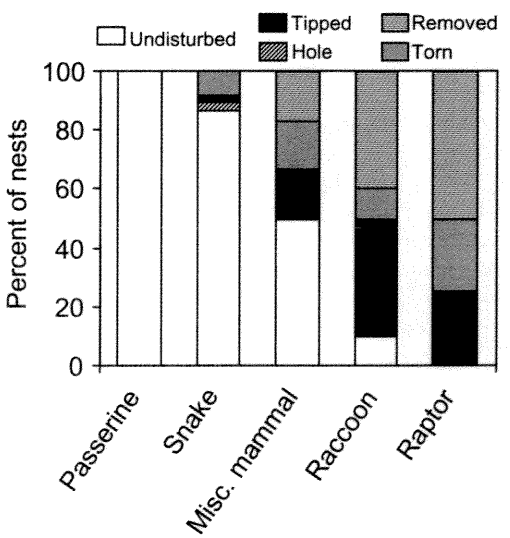

Fig. 3. Condition of songbird nests after predation by predators identified with video cameras in field and forest habitats in Missouri, USA, 1997–1999.

habitats, and only raccoons were more important than snakes in forest habitats. Based on our observations of snakes during routine fieldwork on our study site, snakes appear much more abundant in field than forest habitats (D. E. Burhans, unpublished data). Snakes have been suspected as important nest predators in old-field habitats (Best 1978, Nolan 1978, Zimmerman 1984), and some studies have documented snakes depredating nests in these habitats (Best 1974, Nolan 1978). However, simply because predators are found in a given habitat does not mean that they depredate nests there. Although raccoons were common at grassland sites in North Dakota, Pietz and Granfors (2000) identified a variety of small mammals as the main predators in their video camera study and did not record raccoon predation.

We found little evidence that cameras affected predation. Substantial model selection uncertainty existed among the 4 top models, including 1 with camera as a covariate, and fit of the global model was questionable. In addition, predation estimates based on the best model with camera effects showed inconsistent differences in predation rates between camera and non-camera monitored nests, and the odds ratio for camera was close to 1. We suggest that camera studies can proceed with at least some support that they do not affect nest success any more than traditional visual monitoring. While Pietz and Granfors (2000) found no significant differences, they suggested that a tendency existed for lower predation at video-monitored nests, and hypothesized that nests with a high probability of predation did not survive long enough to become assigned to camera treatments. Buler and Hamilton (2000) found that natural nests monitored with motion-detector cameras had lower predation.

Some studies have used nest damage to infer predator identity, assuming that snakes or songbirds were predators when nests were intact and that mammals were predators when nests were disturbed (Best 1978). Misidentification of predators based on nest evidence may occur because (1) different predators may affect a nest the same way, (2) the same predator may affect a nest in different ways, or (3) several different predators may visit a nest between visits by researchers (Larivière 1999). Hernandez et al. (1997*b*) and Pietz and Granfors (2000) also found interspecific and intraspecific variability in evidence left at nest sites and believed that evidence at the nest was not a good indicator of predator identity. Generally, we found that nests depredated by raccoons and raptors were the most highly disturbed, but raccoons did not always disturb nests. Snakes were the only predator to create a hole in the nest; however, only 1 of 38 observed snakes created a hole. In previous nest-predation studies, we noticed such holes, and at least 1 other study (Best 1978) has mentioned this phenomenon. Overall, condition of the nest could not be reliably used to identify a predator, or even exclude any predator group (except perhaps raptors for undisturbed nests).

The practice of moving cameras gradually toward the nest over a period of days resulted in many fewer nest abandonments, particularly for indigo buntings (see also Thompson et al. 1999). Unfortunately, this practice also resulted in several instances in which we could not identify predators due to the greater distance of cameras from the nest, especially at night. Cameras are available, however, that can monitor nests at night at greater distances. Video cameras usually successfully recorded predation events, and we are aware of no other technique that will reliably identify predators at songbird nests.

MANAGEMENT IMPLICATIONS

Factors affecting nest success vary among studies, and can include nest site (nest height, concealment), habitat-patch (type, patch size, distance to edge), or landscape factors (composition, fragmentation). Researchers have speculated that this variation is the result of predator diversity and differences in predator communities (Tewksberry et al. 1998, Marzluff and Restani 1999, Thompson et al. 2002). We found evidence that the importance of predators can vary within and between adjacent habitats in the same landscape, even for the same or similar nesting species. Therefore, the importance of predators likely may vary among landscapes and geographic areas as well. We suggest that any investigation of factors affecting nest predation should be undertaken or interpreted with some knowledge of the dominant predators. Ideally, this information would come from directly monitoring nests, as in our study, but at a minimum should include identification of potential nest predators in the area, and preferably some information on their abundances in the habitats or landscapes studied. Studies of nest predation will be more informative if factors affecting predation by specific predators are identified. Likewise, conservation efforts to mitigate high nest predation will require knowledge of predators and predator-specific management. Where predators are known,

aspects of the predator's natural history, as well predator responses to nest-site, habitat, and landscape features can be considered in management.

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