CAUSE SPECIFIC MORTALITY AND ANTI-PREDATOR BEHAVIOR IN MIDWESTERN SONGBIRDS

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By

WILLIAM ANDREW COX

John Faaborg, Dissertation Supervisor

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The undersigned, appointed by the dean of the Graduate School,

have examined the Dissertation entitled

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Presented by William Andrew Cox

A candidate for the degree of

Doctor of Philosophy

And hereby certify that, in their opinion, it is worthy of acceptance.

Professor John Faaborg

Professor Frank R. Thompson III

Professor Ray Semlitsch

Professor Lori Eggert

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ABSTRACT

Predation is a ubiquitous selective pressure that profoundly influences plants and animals on evolutionary and ecological time-scales. The influence of predation on the evolution of life-history traits, behavior, morphology and population dynamics has been closely investigated. For many taxa, however, predation events are rare and/or are infrequently observed. As such, we lack estimates of cause-specific mortality and cannot evaluate predator-specific contributions to variation in traits of interest.

We investigated cause-specific nest mortality of breeding songbird nests in the Midwestern United States. Nest predation is the most frequent cause of reproductive failure in birds and has important demographic implications. We used video technology to identify nest predators of the sub-canopy nesting Acadian Flycatcher (*Empidonax virescens*) and a suite of shrub nesting songbird species in forests of Missouri and southern Illinois. In Chapter 1, we evaluated hypotheses of predator-specific nest predation that explained variation of basic traits such as species and nest stage and temporal variables such as nest age and ordinal day. In Chapter 2, we evaluated models that included environmental variables to explain variation in overall predation rates at multiple spatial scales. In Chapter 3, we investigated anti-predator behavior of adult songbirds in response to nest predation risk. Finally, in Chapter 4 we reviewed the use of video equipment at bird nests and summarized the technological options currently available to researchers.

Predation accounted for >90% of all failure for our video-monitored nests, and 20 predator species were identified removing eggs and/or young from nests. Acadian Flycatchers had lower overall predation rates compared to the guild of shrub nesting species. The best supported model for cause-specific nest predation included terms for species and nest stage. Flycatchers exhibited significantly lower predation rates from raptors, other birds, snakes, and were never depredated by a mesopredator. Flycatchers and the shrub nesting guild had lower predation rates during incubation compared to the nestling period because of reduced predation from raptors and snakes.

Overall rates of nest predation were not influenced by landscape forest cover, proximity to habitat edges, or stem density at the nest site. Nevertheless, predation by Brown-headed Cowbirds (*Molothrus ater*) increased as landscape forest cover decreased. Predation by snakes also tended to increase. By contrast, predation by rodents declined dramatically as forest cover decreased. Corvids, rodents, and mesopredators have often been hypothesized to drive increased rates of predation in fragmented landscapes but were not important contributors to overall predation rates in our least forested landscape. Predation by corvids and raptors decreased as stem density near nests increased, though the effect in both cases was marginal.

We recorded nest visitation behaviors for Acadian Flycatchers (*Empidonax virescens*) and Indigo Buntings (*Passerina cyanea*) to determine whether prey species under risk of predation from a broad suite of predator species can accurately assess risk and modify their behavior accordingly. Life-history theory predicts that prey species under relatively low ambient risk of predation may not respond strongly to changes in predation risk, so we evaluated whether adults of species under relatively high (buntings) and low (flycatchers) predation risk modified their behavior to reduce the risk of predation in response to ambient predation risk, imminent predation risk, and diurnal variation in predator activity. We detected low variation in ambient predation risk across study sites, and a corresponding lack of variation in nest visitation rates for both species. In accordance with predictions, buntings responded more strongly to predation risk and visitation rates in the 24 hr period prior to predation were lower for failed nests than fledged nests recorded at a similar time. This was not driven by behavior immediately prior to predation events, as visitation rates were similar for failed and fledged nests in the 1 hr preceding nest predation. Predation events occurred less frequently in the morning for both species. Nest visitation rates were highest for both species in the morning. The early morning peak of visitation rates by buntings may have been a response to temporal variation in predation risk, but it may also reflect a response to adult or nestling loss of energy stores from the previous night. Despite the variation in foraging strategies and activity patterns of predators at our sites, adults adjusted their behavior in response to the imminent risk of predation to their young.

Our review of the literature showed that video technology was most commonly used to study nest predators (*n* = 114), feeding ecology (*n* = 103), and adult behavior (*n* = 81). Most video systems (69%) were partially or completely user-built. Systems that recorded in real-time (≥25 frames per second), time-

lapse (<25 fps), and still images were all common, though their use tended to vary by study objective. Using the time-lapse digital video recording systems we designed, we monitored 184 nests of 15 different species. We generally found these low-cost systems ($350–725 USD per unit) to be reliable. Sources of data loss were variable by study but included digital recorder malfunction, power failure, and video cable damage due to rodents. Our review of the literature and our own experiences suggest that researchers carefully consider their objectives and study system when choosing camera technology.

Estimation of cause-specific mortality rates helped explain overall rates of nest predation within and between species, and across multiple spatial scales. We also documented adult birds mediating nest visitation rates in response to predation risk in an ecosystem with predators that have varying foraging strategies and activity patterns. Our results also reinforce the species-specific nature of predator-prey interactions; the relationship between breeding birds, nest predators, and the landscapes in which they reside are complex, scale-dependent and context-specific.

CHAPTER 1
PREDATOR-SPECIFIC RATES OF PREDATION EXPLAIN VARIATION IN NEST SURVIVAL

ABSTRACT

Studies on nest predation are ubiquitous in the ornithological literature, but few researchers have identified predators and provided quantitative analysis of predator-specific patterns of nest predation. We used video technology to identify nest predators of the sub-canopy nesting Acadian Flycatcher (*Empidonax virescens*) and a suite of shrub nesting species in forests of Missouri and southern Illinois. We grouped predators into five guilds (raptor, other bird, snake, rodent, mesopredator) and evaluated hypotheses within an information-theoretic framework concerning predator-specific nest predation. We hypothesized that species, nest stage, nest height, concealment, nest age, and Julian date would affect predation rates by predator guilds. We found the most support for our species and nest stage hypotheses. Acadian Flycatchers had lower overall predation rates compared to the guild of shrub nesting species. Flycatchers exhibited significantly lower predation rates from raptors, other birds, snakes, and were never depredated by a mesopredator. Flycatchers and the shrub nesting guild had lower predation rates during incubation compared to the nestling period because of reduced predation from raptors and snakes. Putatively important predators that seldom depredated nests included American Crows (*Corvus*

brachyrynchos) and raccoons (*Procyon lotor*). The identification of nest predators can improve our understanding of the breeding biology of birds, better focus research efforts, and inform conservation decisions.

INTRODUCTION

Nest predation is the primary source of reproductive failure for passerines (Ricklefs 1969, Martin 1992) and as such has received much attention from scientists. For example, a keyword search using “nest,” “predation,” and “bird” on Scopus revealed 1041 papers published since 1990 on the topic (accessed 27 August 2010). Statistical approaches to modeling nest survival have shed light on many factors that contribute to variation in predation rates. We know that nest predation varies both within and across habitats (Martin 1993), that birds actively assess the risk of nest predation and attenuate their nest visitation rates accordingly (Fontaine and Martin 2006), and that in the Midwestern United States, the risk of nest predation increases for many forest birds as landscape-level forest cover declines (Robinson et al. 1995). However, patterns of nest predation uncovered by researchers often conflict with one another. For example, the risk of predation can be lowest (Peak et al. 2004) or highest (Cottam et al. 2009) during the laying stage when compared to the incubation and nestling periods, increased nest concealment may (Chapa-Vargas and Robinson 2006) or may not (Howlett and Stutchbury 1996) decrease the risk of predation, and nests early in a breeding season may have higher (Shustack and

Rodewald 2010) or lower (Bowman and Woolfenden 2001) predation rates than those later in the season.

Uncovering the factors that underlie such variation is critical to improving our understanding of patterns of nest predation. Much of the variation is probably due to differences in the abundance or activity of nest predators, as breeding birds face different suites of predators based on their nest site (e.g., on the ground versus in a tree cavity), habitat (e.g., forest versus grassland), and biogeographic location (Thompson 2007). Until recently, however, almost all research focused on patterns of predation rather than nest predators (Marzluff and Sallabanks 1998). Research on nest predators themselves usually correlates predator abundance, richness, or activity with nest survival (reviewed in relation to habitat fragmentation by Chalfoun et al. 2002b; other examples include Patten and Bolger 2003, Cottam et al. 2009). However, the abundance or activity of a putative predator species is of little importance if its actual contribution to overall nest predation rates is low, and the richness of predator species may not be important in systems wherein most instances of nest predation can be attributed to a subset of predators (Weidinger 2009). There is a need for empirical evidence demonstrating predator-specific variation in nest predation rates, but such data are rare because observations of predation events are typically infrequent and cannot be quantitatively analyzed.

The use of video technology to identify nest predators is increasingly common (see Chapter 4). Though the vast majority of studies that have used cameras have presented their data qualitatively (i.e., a table lists all predators and the number of nest failures each is responsible for), several studies provide quantitative evidence to explain variation in predation rates. Thompson and Burhans (2003) showed that snakes contributed most to the overall predation rates for songbird nests in fields, while mammals were dominant nest predators in forests. Weidinger (2009) found that study site best explained variation in which predators were responsible for nest predation in fragmented woodlands. Benson et al. (2010) demonstrated seasonal, nest stage, and edge related predator-specific patterns of predation for Swainson's Warblers (*Limnothlypis swainsonii*). Finally, Reidy and Thompson (in press) found temporal and landscape related predator-specific patterns of nest predation for two endangered songbirds.

These studies suggest that the identification of nest predators can improve our understanding of how and why rates of nest predation vary across space and time. Our goal was to identify predators of the tree-nesting Acadian Flycatcher (*Empidonax virescens*) and a guild of shrub-nesting species in forests in the Midwestern United States to 1) identify which predators or predator guilds contribute most to overall predation rates, and 2) evaluate whether predator-specific predation rates explained variation in overall predation rates. Specifically, we evaluated support for predator-specific hypotheses of nest predation that described differences in overall predation rates between: a) species occupying the same habitat patch but different microhabitats b) incubation and nestling stages, and c) across time. We also evaluated whether two nest site characteristics (nest concealment, nest height) known to influence the risk of predation in our and other study systems (e.g. Burhans and Thompson 1998; Burhans et al. 2002) influenced predator specific predation rates.

METHODS

Study sites and focal species

We selected eight study sites in Missouri and Illinois (Table 1) based on the presence of our focal species, representation of a range of landscape scale forest cover (see Chapter 2), and public access. Sites were characterized by mid- to late successional deciduous forests with overstories dominated by oak (*Quercus sp.)* and hickory (*Carya sp.*), though several sites in Illinois also featured mature Tuliptree (*Liriodendron tulipifera*), Sweetgum (*Liquidambar styraciflua*) and American beech (*Fagus grandifolia*). Sugar Maple (*Acer saccharum)* was a common component of the understory and sub-canopy at most sites.

We conducted field work from May to August during 2006 – 2010. We did not visit all sites in all years because of logistical constraints (Table 1). Our primary focal species were the Acadian Flycatcher and Indigo Bunting (*Passerina cyanea*) because they have previously demonstrated variation in nest predation rates between each other (Robinson et al. 1995), and between nest stages (Peak et al. 2004). The Acadian Flycatcher breeds in the interior of mid-successional to mature forests in the eastern United States and typically nests at the end of slender branches of understory trees. The Indigo Bunting breeds in old fields, forest edges, and forest gaps in the eastern United States north to southern Canada. It often nests in herbaceous shrubs such as blackberry (*Rubus spp.*) and multiflora rose (*Rosa multiflora*), but also builds nests in deciduous and coniferous saplings. Both species are listed as “Least Concern” by the IUCN because of their large ranges and relatively stable populations (IUCN 2010). We also located and monitored nests of other shrub-nesting species, including the Northern Cardinal (*Cardinalis cardinalis*), Yellow-breasted Chat (*Icteria virens*), Field Sparrow (*Spizella pusilla*), and Eastern Towhee (*Pipilo erythrophthalmus*). We grouped buntings and these species into a shrub-nesting guild for our analysis because they share similar breeding ecologies and nest site characteristics. Finally, we opportunistically filmed nests of other species when cameras were available, but we excluded these from quantitative analyses because of small sample sizes and substantially different nesting ecologies and nest placement.

Nest monitoring and camera placement

We located nests using systematic search and behavioral cues. Nests without cameras were monitored every 2 – 4 days following Martin and Geupel (1993). We filmed nests using a combination of vendor (Fuhrman Diversified, Inc.) and user-built video systems (Cox et al. in press). In 2006, we utilized four user-built analog video systems with 850 nm infrared cameras. During 2007 – 2010, we used eight vendor-built digital video systems with 940 nm infrared cameras and 16 user-built digital video systems. Thirteen of the user-built systems had 940 nm infrared cameras and three operated at the 850 nm wavelength. We placed the vendor-built systems 0.5 – 1 m from nests, while the user-built systems were placed 1.5 - 4.5 m from nests. For the user-built systems, we placed cameras on a tripod or affixed them to trees with a spring-loaded metal clip, brown duct tape, or a custom-made cargo strap wrapped around a tree trunk. We camouflaged all components of vendor and user-built systems with small branches, leaves, and other vegetation to reduce the likelihood of the equipment influencing predator behavior (Herranz et al. 2002, Richardson et al. 2009) or inducing nest abandonment. For all mounting methods, we sprayed the extension cable and the camera's exposed wires with Ropel®, a non-toxic, bitter-tasting chemical, to reduce damage from wildlife. We placed the VCR/DVR case 8 – 10 m from nests to minimize disturbance to the nesting bird when changing the battery and memory card. Upon completion of camera setup, we covered the case in a waterproof, camouflage tarp, covered the tarp with leaf litter, and locked the case to a nearby tree to reduce the risk of theft. The total time for camera setup was generally ≤15 min. After setup we walked ~50 m from the nest and waited for the cessation of alarm calls to signal a nesting female's acceptance of the camera. If a female did not accept a camera after 20 minutes, we moved it farther from the nest. If she still did not accept a camera, we removed it. We tended to our cameras every 44 – 52 hr to replace the battery and the SD memory card.

When there were fewer nests available than cameras, we filmed all nests except those from which we could not consistently acquire high quality images.

Generally, we excluded nests if they were beyond the effective range of the infrared of our cameras (1 m for vendor built systems, 5 m for user-built models) or if we felt that the set-up or placement would cause unacceptable disturbance to the vegetation and/or cover surrounding a nest. When there were more nests than cameras, we prioritized nests to 1) avoid filming more than one nest per breeding pair within a season, 2) maximize the distance between cameras, and 3) achieve an adequate sample size for both Acadian Flycatchers and shrub-nesting species.

Covariates

We measured nest height using either a measuring tape or a clinometer. We used a modified version of BBird protocols (Martin et al. 1997) to measure nest concealment. For shrub-nesting species we made visual estimates of the percent of a nest concealed from 1 m at the four ordinal directions, from 1 m above, and from 1 m below. For nests <1 m high we estimated concealment from below using a mirror at ground-level. We used a similar approach for Acadian Flycatchers, but we did not record measurements for nests we deemed too high to accurately estimate concealment.

We calculated nest age by counting the last day an egg was laid as day zero of the nest period. If we did not know when the eggs were laid but obtained a hatch date, we would backdate from the hatch date using the mean incubation period from our data or from Birds of North America Online species accounts (Poole 2005). In some cases poor video quality prevented us from accurately determining the hatch date so we backdated nest ages from the fledge date when possible. Finally, 19 nests were found after laying but were depredated prior to hatching. For these nests we randomly selected nest ages from a range of possible ages constrained by the mean incubation period and number of observation days we had (e.g., if an Indigo Bunting nest was depredated on the eighth day of filming, that day was randomly assigned an age between eight [the minimum age possible] and 11.5 [the mean incubation period for the species]). We estimated ages based on the physical appearance of nestlings for depredated nests that were found after hatch (n = 23).

Analysis

We used multinomial logistic regression in an information-theoretic framework (Burnham and Anderson 2002) to evaluate support for eight predator-specific models of nest predation (see below). We ranked models by Akiake's Information Criteria (AIC_c) and calculated Akaike weights (w_i) for each model. Our use of multinomial regression allowed us to have more responses (described below) than typical binomial (0 = active, 1 = failed) nest fate approaches. We assumed *a priori* that our sample sizes for many predator species would be small, so we grouped predators into five biologically meaningful guilds and had seven total response levels or fates: active, depredated by raptor, other bird, rodent, mesopredator, snake, or other. The "other" category included nests that failed from predators that did not fall into the first five categories (e.g., human), environmental factors (e.g., weather), nest abandonment, nestling mortality, and nests with unknown fates (e.g., because of camera failure or technician error). We considered a nest to fail if at least one nestling was captured by a predator (i.e., partial predations and force fledging events in which a nestling is captured but others leave the nest to escape are both considered failures). The sampling unit for this approach is each 24 hr interval a nest was filmed, which is comparable to nest survival methods that use nest-check intervals as sampling units (Dinsmore et al. 2002, Shaffer 2004). For nests lacking an exact date of fledge or failure because of camera failure, we assigned the midpoint of the interval between nest visits as the date of fledge or failure.

Models

We constructed models to represent our hypotheses that species, nest stage, nest height, concealment, nest age, and Julian date would affect predation rates by predator guilds. We limited the number of covariates in candidate models because of concerns about small sample sizes among predator categories and between species (for simplicity, the “species” covariate in all models refers to the comparison between Acadian Flycatchers and the shrub-nesting guild). Because a coefficient is estimated for each of the six responses for each covariate and results in a 12 point increase in AIC_c scores, we limited the pool of potential covariates to those we thought were most likely to have substantial explanatory power. We included two single-covariate models (nest stage, species) because these two factors are often important predictors of nest survival for birds (reviewed in Martin 1992) and we included both covariates in all other models. We included an interaction term for species and nest height because the height of shrub nests is relatively invariant so we hypothesized the effect of nest height would be smaller for shrub nesters than Acadian Flycatchers. We pooled data across years and did not evaluate a year effect because of small sample sizes at each site in a given year.

Model-selection approaches require that models be compared based on the same set of data; this requires a covariate with missing values be dropped from consideration or that observations with missing values be dropped. Because we only had nest concealment measurements for a subset of nests, we conducted a separate analysis of these nests. We included single covariate models for species and stage, a model that combined species and stage, and a model with species and stage that included nest concealment. We also included a model testing the interaction between species and concealment to reflect the possibility that nest concealment influenced the risk of predation for just one of the species. The AIC_c scores for these models cannot be compared to the previous models, but can be compared to one another to evaluate the relative importance of nest concealment in predicting predator-specific predation rates. We used the best-supported model to generate daily predation rate estimates and odds ratios for coefficient estimates. We calculated overall predation rate estimates by collapsing the predator-specific response variables (excluding “other” fates) into a single variable and weighting observations during incubation and nestling stages to reflect the amount of time each species spends in each stage. All estimates are presented with 95% confidence intervals. We performed all analyses with SAS version 9.2 (2008).

RESULTS

We found 1065 active nests of 26 species and monitored 381 nests of 15 species with cameras.   Adults abandoned eight nests because of the presence of the camera and/or researchers. Of the remaining 373 nests, 185 were Acadian Flycatcher nests and 166 were shrub nests, the majority of which were Indigo Buntings (*n* = 124). The final 22 nests were of species we did not include in the quantitative analysis. The effective sample size was 4087 observation days for the first analysis and 3822 observation days for the nest concealment analysis.

We recorded 174 nest failures for 11 species and personally witnessed one predation event at an unfilmed nest that we included in our analyses (Table 2). We included one predation event from a Red-shouldered Hawk (*Buteo lineatus*) in Table 2 that we excluded from analysis because a hawk visited the nest ~20 min after we set up the camera and an individual of the same species depredated the nest several days later. Raptors (*n* = 54) and other birds (*n* = 39) most frequently depredated nests. Blue Jays (*Cyanocitta cristata*; *n* = 22) and Broad-winged Hawks (*Buteo platypterus*; *n* = 20) were the most common avian predators identified. Snakes (*n* = 34) were also common predators; the majority of predation events were from black ratsnakes (*Elaphe obsoleta*; *n* = 21).   Most of the rodent predation events (*n* = 16) were from mice (*Peromyscus spp.*; *n* =

10), and raccoons (*Procyon lotor;* N=5) were responsible for most of the predation events from mesopredators (n=7). The failure of two nests by humans was the result of vegetation removal by land managers. Adult females were killed during two depredation events; an Eastern Towhee was depredated by a Barred Owl while incubating at night and another Eastern Towhee was depredated by a black ratsnake while brooding her young. All other females were confirmed to have survived nest depredation events.

The model with species and stage was best supported in both the original and concealment set of candidate models and the null model had the least support in both model sets (Table 3). The second ranked model in the original candidate set included a variable for Julian date and the second ranked model in the concealment set included the concealment variable.

We lacked observations of mesopredators depredating nests during the incubation stage for shrub-nesting species and in either nest stage for Acadian Flycatchers, so parameter estimates for this predator guild could not be estimated. This typically does not influence the parameter estimates derived from other response levels (Allison 2008), however, which we confirmed with a *post hoc* analysis on a dummy data set that replaced missing values.

Predation differed between Acadian Flycatchers and shrub nesting species during both nest stages and overall when controlling for nest stage (Fig. 1). The difference between species was driven by three predator guilds; the odds of predation for shrub nesting birds was greater than for Acadian Flycatchers by raptors (249%), snakes (466%), and non-raptorial birds (224%; Fig. 2; Table 4).

Further, mesopredators did not depredate any flycatcher nests. The difference between stages was driven by two guilds; the odds of predation by raptors and snakes was 551% and 356% greater, respectively, during the nestling period than during incubation (Fig. 2; Table 4). Mesopredators depredated shrub nests exclusively during the nestling period. Rates of predation between predator guilds and between nest stages exhibited similar variation for each species (Fig. 3).

DISCUSSION

We identified the source of failure at 174 nests of songbirds breeding in Midwestern forests and evaluated predator-specific patterns of nest predation. Raptors, snakes, and non-raptorial birds were frequent predators of shrub and flycatcher nests. Rodents contributed some to overall predation rates but mesopredators never depredated a flycatcher nest and rarely depredated shrub nests. No single predator guild was responsible for the significant difference in overall predation rates between flycatchers and shrub nesting species. Instead, flycatchers exhibited a reduced risk of nest predation from all predator guilds except rodents.

Raptors were frequent nest predators for shrub-nesting species and for Acadian Flycatchers at our field sites. This contrasts with other studies in which raptors depredated nests less frequently than other predator guilds (Reidy and Thompson in press, control sites of Conner et al. 2010, Benson et al. 2010). Habitat type and biogeographic region are likely responsible for such variation

(Thompson 2007). Thompson and Burhans (2003) also found raptors to be relatively infrequent nest predators at a field site shared by this study, but this is probably a consequence of sampling effort. We focused our monitoring efforts on birds breeding within forests and along forest edges and avoided entering old fields where many shrub nests found by Thompson and Burhans (2003) were filmed. Our most common raptorial predators (Barred Owls and Broad-winged Hawks; Table 2) are forest-dwelling species and may forage more frequently within the forest than they do in old fields, though surprisingly few data on habitat use and selection exist for raptors. The difference in raptor predation between Thompson and Burhans (2003) and this study may also be due to annual variation in predator abundance or activity but our small sample sizes do not allow us to evaluate site-specific year effects on predator-specific predation rates.

Of the non-raptorial avian species, Blue Jays were by far the most frequent nest predator we identified (Table 2). Crows have often been hypothesized to be important nest predators, but our results corroborate those of other researchers (Reidy and Thompson in press, Thompson and Burhans 2003) and it does not appear that they contribute meaningfully to the overall risk of predation for forest-breeding songbirds. Brown-headed Cowbirds were the only other non-raptorial avian species we recorded depredating more than three nests in the five years of our study. Cowbirds usually flew out of the view of the camera with eggs or nestlings in their bills, but we observed three occasions during which nest contents were dropped rather than consumed. Such ransacking of nests provided cowbirds with no nutritive benefits and probably is done to allow for additional reproductive opportunities by forcing the host adults to initiate a new nest (Arcese et al. 1996, Hoover and Robinson 2007). The higher rate of predation on shrub nests versus flycatchers from non-raptorial birds may due to increases in cowbird and/or Blue Jay abundances along forest edges (Chalfoun et al. 2002a). However, while cowbird nest parasitism rates are correlated with proximity to forest edges (Lloyd et al. 2005), densities may not be (Donovan et al. 1997). Surprisingly few data exist on Blue Jay habitat selection and use and it is unclear whether jay abundance or activity is greater near forest edges.

Both Acadian Flycatchers and shrub-nesting species were vulnerable to the risk of predation from snakes, providing further evidence of their importance as an avian nest predator (Weatherhead and Blouin-Demers 2004). Black ratsnakes have been identified as nest predators throughout their range (Thompson et al. 1999, Williams and Wood 2002, Farnsworth and Simons 2000, Benson et al. 2010). They are the most adept climber among snakes at our field sites and were the only species of snake we recorded depredating Acadian Flycatcher nests. The reduced risk of predation for flycatchers from this guild may occur in part because fewer species of snakes can access their nests. Additionally, ratsnakes prefer shrubby habitat near forest edges over the forest interior because of the increased thermoregulatory opportunities such habitat provides (Blouin-Demers & Weatherhead 2001). Other species of snake we encountered but did not record depredating nests include the Timber rattlesnake

(*Crotalus horridus*), Copperhead (*Agkistrodon contortrix*), and Eastern garter snake (*Thamnophis sirtalis sirtalis*).

Mice (*Peromyscus sp.*) were the only mammal for which we recorded more than five depredation events during our study (Table 2). Mesopredators have been implicated as major nest predators (e.g., Crooks and Soulé 1999, Dijak and Thompson 2000) but contributed very little to overall predation rates for shrub-nesting species and no Acadian Flycatcher nest was depredated by a mesopredators, probably because they cannot access typical flycatcher nest-sites. Mesopredators more frequently depredate nests in other systems (e.g., Renfrew and Ribic 2003), and may remain an important source of nest mortality for ground-nesting birds at our field sites; the only two nest predators we identified for Worm-eating Warblers (*Helmitheros vermivorus*) were raccoons. Nevertheless, studies in forests of the eastern United States (Conner et al. 2010, Williams and Wood 2002, Farnsworth and Simons 2000, King et al. 2001) suggest that they are not frequent predators of shrub- and understory-nesting birds. Other putative predators we observed at our field sites that did not depredate filmed nests include Fox squirrels (*Sciurus niger*), Eastern chipmunks (*Tamias striatus*), and Eastern gray squirrels (*Sciurus carolinensis*), of which one individual inspected and left unmolested an active Indigo Bunting nest (W.A. Cox, personal observation).

Acadian Flycatchers and shrub-nesting species both experienced a significantly lower risk of predation during incubation compared to the nestling period. In both cases this was driven by a decline in the risk of predation from snakes and from raptors. Ratsnakes use visual cues to find bird nests (Mullin and Cooper 1998, Lillywhite and Henderson 1993), and visitation rates for Acadian Flycatchers and Indigo Buntings are lower during incubation than during the nestling period (see Chapter 3). Most of the Acadian Flycatcher nests depredated by snakes occurred after dusk (W.A. Cox unpublished data) when adult activity had ceased, however. Whether snakes use information acquired during the day to forage at night is not known, but Stake et al. (2005) documented two ratsnakes near nests during the day that were later depredated by ratsnakes after sunset. Snakes also use olfactory cues to locate prey (Halpern 1992) and such cues may be more prevalent in nests with young compared to those with eggs. However, olfactory cues probably become more prevalent as nestlings grow but we saw no effect of nest age on predator-specific predation rates.

Raptors also use visual cues to locate prey, which may further explain the increased predation rates during the nestling period. The *Accipter* and *Buteo* species we recorded depredating nests are all diurnal, and only two of 12 predation events by Barred Owls occurred between dusk and dawn (see Chapter 3). However, our recordings also provide some anecdotal evidence that raptors may preferentially forage on nestlings. The Red-shouldered Hawk we excluded from analysis appeared to wait until hatching to consume the nest contents. In another nest, a Barred Owl depredated an incubating female but did not consume the eggs. Finally, raptors at two nests with eggs appeared to ransack the nest rather than consume its contents.

None of the other variables we tested explained predator-specific patterns of nest predation. Evidence supporting the hypothesis that increased nest concealment reduces the risk of predation is equivocal in the literature. Such a relationship may be confounded by adult behavior or trade-offs birds face in nest-site selection (reviewed in Lima 2009), which may explain why models including nest concealment were not well supported for birds at our field sites. Birds are capable of responding to variation in a local predator community by altering nest heights (Forstmeier and Weiss 2004, Peluc et al. 2008), which suggests that some predator guilds have reduced access to higher nests. We did not detect such an effect, but this may be due in part to our grouping of predators. For example, “rodents” included terrestrial mice and arboreal flying squirrels which probably reduced the likelihood of nest height influencing predation rates from this guild.

Many passerines exhibit intraseasonal variation in predation rates (e.g., Fisher and Weibe 2006, Post van der Berg et al 2010) but we did not detect an effect of Julian date on predator-specific predation rates. This was surprising because Acadian Flycatchers exhibit an intraseasonal decline of nest predation rates in Ohio (Shustack and Rodewald 2010) and in Missouri, where avian predation rates (raptors and non-raptorial birds) declined as the breeding season progressed (Hirsch-Jacobson et al. in press). A post-hoc analysis of a model that included an interaction term between species and Julian date received less support than the original model, indicating that neither flycatchers nor shrub nesting species are exhibiting pronounced temporal trends in nest survival (W.A.

Cox, unpublished data). Given that the model with Julian date was the second most supported model with a marginal weight of evidence, seasonal effects on nest survival probably exist at our study sites but were significantly less pronounced than the species and stage effects we identified.

We demonstrated that the identification of nest predators and analysis of predator-specific patterns of nest predation can improve our understanding of the factors that underlie variation in the risk of nest predation. Such knowledge can inform conservation decisions and increase our understanding of avian behavior, ecology, and the evolution of life-history traits. Knowledge of the importance of particular predators can also better focus research efforts; Cottam et al. (2009) attempted to use predator density as a predictor for Acadian Flycatcher nest survival in Illinois, but eight of ten putative predators they studied never depredated a flycatcher nest in our study. Future research that identifies predators for a wider suite of species at both local and broader spatial scales will further improve our understanding of the ecology and evolution of breeding birds.

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Table 1. Field sites, locations, and year sampled in a study of nest predation in the Missouri and Illinois, 2006 – 2010.

			Year Sampled				
State	Site	Location	2006	2007	2008	2009	2010
Missouri	Baskett Wildlife Area	38° 44’N, 92° 12’W		x		x	
	Bennitt Conservation Area	39° 15’N, 92° 28’W		x		x	
	Current River Conservation Area	37° 11’N, 91° 02’W	x	x		x	
	Mark Twain National Forest - Doniphan	36° 37’N, 90° 55’W		x		x	
Illinois	Ferne Clyffe State Park	37° 32’N, 89° 01’W			x		x
	Saline Conservation Area	37° 42’N, 88° 24’W			x		x
	Thompsonville private land	37° 56’N, 88° 40’W			x		x
	Trail of Tears State Forest	37° 30’N, 89° 21’W			x		X

Table 2. Fates of video-monitored nests at eight field sites in Missouri and Illinois, 2006 – 2010.

			Shrub-nesting species					Other				
Predator	Total	ACFL[1]	INBU	NOCA	EATO	FISP	YBCH	WOTH	REVI	WEWA	OVEN	WEVI
Raptor	**54**											
Accipiters	3	1	1	1								
(*Accipter sp.*)												
Barred Owl	12	6	4		1			1				
(*Strix varia*)												
Broad-winged Hawk	20	10	8					1				1
(*Buteo platypterus*)												
Buteos (*Buteo spp.*)	3		1	1			1					
Eastern Screech Owl	1		1									
(*Otus asio*)												
Hawk	3		1	2								
(unknown sp.)												
Red-shouldered Hawk	5	2	3									
(*Buteo lineatus*)												
Red-tailed Hawk	4	1	3									
(*Buteo jamaicensis*)												

			Shrub-nesting species					Other				
Predator	Total	ACFL[1]	INBU	NOCA	EATO	FISP	YBCH	WOTH	REVI	WEWA	OVEN	WEVI
Unknown species	3	2	1									
Other birds	**39**											
American Crow (*Corvus brachyrhynchos*)	3	2	1									
Non-raptorial avian (unknown sp.)	1	1										
Blue Jay (*Cyanocitta cristata*)	22	11	8				1		1		1	
Brown-headed Cowbird (*Molothrus ater*)	9	2	7									
Wild Turkey (*Meleagris gallopavo*)	1		1									
Yellow-billed Cuckoo (*Coccyzus americanus*)	3	2	1									
Snake	**34**											
Black ratsnake (*Elaphe obsoleta*)	21	9	6	3	2	1						

			Shrub-nesting species					Other				
Predator	Total	ACFL[1]	INBU	NOCA	EATO	FISP	YBCH	WOTH	REVI	WEWA	OVEN	WEVI
Eastern yellow-bellied racer	4		4									
(*Coluber constrictor*)												
Unknown species	9	1	5	3								
Rodent	**16**											
Wood Rat	1		1									
(*Neotoma sp.*)												
Mouse	10	5	5									
(*Peromyscus sp.*)												
Unknown sp.	3	3										
Southern Flying Squirrel	2	2										
(*Glaucomys volans*)												
Mesopredator	**7**											
Fox	1		1									
(unknown sp.)												
Virginia Opossum	1		1									
(*Didelphis virginiana*)												
Raccoon	5		2	1						2		

Predator	Total	ACFL[1]	Shrub-nesting species					Other				
			INBU	NOCA	EATO	FISP	YBCH	WOTH	REVI	WEWA	OVEN	WEVI
(*Procyon lotor*)												
Other	33											
Abandoned												
Hatching failure	1		1									
Camera/researcher effects	8	3	3		1			1				
Unknown why	5	2	2						1			
Environmental factors (weather, tree fall)	6	3		1		1		1				
Avian - unknown order	1	1										
Human	2		1	1								
Nest breakage	3	2				1						
Nest dislodged	1		1									
Nestling mortality	6	6										
Unknown	**44**											
Camera failure	20	10	4	4		1				1		
Camera removed	9	3	4			1		1				

			Shrub-nesting species					Other				
Predator	Total	ACFL[1]	INBU	NOCA	EATO	FISP	YBCH	WOTH	REVI	WEWA	OVEN	WEVI
Nest out of view	4	2	2									
Predator not identified	5	4			1							
Technician error	6	2	2	1						1		
Total (excluding unknown fates and camera/researcher effects):	**175**	**74**	**71**	**13**	**3**	**3**	**2**	**3**	**2**	**2**	**1**	**1**

[1] Species codes: ACFL – Acadian Flycatcher; INBU – Indigo Bunting; NOCA – Northern Cardinal; EATO – Eastern Towhee; FISP – Field Sparrow; YBCH – Yellow-breasted Chat; WOTH – Wood Thrush (*Hylocichla mustelina*); REVI – Red-eyed Vireo (*Vireo olivaceus*); WEWA – Worm-eating Warbler (*Helmitheros vermivora*); OVEN – Ovenbird (*Seiurus aurocapillus*) ; WEVI - White-eyed Vireo (*Vireo griseus*).

Table 3. Model selection results for *a priori* candidate models describing predator-specific patterns of nest predation for Acadian Flycatchers and shrub-nesting species in a study of nest predation in Missouri and Illinois. 2006 – 2010.

Model	Structure	Log likelihood^1	K^2	AIC$_c^3$	Δ AIC$_c^4$	w_i^5
Species and Nest Stage	$\beta_0 + \beta_1$(Species) + β_2(Stage)	2122.14	18	2158.14	0.00	0.81
Julian date	$\beta_0 + \beta_1$(Species) + β_2(Stage) + β_3(Date)	2113.03	24	2161.03	2.90	0.19
Nest Height	$\beta_0 + \beta_1$(Species*NestHeight) + β_2(Stage)	2120.22	24	2168.22	10.09	0.01
Global Model	$\beta_0 + \beta_1$(Species) + β_2(Stage) + β_3(NestHeight) + β_4(NestAge) + β_6(Date)	2105.16	36	2177.16	19.03	0.00
Nest Age	$\beta_0 + \beta_1$(Species) + β_2(NestAge)	2142.24	18	2178.24	20.11	0.00
Species	$\beta_0 + \beta_1$(Species)	2165.66	12	2189.66	31.52	0.00
Nest Stage	$\beta_0 + \beta_1$(Stage)	2167.45	12	2191.45	33.31	0.00
Null	β_0	2209.65	6	2221.65	63.51	0.00
Concealment candidate models						
Species and Nest Stage	$\beta_0 + \beta_1$(Species) + β_2(Stage)	2023.10	18	2059.10	0.00	0.92

Model	Structure	Log likelihood[1]	K[2]	AIC$_c$[3]	Δ AIC$_c$[4]	w_i[5]
Nest concealment (Global)	$\beta_0 + \beta_1$(Species) + β_2(Stage) + β_3(Concealment)	2016.32	24	2064.32	5.21	0.07
Nest concealment by species	$\beta_0 - \beta_1$(Species*Concealment) + β_2(Stage)	2020.95	24	2067.10	8.00	0.02
Stage	$\beta_0 + \beta_1$(Stage)	2066.13	12	2090.13	31.02	0.00
Species	$\beta_0 + \beta_1$(Species)	2068.86	12	2092.86	33.76	0.00
Null	β_0	2111.01	6	2123.01	63.91	0.00

[1] Log likelihood score from PROC LOGISTIC in SAS.

[2] Number of parameters in the model.

[3] Akaike's Information Criteria.

[4] The difference between the current and top-ranked model's AIC$_c$ score.

[5] Weight of evidence supporting the model.

Table 4. Coefficient and odds ratio estimates for parameters from the top-ranked model (Species + Stage) in a study of nest predation in the Midwestern United States, 2006 – 2010. Odds ratios in bold are considered significant because their 95% confidence intervals do not overlap 1. Missing values for both variables in the model prevented generation of estimates for mesopredators.

			Odds Ratio		
Variable	Coefficient (β)	SE	Estimate	95% CI	
Species[1]					
Raptor	0.46	0.14	**2.49**	1.42	4.37
Snake	0.77	0.19	**4.66**	2.22	9.79
Other bird	0.40	0.16	**2.24**	1.19	4.22
Mesopredator	NA	NA	NA	NA	NA
Rodent	0.07	0.26	1.14	0.42	3.16
Stage[2]					
Raptor	0.85	0.22	**5.51**	2.34	12.98
Snake	0.64	0.23	**3.56**	1.47	8.62
Other bird	0.26	0.17	1.69	0.85	3.34
Mesopredator	NA	NA	NA	NA	NA
Rodent	0.10	0.26	1.23	0.45	3.39

[1] Odds ratios presented compare predation rates of shrub-nesting species to that of Acadian Flycatchers (i.e., shrub-nesters were 2.49 times more likely than flycatchers to be depredated by a raptor).

[2] Odds ratios presented compare the nestling period to the incubation period.

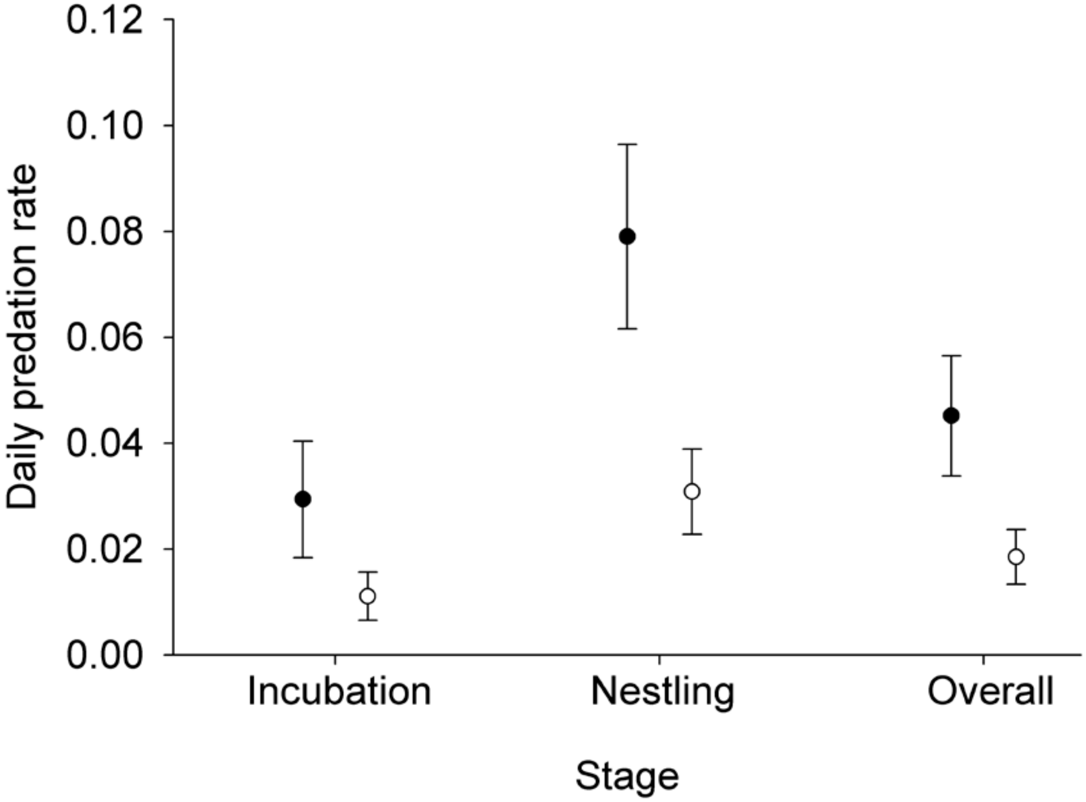

Figure 1. Overall rates of predation for Acadian Flycatchers (white circles) and shrub-nesting species (black circles) estimated from the top-ranked model in a study of nest predation in the Midwestern United States, 2006 – 2010.

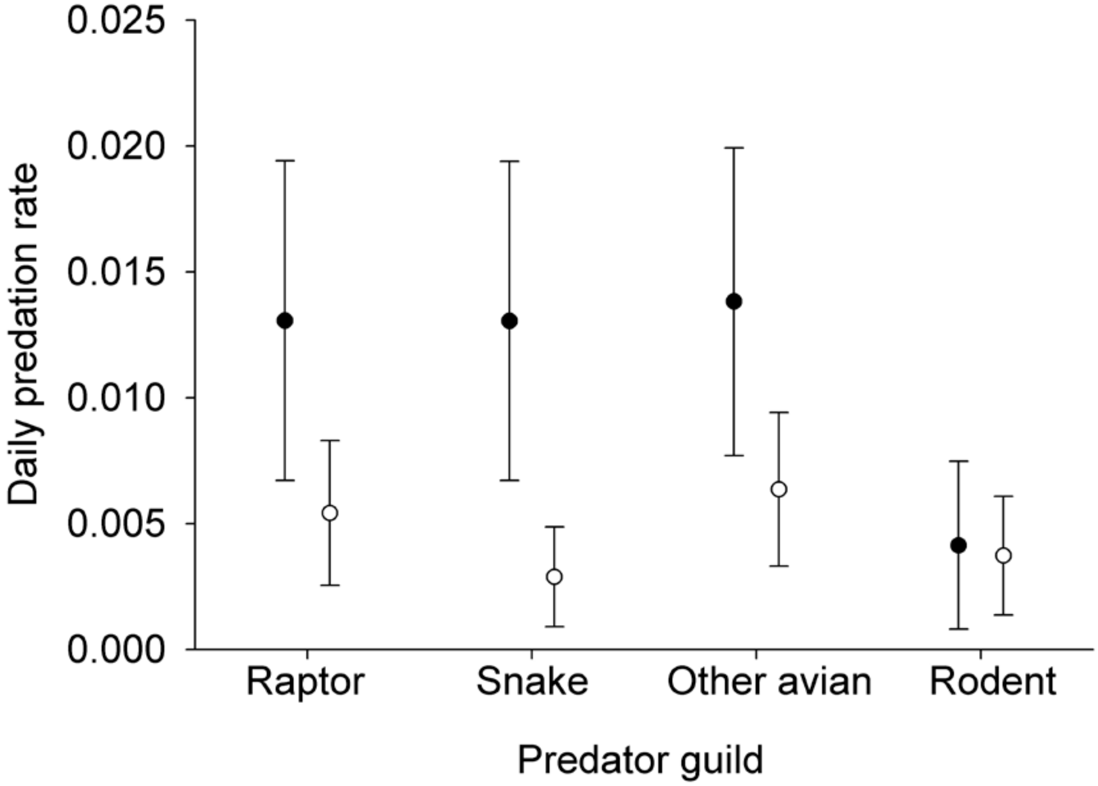

Figure 2. Predator-specific nest predation rates for shrub nesting species (black circles) and Acadian Flycatchers (white circles) estimated from the top-ranked model (Species + Stage) in a study of nest predation in the Midwestern United States, 2006 – 2010. Missing values for both variables in the model prevented generation of estimates of predation rates for mesopredators.

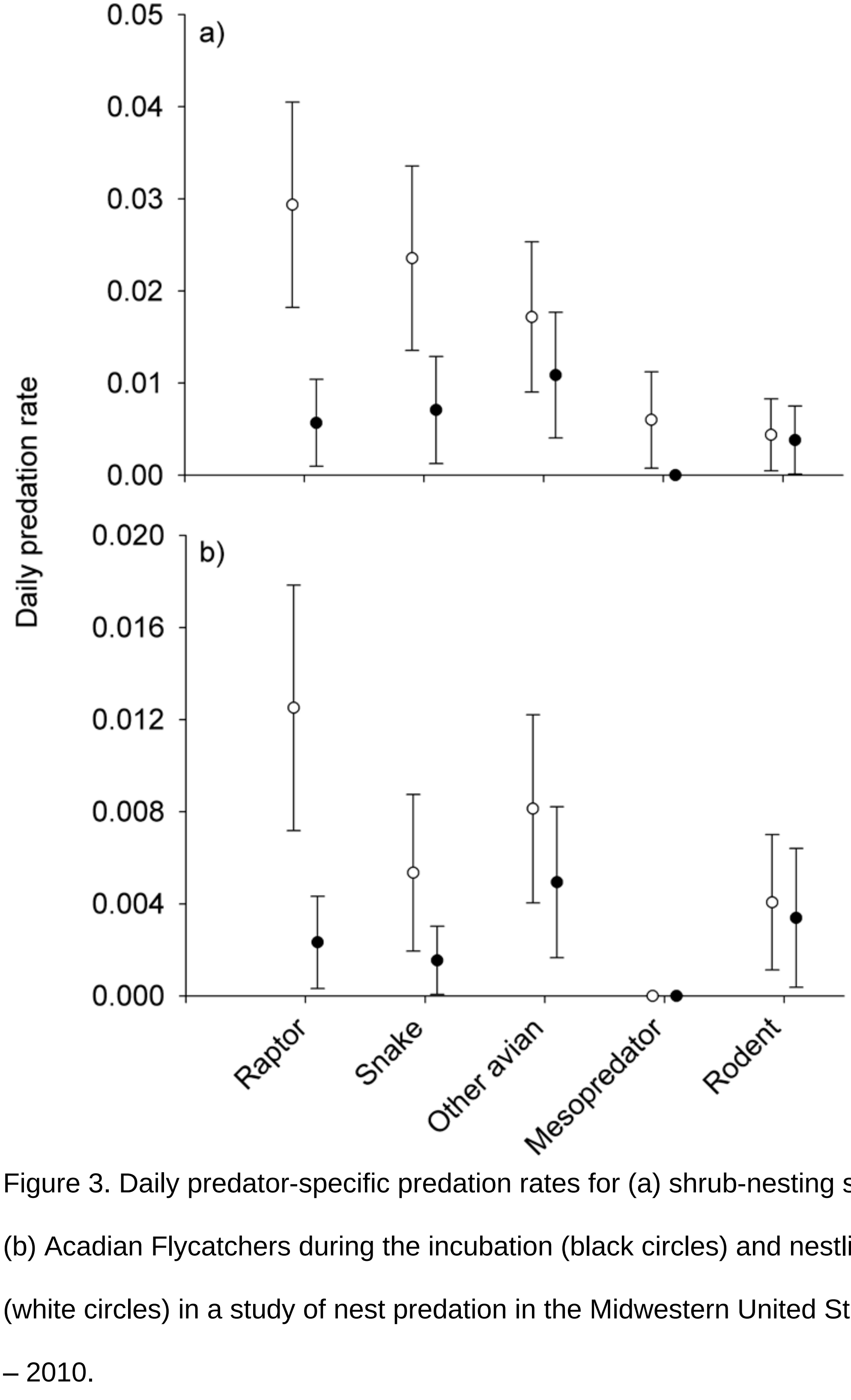

Figure 3. Daily predator-specific predation rates for (a) shrub-nesting species and (b) Acadian Flycatchers during the incubation (black circles) and nestling period (white circles) in a study of nest predation in the Midwestern United States, 2006 – 2010.

CHAPTER 2
LANDSCAPE AND NEST SITE FACTORS INFLUENCE PREDATOR-SPECIFIC RATES OF NEST PREDATION

ABSTRACT

Rates of nest predation for birds vary between and within species across multiple spatial scales. At the landscape scale, forest songbirds in the Midwestern United States exhibit increased rates of predation as forest cover declines. At the patch scale, proximity to forest edges has been associated with increased rates of nest predation. At the nest-site scale, increased foliage density near nests can reduce the risk of predation. We documented predators at the nests of Acadian Flycatchers (*Empidonax virescens*) and a guild of shrub nesting species at eight study sites in the Midwestern United States to evaluate hypotheses concerning factors affecting predator-specific rates of predation and how these related to overall patterns of nest predation at three spatial scales. The best supported models as determined using an information-theoretic approach included covariates for landscape-level forest cover and stem density at the nest-site. Predation by Brown-headed Cowbirds (*Molothrus ater*) increased as landscape forest cover decreased. Predation by snakes also tended to increase. By contrast, predation by rodents declined dramatically as forest cover decreased. Predation by corvids and raptors tended to decrease as stem density near nests increased, though the effect in both cases was marginal.

Despite the predator-specific patterns we detected, none of the covariates tested explained any variation in overall rates of predation. The interactions between breeding birds, nest predators, and the landscapes in which they reside are complex, scale-dependent and context-specific, and may be resistant to broad conceptual management recommendations.

INTRODUCTION

Anthropogenic habitat loss can have pervasive negative effects on wildlife (Fahrig 2003), which may extend beyond the obvious reduction in habitat. The quality of remaining habitat may also be affected, resulting in reductions in species richess, abundance, and important demographic parameters (Lindenmayer and Fischer 2006). Birds have often demonstrated sensitivity to factors related to habitat fragmentation and loss at multiple spatial scales (Faaborg et al. 1995). Effects on nest predation rates for breeding songbirds has been particularly well studied because nest survival is an important component of songbird demography (Donovan and Thompson 2001) and many species have experienced long-term population declines on the breeding (Robbins et al. 1989) and wintering grounds (J. Faaborg, unpublished data). Rates of nest predation may increase for forest songbirds as landscapes become less forested (Robinson et al. 1995), which in combination with a concomitant increase in rates of brood parasitism contributes to reduced population growth rates for songbirds across the United States (Lloyd et al. 2005). Proximity to forest edges can further exacerbate this problem by increasing the risk of nest predation for many species even when controlling for other landscape effects (Lloyd et al. 2005).

In many cases, however, habitat fragmentation and edge effects have not had demonstrable effects on nest predation. For example, edge effects may only be pronounced in moderately fragmented landscapes (Donovan et al. 1997) and more generally may be context dependent, influenced by biogeographic region, habitat type, and nest guild (Batáry and Báldi 2004). Further, in biogeographic regions with historically fragmented forests, nest predation rates may actually decline as fragmentation increases (Tewksbury et al. 1998). Thompson et al. (2002) proposed a hierarchical model to explain these discrepancies, in which factors that affect the risk of nest predation for songbirds operate at multiple spatial scales, with those operating at broad spatial scales providing constraints on local processes.

To explain variation across spatial scales, most researchers predictably invoke hypotheses about the identification, abundance, and/or activity of nest predators. The taxonomic focus of existing nest predator studies reveals the hypothesized mechanisms behind observed patterns of nest predation, as hypotheses typically focus on changes in abundance or activity of corvids, mesopredators (e.g., raccoons and opossums), and rodents (e.g., mice and squirrels; [Chalfoun et al. 2002b]). Actual tests of such hypotheses are relatively rare and exhibit highly variable results, in part due to the taxon and context-dependent nature of the effects of forest fragmentation (Chalfoun et al. 2002b). However, most studies of fragmentation effects on nest predators also suffer from a fundamental problem: the predators being investigated are only putatively important. Identifying species that are dominant nest predators in any habitat has proven difficult because nest predation events are infrequently observed and because artificial nest experiments designed to identify predators are biased (Faaborg 2004). In one study, for example, a predator guild (snakes) that commonly depredated real nests was never recorded depredating an artificial nest, and video recordings showed that predators could not be reliably identified from marks made in plasticine eggs (Thompson and Burhans 2004).

The identification of nest predators is an imperative step in understanding why nest predation rates vary across and within landscapes (Stephens et al. 2003). We used video cameras to identify predators at the nests of forest songbirds at eight sites in Missouri and Illinois that span a gradient of landscape-level forest cover. Our objective was to determine whether patterns of nest predation that have been identified at three spatial scales can be explained by variation in predator-specific nest predation rates. Specifically, we assessed previously invoked hypotheses about the mechanisms that drive increased rates of nest predation as landscape-scale forest cover declines (Robinson et al. 1995) and as proximity to forest edges increases (Hoover et al. 2006). At a local scale we assessed whether nest-site foliage density, a habitat feature known to influence the risk of nest predation (Martin 1992) and one that can be controlled by land managers, influenced predator-specific predation rates. We predicted that these patterns would be driven by variation in predation rates by mesopredators, corvids, rodents, and snakes, as each may vary in abundance, species richness, or activity in landscape and/or edge contexts (Chalfoun et al. 2002b). We also considered raptors in our analyses as they are the most frequent predator of songbird nests at our study sites (see Chapter 1). Finally, the well established pattern of increased cowbird abundance and brood parasitism with increasing fragmentation (Chace et al. 2005) coupled with strong evidence that Brown-headed Cowbirds (*Molothrus ater*) depredate nests (Arcese et al. 1996, Hoover and Robinson 2007) led us to predict that cowbirds may contribute to patterns of nest survival.

METHODS

Data collection

We selected eight study sites in Missouri and Illinois based on the presence of our focal species and a representative range of landscape-scale forest cover in the Midwestern United States (Fig 1). All sites were >20 km from one another to ensure independence at the landscape-scale (see below). We collected data from May to August during 2007 – 2010. We studied four sites in Missouri in 2007 and 2009 and four sites in Illinois in 2008 and 2010. Our primary focal species were the tree-nesting Acadian Flycatcher (*Empidonax virescens*) and shrub-nesting Indigo Bunting (*Passerina cyanea*), which have shown differing responses to habitat fragmentation (Robinson et al. 1995). We also located and monitored nests of other shrub-nesting species, including the Northern Cardinal (*Cardinalis cardinalis*), Yellow-breasted Chat (*Icteria virens*), Field Sparrow (*Spizella pusilla*), and Eastern Towhee (*Pipilo erythrophthalmus*).

We grouped buntings and these species into a shrub-nesting guild for our analysis because they share similar breeding ecologies and nest site characteristics. We filmed nests using a combination of vendor (Fuhrman Diversified, Inc.) and user-built video systems (see Chapter 4 for a full description). Camera set-up and protocols are described in Chapter 1.

We used ArcMap 9.3 (2008) to calculate landscape and edge metrics for each nest. We merged land cover data for Regions 9, 11, and 12 from the 2001 National Land Cover Database (http://www.mrlc.gov) and reclassified land cover as forest or non-forest (see Appendix I). We calculated percent forest cover in a 10 km radius around each nest using the Zonal Statistics tool in Hawth's Tools (Beyer 2004). We chose a 10 km buffer because it best explains variation in nest predation for forest songbirds in the United States (Lloyd et al. 2005). We digitized edges at our field sites using orthophotos from the 2009 National Agriculture Imagery Program (available at http://www.apfo.usda.gov/FSA). We treated all anthropogenic openings (e.g., large agricultural fields, open canopy roads, powerlines, and wildlife food plots) as edges because the variation in predator-specific nest predation rates between birds that typically nest in these locations versus the forest interior suggest that they are preferentially used by nest predators (see Chapter 1). We did not consider water/forest interfaces as edges. We then used the Nearest Feature tool to calculate the distance between each nest and the nearest edge. Thirteen shrub nests were located just outside the forest canopy in winged sumac (*Rhus copallinum*), blackberry (*Rubus sp.*) or other shrubby patches that composed a soft edge; these were assigned a distance of zero. We calculated stem density at each nest by counting all woody stems and trees greater than 1.3 m in height within a 5.64 m radius (i.e., 100 m^2).

Analysis

We used multinomial logistic regression within an information-theoretic framework (Burnham and Anderson 2002) to evaluate relative support for predator-specific models of nest predation (see below). We ranked models by calculating Akiake's Information Criteria (AIC_c) and each model's associated weight (w_i). Our use of multinomial regression allowed us to have more response variables than typical binomial (0=active, 1=failed) nest fate approaches. Our response variables were: active, depredated by corvid, rodent, mesopredator, cowbird snake, raptor (i.e., hawks and owls) or other. We did not consider host eggs lost to cowbirds during laying to be a predation event. The "other" category included nests that failed from predators that did not fall into the first five categories (e.g., other birds, humans), acts of god (e.g., weather), nest abandonment, nestling mortality, and nests with unknown fates (e.g., because of camera failure or technician error). We considered a nest to fail if at least one nestling or egg was captured by a predator.

The sample unit for our models was each 24 hr interval a nest was filmed, which is comparable to nest survival methods that use nest-check intervals as sampling units and the number of observation days as the effective sample size (Dinsmore et al. 2002, Shaffer 2004). For nests lacking an exact date of fledge or failure because of camera failure, the midpoint of the interval between nest visits was assigned as the date of fledge or failure. In six cases a nest was depredated the same day a camera was placed at the nest which resulted in zero complete sampling units; we retained these nests in the study by backdating our observations a day.

Study sites in Illinois were generally located in less forested landscapes than those in Missouri (Fig. 1), and because we never sampled sites in Missouri and Illinois in the same year it is possible that our landscape forest cover covariate was confounded with year effects. We could not assess this directly, but we evaluated the presence of year effects between Illinois sites in 2008 and 2010 and between Missouri sites in 2007 and 2009 by considering evidence ratios (i.e., ratio of Akiake weights between two models) for a model with terms for species and stage (i.e., null; see below) and one that also included a term for year.

We evaluated eight models representing predator-specific hypotheses of nest predation (Table 1). All models included a term for nest stage and species, as each is an important predictor of predator-specific rates of nest predation (see Chapter 1). A preliminary tolerance analysis of all covariates indicated no multicollinearity ([Allison 1999]; all tolerance values ≥ 0.95), so we were able to include any combination of our three covariates (forest cover, distance to edge, stem density) in our models. Our global model included all three covariates. We also evaluated two models wherein landscape forest cover constrained edge effects or nest-site effects, a model with only landscape forest cover and another with only edge effects. We did not evaluate a model with only stem density as we hypothesized that any nest-site effects would be constrained by processes at broader spatial scales (Thompson et al. 2002). We also included models with species interaction terms, as flycatchers and shrub-nesting species have previously demonstrated differing responses to landscape forest cover (Robinson et al. 1995) and because responses to increased proximity to forest edges can be highly variable (Batáry and Báldi 2004).

We used the most supported model to generate predicted probabilities of nest predation unless otherwise noted. To evaluate whether the best model also described overall (non-predator specific) rates of predation, we collapsed the predator response levels into one response level and compared evidence ratios between a null model and models with each of the covariates from the best model. We knew *a priori* that we could not generate estimates for mesopredators because we lacked observations of predation events for flycatchers and for shrub-nesting species during incubation (see chapter 1). To account for this, we changed the species and stage codes for three mesopredator predation events. This allowed us to model mesopredator nest predation rates as a function of our habitat covariates when stage and species were held constant. All other predicted probabilities were generated from the original dataset and are reported with 95% confidence intervals. We also report whether 85% confidence intervals for parameter odds ratios include one, as the use of model selection approaches with AIC supports parameters as informative at this level (Arnold 2010). Mean values for covariates are presented with standard errors. All analysis was performed using SAS version 9.2 (2008).

RESULTS

We filmed 328 nests and had a total of 3912 observation days during 2007-2010. We identified 136 predators that we placed into the six predator guilds. Predators identified included 22 corvids, 34 snakes, five mesopredators, nine cowbirds, 16 rodents, and 50 raptors (see Chapter 1 for a detailed list of predator species). Study sites ranged from ~33 – 87% forest cover in a 10 km radius surrounding their center (Fig. 1). Mean values and ranges of forest cover, distance to edge, and stem density are reported in Table 1.

The evidence ratios (Missouri: 27.0; Illinois: 24.8) for a null model versus a model that also included a year term provide little evidence of year effects in either state. The top ranked model included a term for landscape, while the second ranked model included landscape and a term for stem density (Table 2). No model that included the distance to edge covariate was well supported. Ninety-five percent confidence intervals for odds ratios derived from the top ranked model indicated that nest predation by Brown-headed Cowbirds decreased with increasing landscape forest cover, while the odds of predation by rodents increased with increasing forest cover (Table 2; Fig. 2). The risk of predation from snakes declined with increased forest cover (0.15; 85% CI: 0.03-0.73), but 95% odds ratio confidence intervals overlapped one. We found limited support for the addition of stem density in the second ranked model. Odds ratio 95% confidence intervals overlapped one for all predator guilds (Table 2), but at the 85% confidence level estimates for corvids (0.97,: 85% CI: 0.94-1.00) and raptors (0.98; CI: 0.96-1.00) suggest that predation from these two guilds declined with increasing stem density (Fig. 3). While we found support for landscape and nest site effects on predation by specific predator guilds, the evidence ratio for a null model versus models with a term for each variable when all predators were pooled indicated no support for forest cover effects on overall predation rates (ratio: 6.8), but some support for stem density (ratio: 0.8).

DISCUSSION

We identified predators responsible for 136 predation events at forest songbird nests at eight sites in Missouri and Illinois. We found support for our hypotheses that landscape and nest-site effects on the probability of predation differed among predator guilds. Though some effects were marginal, all but one predator guild (mesopredators) were influenced by either forest cover or stem density. Effects varied in direction and magnitude by predator guild, so much so that we detected no net effect of forest cover and a modest effect of stem density on overall predation rates (i.e. all predators pooled).

The risk of nest predation from raptors and corvids (primarily Blue Jays [*Cyanocitta cristata*]) remained relatively constant across the gradient of landscape forest cover. Studies suggest that there are landscape-level effects on corvid abundance and/or activity (Chalfoun et al. 2002b). Blue Jays were common at all of our sites, however (W.A. Cox, personal observation), and whatever variation that did exist between sites did not result in meaningfully different rates of nest predation. We included raptors in our analysis because they are the most frequent nest predators at our study sites (see Chapter 1). We observed individuals of most species at all field sites, with the exception of Broad-winged Hawks (*Buteo platypterus*), which we did not hear or see at our study site in the least forested landscape (W.A. Cox, personal observation). Raptor nest predation probably remained steady across the forest cover gradient because the assemblage remained largely intact and because raptors generally occur at low densities.

Predation by cowbirds increased as forest cover declined. Factors that influence the abundance and distribution of cowbirds are well studied (reviewed in Chace et al. 2005), as are their impacts as brood parasites on the demography of host species (Trine et al. 1998). Their role as a nest predator has been previously explored in several rigorous experiments (Arcese et al. 1996, Smith et al. 2003, Hoover and Robinson 2007), but in general it has received much less attention than their role as a brood parasite. For example, in Chalfoun et al.'s (2002b) review of nest predators, zero of 106 hypothesis tests of predator-specific responses to landscape metrics at three spatial scales involved cowbirds. Given that they are recognized nest predators and that their abundance increases with decreasing landscape forest cover (Thompson et al. 2000, Chace et al. 2005), it is not surprising that the risk of predation from cowbirds increases as well. We recommend that researchers interested in spatial patterns of nest predation consider cowbirds as a potential causal agent of such variation, especially in landscapes where brood parasitism rates are high and competition for host nests promotes ransacking of nests to gain additional reproductive opportunities (Arcese et al. 1996, Hoover and Robinson 2007).

Snakes are important predators of songbird nests in a variety of habitats and biogeographic regions (Weatherhead and Blouin-Demers 2004, Thompson 2007). They prefer edge habitat for thermoregulation (Blouin-Demers and Weatherhead 2001), and have been found in higher abundances near edges (Chalfoun et al. 2002a). Edge density decreases with increasing forest cover in Midwestern landscapes (Faaborg et al. 1995), so landscapes with less forest cover may provide the edge or habitat heterogeneity to support greater snake populations. As hypothesized, snake predation decreased with forest cover (Fig. 2) but we did not find support for edge effects. Density estimates for snakes are notoriously difficult to acquire (Weatherhead et al. 2010), but more work in this area is needed if we are to link snakes to changes in rates of predation across landscapes.

In contrast with cowbirds and snakes, the risk of predation from rodents (primarily *Peromyscus* sp. – see Chapter 1) increased dramatically as landscapes became more forested. Red squirrels (*Tamiasciurus* hudsonicus) may drive landscape-level patterns of nest predation in the Western United States (Tewksbury et al. 1998), but sciurids at our sites rarely depredated nests (see Chapter 1). Most studies that have investigated landscape effects on rodent abundance and/or activity have not found effects (Chalfoun et al. 2002b), and those that have offer conflicting results. Mouse densities may be similar in contiguous versus less forested landscapes even when edge effects are present (Bayne and Hobson 1998), or much lower in contiguous forests (Nupp and Swihart 2000). Densities can also be higher in forest interiors than near forest edges (Wolf and Batzli 2002) because of increased rates of predation near edges (Morris and Davidson 2000, Wolf and Batzli 2004), which would lead to higher densities in more contiguous forests. Clearly, estimation of predator abundance in conjunction with the use of cameras at nests would further strengthen our understanding of the mechanisms behind the patterns we observed.

Despite the predator-specific patterns of predation at the landscape scale we observed for cowbirds and snakes, it remains unclear whether either predator guild is an important driver of overall increased rates of nest predation in fragmented landscapes as seen in Robinson et al. (1995). In this study, increased predation rates by both guilds appeared to be compensatory, as rates of predation from rodents were lower in less forested landscapes and overall predation rates remained constant across landscapes. Further, even at the low end of the forest cover gradient where their impact was greatest, cowbirds accounted for a small fraction (~13%) of the overall predation rate. While snakes became the most frequent predator in the least forested landscapes and accounted for ~33% of the overall predation rate, they contributed significantly to overall predation rates at all levels of forest cover. Greater insights into whether these predators drive increased rates of predation in highly fragmented landscapes will probably require sampling in areas that are less forested (i.e., <30%) than those we studied.

Edge effects on nest predation may occur infrequently (Lahti 2001) and studies investigating predator-specific responses to edges usually fail to detect effects on predator abundance or activity (Chalfoun et al. 2002b). Nevertheless, we hypothesized that predator-specific edge effects would exist at our sites for four reasons: 1) snakes, cowbirds and corvids have all been positively associated with edge habitat in Missouri (Chalfoun et al. 2002a) and other locations (Blouin-Demers and Weatherhead 2001, Sperry et al. 2009), 2) mesopredators such as raccoons prefer forest edges in the Midwestern United States (Dijak and Thompson 2000, Barding and Nelson 2008), 3) the shrub-nesting species we studied are primarily found near forest edges and exhibit much higher overall rates of predation than Acadian Flycatchers (see Chapter 1), 4) Acadian Flycatchers have exhibited edge effects in forests near some of our study sites (Hoover et al. 2006). Nevertheless, the distance between nests and forest edges had no discernible effect on predator-specific predation rates. We may have lacked the temporal replication required to detect edge effects (Stephens et al. 2003) and may have benefitted by incorporating edge type into our analysis (Murcia 1995, but see Chapa-Vargas and Robinson 2006). In addition, edge effects are not always linear with respect to landscape (Donovan et al. 1997) but concerns about our sample size precluded us from including additional interaction terms in our models. Even with relatively simple models, our sample sizes for some predator guilds (e.g., mesopredators, cowbirds) were small, making it difficult for us to detect effects for any of our covariates. Subtle edge effects may exist for these predators, but within the range of landscapes we studied they are not likely to significantly impact songbird productivity. Nevertheless, greater sampling effort over longer time periods is needed to evaluate complex models that represent all plausible biological hypotheses.

The nest-site variable stem density did not appear in the top model, but it did occur in the second ranked model (ΔAIC_c = 2.82), which was a plausible candidate for the top model. The modest support for this term indicate that these data should be considered exploratory rather than confirmatory. Nevertheless, our results for raptors and corvids are in line with previous studies which suggest that dense foliage surrounding a nest can hinder some predators from finding or accessing nests (Martin 1992).

Landscape metrics often fail to explain variation in songbird nest survival (Cottam et al. 2009, Falk et al. 2011), and in this study none of the metrics we quantified were correlated with overall rates of nest predation. However, similar to Benson et al. (2010), we found several predator-specific patterns of nest predation despite the lack of trends in overall predation rates. The management implications of these data are twofold. First, the rate of predation on songbird nests in mostly forested landscapes was similar to that in landscapes dominated by agriculture. The point at which nest survival declines for some species in fragmented landscapes may lie outside the range we sampled (i.e., < 30% forest cover). Nevertheless, a demographic model for Acadian Flycatchers (R. Hirsch-Jacobson, unpublished data) and data from other studies on Indigo Buntings (Payne 1989, Weldon and Haddad 2005) suggests that the rates of nest predation we observed are sufficient for population persistence. Second, there are significant challenges facing managers attempting to optimize habitat for breeding songbirds. The suite of predators we identified was diverse and responded differently to both landscape and nest-site factors. As such, managing habitat to reduce the impact of one predator guild may result in compensatory predation by another guild. Further, managers cannot assume that the suite of predators primarily responsible for nest failure at one site is the same at another, even when the same predator species exist at both sites. Finally, even though the lack of an interaction term in our best supported model suggested that flycatchers and shrub nesters responded similarly to landscape forest cover, this may not be true for ground or canopy nesting species. Landscape effects are often species-specific for birds (Robinson et al. 1995) and other taxa (Cushman 2006); species with different breeding phenologies or nest site locations may exhibit substantially different responses to the metrics we measured. The interactions between breeding birds, nest predators, and the landscapes in which they reside are complex, scale-dependent and context-specific, and may be resistant to broad conceptual management recommendations.

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Table 1. Mean, standard error (SE), minimum and maximum values of covariates used in analysis of predator-specific predation in Missouri and Illinois, 2006 – 2010.

	Acadian Flycatcher (*n* = 175)				Shrub-nesting species (*n* = 153)			
Variable	Mean	SE	Min	Max	Mean	SE	Min	Max
Forest cover (%/10 km^2)	58.2	1.2	32.2	88.4	55.7	1.4	32.3	88.5
Distance to edge (m)	208.4	15.0	9.3	1164.2	57.3	9.1	0.0	850.6
Stem density (stems/100 m^2)	25.8	1.0	2.0	126.0	24.8	1.3	0.0	93.0

Table 2. Model selection results for *a priori* candidate models describing predator-specific patterns of nest predation for Acadian Flycatchers and shrub nesting species in the Midwestern United States, 2007-2010.

Model	Structure	-2LogL[1]	K[2]	AIC_c[3]	Δ AIC_c[4]	w_i[5]
Landscape	β_0 + β_1(Species) + β_2(Stage) + β_3(10kmforest)	2066.86	28	2122.86	0.00	0.62
Landscape + Stem	β_0 + β_1(Species) + β_2(Stage) + β_3(10kmforest) + β_4(stemcount)	2055.68	35	2125.68	2.82	0.15
Null	β_0 + β_1(Species) + β_2(Stage)	2084.58	21	2126.58	3.72	0.10
Landscape + Edge	β_0 + β_1(Species) + β_2(Stage) + β_3(10kmforest) + β_4(distedge)	2056.73	35	2126.73	3.87	0.09
Global	β_0 + β_1(Species) + β_2(Stage) + β_3(10kmforest) + β_4(distedge) + β_5(stemcount)	2045.44	42	2129.44	6.58	0.02
Edge	β_0 + β_1(Species) + β_2(Stage) + β_3(distedge)	2075.49	28	2131.49	8.63	0.01
Edge × species	β_0 + β_1(Species) + β_2(Stage) + β_3(Species*10kmforest)	2075.88	28	2131.88	9.02	0.01
Landscape × species	β_0 + β_1(Species) + β_2(Stage) + β_3(Species*10kmforest)	2077.38	28	2133.38	10.52	0.00

[1] -2 × Log likelihood.

[2] Number of parameters in the model.

[3] Akaike's Information Criteria.

[4] The difference between the current and top-ranked model's AIC_c score.

[5] Weight of evidence supporting the model.

Table 3. Coefficient and odds ratio estimates for parameters in a study of nest predation in the Midwestern United States, 2007-2010. Coefficients for the landscape parameter were estimated from the top ranked model, while those from stem density come from the second ranked model. Odds ratios in bold are considered significant because their confidence intervals do not overlap one.

			Odds Ratio		
Parameter	Coefficient (β)	SE	Estimate	95% CI	
Landscape					
Corvid	0.57	1.27	1.77	0.14	20.31
Snake[1]	-1.93	1.15	0.15	0.01	1.27
Mesopredator[2]	-3.43	3.29	0.03	0.00	9.98
Cowbird	-6.68	3.03	**<0.01**	0.00	0.24
Raptor	0.78	0.84	2.17	0.41	11.02
Rodent	3.50	1.45	**33.14**	1.95	623.54
Stem density					
Corvid[1]	-0.03	0.02	0.97	0.93	1.01
Snake	<0.01	0.01	1.00	0.98	1.02
Mesopredator[2]	-0.03	0.04	0.97	0.88	1.03
Cowbird	<0.01	0.02	1.01	0.90	1.04
Raptor[1]	-0.02	0.01	0.98	0.96	1.00
Rodent	-0.02	0.01	1.02	0.96	1.00

[1] 85% odds ratio confidence interval does not include one. See Arnold (2010) for a discussion on odds ratios and model support in information-theoretic frameworks using AIC.

[2] Mesopredator parameter estimates and odds ratios are derived from a modified dataset that filled in missing observation values (see methods).

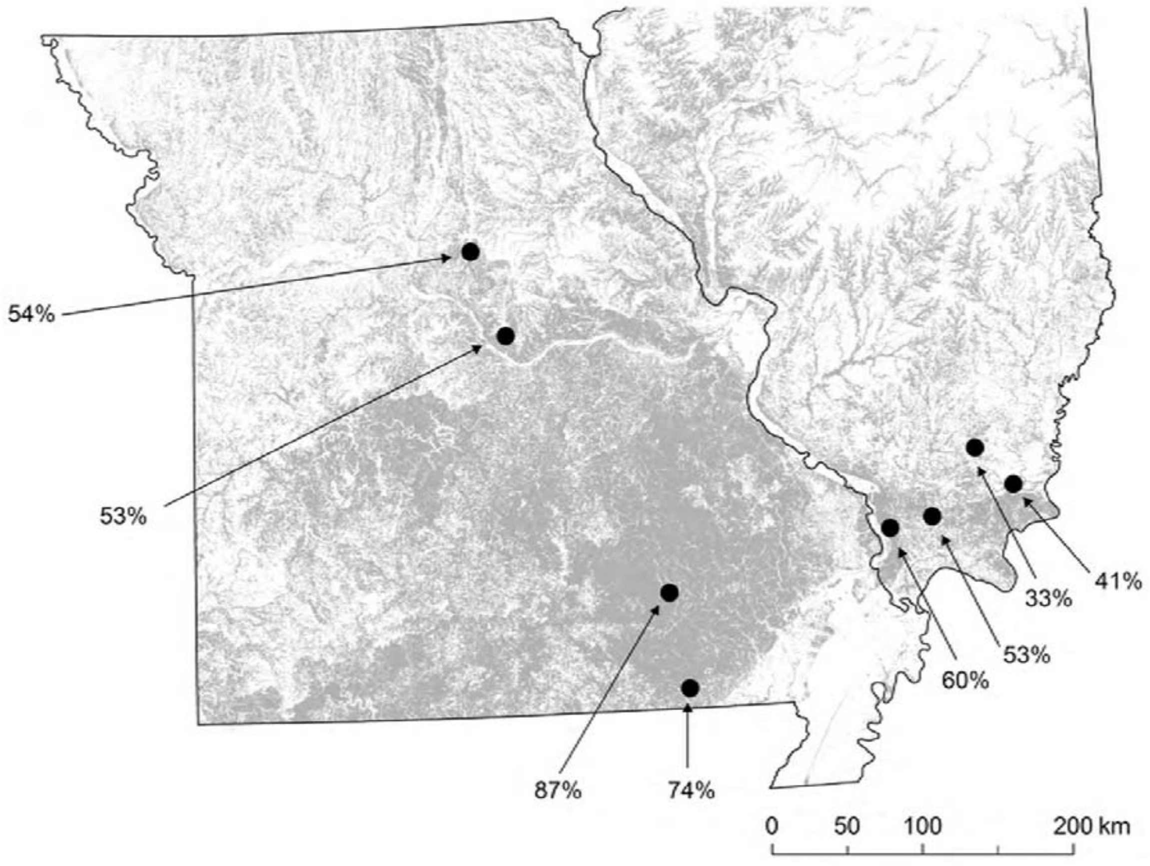

Figure 1. Location of eight sites in a study of nest predation in Missouri and Illinois, 2007-2010. Percentages indicate amount of forest cover in a 10 km radius extending from the center of each study site.

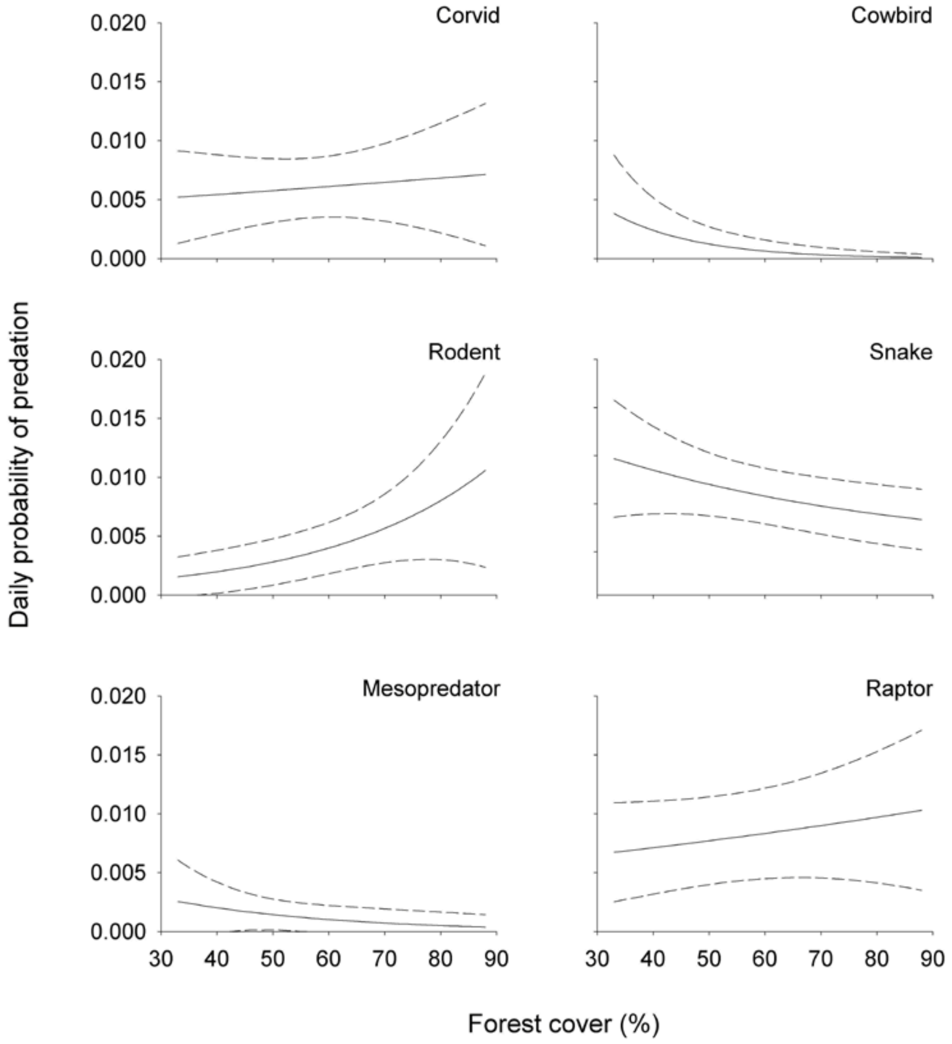

Figure 2. Daily probability of nest predation for forest songbirds from six predator guilds as a function of landscape-scale forest cover, estimated from the top ranked model with species and nest stage held constant in a study of nest predation in the Midwestern United States, 2007-2010. Dashed lines indicate 95% confidence intervals.

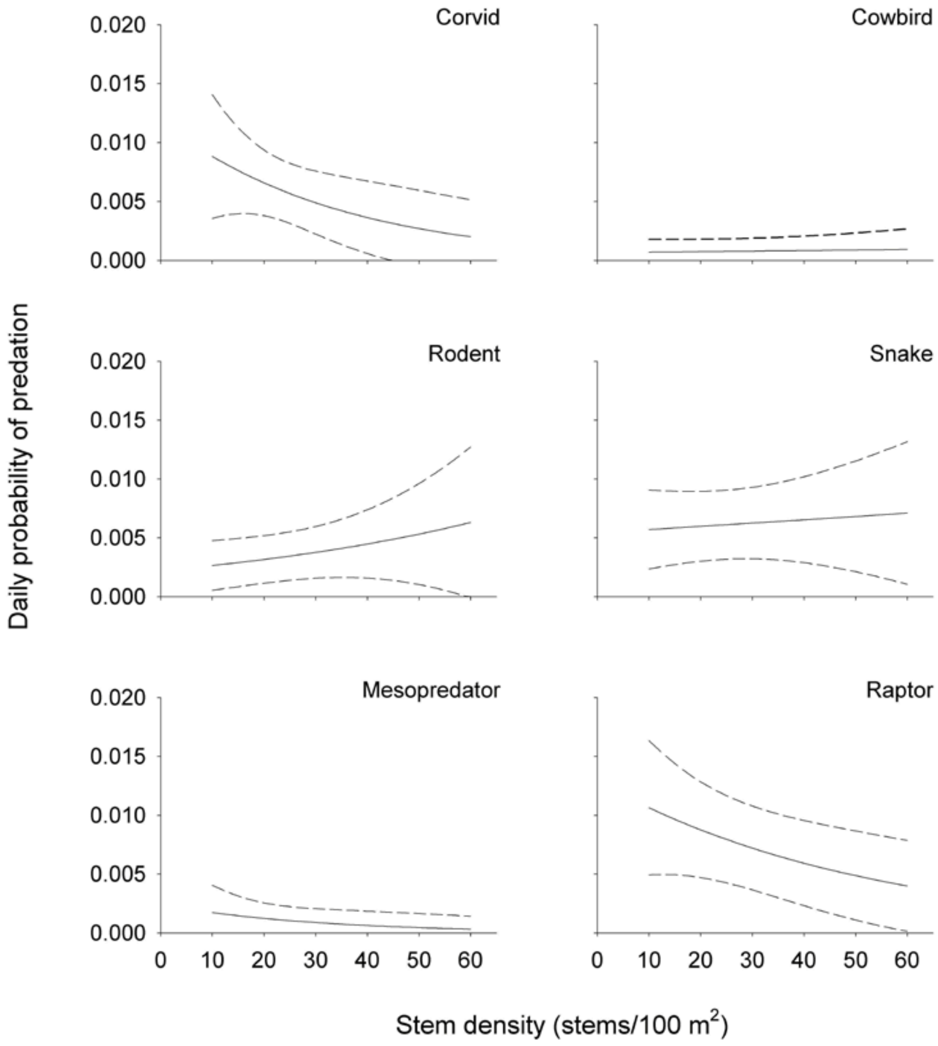

Figure 3. Daily probability of nest predation for forest songbirds from six predator guilds as a function of nest-site stem density in a study of nest predation in the Midwestern United States, 2007-2010. Dashed lines indicated 95% confidence intervals. Estimates are from the second ranked model with species and nest stage held constant and forest cover held at its mean value (57%).

Appendix 1. Reclassification of land cover categories from National Land Cover Database (NLCD) datasets.

NLCD Classes	Reclassified
Open Water	Non-forest
Developed, Open Space	
Developed, Low Intensity	
Developed, Medium Intensity	
Developed, High Intensity	
Barren Land	
Dwarf Scrub	
Grassland/Herbaceous	
Sedge/Herbaceous	
Moss	
Pasture Hay	
Cultivated Crops	
Emergent Herbaceous	
Wetlands	
Deciduous Forest	Forest
Evergreen Forest	
Mixed Forest	
Shrub/Scrub	
Woody Wetlands	

CHAPTER 3
NEST VISITATION RATES VARY IN RESPONSE TO PREDATION RISK FROM A DIVERSE SUITE OF PREDATORS

ABSTRACT

Predator-induced behavioral plasticity in animals is a well-established phenomenon, but most studies have focused on interactions between a single predator and prey species or have been performed in relatively simple ecosystems in which the threat of predation is predictable and easily assessable. When the risk of predation is variable and the sources of predation are more diverse, however, prey species may not be able to accurately assess risk and modify their behavior accordingly. Further, life-history theory predicts that prey species under relatively low ambient risk of predation may not respond strongly to changes in predation risk. We recorded nest visitation behaviors for Acadian Flycatchers (*Empidonax virescens*) and Indigo Buntings (*Passerina cyanea*) at eight study sites in Missouri and Illinois, the dependent young of which were under threat of predation from a diverse suite of predators with varying activity patterns and foraging strategies. Our goal was to determine whether adults of species under relatively high (buntings) and low (flycatchers) predation risk modified their behavior to reduce the risk of predation in response to ambient predation risk, imminent predation risk, and diurnal variation in predator activity. We detected low variation in ambient predation risk across study sites, and a corresponding lack of variation in nest visitation rates for both species. In accordance with predictions, buntings responded more strongly to predation risk and visitation rates in the 24 hr period prior to predation were lower for failed nests than fledged nests recorded at a similar time. This was not driven by behavior immediately prior to predation events, as visitation rates were similar for failed and fledged nests in the 1 hr preceding nest predation. Predation events occurred less frequently in the morning for both species, when nest visitation rates were highest for both species. Our results indicate that adult birds can adjust behavior in response to imminent predation risk despite the variation in foraging strategies and activity patterns of predators at our sites.

INTRODUCTION

Predation is a ubiquitous selective pressure that profoundly influences plants and animals on evolutionary and ecological time-scales. Species under consistent threat of predation have evolved morphological, chemical, and behavioral defenses to reduce direct and indirect costs associated with predation. Anti-predator defenses can be costly, however, and many taxa assess the risk of predation in their local environment and only induce defenses when threatened (Benard 2004, Greenstone and Dickens 2005, Callahan et al. 2008). Predator-induced modifications of animal behavior have long been of interest to ecologists, and there are numerous studies that document complex behavioral responses of prey to the presence of predators and the costs associated with them (Lima and Dill 1990). However, much of the literature on predator-induced behavioral plasticity has been focused on interactions between single predator and prey species (Relyea 2005). It is less clear whether animals under threat of predation from a diverse suite of predators can accurately assess the risk of predation and modify their behavior accordingly.

Predator induced behavioral plasticity by birds to reduce the risk of predation to themselves or their young is a well-studied phenomenon (Lima 2009). Predation of eggs and young in nests is the primary source of reproductive failure for many avian species (Ricklefs 1969, Martin 1992), and much of the literature on behavioral responses to predation focuses on active nest defense (e.g., distraction displays, predator mobbing) when adults put themselves at risk to defend their nest from imminent predation (*sensu* Montgomerie and Weatherhead 1988). Another behavioral defense is the mediation of nest visitation rates by adults, where birds reduce the risk of nest predation by decreasing nest visitation rates on both ecological and evolutionary timescales (Skutch 1949, Martin et al. 2000b). The reduction of nest visitation rates when a predator is obviously present has been demonstrated for songbirds via model presentation experiments (Peluc et al. 2008, Kovařík and Pavel 2011). There is also strong experimental evidence that birds can actively assess the ambient risk of nest predation and adjust their behavior accordingly. For example, when the ambient risk of predation was reduced via predator removal, adult birds responded with increased nestling feeding rates and reduced incubation duration (Fontaine and Martin 2006). Further, Siberian Jays (*Perisoreus infaustus*) responded to afternoon predator playbacks by increasing nest visitation rates in the morning and reducing them in the afternoon (Eggers et al. 2005), in support of the predation risk allocation hypothesis (Lima and Bednekoff 1999). Martin and Briskie (2009) summarized the relationship between nest visitation rates and the risk of predation by suggesting that 1) predation risk increases with increased feeding rates more sharply for species with higher ambient predation risk compared to those with a lower ambient risk, and 2) because the cost of visiting the nest is low for species with low ambient risk, they will make relatively smaller behavioral modifications in response to changes in predation risk.

Much of the research on the relationship between behavioral plasticity and nest predation in birds has occurred in relatively predictable environments with a small set of diurnal, visually oriented predator species (but see Chalfoun and Martin 2010). It is less clear whether birds that are under threat from a diverse suite of predators with varying foraging strategies can accurately assess the risk of predation or have opportunities to mediate their behavior. For example, nest visitation rates are unlikely to be relevant in systems where predation events usually occur at night (e.g., Reidy and Thompson in press), or are primarily due to predators that do not use visual cues (e.g., red imported fire ants [*Solenopsis invicta*]). Further, if the risk of predation is invariant throughout the day, temporal shifts in visitation rates to avoid periods of high predator activity are not possible. Nevertheless, the overall diversity of predator species does not reflect potential overlap in predator morphologies, foraging strategies, or activity patterns. In addition, some predator species rarely depredate nests (see chapter 1). Adults may only need to assess danger from a subset of predators, many of which belong to similar guilds (e.g., hawks, snakes).

We examined the relationship between nest predation risk and parental behavior in two songbird species with different ambient rates of nest predation in an ecosystem with a diverse predator community (19 documented predator species; see Chapter 1) using a data set in which the predators of failed nests were known. Our goals were to assess how avian species in this environment adjusted their behavior in response to the risk of predation and to determine whether opportunities of low risk existed for adults to exploit. We hypothesized that adults would respond to predation risk and mediate their behavior despite the diversity of predators at our study sites. We predicted that visitation rates would be highest at study sites with the lowest ambient risk of predation, and that the effect size would be larger for a species under lower inherent risk of predation. We predicted that adults with nests in imminent danger of failure would be aware of a predators presence and reduce visitation rates to reduce the risk of predation. Finally, we predicted that diverse predator communities would eliminate pronounced diel patterns of predator activity and thus prevent adults from taking advantage of periods of low risk to increase nest visitation rates.

METHODS

Data collection

We selected eight study sites in Missouri and Illinois based on the presence of our focal species and a representative range of landscape-scale forest cover in the Midwestern United States (see Chapter 1 for details on study sites and years sampled). We collected data from May to August during 2006 – 2010. Our focal species were the tree-nesting Acadian Flycatcher (*Empidonax virescens*) and shrub-nesting Indigo Bunting (*Passerina cyanea*). Nest predation rates differed significantly between the species, with flycatchers having a lower ambient risk of predation than buntings (see Chapter 1). We monitored nests using a combination of vendor (Fuhrman Diversified, Inc.) and user-built video systems (see Chapter 1 for methods 4 for a description of equipment).

We recorded adult behavior at nests during daylight hours for a 24 hr period prior to each predation event. We calculated the nest visitation rate as the total number of adult visits divided by the total time captured on film, excluding the hours between dusk and dawn. To reduce any bias associated with our presence at nests, we removed all observations that occurred 30 min before and 30 min after technician visits and reduced the total time captured on film accordingly. We also reduced the total time captured on film when we could not record adult behavior because of obstructed views or camera failure.

We selected 24 hr periods from video-monitored by pairing periods from a depredated nest and a fledged nest. To ensure a balanced sample, we paired all nests by species and stage because visitation rates vary widely across species and nest stages (Martin et al. 2000a). When possible, we also paired nests by study site, the presence of cowbird young, and nest age. A Pearson correlation test indicated that year and study site covaried ($r_s = 0.64$, $p < 0.01$), probably because we visited sites in Illinois and Missouri in different years. Nevertheless, we also paired nests by year whenever possible.

We aged nests during incubation based on lay dates. When we found nests after lay, we aged them by backdating 14 d and 11 d for flycatchers and buntings, respectively, from hatch day based on mean incubation periods from our study sites (13.9 ± 0.1 d, $n = 33$ for Acadian Flycatchers, 11.2 ± 0.3 d, $n = 8$ for Indigo Buntings). We did not have lay or hatch dates for four nests depredated during incubation, so we randomly selected the age from a set of numbers between the mean incubation period and the number of days we had observed the nest before it was depredated. We aged nests similarly for the nestling period using hatch and fledge dates, except that we randomly selected the age at fledge from one of the two integers that surrounded the mean nestling period for each species (13.6 ± 0.1 d, $n = 41$ for Acadian Flycatchers, 9.7 ± 0.2 d, $n = 19$ for Indigo Buntings).

Analysis

We calculated site-specific rates of nest predation using the logistic-exposure method (Shaffer 2004). We modeled nest predation for each species and included a covariate for nest stage to control for stage-specific variation in rates of predation. We estimated rates for each species for a balanced sample of nests across nest stages, based on the number of days spent in each nest stage, so estimates would reflect population level estimates at each site rather than potential sampling biases (Thompson and Shaffer 2007). We excluded nests from analysis that were abandoned or failed for reasons other than predation.

We used analysis of covariance to estimate mean visitation rates across a balanced population for each study site. We ran models for each species separately and estimated least square mean values for each study site using a model that included a variable for nest stage, and terms for its interactions with nest age and the number of young as covariates to control for their potential influence on visitation rates. We excluded a covariate for year because it was correlated with study site and several sites had too few nests within a year to reliably estimate nest survival. We used the same approach to estimate visitation rates for failed and fledged nests. For both analyses we excluded paired nests in which the failed nest was depredated on hatch day because visitation rates could not be assigned to a single nest stage.

We estimated diurnal patterns of nest visitation by calculating hourly rates for each bird and incorporating them into ANCOVA models similar to those previously described. We removed any hour for nests which had incomplete data due to video loss, dawn, dusk, or nest failure. We also removed any hour within 30 min of a technician's visit to the nest. We assumed that there would be an inverse relationship between nest visitation rates and the diurnal timing of predation events if adults were adjusting their behavior to avoid feeding young during periods of high predator activity. To determine this we used Akiake's information criteria (AIC) to evaluate whether a linear, quadratic, cubic, or quartic model best described the relationship between time of day and visitation rates for each species. We then used the same approach to evaluate the relationship between time of day and the timing of predation events and compared the direction and order of the resulting models. All analyses were performed using SAS (2008).

RESULTS

We found and monitored 407 Acadian Flycatcher nests (*n* = 24 – 69 per site) and 220 Indigo Bunting nests (*n* = 12 – 51 per site) that we included in our analysis of site-specific rates of predation. Rates of predation were relatively invariant across sites for Acadian Flycatchers (low: 0.024, 95% CI: 0.017 – 0.032; high: 0.036, 95% CI: 0.026 – 0.049) or for Indigo Buntings (low: 0.054, 95% CI: 0.039 – 0.076; high: 0.081, 95% CI: 0.058 – 0.112), with pairwise comparisons of rates indicating that only two sites for Acadian Flycatchers differed significantly (South and Trail of Tears; P = 0.04, uncorrected for multiple comparisons). No other sites differed for either species.

We video-monitored 185 Acadian Flycatcher nests and identified 61 predators and video-monitored 124 Indigo Bunting nests and identified 67 predators (Chapter 1, Table 2). We did not calculate nest visitation rates for 52 depredated nests because we could not reliably age the nest contents, did not have an appropriate fledged nest for pairing, or because the video was no longer accessible because of hard drive failure or reuse of video cassette tapes. As such, we recorded behavioral data for 76 depredated nests and paired them to fledged nests. All flycatcher pairs (*n* = 43) were matched by their estimated age within 1.5 d during incubation and 1.5 d during the nestling period. Thirty-two (74%) flycatcher nest pairs were matched by location and year. Seven (16%) were matched by location, two by year (5%), and two (5%) were not matched by year or location. All bunting pairs (*n* = 33) were matched by their estimated age within 2 d during incubation and 0.5 d during the nestling period. Nine (27%) were matched by location and year. Two (6%) were matched by location, 10 by year (30%), and 12 (36%) were not matched by year or location. No nest was used more than once.

Visual inspection of residual probability plots for all ANCOVA models indicated that data met normality assumptions. Nest visitation rates were not associated with site-specific ambient predation risk for either Acadian Flycatchers ($F_{1,6} = 2.23$, P= 0.19; Fig. 1) or Indigo Buntings ($F_{1,6} = 0.11$, P = 0.75; Fig. 1). Most predation events (73%) occurred during the day. Some predator species exhibited diurnal variation in the timing of predation events; Blue Jays (*Cyanocitta cristata*) did not depredate a nest until ~4 hr past dawn, while mesopredators and mice (*Peromyscus sp.*) were exclusively nocturnal (Fig. 2). The diurnal pattern of nest predation for Acadian Flycatchers was best described by a cubic model, with fewer predation events occurring in the morning (Table 1, Fig. 3a). The diurnal pattern of nest predation for Indigo Buntings was best described by a linear model, again with fewer predation events occurring in the morning (Table 1, Fig. 4a). Both species exhibited diurnal variation in nest visitation rates and visited the nest most frequently in the morning. Acadian Flycatcher visitation rates were best described by a quadratic model (Table 1,

Fig. 3b), while Indigo Bunting visitation rates were best described by a cubic model (Table 1, Fig. 4b).

Nest visitation rates were 22% greater for fledged versus failed nests for flycatchers but the difference was not significant (*n* = 86, P = 0.11; Table 2, Fig. 5). Visit rates were 37% greater for fledged versus failed nests for buntings (*n* = 66, P = 0.05; Table 2, Fig. 5). No predator-specific patterns were evident for either species (all P > 0.05; Fig. 5). We questioned whether the higher visitation rates for fledged nests compared to failed nests might be driven by drastic reductions in visitation rates just before predation events occurred, so we performed a *post-hoc* analysis of visitation rates using two subsets of data from each nest. First, for each set of paired of nests we selected the first four hours of video that was not interrupted by dawn, dusk, video loss, or a field technician. Second, we selected the last hour of video prior to time of nest failure for the depredated nest. For both species, visit rates were higher for fledged versus failed nests during the first 4 hr of video and for the last 1 hr of video prior to predation, but none of the differences were significant (Table 2).

DISCUSSION

We identified predators and recorded nest visitation rates for two avian species at eight study sites to assess the ability of animals to adjust parental behavior in response to the threat of predation from a broad suite of predators. Animals do not always accurately assess the risk of predation (Lima and Steury 2005), but adults at our study sites adjusted their behavior in response to imminent predation risk despite the diverse suite of predators that included species such as the Barred Owl (*Strix varia*) and Broad-winged Hawks (*Buteo platypterus*) that conceal their presence via sit-and-wait hunting strategies. Indigo Buntings (high ambient risk of predation) exhibited higher visitation rates for fledged versus failed nests, while Acadian Flycatchers (low ambient risk of predation), exhibited marginally higher visitation rates for fledged versus failed nests. We detected this difference despite the fact that nearly a fourth of failed nests included in our analyses were depredated at night, which we expected to reduce differences in visitation rates between failed and fledged nests.

Our findings are contrary to our predictions and to other studies (e.g., (Martin et al. 2000a, Muchai and Du Plessis 2005) in which failed nests had higher visitation rates than fledged nests. Although the patterns we observed were not due to behavioral changes in the hour prior to nest predation events, our video data suggests that some raptors may not depredate nests when they first locate them (see Chapter 1). This may also be the case for snakes (Withgott 1990, Stake et al. 2005). If this foraging strategy by predators is common, adults at failed nests may have already acquired the prior information (via predator encounters) required to update rules of behavior (Lima and Steury 2005), as has been observed in other avian species (Chalfoun and Martin 2010). Alternatively, adults at failed nests may occupy territories in which the ambient risk of predation is greater because of spatial heterogeneity in predator density, diversity, or activity. We lack data on within-site variation to assess this possibility, however, and the overall risk of predation between sites was probably too invariant for us to detect whether adults were capable of responding to the ambient risk of predation at that spatial scale. Regardless, our data suggest that adults are able to assess danger from a suite of predators that spans multiple taxa with markedly different morphologies and/or foraging strategies. Such behavior may be a consequence of adopting a relatively simple rule of behavior in which birds overestimate the risk of danger. Adults may simply treat most conspecifics as predators and respond accordingly, as the costs of such a rule (e.g., reduced development during incubation [Martin et al. 2007] and the nestling period [Scheuerlein and Gwinner 2006]) are usually outweighed by the obvious benefit of avoiding predation (Bouskila and Blumstein 1992). Further, the direction of the response of the defense measured here (i.e., reduction of nest visitation rates) is the same for all predators, making it easier for adults to formulate a simple decision rule for multiple predators (Relyea 2003).

The predation risk allocation hypothesis (Lima and Bednekoff 1999) posits that animals should forage more frequently when the risk of predation is low and illicit anti-predator behaviors when the risk of predation is high. Evidence supporting the hypothesis has been mixed (reviewed in Ferrari et al. 2009), but experimental studies have demonstrated that birds (Eggers et al. 2005), amphibians (Ferrari and Chivers 2009), fish (Brown et al. 2006) and other taxa modify timing of diel activities to reduce the risk of predation. Here, despite the potential of the varied activity patterns of predators to preclude the possibility of diurnal variation in predation risk, fewer predation events occurred in the morning. Further, both species visited the nest most frequently in the morning.

The morning peak of foraging activity for songbirds serves to replenish energy stores lost the previous night (Clark 1979). Such self-maintenance coupled with the thermoregulatory and developmental requirements of eggs and young constrain adult behavior and limit the scale of reaction norms in response to predation risk. Nevertheless, birds can compensate for reduced visitation rates via increased on-bout lengths during incubation and increased food loads during the nestling period (Martin and Briskie 2009), so alterations in diurnal patterns of nest visitation rates are possible for small passerines. As such, peak morning activity may also represent a response to high predation risk to adults (Roth and Lima 2007) and/or young (our study), with the disconnect between predator and prey activity maintained by nest predators tracking the activity patterns of other prey species or avoiding periods of high activity of their own predators (Roth and Lima 2007).

Our study illustrates predator-induced behavioral plasticity occurring in an ecosystem with a diverse suite of predators that utilize varied foraging strategies. Activity was higher for both species for fledged nests versus failed nests and during the morning when the fewest predation events occurred. In accordance with predictions (Martin and Briskie 2009), the relationship between predation risk and nest visitation rates was stronger for a species under higher ambient risk of predation. Rather than nest predation resulting from the actions of oblivious parents, our data suggest that most adults are aware of the presence of predators and respond accordingly by reducing risk as much as possible given the constraints of raising dependent young. Ultimately, the diversity of predators may not be a good predictor of prey response to the risk of predation. A subset of predators may utilize foraging strategies that preclude effective responses by adults (e.g., nocturnal foraging), while others may be infrequent or opportunistic predators that do not locate nests via parental behavior. Finally, morphology and foraging strategies shared by some predator species (e.g., raptors), may reduce the diversity to which adult birds must respond. Regardless, given that predation is a pervasive selective pressure under which prey have evolved, it is perhaps not surprising that they are remarkably adept at recognizing threats of all shapes and sizes and are able to respond accordingly.

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Table 1. Model selection results comparing 1^{st} – 4^{th} order equations describing temporal variation in the timing of nest predation and adult nest visitation rates for two songbird species in Missouri and Illinois, 2005 – 2010. Results from the top ranked model in each set are in bold.

		Acadian Flycatcher				Indigo Bunting			
		Predation timing		Visitation rates		Predation timing		Visitation rates	
Order	K	Δ AIC	w_i	Δ AIC	w_i	Δ AIC	w_i	Δ AIC	w_i
Linear	2	0.62	0.28	6.81	0.02	**0.00**	**0.64**	2.16	0.17
Quadratic	3	1.39	0.19	**0.00**	**0.57**	1.99	0.24	2.67	0.13
Cubic	4	**0.00**	**0.38**	1.33	0.29	3.96	0.09	**0.00**	**0.50**
Quartic	5	1.75	0.16	3.21	0.11	5.60	0.04	1.92	0.19

Table 2. Nest visitation rates for three time periods for two songbird species in Missouri and Illinois, 2005 – 2010. Estimates are least squares mean values with study site, nest stage, and a term for nest stage interactions with nest age and number of young included as covariates.

	Indigo Bunting			Acadian Flycatcher		
Time	Fledge	Fail	P-value	Fledge	Fail	P-value
All video	3.76 ± 0.38	2.74 ± 0.42	0.05	5.97 ± 0.60	4.91 ± 0.58	0.11
First 4 hr of video	3.69 ± 0.30	3.27 ± 0.33	0.29	5.94 ± 0.75	5.52 ± 0.73	0.61
1 hr prior to predation	3.26 ± 0.66	3.13 ± 0.69	0.87	6.27 ± 1.06	4.73 ± 1.04	0.21

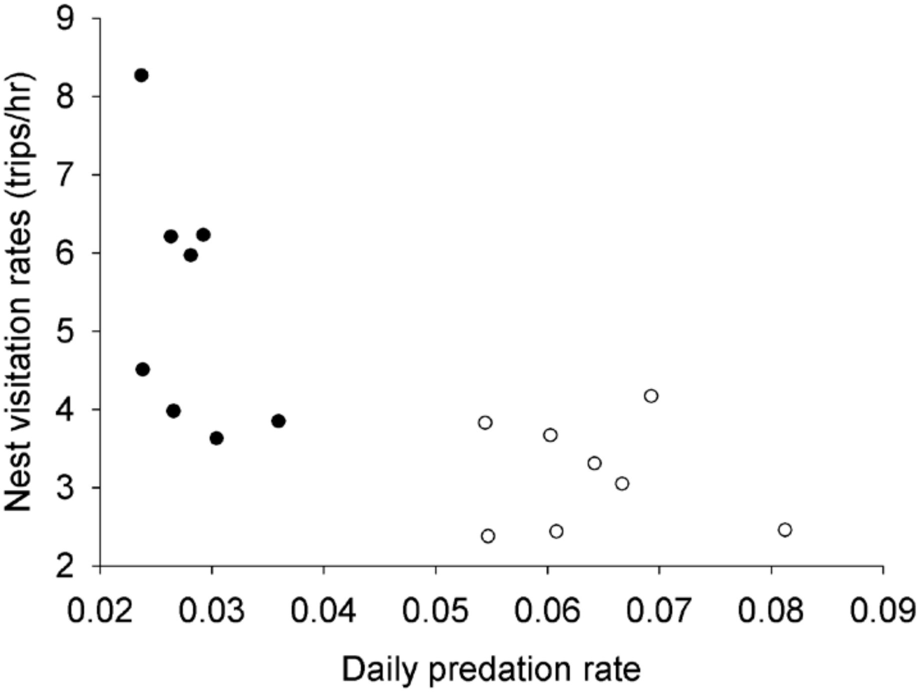

Figure 1. Relationship between daily predation rates and nest visitation rates for Acadian Flycatchers (black circles) and Indigo Buntings (white circles) in Missouri and Illinois, 2005 – 2010. Each point indicates a study site. Visitation rates are least squares mean values as calculated from ANCOVA models that include covariates for nest stage and terms for its interactions with nest age and the number of young in the nest.

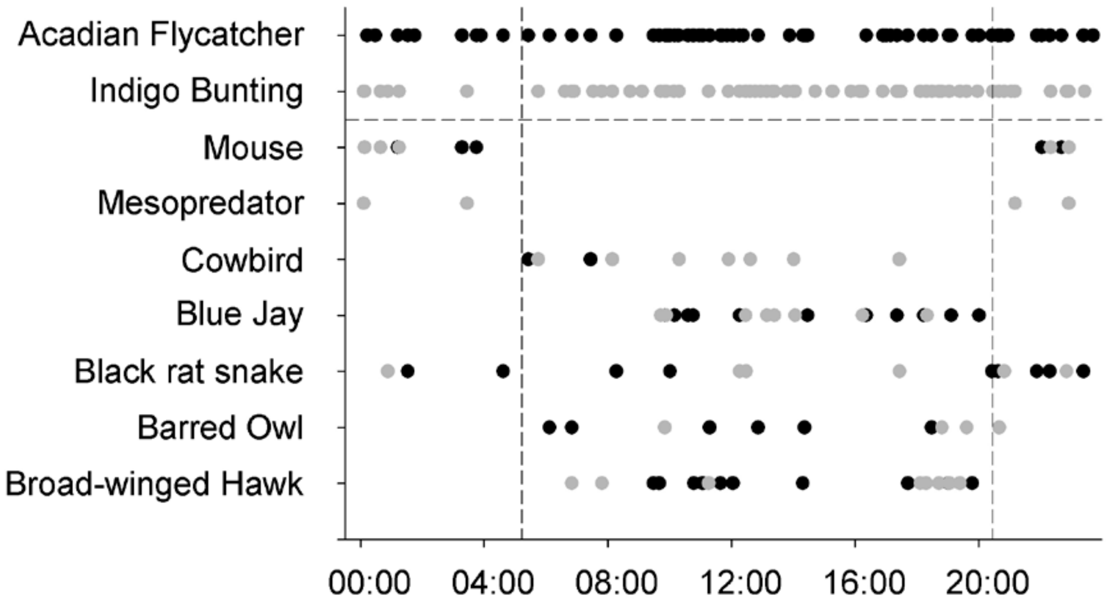

Figure 2. Timing of all predation events for two songbird species (above the horizontal dotted line) and from a subset of predators (below the horizontal dotted line) at eight study sites in Missouri and Illinois, 2005 – 2010. Black circles indicate predation of flycatcher nests and gray circles indicate predation of bunting nests. The mesopredator category includes two raccoons (*Procyon lotor*), one fox (unknown sp.) and one Virginia opossum (*Didelphis virginiana*). Predation events between the vertical dashed lines occurred during daylight hours.

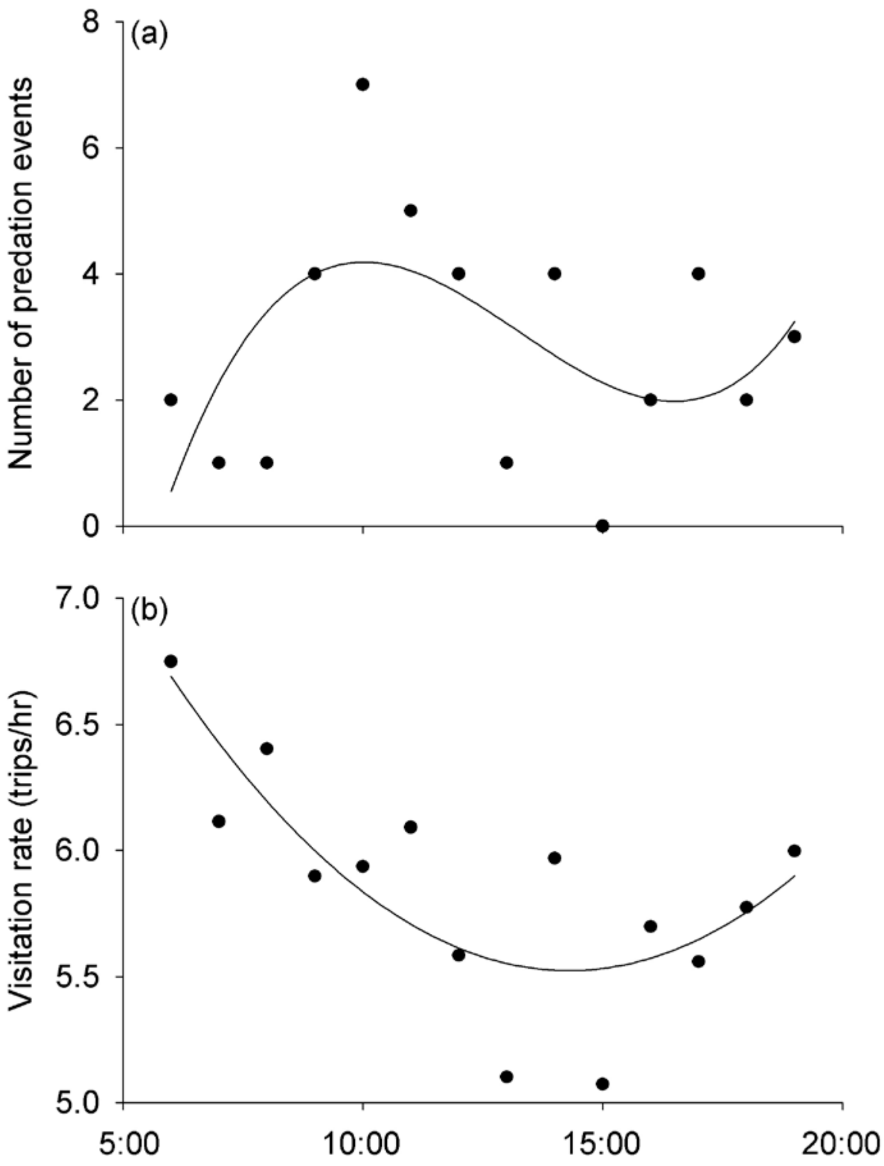

Figure 3. Diurnal patterns of (a) predation events and (b) nest visitation rates for Acadian Flycatchers in Missouri and Illinois, 2005 – 2010. Estimates for each hour in (b) are least squares mean values with study site, nest stage, and a term for nest stage interactions with nest age and number of young included as covariates (*n* = 63 – 83 nests for each hour). The regression line in each figure is from the top-ranked model as determined by AIC scores.

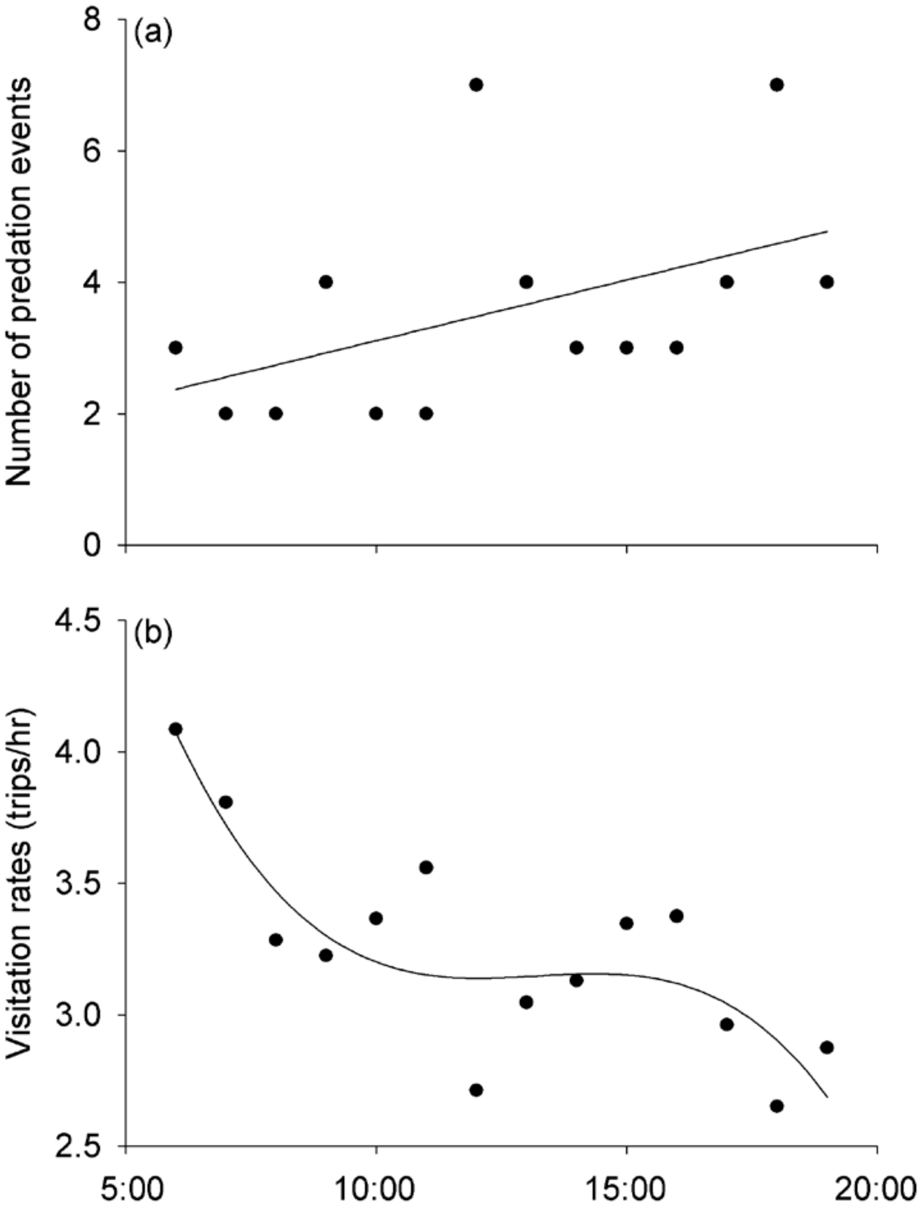

Figure 4. Diurnal patterns of (a) predation events and (b) nest visitation rates for Indigo Buntings in Missouri and Illinois, 2005 – 2010. Estimates for each hour in (b) are least squares mean values with study site, nest stage, and a term for nest stage interactions with nest age and number of young included as covariates (*n* = 43 – 62 nests for each hour). The regression line in each figure is from the top-ranked model as determined by AIC scores.

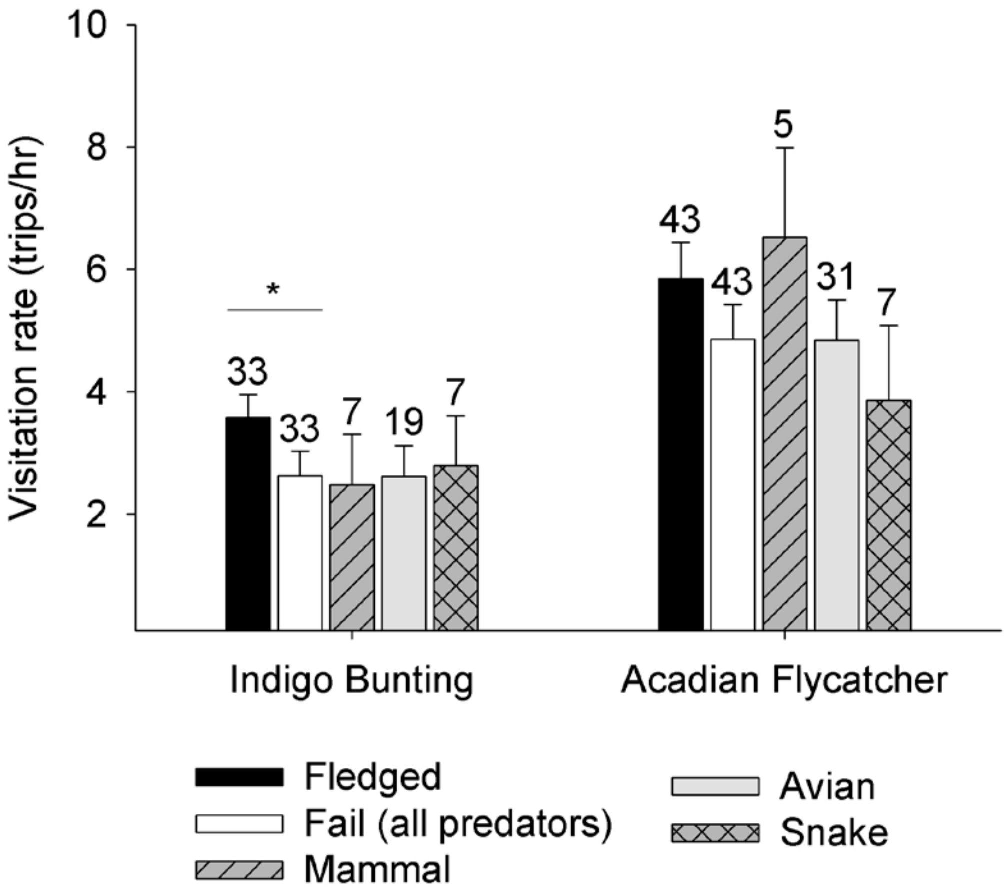

Figure 5. Visitation rates for fledged nests, failed nests, and for nests that failed from known predator guilds for two songbird species in Missouri and Illinois, 2005 – 2010. Rates are presented with standard errors. Numbers above the bars represent sample sizes for each category. An asterisk indicates a significant difference between fledged and failed nests.

CHAPTER 4
DEVELOPMENT OF CAMERA TECHNOLOGY FOR MONITORING NESTS

W. Andrew Cox, M. Shane Pruett, Thomas J. Benson, Scott J. Chiavacci, and Frank R. Thompson III

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ABSTRACT

Photo and video technology has become increasingly useful in the study of avian nesting ecology. However, researchers interested in using camera systems are often faced with insufficient information on the types and relative advantages of available technologies. We reviewed the literature for studies of nests that used cameras and summarized them based on study objective and the type of technology used. We also designed and tested two video systems that we used for three nest predator and behavioral studies. We found 327 studies that recorded 255 bird species spanning 19 orders. Cameras were most commonly used to study nest predators (*n* = 114), feeding ecology (*n* = 103), adult behavior (*n* = 81). Most systems (69%) were partially or completely user-built. Systems that recorded in real-time (≥25 frames per second), time-lapse (<25 fps), and still images were all common, though their use tended to vary by study objective. Using the time-lapse digital video recording systems we designed, we monitored 184 nests of 15 different species. We generally found these low-cost systems ($350–725 USD per unit) to be reliable. Sources of data loss were variable by study but included digital recorder malfunction, power

failure, and video cable damage due to rodents. Our review of the literature and our own experiences suggest that researchers carefully consider their objectives and study system when choosing camera technology. To facilitate selection of the appropriate system, we describe general video system design and offer recommendations for researchers based on commercially available system components.

INTRODUCTION

In 1956, Gysel and Davis presented an “automatic photographic unit for wildlife research” which they baited with dove eggs to identify potential predators. Three years later, Royama (1959) published the specifications for an “auto-cinematic food-recorder” which automatically triggered photographs of prey in the bills of Great Tits (*Parus major*) each time they perched on a trigger mechanism at the entrance of their nest-box. In the subsequent 50 years, ornithologists have employed photo and video technology to study birds at their nests with increasing frequency. Such technology allows for the collection of data that would otherwise be impractical to obtain because of logistical and/or financial constraints. Common research questions that can be addressed with cameras include nest predator identification (e.g., Hussell 1974, Thompson et al. 1999, Pietz and Granfors 2000), parental care (e.g., Grundel 1987, Cartar and Montgomerie 1987), prey identification (e.g., Grønnesby and Nygård 2000, Hanula and Franzreb 1995), and nestling behavior (e.g., McRae et al. 1993, Nathan et al. 2001). Cameras also provide researchers with glimpses of extremely rare events or unknown behaviors (e.g., egg and nestling cannibalism [Gilbert et al. 2005, Ben-Dov et al. 2006]; helping at nests of non-cooperatively breeding species [Guzy et al. 2002]) that would otherwise go undetected.

Despite the obvious value and increasingly common use of camera technology, ornithologists are often faced with more questions than answers when it comes to deciding on the type of equipment to use. Furthermore, reliable implementation of wildlife surveillance equipment is sometimes easier said than done; adverse field conditions or a lack of technical expertise can seriously hinder data collection. There have been two previous literature reviews that offered guidance on the video surveillance of nests. Cutler and Swann (1999) provided a useful guide to equipment based on study objectives, though it is now nearly a decade old and provides little practical technical help given the rapid pace of innovation. Reif and Tornberg (2006) filled this gap in their more recent review, which focuses on use of digital video systems. Both papers should be read by any researcher interested in using cameras at avian nests. Our objectives were to: 1) provide an updated review of camera studies focusing on the technology used to address common research questions, 2) report on user-built systems we used to monitor nests, and 3) provide recommendations on technical aspects of video systems for nest surveillance.

METHODS

Literature review

In January 2009 we used Biblioline Wildlife and Ecology Studies Worldwide and Scopus to find original, peer-reviewed research which used camera technology to monitor avian nests. We used the keyword *nest* with keywords *photo, video,* or *camera.* We read all bird-related papers from the resulting output and used their cited literature to find other papers not captured by our search criteria. This approach did not provide a comprehensive list of studies that used video technology because these databases only index titles, keywords, and abstracts, whereas in many cases the use of video technology is first mentioned when methods are presented. Nevertheless, our approach provided us with an ample number of papers for this review. We noted whether the study used analog (i.e., VCR) or digital recording units; the method of recording (e.g., still photos, real-time [≥25 frames per sec] or time-lapse [<25 frames per sec] video, 24-hr [continuous] or subsampled hours, with or without triggering mechanism); and the source of equipment (i.e., vendor-built [professionally designed and constructed] or user-built [at least partially designed and constructed by the researcher]). We assumed that papers using camera systems more complex than a simple hand-held recorder would provide vendor information when applicable. We also recorded whether the camera system was used with artificial or real nests and in the latter case we recorded the focal species studied. Finally, we recorded the stated objective(s) for each study. In many papers we could not adequately determine some of the information we were seeking, so sample sizes for summary statistics presented below are variable.

Case studies

In 2007–2009 we designed and tested two user-built digital video monitoring systems (referred to as System One and System Two when necessary hereafter; see Appendix 1 for a detailed list of components). Both systems consisted of a miniature digital video recorder (DVR), a battery, and a BNC power/video extension cable (10–30 m) that connected the recorder to a weatherproof, day/night security camera (Fig. 1). System One included a voltage converter because the DVR and camera operated at different voltages. We housed the recorder, voltage converter and battery in either a waterproof Pelican™ 1500 case or a camouflaged 18–30 gallon plastic container.

We used six different fixed-focus camera models that ranged from $30–170 (USD). All but the two least expensive models were weather-proof; we sealed the latter models with a plastic coating and housed them within a PVC cap to prevent moisture penetration. For nighttime illumination, the most expensive model was equipped with infrared (IR) light-emitting diodes (LEDs) that emitted light at a peak wavelength of 940 nm; the rest had LEDs with a peak wavelength of 850 nm. We had the vendor replace the wide-angle 3.6-mm lens with a 12-mm lens on the most expensive model which allowed for camera placement at greater distances from nests. The lenses on the remaining five models ranged from 3.6–8 mm. We used paint, natural vegetation, and/or tree bark to improve camera concealment.

We used two different DVR models. The DVR for System One allowed for three resolution settings up to 704 x 480 (vertical x horizontal lines) while System Two's DVR only recorded at a low resolution (352 x 240). Image compression rate options (i.e., the amount of detail stored per frame) provided three different recording qualities, and the number of frames recorded per second (fps) ranged from 1 to 30. Time and date stamps could also be added to the video. Images were stored on 4–8 GB SD or SDHC memory cards (not supplied with the DVR). The typical duration of a recording period was 2–4 d and was dependent upon the settings we chose (usually 6 fps of normal or high quality video at the lowest resolution) and the memory card capacity. However, both DVRs used a memory-saving algorithm which resulted in differing memory requirements for each nest (i.e., the number of hours of video that could be recorded differed based on camera field of view, amount of movement within the field of view, etc.), so we would adjust settings in the field as needed. Both DVRs also had a motion-detection feature that could save substantial storage space (see discussion), but we did not test this option.

We powered each unit with a single deep-cycle marine battery (75–125 amp hr) or a sealed lead-acid battery (26 amp hr). The total cost per system, including SD cards, batteries, chargers, and a small digital monitor for confirming system function and checking camera alignment ranged from $350–725 per unit when multiple units are purchased (if cameras are tended to on alternating days, two units can share a battery charger, replacement batteries, and SD cards).

We tested our video systems in 2007–2009 at field sites in Missouri, Illinois, and Arkansas. In Missouri and Illinois we deployed cameras at passerine nests in shrublands and forests. We typically placed cameras 1–4 m from nests, mounted on a tripod or wooden dowel, attached to thin (~1–4 cm) branches with a spring-loaded metal clip, or affixed to a tree trunk with brown duct tape or with a custom-made cargo strap. In Arkansas we deployed cameras at Mississippi Kite (*Ictinia mississippiensis*) nests. Because these nests may be located >30 m above the ground, we sometimes joined multiple 30-m BNC cables using female-female BNC couplers prior to climbing to the nest. The camera was attached to the limb of the nest tree, 0.4–0.5 m above the nest using camouflaged plastic cable ties. For all mounting methods, we sprayed the extension cable and exposed camera wires with Ropel®, a non-toxic chemical, to deter wildlife from damaging them. We camouflaged all components of the system with small branches, leaves, and other vegetation to prevent predators from being affected by the equipment (Herranz et al. 2002, Richardson et al. 2009) and to maximize the likelihood of nesting birds accepting the camera. We placed the waterproof case 8–10 m from passerine nests and approximately 30 m from raptor nests to minimize disturbance to the nesting bird when changing the battery and memory card. The total time for camera setup was generally ≤15 min for one person at passerine nests and ~1 hr for two people at raptor nests.

Once out of the field, we downloaded data from the SD cards to an external hard drive using a standard SD card reader. The more expensive DVR broke the total time recorded into separate 1-MB files. This resulted in thousands of files for a 48-hr recording period, but it also allowed for easy manipulation of files (e.g., sections of video were easily deleted or stored in separate places). The files were in MPEG-4 format, which is compatible with many freely available media players, but we chose to use Windows Media Player 11 because it allows multiple files to be queued for sequential play. The other DVR stored files in 30-min increments in a proprietary format that required special software to view, but those files could also be converted to a commonly used file format for viewing on most players.

RESULTS

Literature Review

We found 327 journal articles that mentioned use of photo or video technology (Table 1), the frequency of which increased over time (Fig. 2; see Appendix 2 for a complete list of articles). Three primary types of recording equipment were used. Systems that record in real-time (≥25 fps) were regularly used (27% of all publications), but most of these did not continuously record data at nests 24 hr per day (e.g., many recorded 2- or 4-hr samples). Time-lapse video systems, which record at <25 fps, were most common (38%). Systems with manual or IR triggers that took still photos of nests were also common (33%). Less commonly used were video systems that did not record images (8%;

usually associated with checking nest contents). Digital technology was used in 11% of studies since its first use in 2003 and in 21% of studies since 2006.

Twenty percent of these systems were built by vendors and 11% were unmodified hand-held video cameras. The remaining 69% of systems required some assembly by the end-user. The user-built video systems varied greatly in sophistication and purpose. Nest-checking equipment included cameras designed to allow access to nests of canopy, cavity, or burrow-nesting species that would otherwise be unreachable (e.g., Dyer and Hill 1991, Proudfoot 1996). Systems for monitoring adult behavior were often simple modifications of hand-held camcorders (e.g., Honza and Moskát 2008) but also included some impressive uses of wireless (King et al. 2001), solar (e.g., Margalida et al. 2006), and satellite (e.g., Momose et al. 2003) technology.

The studies using camera technology recorded data for 255 species from 19 orders. We identified eight broad categories that encompassed most papers' study objectives (Table 1). Cameras were most commonly used to identify nest predators, but they also were frequently used in studies of adult and nestling behavior, especially related to feeding ecology. Many papers presented user-built video systems, including systems used to identify the contents of otherwise inaccessible nests. Studies reporting extra-pair adults (conspecific and otherwise) that visited the nest were less common. Finally, a small number of studies evaluated the impact or efficacy of video cameras or other technology (e.g., radio transmitters) at avian nests.

Case Studies

We obtained video footage at 125 nests of 10 species and determined the cause of failure at 53 of 66 unsuccessful nests with System One. At one nest, the female disappeared 9 d after camera setup, but the extended period between camera installation and the female's disappearance suggests the abandonment was not caused by our activities. At two nests we were not able to identify a predator even though the camera was functioning correctly. We removed cameras at four nests prior to nest failure, and we failed to record predation events at seven nests because of technician error (*n* = 3), video system malfunction (*n* = 3), or because a camera fell (*n* = 1). In all other cases, predators were identified to guild (e.g., raptor, mouse, snake). Although many images were clear (Fig. 3a), poor video quality associated with the distance between the nest and the camera (i.e., cameras too close too nests were out of focus and those that were too far had insufficient detail to identify small predators) prevented species identification of 16 of 50 (31%) of the recorded predators (Fig. 3b). In 2009 we tested a color camera with manual focus and zoom controls to alleviate this problem, but image quality was generally worse (Fig. 3c). Predators not identified to species included all rodents (*n* = 7), five of 22 raptors, and four of seven snakes.

We obtained video footage at 53 nests of nine passerine species using System Two and determined the cause of failure at 27 of 29 failed nests. Image quality was generally quite good (Fig. 3d) and we were able to identify all predators except for one mammal to species. In Arkansas, we collected video data from six Mississippi Kite nests. We recorded one predation event by a black rat snake (*Elaphe obsoleta*) and documented a non-predator related failure caused by a severe thunderstorm that degraded the nest, causing the egg to fall through it while the adult was incubating.

System One's reliability was lower than expected in 2007. We failed to record data on 121.5 of 758 d (16% failure rate). Of all causes of system failure, the most frequent were a DVR firmware malfunction that prevented the download of files (64% of failure days) and faulty wiring between the battery and the recorder (10%). We installed a firmware upgrade from the DVR manufacturer prior to the 2008 season and the reliability of our systems improved; we failed to record data on 51 of 928 d (6% failure rate). However, our voltage converters did not function as expected and several DVRs began to perform erratically or fail completely (30% of all failure days). The second video system generally performed reliably; we only failed to record data on 32 of 743 d in the field (4% failure rate) and did not have any notable technical problems. Causes of failure common to both systems include: exceeding the capacity of memory cards prior to the end of the recording period (8% of combined failure days for both systems), power failure when batteries died prematurely (7%), and rodents chewing through wiring (6%).

DISCUSSION

Video systems are being used with increasing frequency because they facilitate efficient collection of data on many aspects of avian reproductive biology that would otherwise be impractical or impossible to obtain. Their use across a broad array of avian taxa and study objectives demonstrates their wide range of utility but also indicates that there is no single ideal system. As such, it can be difficult to determine what kind of system is optimal for a particular study. Our literature review and experience in the field suggest that careful consideration of one's study objectives combined with an understanding of the components of commonly used video systems are needed to choose the right system. Although we cannot offer advice related to study objectives, we believe the following guide can help researchers understand the basic technology involved in most video systems used to monitor bird nests.

Camcorders, trail cameras, and still-frame cameras

The first question a researcher should ask is whether off-the-shelf equipment will suffice to meet their study objectives. These are often the least expensive, least time consuming options (e.g., hand-held camcorders, trail cameras, still-frame cameras) and do not require separate camera and recording components. Clearly, commercially available video cameras that record in real-time for relatively short durations are not desirable for nest predation studies, but their relatively low cost (many models are available for <$300) and ease of use make them well suited for behavioral studies where sub-sampled time periods are standardized among nests (e.g., food-provisioning or incubation behavior). These cameras, however, are generally not designed for prolonged outdoor use and measures should be taken to safeguard equipment from adverse field conditions.

Still-frame cameras have been used primarily for nest predator identification and feeding ecology studies (the latter almost exclusively with cavity-nesting species). For both study objectives, researchers have typically used systems that only record images when a mechanical or IR trigger is tripped (reviewed in Reif and Tornberg 2006). Mechanical triggers coupled with still-frame cameras are now used primarily in conjunction with artificial nests to identify nest predators (79% of studies from 1990–2007), but such use may not be warranted. In addition to the biases associated with artificial nests (e.g., Buler and Hamilton 2000, Thompson and Burhans 2004), camera shutter sounds can disrupt predation events and single images (many still-frame models cannot take rapid successive photos) may not provide conclusive evidence of a predation event (Pietz and Granfors 2000). Further, even when used at real nests, still-frame cameras and mechanical triggers may systematically under-sample certain predator guilds during the nestling stage (Liebezeit and George 2003).

IR triggers can be active (a transmitter emits an IR beam to a receiver placed on the opposite side of the nest) or passive (a receiver detects changes in radiant IR levels). Active triggers take longer to set up and may not perform as well as passive ones (Bolton et al. 2007), but researchers have experienced problems with passive triggers as well (Hernandez et al. 1997). For example, passive triggers may be activated by abiotic factors such as temperature and/or sunlight changes, and they may not be sensitive to the movement of small animals

(Brown and Gehrt 2009). Both passive and active IR triggers used with either camcorders or still-frame cameras are external to the recording device, which results in a pause (typically ≤0.5 sec) between motion detection and camera activation. The newest triggers can have very short pauses (≤0.15 sec) that minimize the risk of lost data. Nevertheless, in some study systems certain events (e.g., nest predation by ants [Stake and Cimprich 2003, Connor et al. 2010] or harvestmen [Benson et al. 2010]) may not activate triggers, while in other cases they may be frequently activated by non-targeted events such as moving vegetation.

Trail cameras, such as those used by hunters to identify game animals, usually integrate passive IR triggers and cameras (typically still-frame, but newer models offer video as well) into a single unit and are explicitly designed for extended deployment in the field. They are more energy efficient than systems that record continuously, so most models run off household batteries. Many models are larger than cameras used in other nest monitoring systems and are usually equipped with wide-angle lenses; these factors make them impractical for some species but they may be cost effective, off-the-shelf tools for recording images at nests of larger species (e.g., Dreilbelbis et al. 2008). The newest, most expensive models are more compact and have been used with passerines, but even those placed within one meter of the nest did not capture all predation events because the IR trigger sometimes failed to detect movement at the nest (G. Londoño, pers. comm.).

Digital recorders

While systems that record continuously for extended durations may be too expensive and unneeded for many study objectives, they are usually necessary for identifying nest predators. Rapid advances in digital technology have resulted in the production of sophisticated DVRs and high capacity flash memory, which allow for the capture and storage of high quality digital video. These devices can be integrated by vendors or end users into video monitoring systems like those used in our case studies. Digital equipment is lighter, more reliable, less expensive, and uses less power than comparable analog components that were commonly used in the past; we see little reason for researchers to consider analog equipment.

There is a variety of DVRs available in the marketplace suitable for monitoring bird nests. The models we used in our case studies were small (both DVRs we used were ≤ 6 x 9 x 2 cm) and offered a number of options (e.g., resolution, frame rate, video quality) often found in other models as well. One feature we did not test was the integrated passive triggers (i.e., motion detection recording options) that eliminate the pause between the trigger and camera activation previously described by including 0.5 sec of video prior to activation of the trigger. This kind of trigger was tested by Bolton et al. (2007), was successfully used in several subsequent studies (Stevens 2008, Morris and Gilroy 2008), and can drastically reduce memory usage. Regardless, we chose not to use the motion detection options of our DVRs because of concerns about the detectability of some predators.

Several options our DVRs lacked may be useful to other researchers. First, many portable DVRs have integrated hard disk drives which offer greater storage capacity than the SD cards we used with our DVRs. These DVRs can significantly extend deployment periods or allow researchers to gather higher quality video (i.e., increased resolution or frame rate). However, downloading the data from the DVR in the field can be time consuming and may require a laptop or extra DVRs to replace those with full hard-drives (e.g., Pierce and Pobprasert 2007). Second, our DVRs required a small portable monitor to view the recording settings, but other models have integrated liquid crystal displays (LCDs) which eliminate the need for an external monitor. Portable monitors are relatively inexpensive and have other uses as well (see below), so integrated LCDs may not be worth the extra cost for some researchers. Finally, for study systems with high nest densities, multi-channel DVRs allow researchers to simultaneously record video from multiple nests (e.g., Colombelli-Négrel et al. 2009).

Cameras for use with DVRs

Many types of cameras can be effectively deployed at nests, but the most useful types are likely those designed for security applications. A major advantage of these cameras is that many are designed for outdoor use and are therefore able to withstand extreme temperatures and precipitation, and most are designed to use a 12-volt DC power source. Depending on the features included, these cameras vary greatly in size and in the power they consume.

Price also tends to vary with the features included, but many field-worthy cameras are available for <$150. Cameras offer different levels of resolution (described by the number of horizontal lines that compose a frame, also called TVL), but researchers will only benefit from increased camera resolution if they are also recording in high resolution. For example, if a DVR is recording at low resolution (352 x 240), then images from all cameras with ≥240 TVL will have the same resolution when played back.

Cameras come with or without IR LEDs for night recording; models that provide nighttime illumination have variable effective ranges depending upon the type and number of LEDs. Some substrates absorb rather than reflect IR light, which can result in an effective range that is smaller than that specified by the camera manufacturer (e.g., Sabine et al. 2005). Separate IR illuminators can also be used to provide additional light for night recording, but these can only be used with cameras that have lenses sensitive to infrared light. An important consideration when choosing an IR illuminator or camera is the wavelength of light emitted by its LEDs. LEDs with shorter (e.g., 850 nm) versus longer (e.g., 940 nm) peak wavelengths tend to provide better lighting in near to total darkness and are much more commonly available, but they emit some light in the visible spectrum which appears to humans as a faint red glow; LEDs with longer peak wavelengths emit light that is invisible to humans. The glow is only visible from a relatively narrow range of viewing angles and does not seem to affect predation rates (Sanders and Maloney 2002, this study’s AR and IL data), but to our knowledge no studies have explicitly investigated its influence on predator behavior.

The focal length of camera lenses should also be taken into account when choosing a camera. Those with wide-angle lenses have shorter focal lengths, requiring them to be relatively closer to nests, but because cameras with wide-angle lenses remain focused at variable distances, the distance from camera to nest does not need to be exact to preserve picture quality. Lenses with longer focal lengths on the other hand, can be situated farther from nests because they provide greater magnification, but they need to be placed at a more precise distance from the nest to avoid reduced picture quality. Our experience suggests that cameras with relatively wide-angle lenses (≤8 mm focal length) work well when cameras can be placed close (e.g., ≤2 m) to nests. We used a camera with a longer focal length (12 mm) to film Acadian Flycatchers because their nest placement generally did not allow for cameras to be closer than 3 m. We recently disassembled two different fixed-focus camera models and found that adjusting the focal point of the lens can be done rapidly and easily, so we plan to do this during setup at nests in future years. However, we must caution that IR LEDs are matched with lenses to provide optimal lighting at specific distances, so adjusting or replacing lenses may reduce nighttime image quality. Many newer models offer variable zoom and focus options which can improve the flexibility of camera set-up and placement without such a sacrifice, as the LEDs are configured to match the variable focal distances of the camera. However, even though the 940-nm camera we tested in 2009 had a 9–22 mm zoom color lens and manual focus controls, it did not operate well during the day in low light and image quality was very poor in heavily shaded habitats or at dusk and dawn.

Color cameras will be necessary for researchers recording marked birds and many of our color models performed quite well. But color images require more memory than black-and-white images and our experience suggests that with some models colors can appear dull or washed out even when lighting is good, which limits their use for identifying color-banded birds. Our conversations with vendors suggest that in general, black-and-white cameras tend to produce sharper, less pixelated images, especially in cameras equipped with 940-nm

LEDs

Recent advances in IR LEDs should result in cameras that provide brighter images at greater distances more efficiently than current models, and new lenses are being developed that provide increased clarity of IR-illuminated images. Other new technologies that may improve cameras for avian nest studies include digital noise reduction (DNR) and wide-dynamic range (WDR) cameras, both of which are intended to improve image quality and reduce pixelation in low-light conditions. Furthermore, new cameras are commercially available that amplify ambient light and do not require IR LEDs when recording at night, although we have not tested these. Regardless of the model chosen, we recommend that researchers test it under normal field conditions prior to purchasing in quantity or relying on it for high-quality data collection. Security cameras are not designed specifically for wildlife studies and not all models will perform as desired. For example, some of our cameras did not function well unless placed near enough to a nest for it to occupy a substantial portion of the field of view, which was not always possible. Furthermore, some species are much more sensitive than others to the presence of cameras and may require special models; adults at three Kentucky Warbler (*Oporornis formosus*) nests would not accept camouflaged cameras even when placed 4–5 m from the nest (W. Cox, personal observation).

Other technical considerations

Most of the video systems we found in the literature were powered by traditional lead-acid batteries. Deep-cycle marine batteries are cost effective and typically have high charge capacities but are relatively heavy (23–30 kg); sealed lead-acid batteries can be significantly lighter and are safer (there is little danger of acid burns) but are also more expensive. Lithium batteries are much more expensive than their lead acid counterparts but are an effective way to drastically reduce the size and weight of a video system. Batteries have variable lifespans, but many can be used for five field seasons or more. To maximize lifespan, batteries of all types should be charged at a low amperage (e.g., 2−6 amps) and should be charged periodically when not in use for extended periods. Solar panels have been used frequently over the past decade and when combined with wireless transmitting technology they offer an ideal solution for researchers working in remote areas or with species whose nests are difficult to access (e.g., Margalida 2006). Fuel cells are another expensive but useful power option for researchers lacking frequent access to nests and/or a power grid (e.g., www.sandpipertech.com/remote_power.html).

Cables and connectors are also required in most systems to provide power to the components and transmit the video data to the recorder. The distance between the camera and its associated recording equipment and power supply should be great enough to allow researchers to download data and exchange batteries without flushing adult birds from the nest or inciting alarm calls from adults attending nestlings. Cables can be purchased in varying lengths or connected in series to allow the recording equipment to be placed far from the nest without noticeable signal degradation. Although separate power and video cables can be purchased, cables that combine both functions are commercially available, generally sturdy enough for field use, and relatively inexpensive. In addition to these cables, connectors that convert between RCA and BNC plug types are generally needed, and short connectors with alligator clips that facilitate attachment to the battery are also useful; these are available from several sources including stores that sell electronics components. To prevent damage to the video/power cable, primarily by gnawing mammals, chemical deterrents are available (e.g., Ropel®) but do not always work. Other researchers have wrapped cables in aluminum tape (Booms and Fuller 2003) or buried them (Coates et al. 2008) to reduce the risk of damage. In areas where rodent damage was severe we handled our cables with rubber gloves to reduce scent and mineral deposition and we concealed metal connectors with electric tape to prevent their theft by wood rats (*Neotoma spp.*). However, even with these deterrents occasional cable damage is likely inevitable and researchers should purchase spare cables to prepare for this possibility. Some researchers (e.g., Pechacek 2005, King and DeGraaf 2006) have used wireless technology instead of cables to connect a camera to a DVR (reviewed in Reif and Tornberg 2006). This eliminates the risk of cable damage from rodents and allows for the study of nests that are difficult to access (e.g., Margalida et al. 2006), though a separate power source for the camera and transmitter is required and systems may require line-of-sight between transmitting and receiving antennas.

A portable LCD viewing monitor is necessary for some DVRs and can be helpful during set-up and nest checks for most systems. Monitors can be connected directly to a camera, which allows for efficient and exact camera placement. For DVR models without video screens, monitors are required to ensure proper camera placement, view DVR menu options when changing recording settings (e.g., fps, resolution, picture quality), and to check the remaining memory on cards.

Finally, some recent video systems have integrated computers which help researchers control and store data. Colombelli-Négrel et al. (2009) designed a system that used a computer to manage data from multiple video and audio recorders, while Grivas et al. (2009) constructed a wireless video/audio monitoring system that had a local computer receive, record, and transmit data to a remote computer (145 km from the nest) from which researchers could control the system.

User- versus vendor-built systems

For those who require a system more specialized than what is available off the shelf, an important consideration is whether to build your own or purchase one from a vendor. The majority of video systems used in the reviewed papers were at least partially user-built. Relative to vendor-built systems, a primary advantage of user-built systems is lower cost. For example, our systems cost approximately $350–725 per unit, which is significantly less than comparable vendor-built units (e.g., System One cost ~33% of a comparable vendor–built unit at the time it was constructed in 2007). Repair costs are typically less expensive as well, as no labor charges or markups on components occur. Other researchers presenting user-built systems noted similar savings (e.g., King et al. 2001, Hudson and Bird 2006). These savings are especially pertinent for researchers using cameras to identify nest predators because sample sizes are often small and constrained by the number of cameras available.

A user-built video system may not be the best choice for all biologists. Considerable time and effort went into manufacturing each system and our initial experiences with System One were not wholly positive. We were unable to address image-quality issues associated with our fixed-focus cameras because we did not have the expertise to build a camera that fit our exact specifications and none were available commercially (most IR cameras have a peak wavelength of 850 nm).   Furthermore, the reliability problems associated with our DVR and voltage converter were not easily diagnosed and resulted in the loss of data. Finally, our system lacks reverse polarity protection, so operator error can result in catastrophic failure of some system components. By contrast, vendor-built systems may offer greater reliability, more flexibility in system design, and do not require the user to diagnose and repair malfunctioning equipment.

We cannot make an unambiguous recommendation as to whether researchers should use vendor or user-built video systems. Vendor-built systems are often relatively expensive and repairing them may not be possible in the field. But they can also offer researchers greater ease, reliability, and technical sophistication. User-built systems are much cheaper but require more knowledge, time, and effort to build. For researchers who do wish to explore building their own systems, we first recommend that they consult the literature (including this study) to learn what, if any, systems have been designed and used for their species and/or study objective. There are many good examples of video systems in the literature that can provide excellent guidance on general system design despite the fact that the rapid pace of technological developments makes many past systems functionally obsolete. We also think that researchers who custom build a video system may benefit by consulting someone with electronics experience who can help identify potential pitfalls in design and component selection. In 2009, for example, we purchased inexpensive, professionally constructed voltage converters (ESCO-Ohio.com) to replace the problematic ones in our first case study; this fully resolved our problems with DVR failure (W. Cox, unpublished data).

Conclusions

Miniaturized cameras coupled with digital recording and data storage are changing how we approach the study of avian reproductive ecology. The amount and quality of data that can be collected in a season with even a few well placed cameras far exceeds what was previously possible with systematic or opportunistic observation by human observers. Furthermore, for some study objectives, cameras have demonstrated that older methods of data collection were either unreliable (e.g., Thompson and Burhans 2003) or heavily biased (e.g., Thompson and Burhans 2004). Video is not a bias-free panacea; nests monitored with cameras may have lower predation rates than those without cameras (Richardson et al. 2009) and care must be taken to minimize any effects on nesting birds or their predators. Regardless, video systems offer the promise of large volumes of high quality data and are increasingly being used by ecologists to document and quantify events and behaviors that are difficult or impossible to observe directly. The study species and objectives will largely dictate specific needs, but the availability of funds for purchasing and maintaining multiple systems is a constraint for most studies. Once a system has been chosen, field tests are critical for assessing functionality, identifying potential problems, and developing protocols to troubleshoot those problems (e.g., availability of extra parts or on-site expertise).

The use of stationary cameras to monitor nests is a well established practice, but we are now reaching a degree of technological sophistication that will no longer restrict researchers to a stationary observation site. Perhaps the most exciting recent use of video is that of Rutz et al. (2007), who attached miniature cameras to New Caledonian Crows (*Corvus moneduloides*) to collect data on foraging behavior and tool use. These tiny cameras were combined with VHF radio transmitters, allowing the researchers to couple fine-scale foraging data with larger-scale spatial data. Given the accelerated rate of microcircuitry miniaturization, researchers may be able to obtain similar video images from all but the smallest of avian species in the near future.

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Table 1. Number of studies published during 1956 – January 2009 that utilized camera technology (see Appendix 2), listed by study objective and type of recording technology used.

		% of studies in category [b]		
Study category [a]	No. studies	Still [c]	Time-lapse [c]	Real-time[c]
Nest predator identification	114	50	43	6
Feeding ecology [d]	103	28	32	40
Adult behavior [e]	81	6	45	43
Present a user-built system	32	39	35	26
Nest contents identification [f]	23			
Nestling behavior	19	0	21	79
Camera or technique evaluation	15	25	58	17
Intruder behavior [g]	13	0	45	55
Other	7	0	60	40

[a] Studies that had multiple objectives are included in more than one category.

[b] Excludes systems that were not adequately described or did not have a recording unit.

[c] Mechanical or infrared triggers were used in all but one still-frame system, which used digiscoped photos. Triggers were used in 4% of time-lapse systems and 12% of systems that provided real-time (≥25fps) video.

[d] Includes studies on provisioning rates, food loads, and prey identification.

[e] Includes studies on nest defense by parent birds and helpers of cooperatively breeding species and on breeding behavior other than feeding (e.g., nest attentiveness).

[f] With one exception (Hudson and Bird 2006), systems used to check nest contents relayed images to a video screen but did not record them.

[g] Includes studies on brood parasites and conspecific adults of non-cooperatively breeding species.

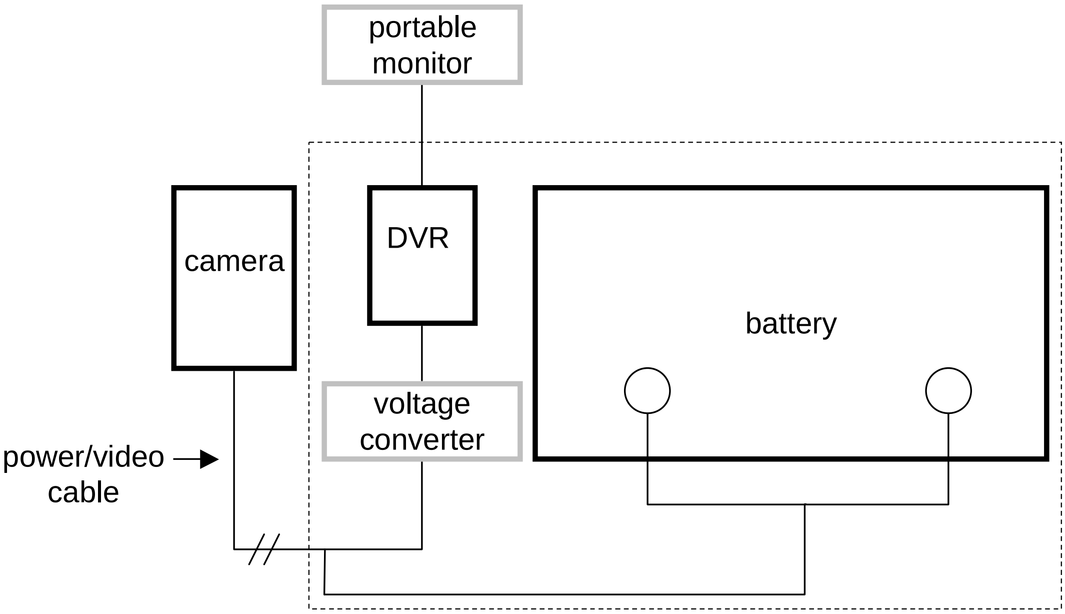

Figure 1. Schematic of a user-built digital video recording (DVR) system. The dashed line surrounds components housed in a waterproof case. Components in gray boxes may not be required; some DVR models have integrated LCDs and some may operate at the same voltage as the camera (typically 12 volts).

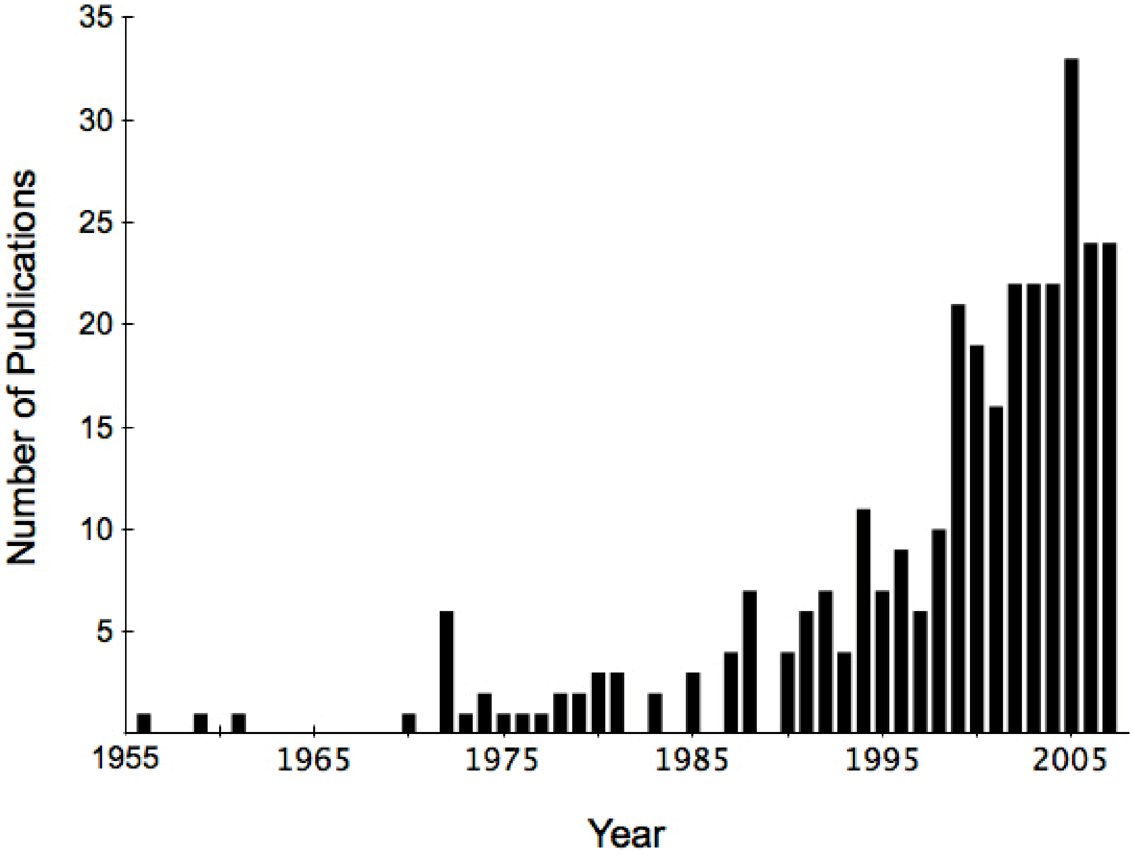

Figure 2. Camera technology has been used with increasing frequency between 1956 and 2007, the last year in which papers were fully indexed when we performed our literature search.


A
2007/07/03 11:04:29
B
2007/06/24 22:20:33
C
2009/06/14 17:09:38
D
2009-07-14 14:01:39

Figure 3. Sample images from our case studies. In (a), a Broad-winged Hawk (*Buteo platypterus*) depredates an Acadian Flycatcher nest. The same fixed-focus camera provided lower quality images when placed too close to a nest. The video was out of focus in the day and worse at night; the Indigo Bunting in (b) (top arrow) is barely visible and the mouse (bottom arrow) cannot be identified to species. Some camera models rarely provided good images; the camera that recorded the image of a hawk (top arrow) depredating an Acadian Flycatcher nest (bottom arrow) in (c) usually produced pixelated images with poor contrast despite the fact that it had manual focus and zoom controls. In contrast, the fixed-focus model used to record the black rat snake in (d) typically provided high quality color.

Appendix 1. List of major components and their costs (USD) for two user-built digital video systems designed for nest predator identification studies.

Component	System One	Cost	System Two	Cost
DVR	Yoko Tech RYK9122	$190	Seorim AKR-100	$150
Camera[a]	Rainbow CCTV BB22WIRC*	$160	Supercircuits PC6EX-3*	$30
			Supercircuits PC6EX-4	$50
			Supercircuits PC331-IR	$70
			Supercircuits PC506-IR	$90
			Supercircuits PC168-IR	$90
Voltage converter	ESCO-Ohio 3-terminal	$20		
Waterproof case	Pelican™ 1500	$70	plastic container	$3, $10
Video/power cable	15 m BNC	$20	30 m BNC	$25
Battery	Sealed lead-acid Werker WKA11226NB	$85	deep-cycle (various)	$60–80
Battery charger	Schumaker SC-600A	$40	various	$25–60
Memory cards	various (4GB)	$10	various (8GB)	$20
Portable monitor	Supercircuits MON-1	$100	various	$80–435

[a] Camera models recorded color images except those marked with an asterisk (*), which recorded monochrome images.

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VITA

W. Andrew Cox was born in New Jersey and raised in southwest Florida. He received his B.A. in English from the University of Florida in 1997, where he fell in love with college football and his wife. He held a series of corporate jobs from 1997 to 2003, when his early mid-life crisis precipitated a return to the University of Florida for a year of biology classes. He and his wife left Florida in 2004 to work with birds in Arizona, Hawaii, and Venezuela. They moved to Columbia in 2005 when Andrew began graduate school. There they happily reside with two cats, a garden, and a fenced yard. The American dream!