



SPECIES AND TEMPORAL FACTORS AFFECT PREDATOR-SPECIFIC RATES OF NEST PREDATION FOR FOREST SONGBIRDS IN THE MIDWEST

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ABSTRACT.—Knowledge of the relative contributions of predator species to overall rates of nest predation can improve our understanding of why predation risk varies, but the identity of predators is seldom known. We used video technology to identify nest predators of the tree-nesting Acadian Flycatcher (*Empidonax vireescens*) and the shrub-nesting Indigo Bunting (*Passerina cyanea*) in forests of Missouri and southern Illinois. Raptors, snakes, and nonraptorial birds were the most frequent nest predators; rodents depredated fewer nests; and mesopredators rarely depredated nests. We tested hypotheses concerning effects of songbird species, ordinal date, nest stage, height, and age on overall and predator-specific predation rates to determine whether variation in overall predation rates was attributable to a subset of nest predators. Overall predation rates were higher for Indigo Buntings than for Acadian flycatchers, were higher during the nestling stage than during incubation, and exhibited a midseason peak. Compared with Indigo Buntings, Acadian Flycatchers experienced significantly lower predation by raptors, nonraptorial birds, and snakes and were never depredated by a mesopredator. Nests of both species had higher predation rates during the nestling stage than during incubation because of increased predation by raptors and snakes. Raptors, nonraptorial birds, snakes, and rodents all exhibited a midseason peak in predation rates. Estimating the contribution of specific predators to overall predation rates can increase our mechanistic understanding of why predation risk varies and thus improve our understanding of antipredator behavior and increase our ability to predict how anthropogenic habitat and climate change will influence avian productivity. Received 1 August 2011, accepted 3 December 2011.

Key words: Acadian Flycatcher, cause-specific mortality, *Empidonax vireescens*, Indigo Bunting, nest predation, nest predators, *Passerina cyanea*, passerines.

Eas Especies y los Factores Temporales Afectan las Tasas de Depredación de Nidos de Aves Canoras por Depredadores Específicos en el Medio Oeste

RESUMEN.—El conocimiento sobre la contribución relativa de las especies depredadoras sobre las tasas totales de depredación de nidos puede mejorar nuestro entendimiento sobre el porqué de la variación en el riesgo de depredación, pero la identidad de los depredadores rara vez se conoce. Usamos tecnología de vídeo para identificar los depredadores de nidos en árboles de *Empidonax vireescens*, especie que anida en árboles, y de *Passerina cyanea*, que anida en arbustos, en bosques de Missouri y el sur de Illinois. Aves rapaces, serpientes y aves no rapaces fueron los depredadores más frecuentes de los nidos; los roedores depredaron menos nidos. Pusimos a prueba hipótesis sobre los efectos de la especie de ave, fecha ordinal, etapa del nido, altura y edad sobre las tasas totales y específicas de depredación para determinar si la variación en las tasas totales de depredación era atribuible a un subconjunto de los depredadores de nidos. Las tasas totales de depredación fueron mayores para *P. cyanea* que para *E. vireescens*, fueron mayores durante las etapas con polluelos que durante la incubación y exhibieron un pico en la mitad de la temporada. En comparación con *P. cyanea*, *E. vireescens* experimentó una depredación significativamente menor por parte de aves rapaces, aves no rapaces y serpientes y sus nidos nunca fueron depredados por un mesodepredador. Los nidos de ambas especies tuvieron mayores tasas de depredación durante la etapa con polluelos que durante la incubación debido a un incremento en la depredación por parte de aves rapaces y serpientes. Las aves rapaces, aves no rapaces, serpientes y roedores exhibieron un pico en la mitad de la temporada en las tasas de depredación. Estimar la contribución de depredadores específicos a las tasas totales de depredación puede incrementar nuestro entendimiento de los mecanismos que explican por qué varía el riesgo de depredación, y por ende mejorar nuestro entendimiento del comportamiento antipredatorio e incrementar nuestra habilidad para predecir cómo los cambios antropogénicos y climáticos en el hábitat van a influir en la productividad aviar.

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NEST PREDATION IS the primary source of reproductive failure in passerines (Ricklefs 1969, Martin 1992) and can have significant negative consequences for populations (Donovan and Thompson 2001). Rates of nest predation can vary widely between species within a habitat (Martin 1993), between nest stages (Peak et al. 2004, Cottam et al. 2009), intraseasonally within a species (Shustack and Rodewald 2010), and across numerous other factors of interest to biologists. 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, depending on their nest site (e.g., on the ground vs. in a tree cavity), habitat (e.g., forest vs. grassland), and geographic location (Thompson 2007). However, most studies have focused on describing variation in predation rates rather than on nest predators (Marzluff and Sallabanks 1998).

Studies on nest predators themselves usually relate predator abundance, richness, or activity with nest survival (reviewed in relation to habitat fragmentation by Chalfoun et al. 2002b; see also 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 in which most nest predation can be attributed to a subset of predators (Weidinger 2009). We need to better understand the relative contributions of different predators to overall rates of predation, 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 (Cox et al. 2012). Most camera studies present qualitative data (i.e., number of nest failures attributable to different predators), but several have demonstrated that a subset of predators can drive overall variation in predation rates. Thompson and Burhans (2003) showed that snakes contributed most to the overall predation rates for songbird nests in fields, whereas mammals were dominant nest predators in forests. Weidinger (2009) found that important predators varied by study site and that larger songbirds lost nests to a subset of the predators responsible for nest predation on smaller species. Benson et al. (2010) demonstrated that raptors and snakes depredated Swainson's Warbler (*Limnothlypis swainsonii*) nests during the nestling stage more often than during incubation, and that predation by raptors and Brown-headed Cowbirds (*Molothrus ater*) decreased seasonally, whereas predation by Black Ratsnakes (*Elaphe obsoleta*) increased. Reidy and Thompson (2012) also observed seasonal patterns: nest predation by cowbirds and mammals increased whereas nest predation by snakes decreased as the breeding season progressed.

The results of these studies suggest that the identification of nest predators can clarify causes of variation in rates of nest predation. We used video technology to document predators of the tree-nesting Acadian Flycatcher (*Empidonax vireescens*; hereafter "flycatcher") and the shrub-nesting Indigo Bunting (*Passerina cyanea*; hereafter "bunting") in forests in the midwestern United States to address two objectives. First, we sought to identify which nest predators contributed meaningfully to overall predation rates. Second, we tested hypotheses concerning effects of songbird species, ordinal date, nest stage, height, and age on overall and predator-specific predation rates to determine whether

variation in overall predation rates was attributable to variation in predation rates by a subset of predators.

Prior analysis showed that flycatchers experienced lower nest predation rates than buntings at our study sites (W. A. Cox unpubl. data). We predicted that this was because the location of flycatcher nests at the ends of slender tree branches inhibited access by snakes and by mesopredators such as Raccoons (*Procyon lotor*), Virginia Opossums (*Didelphis virginiana*), and foxes. Previous studies (Peak et al. 2004, Cottam et al. 2009) of both bird species showed that rates of nest predation were lower during incubation than during the nestling stage. Thus, we predicted that predation by snakes and avian predators would increase during the nestling stage or as nests aged because increased parental activity at the nest may draw the attention of visually oriented snake and avian nest predators (Lillywhite and Henderson 1993, Mullin and Cooper 1998). Individual birds may increase nest height following failure, to reduce the risk of predation by terrestrial predators (Peluc et al. 2008), so we predicted that reduced predation associated with increased height within a species (e.g., Wilson and Cooper 1998a) would be driven by rodents and mesopredators. Finally, seasonal variation in passerine nest predation is relatively common (e.g., Wilson and Cooper 1998b, Post van der Burg et al. 2010) as predator activity patterns (Sperry et al. 2008) or diet (Sieving and Willson 1999) shift across the breeding season. Songbirds in midwestern forests have shown linear seasonal declines (Shustack and Rodewald 2010, 2011) as well as midseason peaks of nest predation (Hirsch-Jacobson et al. 2012), so we assessed both possibilities. We predicted a linear seasonal decline in nest predation (e.g., Wilson and Cooper 1998b, Shustack and Rodewald 2010) due to reduced losses to avian predators—which may become less abundant because of low postfledging survival of raptors (e.g., McFadzen and Marzluff 1996, Sunde 2005) or postbreeding dietary shifts in corvids (Sieving and Willson 1999)—whereas a midseason peak in predation would occur from a broad suite of predators responding to a pulse in an available resource (Schmidt 1999).

METHODS

Data collection.—We selected eight study sites in Missouri and Illinois (Table 1) on the basis of the presence of our focal species, existence of typical midwestern landscape-scale forest cover, and public access. Sites were characterized by mid- to late-successional deciduous forests with overstories dominated mainly by oaks (*Quercus* spp.) and hickories (*Carya* spp.) but including mature Tuliptree (*Liriodendron tulipifera*), Sweetgum (*Liquidambar styraciflua*), and American Beech (*Fagus grandifolia*) at some Illinois sites. Sugar Maple (*Acer saccharum*) was common in the understory and subcanopy at most sites.

We conducted field work from May to August during 2006–2010. Because of logistical constraints, we did not visit all sites in all years (Table 1). Flycatchers typically nest at the end of slender branches of understory trees in the interior of midsuccessional to mature forests. By contrast, the bunting breeds in old fields, forest edges, and forest gaps and builds nests in herbaceous shrubs such as blackberries (*Rubus* spp.) and Multiflora Rose (*Rosa multiflora*) and in deciduous and coniferous saplings. Both species begin breeding in mid-May and have been documented with active nests into September in Missouri (R. Hirsch-Jacobson and

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

Site	Location	Year sampled				
		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	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

D. Morris pers. comm.). We located nests using systematic search and behavioral cues. Nests without cameras were monitored every 2 to 4 days, following Martin and Geupel (1993). We filmed nests using a combination of vendor-built (Fuhrman Diversified, Seabrook, Texas) and user-built video systems (Cox et al. 2012). In 2006, we used four user-built analog video systems. During 2007–2010, we used eight vendor-built digital video systems and 16 user-built digital video systems. We placed the vendor-built systems 0.5–1 m from nests, and the user-built systems 1.5–4.5 m from nests. We camouflaged all components with small branches, leaves, and other vegetation to reduce the likelihood that the equipment would either attract (Thompson and Burhans 2004) or repel (Herranz et al. 2002, Richardson et al. 2009) nest predators. Batteries and SD memory cards of cameras were replaced every 44–52 h.

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 infrared range of our cameras or if we felt that the setup or placement would cause unacceptable disturbance to the vegetation or the 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 species.

We measured nest height using a measuring tape for nests ≤4 m above ground and a clinometer for higher nests. We calculated nest age of flycatchers and buntings by counting the last day an egg was laid as day zero of the nest cycle. If we did not know when the eggs were laid but obtained a hatch date ($n = 110$), we backdated from the hatch date using the mean incubation period (flycatchers: 13.9 ± 0.1 days, $n = 33$; buntings: 11.2 ± 0.3 days, $n = 8$; W. A. Cox unpubl. data). Fifteen 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. For example, if a bunting nest was depredated on the eighth day of filming, that day was randomly assigned an age between 8 (minimum age possible) and 11.2 (mean incubation period for the species). We backdated nest ages from the fledge date using the mean nestling period (flycatchers: 13.6 ± 0.1 days, $n = 41$; buntings: 9.7 ± 0.2 days, $n = 19$) for nests found after hatch when possible ($n = 26$). For nests found after hatching that were

eventually depredated, we estimated nestling ages based on their physical appearance ($n = 21$).

Analysis.—We used logistic regression in an information-theoretic framework (Burnham and Anderson 2002) to evaluate support for eight models of nest predation (see below). We used the same set of candidate models to evaluate two sets of hypotheses concerning (1) factors that affect overall nest predation and (2) factors that affect predator-specific nest predation. We ranked models by Akaike’s information criterion (AIC_c) and calculated Akaike weights (w_i) for each model. We considered models that comprised the top 90% of the total weight to be well supported (Burnham and Anderson 2002). We were interested in rates of predation rather than nest survival per se, so our response levels differed from typical nest survival analyses. For our analyses of overall predation rates, we used a binary response variable to distinguish between a nest that was (0) or was not (1) depredated during the observation interval. The latter included nests that remained active or that failed for reasons other than predation. For our analysis of predator-specific nest failure, we used multinomial regression with six response categories. We assumed *a priori* that our sample sizes for many predator species would be small, so for the predator-specific analysis we grouped predators into five biologically meaningful groups representing five of the response categories: depredated by raptor (i.e., hawks and owls), nonraptorial bird, rodent (i.e., mice, rats, sciurids), mesopredator, or snake. We included a sixth response, “other,” that included active nests and those that failed from a predator that did not fall into the first five categories (e.g., human), environmental factors (e.g., weather), nest abandonment, nestling mortality not caused by depredation, and nests with unknown fates (e.g., because of camera failure or technician error). Typical nest survival analyses consider a partial predation event to be a successful interval because ≥1 egg or nestling is still present and attended by adult birds. By contrast, we treated partial predation events as an unsuccessful interval. Therefore, the predation rates we present should be interpreted not as the inverse of standard nest survival rates but, rather, as rates of successful predator attacks. The sampling unit for this approach is each 24-h interval during which a nest was filmed, which is comparable to methods that use nest-check intervals as sampling units (Dinsmore et al. 2002, Shaffer 2004).

We constructed models to represent our hypotheses that bird species, nest stage, nest height, nest age, and ordinal date would

affect overall and predator-specific rates of predation. We limited analysis to these variables because of potential limitations related to our predator-specific data. First, given our expected small sample sizes for some predator categories, we chose to keep the models relatively simple. Second, a coefficient is estimated for each of the five response levels for each covariate and results in a 10-point increase in AIC_c scores, so we limited the pool of potential covariates to those that we thought were most likely to have substantial explanatory power. We included two single-covariate models, nest stage and species, because these two factors are often important predictors of nest survival in birds (reviewed in Martin 1992), and we included one or both covariates in all other models. We included an interaction term for species and nest height because the height of bunting nests is relatively invariant and, thus, we hypothesized that the effect of nest height would be smaller for buntings than for flycatchers. We pooled data across years and did not evaluate a year effect because of small sample sizes of identified predators at each site in a given year. We used the best-supported model to generate estimates of daily predation rate and odds ratios for coefficient estimates. Estimates are presented with 95% confidence intervals. We performed all analyses with SAS, version 9.2 (SAS Institute, Cary, North Carolina).

RESULTS

We found 407 active flycatcher nests and 220 bunting nests and video-monitored 182 flycatcher nests and 122 bunting nests. Adults abandoned six nests because of the presence of the camera or researchers. We recorded 144 nest failures and personally observed a Blue Jay (*Cyanocitta cristata*) depredate an unfilmed flycatcher nest that we included in our analyses (Table 2). We identified predators at two nests of three breeding pairs; no other breeding pair is represented more than once in Table 2. We included one predation event from a Red-shouldered Hawk (*Buteo lineatus*) in Table 2 that we excluded from analysis because of potential researcher effects; a hawk visited a bunting nest ~20 min after we set up the camera, and an individual of the same species depredated the nest several days later. Raptors ($n = 45$) and non-raptorial birds ($n = 36$) were most frequently recorded depredating nests. Blue Jays ($n = 19$) and Broad-winged Hawks (*B. platypterus*, $n = 18$) were the most common avian predators identified. Snakes ($n = 25$) were also common predators; the majority of predation events were by Black Ratsnakes ($n = 15$). Most of the rodent predation events ($n = 16$) were by mice (*Peromyscus* spp.; $n = 10$), and mesopredators ($n = 4$) rarely depredated nests. The failure of one nest by humans was the result of vegetation removal by land managers. No adult females were depredated while on the nest during our study.

Our estimates of overall and predator-specific predation rates were based on 3,765 total observation days (incubation: 1,553 days; nestling: 2,212 days). The same model was the best supported in both the overall and the predator-specific analyses and included terms for bird species, nest stage, and a quadratic effect for date (Table 3). In both analyses the second-ranked model also had support ($\Delta AIC_c \leq 2$), but we did not model-average in either case. For the analysis of overall rates, the top- and second-ranked models differed only by a single parameter (species \times height interaction), so the approximately 2-point difference in AIC scores between the

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

Predator group	Species	Acadian Flycatcher	Indigo Bunting	Total	
Raptors ($n = 45$)	Accipiters (<i>Accipiter</i> spp.)	1	1	2	
	Barred Owl (<i>Strix varia</i>)	6	4	10	
	Broad-winged Hawk (<i>Buteo platypterus</i>)	10	8	18	
	Buteos (<i>Buteo</i> spp.)		1	1	
	Eastern Screech Owl (<i>Otus asio</i>)		1	1	
	Hawk (unknown spp.)		1	1	
	Raptor (unknown spp.)	2	1	3	
	Red-shouldered Hawk (<i>B. lineatus</i>)	2	3	5	
	Red-tailed Hawk (<i>B. jamaicensis</i>)	1	3	4	
	Nonraptorial birds ($n = 36$)	American Crow (<i>Corvus brachyrhynchos</i>)	2	1	3
		Avian (nonraptor, unknown spp.)	1		1
		Blue Jay (<i>Cyanocitta cristata</i>)	11	8	19
		Brown-headed Cowbird (<i>Molothrus ater</i>)	2	7	9
Wild Turkey (<i>Meleagris gallopavo</i>)			1	1	
Yellow-billed Cuckoo (<i>Coccyzus americanus</i>)		2	1	3	
Snakes ($n = 25$)		Black Ratsnake (<i>Elaphe obsoleta</i>)	9	6	15
		Eastern Yellow-bellied Racer (<i>Coluber constrictor</i>)		4	4
	Snake (unknown spp.)	1	5	6	
Rodent ($n = 16$)	Wood Rat (<i>Neotoma</i> spp.)		1	1	
	Mouse (<i>Peromyscus</i> spp.)	5	5	10	
	Rodent (unknown spp.)	3		3	
	Southern Flying Squirrel (<i>Glaucomys volans</i>)	2		2	
Mesopredators ($n = 4$)	Fox (unknown spp.)		1	1	
	Virginia Opossum (<i>Didelphis virginiana</i>)		1	1	
	Raccoon (<i>Procyon lotor</i>)		2	2	
Other ($n = 19$)	Abandoned	2	3	5	
	Environment (weather, tree fall)	3		3	
	Avian (unknown order)	1		1	
	Human		1	1	
	Nest dislodged or broken	2	1	3	
	Nestling mortality	6		6	
Total ^a		74	71	145	

^aExcludes nests abandoned because of research activities ($n = 6$) and nests with unknown fates because of equipment failure ($n = 14$), technician error ($n = 4$), removal of a camera prior to a predation event ($n = 7$), or failure to identify a predator ($n = 8$).

models reflects the +2 AIC point penalty associated with the additional parameter (Arnold 2010). For the predator-specific analysis, we followed Burnham and Anderson (2002), who discouraged model averaging when a term is linear in one model but not in others.

Predation rates on flycatcher nests were lower than those on bunting nests during both incubation and the nestling stage and

TABLE 3. Model selection results for *a priori* candidate models describing predator-specific patterns of nest predation for Acadian Flycatchers and Indigo Buntings in a study of nest predation in Missouri and Illinois, 2006–2010. (AIC_c is Akaike’s information criterion, ΔAIC_c is the difference between the current and top-ranked model’s AIC_c score, *w_i* is the weight of evidence supporting the model, and *k* is the number of parameters in the model.)

Model	Overall				Predator-specific			
	AIC _c	ΔAIC _c	<i>w_i</i>	<i>k</i>	AIC _c	ΔAIC _c	<i>w_i</i>	<i>k</i>
Species + Stage + Date + Date ²	1,066.64	0.00	0.67	5	1,431.85	0.00	0.63	25
Species + Stage + (Species × Height) + Date + Date ²	1,068.44	1.80	0.27	6	1,441.17	9.33	0.01	30
Species + Stage + Date	1,072.55	5.91	0.04	4	1,437.41	5.56	0.04	20
Species + Stage	1,074.87	8.22	0.01	3	1,433.19	1.35	0.32	15
Species + Stage + (Species × Height)	1,076.76	10.12	0.00	4	1,441.64	9.79	0.00	20
Species + Nest Age	1,094.95	28.31	0.00	3	1,454.79	22.94	0.00	15
Species	1,103.21	36.57	0.00	2	1,462.09	30.25	0.00	10
Stage	1,105.00	38.36	0.00	2	1,462.61	30.77	0.00	10

over the entire nest cycle (Fig. 1A), whereas predation rates for both species peaked in the middle of the breeding season (Fig. 1B). The odds of predation for buntings was greater than for flycatchers by raptors (150%), snakes (301%), and nonraptorial birds (177%; Table 4). Mesopredators did not depredate any flycatcher nests and depredated bunting nests (*n* = 4) only during the nestling stage. The odds of predation by raptors and snakes were 488% and 474% greater, respectively, during the nestling stage than during incubation (Fig. 2 and Table 4). Rates of predation differed by nest stage for each predator guild in a similar manner for flycatchers and buntings (Fig. 2). Each of the four predator guilds for which we could estimate predation rates exhibited a midseason peak in predation (Fig. 3), but the relative change from the beginning of the breeding season to the peak differed for each guild (raptors: 110% increase; snakes: 234%; nonraptorial birds: 228%; rodents: 990%).

DISCUSSION

Predator-specific hypotheses are often proposed but rarely evaluated in nest predation studies (Chalfoun et al. 2002b), which undoubtedly hinders our ability to make inferences about nest predation. For example, American Crows and mesopredators have often been hypothesized to be important nest predators (Chalfoun et al. 2002b), but the present study and others (Conner et al. 2010, Reidy and Thompson 2012) suggest that they do not contribute meaningfully to the overall risk of predation for many songbirds. Further, Cottam et al. (2009) attempted to use predator density as a predictor for flycatcher nest survival in Illinois, but 8 of 10 putative predators (e.g., Virginia Opossum, Raccoon, and Bobcat [*Lynx rufus*]) that they surveyed never depredated a flycatcher nest in our study. Clearly, studying the wrong nest predators is unlikely to prove fruitful, and we suggest that any long-term nest-predation study will benefit greatly by identifying predators at nests.

Raptors were the most frequently observed predators at our study sites (Table 2). However, our model-based approach produced estimates for the population of interest rather than the sample (which was biased toward nests with nestlings; see Shaffer and Thompson 2007) and indicated that nonraptorial birds were the most important contributor to overall predation rates of

flycatcher and bunting nests in Midwestern forests (Fig. 2). Both flycatchers and buntings were also vulnerable to predation by snakes, which provides further evidence of their importance as an avian nest predator (Weatherhead and Blouin-Demers 2004). The Black Ratsnake has been identified as a nest predator throughout its range (Thompson et al. 1999, Farnsworth and Simons 2000, Williams and Wood 2002, Benson et al. 2010) and was the predator at 79% of the 19 nests for which snakes were identified to species. Rodents contributed less to overall predation rates than snakes, raptors, and nonraptorial birds. Mice (*Peromyscus* sp.) were the only rodent for which we recorded more than five depredation events during our study, and we did not record an Eastern

TABLE 4. Coefficient and odds ratio estimates for species and nest-stage parameters from the top-ranked predator-specific multinomial model in a study of nest predation on Acadian Flycatchers and Indigo Buntings 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.

Parameter	Coefficient (β)	SE	Odds ratio	
			Estimate	95% CI
Species ^a				
Raptor	0.46	0.15	2.50	1.37 4.54
Snake	0.69	0.20	4.01	1.81 8.89
Nonraptorial bird	0.50	0.16	2.77	1.46 5.25
Mesopredator	NA	NA	NA	NA NA
Rodent	0.19	0.26	1.46	0.53 4.02
Stage ^b				
Raptor	1.77	0.49	5.88	2.24 15.40
Snake	1.75	0.63	5.74	1.67 19.75
Nonraptorial bird	0.60	0.38	1.83	0.87 3.82
Mesopredator	NA	NA	NA	NA NA
Rodent	0.05	0.53	1.05	0.37 2.98

^aOdds ratios compare predation rates of buntings to that of flycatchers (i.e., the odds of predation by raptors on buntings was 150% [odds ratio – 1 × 100] greater than on flycatchers).

^bOdds ratios compare the nestling stage to the incubation stage.

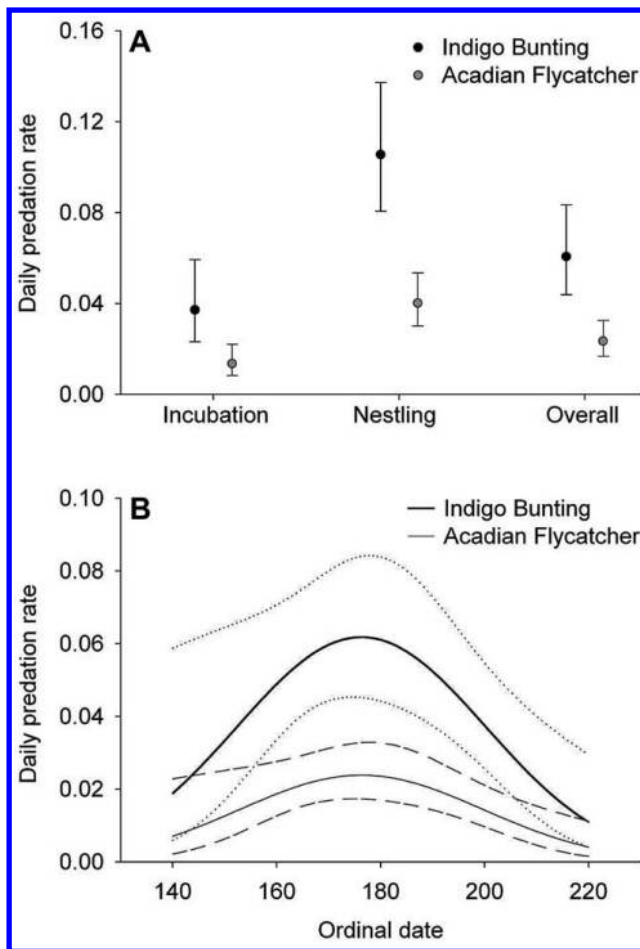


FIG. 1. Nest predation rates for Acadian Flycatchers and Indigo Buntings (A) during incubation, the nestling stage, and overall; and (B) across the breeding season, estimated from the top-ranked model in a study of nest predation in the midwestern United States, 2006–2010. Estimates in A are for ordinal day 181 (29 June), the mean date in our sample, and estimates in A and B are for a population balanced between incubation and nestling stages based on the proportion of the nest cycle spent in each stage. Error bars in A and dashed lines in B indicate 95% confidence intervals.

Gray Squirrel (*Sciurus carolinensis*) or a Fox Squirrel (*Sciurus niger*) depredating a nest, despite their ubiquitous presence at all of our study sites (W. A. Cox pers. obs.), our extensive sampling (>10 years of observation days), and their confirmed identity as a nest predator (Thompson and Burhans 2003, Rodewald et al. 2011). Animal matter is a small component of both species' diets in the summer (Korschgen 1981), so we suggest that they are infrequent, opportunistic nest predators.

We found support for effects of bird species, nest stage, and date on overall and predator-specific predation rates, though some of our predictions had limited support. For example, we predicted that increased predation by snakes and mesopredators on bunting nests compared with flycatcher nests would contribute to higher overall predation rates on bunting nests. Snakes were frequent nest predators and indeed depredated bunting nests more frequently than flycatcher nests. Black Ratsnakes are the most

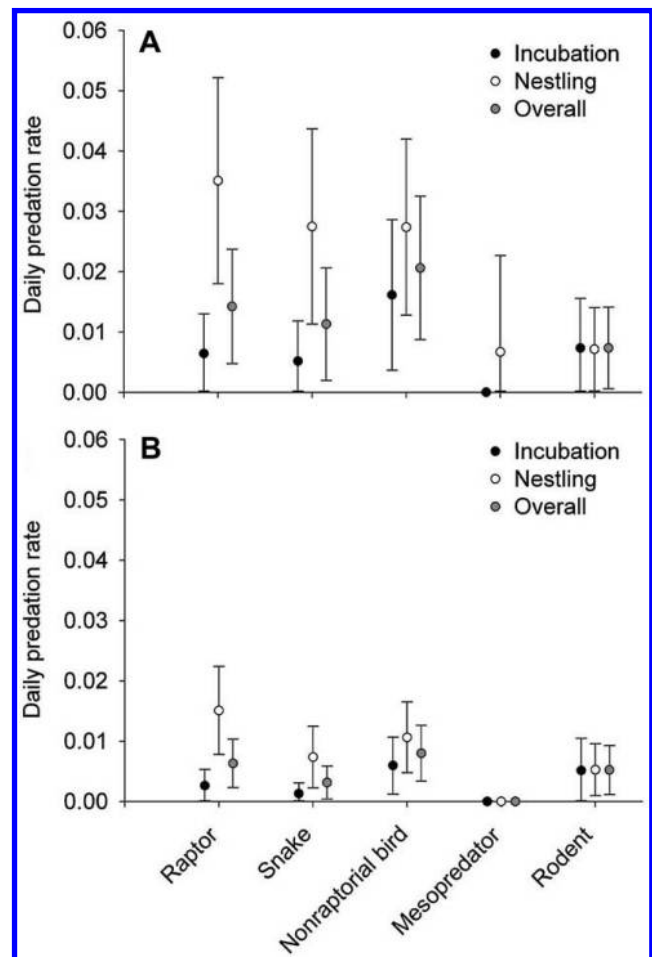


FIG. 2. Daily predator-specific predation rates estimated from the top-ranked model for (A) Indigo Buntings and (B) Acadian Flycatchers during incubation, the nestling stage, and overall in a study of nest predation in the midwestern United States, 2006–2010. Lack of predation on bunting nests during incubation prevented estimation of overall mesopredator predation rates. Estimates are for ordinal day 181 (29 June), the mean value for date in our sample. Error bars indicate 95% confidence intervals.

adept climbers among snakes at our field sites and were the only species of snake recorded depredating flycatcher nests. The only other species of snake that we recorded depredating nests, the Eastern Yellow-bellied Racer (*Coluber constrictor*), is more terrestrial than the Black Ratsnake (Keller and Heske 2000) and probably has difficulty accessing flycatcher nests, which may contribute to lower predation rates from this predator group. Additionally, both snake species prefer shrubby habitat near forest edges where buntings typically nest over the forest interior (Blouin-Demers and Weatherhead 2001, Carfagno et al. 2006). Mesopredators never depredated a flycatcher nest, probably because they cannot access them or because they do not opportunistically encounter them because of their placement at the ends of slender branches. However, the lack of predation by mesopredators on flycatcher nests did not contribute meaningfully to the difference in overall predation rates between the species because mesopredators rarely

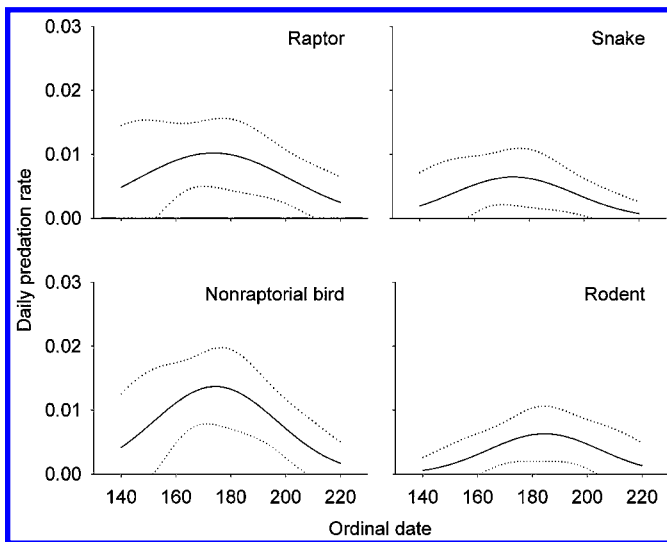


FIG. 3. Temporal patterns of nest predation for Indigo Buntings and Acadian Flycatchers from four predator guilds in a study of nest predation in the midwestern United States, 2006–2010. Estimates are from the top-ranked model for a population with equal numbers of both bird species balanced between incubation and nestling stages based on the average proportion of the nest cycle spent in each stage. Dotted lines indicate 95% confidence intervals.

depredated bunting nests either. Also contrary to our predictions, buntings experienced higher predation from raptors and nonraptorial birds compared to flycatchers. That four of five predator guilds depredated bunting nests more frequently than flycatcher nests indicates that the latter are inherently safer from most predators. We do not believe that this is a consequence of differences in antipredator behavior or nest detectability, because flycatchers had less-concealed nests and higher nest visitation rates than buntings (Cox 2011). Such differences may instead be a result of resource selection and habitat use by predators. Cowbirds, Blue Jays, and snakes may all occur in greater abundance near forest edges (Chalfoun et al. 2002a; but for cowbirds, see Donovan et al. 1997), but surprisingly few data exist on habitat selection and activity patterns for some of the most frequent nest predators (e.g., Broad-winged Hawks and Barred Owls).

As we predicted, snakes and avian predators depredated nests more frequently during the nestling stage than during incubation. Ratsnakes use visual cues to find bird nests (Lillywhite and Henderson 1993, Mullin and Cooper 1998), and visitation rates for flycatchers and buntings are lower during incubation than during the nestling stage (Cox 2011). Most of the flycatcher nests depredated by snakes occurred after dusk when adult activity had ceased (Cox 2011), but diurnal raptors are important predators of ratsnakes (Fitch 1963), and snakes may use information acquired during the day to forage at night to reduce the risk of predation (Stake et al. 2005). Snakes also use olfactory cues to locate prey (Halpern 1992), and such cues may be more prevalent in nests with young than in those with eggs. However, olfactory cues probably become more important as nestlings grow, but we saw no effect of nest age on predation rates.

Raptors also use visual cues to locate prey, which may further explain the increased predation rates during the nestling stage. The *Accipiter* and *Buteo* species that we recorded depredating nests are all diurnal, and only 1 of 10 predation events by Barred Owls occurred between dusk and dawn (Cox 2011). However, we also observed several instances of raptors failing to consume nest contents during incubation (Cox 2011), and it may be that some raptors that find nests during incubation wait until the nestling stage to depredate them. Contrary to our prediction, nonraptorial birds (presumably also visually oriented predators) depredated nests during incubation and during the nestling stage with similar frequency. It may be that corvids locate nests incidentally (Vigalón and Marzluff 2005) rather than using cues such as nestling and parental behavior.

Our previous work detected a modest linear seasonal decline in predation by birds on flycatcher nests (Hirsch-Jacobson et al. 2012). Here, with more robust sampling across two songbird species, we observed a midseason peak in overall predation rates and in predation by raptors, nonraptorial birds, snakes, and rodents. The most pronounced relative seasonal increase came from rodents, but this reflects their virtual absence as a nest predator early in the season. Nonraptorial birds exhibited the greatest absolute increase in predation rates at midseason and were important drivers of overall seasonal patterns. They and other frequent predators that we identified (e.g., Black Ratsnakes and Broad-winged Hawks) are generalists and may prey on songbird nests as more birds are breeding but switch to other prey items when searching for active nests becomes less profitable (Schmidt 1999). Other species of songbirds have exhibited linear increases (Shustack and Rodewald 2011) or decreases (Small et al. 2007) in nest survival across the breeding season. Such differences could be attributable to differences in the activity or species composition of the local predator communities or to the breeding phenology of the prey species in relation to the seasonal activity of the local predator community (i.e., the midseason pulse in predation observed in our focal species may coincide with the end of a nesting season of an early-nesting species, resulting in a linear increase in nest predation for the latter species).

By moving beyond a qualitative description of nest predators, we were able to gain insight into which predators drove variation in predation rates between songbird species, nest stages, and across the breeding season. To better understand why a broad suite of predators are influenced by some factors (e.g., songbird species and date) whereas only a subset of predators are influenced by others (e.g., nest stage), researchers should focus on the mechanisms by which predators encounter nests and patterns of predator resource selection and habitat use. Doing so will improve our mechanistic understanding of why the risk of nest predation varies and, thus, improve our ability to predict how anthropogenic habitat and climate change will influence avian productivity. Knowledge of which predators contribute most to overall predation rates should also improve our understanding of antipredator defenses and the evolution of life-history traits in response to nest predation. Estimating predator-specific predation rates can also help us move beyond investigations of the effect of predation on birds and toward a greater understanding of the role of songbird eggs and nestlings within food webs.

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