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Timing of Songbird Nest Predation as Revealed by Video Surveillance

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ABSTRACT.—The use of video to monitor nests has increased in frequency over the past 25 years and new research using this technology has shed light on many aspects of the interactions between predators and nesting birds. We used video cameras to describe the timing of nest predation events for Acadian Flycatchers (*Empidonax virescens*), Indigo Buntings (*Passerina cyanea*), and other forest-dwelling songbird species. Seventy-four percent (111 of 151) of nest predation events occurred during diurnal hours for both focal species. Although some of our observations were unexpected (e.g., Barred Owls [*Strix varia*] were primarily diurnal nest predators), many of the predator-specific temporal patterns we observed were consistent with prior knowledge. Understanding diel patterns of nest predation in conjunction with identification of the suite of predators that contribute to overall predation rates will improve our understanding of how birds recognize and respond to the risk of nest predation across ecological and evolutionary time scales. *Received 27 February 2015. Accepted 25 July 2015.*

Key words: nest predation, nest predator ecology, nest visitation, songbird ecology, video surveillance.

Predation is the primary source of nest failure for many species of songbirds (Ricklefs 1969, Martin 1992) and has received much attention from ecologists and evolutionary biologists. Until recently, however, the identification of predators responsible for nest failure was largely anecdotal or based on potentially biased methods such as the use of artificial nests (Thompson and Burhans 2004). The use of video to monitor nests has increased in frequency over the past 25 years (Cox et al. 2012), and new research using this technology has shed light on many aspects of the interactions between predators and nesting birds (Ribic et al. 2012). Despite their increased use, the expense and labor-intensive nature of video cameras and recording systems has limited their application and many fundamental aspects of songbird nest predator ecology captured by video cameras remain underreported in the literature. For example, we still know relatively little about the timing of predation (but see Stake et al. 2005, Rodewald and Kearns 2011, Davis et al. 2012), which has important implications with regard to nest defense. Adult birds will put themselves at risk to defend their nest from imminent predation (*sensu* Montgomerie and Weatherhead 1988) or when brooding, especially at night (Reidy et al. 2009). Adult birds also indirectly reduce the risk of predation by mediating the timing (Eggers et al. 2005) or rates of nest visitation (Ghalambor and Martin 2002) in support of the predation risk allocation hypothesis (Lima and Bednekoff 1999), which posits that animals should forage more frequently when the risk of predation is low and

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illicit anti-predator behaviors when the risk of predation is high. The degree to which these defense mechanisms are useful to birds depends in large part upon the timing of predation, however. For example, nest visitation rates are unlikely to be relevant in systems where predation events usually occur at night (e.g., Reidy and Thompson 2012), or are primarily due to predators that do not use visual cues (e.g., red imported fire ants [*Solenopsis invicta*], as observed by Conner et al. [2010] and Reidy and Thompson [2012]). 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. Here, we present predator-specific data on the timing of nest predation based on video surveillance of nests of Indigo Bunting (*Passerina cyanea*) and Acadian Flycatcher (*Empidonax virescens*), and other forest-breeding songbirds in the Midwestern United States (Cox 2011).

METHODS

Data were collected May to August during 2006–2010 at eight upland sites in Missouri and Illinois that were characterized by mid- to late successional deciduous forests with overstories consisting mainly of oak (*Quercus* sp.) and hickory (*Carya* sp.) trees. Our two primary study species were the tree-nesting Acadian Flycatcher and shrub-nesting Indigo Bunting, but we opportunistically included Northern Cardinal (*Cardinalis cardinalis*), Eastern Towhee (*Pipilo erythrophthalmus*), Field Sparrow (*Spizella pusilla*), Yellow-breasted Chat (*Icteria virens*), Wood Thrush (*Hylocichla mustelina*), Red-eyed Vireo (*Vireo olivaceus*), Worm-eating Warbler (*Helmitheros vermivora*), Ovenbird (*Seiurus aurocapillus*), and White-eyed Vireo (*Vireo griseus*).

We located nests using systematic searches and behavioral cues. Nests were typically monitored every 2–4 days following Martin and Geupel (1993). A subset of nests was monitored continuously via vendor-built (Fuhrman Diversified Inc., Seabrook, TX, USA) and user-built constant surveillance video systems, which were placed 0.5–5 m from nests and visited every 2 days to replace batteries and memory cards (see Cox et al. [2012b] for detailed descriptions of the cameras and their setup at nests). When the number of active nests exceeded available video systems, we selected nests that would allow us to avoid filming more than one nest per breeding pair in a given season, maximize the distance between cameras, and achieve adequate sample size for both focal species. We determined the timing of predation events by reviewing time- and date-stamped video footage after the eggs or nestlings at each nest disappeared.

Most depredation events were easily classified as diurnal or nocturnal. We classified those that occurred near dawn or dusk ($n = 7$) on the basis of ambient light levels in videos because birds were often active prior to dawn or after dusk as determined by local sunrise and sunset times. We estimated the average number of daylight hours during the breeding season using local sunrise and sunset times during 15 May–1 August, and used the daylight and overall number of hours to estimate expected values in chi-square tests to assess whether predation events occurred more or less frequently than expected during the day versus the night.

RESULTS

We recorded 151 predation events for which we could identify the predator guild and time (Fig. 1). Sixty-three (42%) of the predation events were recorded at nests of tree-nesting species, 85 (56%) at nests of shrub-nesting species, and the remaining 3 events (2%) were filmed at ground nests. Predation events at 111 (74%) nests occurred during daylight hours which was somewhat more than expected ($X^2_{1,302} = 4.21$, $P = 0.04$) given the average amount of daylight during each day (15 of 24 hrs; 63%) during the study. Both focal species qualitatively exhibited similar patterns; 41 of 60 (68%) predation events at Acadian Flycatcher nests and 50 of 67 (75%) events at Indigo Bunting nests occurred during the day, but neither was statistically significant (flycatcher: $X^2_{1,120} = 0.45$, $P = 0.50$; bunting: $X^2_{1,134} = 2.29$, $P = 0.13$). A *post-hoc* assessment of the data presented in Figure 1 suggests that nest predation occurred less frequently during the early morning (0530–0930) when compared to the remaining daylight hours ($X^2_{1,222} = 5.10$, $P = 0.02$).

Mesopredators ($n = 7$; $X^2_{1,14} = 6.36$, $P = 0.01$) and small mammals ($n = 16$; $X^2_{1,32} = 14.55$, $P < 0.01$) only depredated nests at night. Raptors ($n = 54$; $X^2_{1,108} = 14.04$, $P < 0.01$) and non-raptorial avian predators ($n = 39$; $X^2_{1,78} = 18.00$, $P < 0.01$) almost exclusively depredated nests during the day, with the exception of two nocturnal predation events by Barred Owls (*Strix varia*; 17% of all Barred Owl predation events), one by an Eastern Screech Owl (*Megascops asio*),

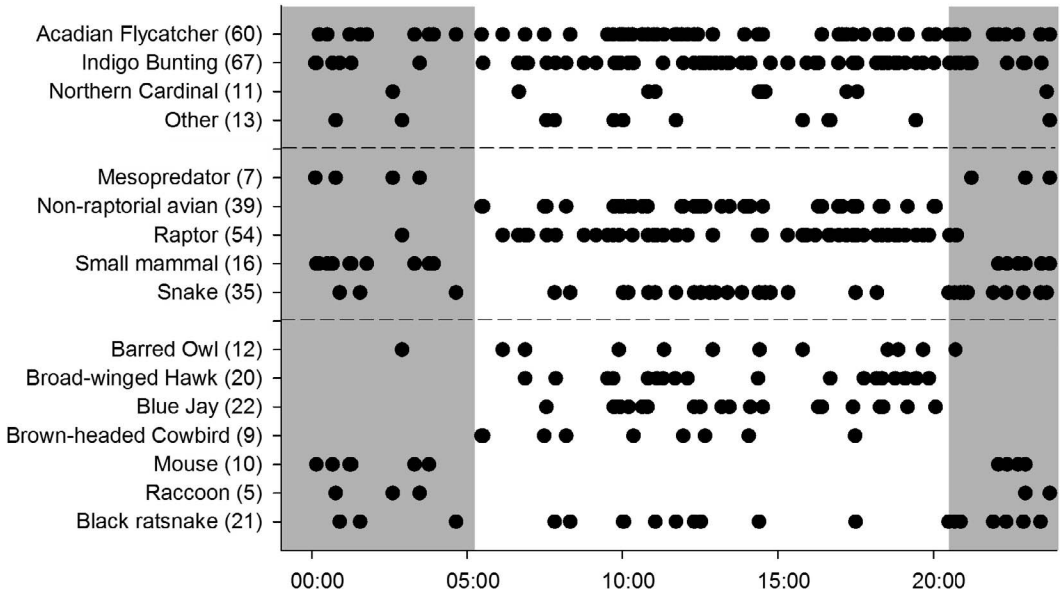

FIG. 1. Timing of 151 nest predation events recorded on video during 2006–2010 in Missouri and Illinois. Horizontal dashed lines separate prey species (top), predator guilds (center), and predator species with substantial sample sizes (bottom), with sample sizes in parentheses. The exact time of dawn and dusk varied during the breeding season, but predation events partly or entirely in shaded areas occurred during night hours.

and one by an unknown raptor. Predation by snakes ($n = 35$; $X^2_{1,70} = 0.29$, $P = 0.59$) occurred throughout the 24-hr diel cycle, with events occurring during the day in 24 of 35 instances (69%). See Cox et al. (2011) for a complete list of species associated with each predator guild.

DISCUSSION

Predation may have occurred slightly more often than expected during the daylight versus nighttime hours, but predation still occurred throughout the night (Fig. 1), which is unsurprising given the diversity of confirmed nest predators (19 species; Cox et al. 2012a) and associated foraging strategies and behaviors present at our study sites. We caution that the patterns we observed are likely influenced by our sampling as we recorded predation events at just three ground nests, which may be more susceptible to nocturnal terrestrial predators such as raccoons (*Procyon lotor*) or Virginia opossums (*Didelphis virginiana*), and it is likely that the timing of nest predation is species- and habitat-specific in most cases.

Buntings and flycatchers at our sites exhibit the highest nest visitation rates during early morning (Cox 2011), which may in part reflect support for the predation risk allocation hypothesis (Lima and Bednekoff 1999), with both species visiting nests at greater rates in the morning than during the rest of the day when nest predation is more frequent. However, stronger data, probably within a manipulative experimental context, are needed, as this variation may also be a consequence of diel patterns of physiological and/or nutritional needs of adult and nestling birds.

Although some of our observations were unexpected (e.g., most predation events by Barred Owls also occurred during the day even though they are typically considered a crepuscular or nocturnal species [Mazur and James 2000]), many of the predator-specific temporal patterns we observed were consistent with prior knowledge. For example, mesopredators were exclusively nocturnal nest predators, and Blue Jays (*Cyanocitta cristata*), Broad-winged Hawks (*Buteo platypterus*), and Brown-headed Cowbirds (*Molothrus ater*) exclusively depredated nests during the day, all of which conforms to what we know of their behavioral ecology. Nevertheless, predator identification did contribute to our understanding of the diel variation in predation; that there were somewhat fewer predation events at night is

probably because mesopredators and smaller mammals were less important predators in our study system than prior studies have suggested (Cox et al. 2012a). Ultimately, understanding diel patterns of nest predation in conjunction with identification of the suite of predators that contribute to overall predation rates will improve our understanding of how birds recognize and respond to the risk of nest predation across ecological and evolutionary time scales.

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