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Preface

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Southern Flying Squirrels (*Glaucomys volans*) as Major Predators of Avian Nest Boxes in Conecuh National Forest, Alabama

Abstract - Bird population dynamics are strongly affected by the ability to successfully reproduce, and nest predation is the primary cause of reproductive failure for most birds. Efforts to understand nest predation and manage its effects on species of conservation concern require knowledge of the ecology of associated predator assemblages. Recently, studies using cameras to record events at nests have illuminated this previously under-studied avian life stage, but such studies have been largely limited to open-cup nests. Cavity nests may be depredated by a different suite of predators, and incubating or brooding females occupying such nests may be more vulnerable to predation relative to open-cup nests. Here, we used motion-activated, infrared trail cameras to record predators of artificial nest boxes in a *Pinus palustris* Mill. (Longleaf Pine) forest in southern Alabama. Although *Glaucomys volans* L. (Southern Flying Squirrel) have only rarely been captured on film preying on nests, we found them to be responsible for the vast majority (84%) of bird-nest depredations at nest boxes, and these depredations contributed to a surprisingly low overall rate of nest success (~20%). These results may have implications for the conservation of birds that nest in artificial cavities in Longleaf Pine forests and highlight the importance of further studies on predator assemblages and their effects on nesting birds.

Introduction

Predation is the primary cause of nest failure for many birds (Martin 1993, Ricklefs 1969) and contributes strongly to variation in reproductive success. Thus, nest predation has played an extensive role in the evolution of avian life-history strategy (Latif et al. 2012, Martin 1988). Despite considerable work on the consequences of nest predation for birds, a deeper understanding of nest predation has been stalled by our lack of dependable information on the identity of the predators (Benson et al. 2010). Because different predators employ varied foraging strategies, identifying local predators within a system informs our understanding of how birds might reduce their risk of nest predation. Furthermore, because nest predation can also limit the viability of bird populations (Robinson and Wilcove 1994), management and conservation plans to reduce predation will benefit from knowing which predator species are most likely to influence avian populations.

The increased adoption of miniaturized remote cameras for identifying predators at nests has vastly improved our understanding of avian ecology and nest predator identity (Cox et al. 2012a). Armed with the identity of nest predators within a system, biologists are better able to understand the interactions between nest predators and breeding birds. For instance, *Pantherophis obsoletus* Say (Western Ratsnake) often use forest edges (Blouin-Demers and Weatherhead 2002), which results in increased nest predation by snakes near edges (Cox et al. 2012b, DeGregorio et al. 2014a). Similarly, nest camera studies have provided novel insights into how proximity to forest edges and other landscape features such as powerline right-of-ways can make bird nests more vulnerable to avian predators and brood parasites (Cox et al. 2012b, DeGregorio et al. 2014b, Rodewald and Kearns 2011). Although the number of nest studies employing video cameras has steadily increased, a recent review of research using nest cameras across North America found that studies on cavity-nesting birds are particularly under-represented in the literature (DeGregorio et al. 2016). Here, we address this gap using motion-activated trail cameras to investigate the identity and behavior of predators at artificial nest boxes in *Pinus palustris* Mill. (Longleaf Pine) forests of Alabama.

One potential predator of cavity-nesting birds in the southeastern United States is *Glaucomys volans* L. (Southern Flying Squirrel, hereafter Flying Squirrel), a small (60–80 g) arboreal nocturnal sciurid found throughout much of the central and eastern United States. The species nests, roosts, and stores food in tree cavities, a habitat that can bring Flying Squirrels into conflict with birds such as the endangered *Leuconotopicus borealis* Viellot (Red-cockaded Woodpecker) as well as the biologists tasked with helping them to recover. Flying Squirrels are often cited as potential predators of Red-cockaded Woodpecker nests (Laves 1996, Loeb 1993) or competitors for their cavities (Rudolph et al. 1990), and some management plans, particularly for small recovery populations, call for the control of squirrels near woodpecker clusters (Gaines et al. 1995).

Our specific objectives here were to use nest cameras to (1) document predator identity at avian nest boxes, and (2) quantify the relative importance of predators within the assemblage. After Flying Squirrels were revealed to be the major nest predator in this system, we added a third objective: (3) explore the factors that influenced the vulnerability of nest boxes to Flying Squirrels. Understanding the timing of predation by Flying Squirrels, the stage of nesting that is most vulnerable to these predators, and the outcomes of predation events can inform future research and conservation efforts related to birds that may be impacted by these little-known nest predators. We chose to monitor predation at artificial nest boxes because they allowed us to generate large sample sizes for comparing trends among 3 primary study sites. Nest boxes may provide nesting opportunities for numerous species of bird in our study area and are easily monitored (Newton 1994). Typically, nest boxes experience lower predation rates and higher survival than natural cavities (Møller 1989, Nilsson 1984, Purcell et al. 1997) but nevertheless can provide useful information for making inferences regarding natural predator rates at a particular site.

Field-Site Description

Our study took place from March to July of 2015 and 2016 at Conecuh National Forest in Alabama. Conecuh National Forest is ~34,000 ha of Longleaf Pine forest adjacent to Blackwater River State Forest in neighboring Florida. We established 3 study plots in similar, contiguous pine forest. The 3 plots were components of a before–after, control–impact study evaluating ecological effects associated with the attempted reintroduction of *Drymarchon couperi* Holbrook (Eastern Indigo Snakes: Gitzen et al. 2017). Plot 1 consisted of Longleaf Pine trees aged ~80 yrs, with a relative basal area for the stand of 22 m² ha⁻¹. Since year 2000, this plot has been on a 2-yr fire-return interval. There were ~3 ha of maintained wildlife openings interspersed throughout the pine forest. Plot 2 consisted of Longleaf Pine forest aged ~80 yrs at a relative basal area of 13.8 m² ha⁻¹. However, until year 2016, the basal area of this site had been 22.9 m² ha⁻¹ prior to forest thinning. Plot 2 contained ~11 ha of maintained wildlife openings. Similar to Plot 1, this site was placed on a 2-yr fire-return interval starting in the year 2000. Finally, Plot 3 was aged 80 yrs old, had a basal area of 18.4 m² ha⁻¹, contained 7 ha of wildlife openings, and was on a fire-return interval of 3 yrs. Each of these 3 plots were located within the Blue Spring Wildlife Management Area.

Methods

Nest boxes

In this study, we used artificial nest boxes to make inferences about the natural predator assemblage and its effects on nesting birds; however, an extensive body of literature exists regarding potential biases associated with this methodology (reviewed in Lambrechts et al. 2010). We are therefore conservative when using the data we collected from nest boxes to make conclusions about birds nesting in natural cavities. We constructed nest boxes using untreated cedar fence boards. Each box was 30 cm x 14 cm x 12 cm. We cut circular entrance holes of 3.8 cm, which is the generally recommended diameter opening for nest boxes intended for *Sialia sialis* L. (Eastern Bluebird) but is also suitable for a wide array of other cavity-nesting birds. We made the top of each nest box hinged so we could easily survey nest contents when necessary.

In February of 2015, we established 3 grids for placing nest boxes. Grids were centered in each of three 2-km² areas associated with a long-term study to determine the effects of Indigo Snake reintroductions on the ecology of the Longleaf Pine ecosystem. At the time of the study, only 1 of the 3 plots had experienced Indigo Snake releases. We placed a total of 251 nest boxes in the 3 plots ($n = 76, 87,$ and $88,$ respectively, in each plot). We placed boxes ~50 m apart in approximate 10 x 10 grids, although the numbers of boxes in each site varied based on the boundaries of our site and the presence of features such as roads, clearings, or waterbodies that prevented the placement of boxes. Each box was mounted to the side of a tree approximately 1.5–2 m off the ground. If a tree was not present at the determined point location (~5% of the time), we hung boxes on metal garden poles ~1.75 m off

the ground. When mounting boxes, we oriented them to avoid having branches and vegetation within 1.5 m of the entrance hole that might dissuade bird colonization or obscure the view from the cameras.

Nest monitoring

We checked all nest boxes for bird occupancy at least twice per month (min–max = 5–17 days). When a box was determined to have an active nest in it—evidenced by the presence of a fully or partially constructed nest, eggs, or active building behavior by birds—we immediately placed a camera at the nest. The open understory of this habitat allowed us to use motion-activated, infrared trail cameras (Bushnell Aggressor Trophy Cam 20MP HD, Bushnell Outdoor Products, Overland Park, KS) to monitor nests. We placed cameras on tripods or garden stakes ~5 m away from each nest box. We programmed cameras to take a burst of 3 photographs every time the motion trigger was activated. Each camera had a 32-GB memory card in it capable of storing upwards of 30,000 photographs. We visited cameras every 5–9 days to replace batteries and download memory cards. We checked the status of the nests during each visit by partially opening the lid of the nest box and using a mirror to view the nest contents and condition. At each nest check, we noted the nest contents (# eggs and/or nestlings, the presence of parents, the condition of the nest) and attempted to age nestlings when appropriate. We removed cameras after nests had been depredated or successfully fledged young. We considered a nest to have fledged young when the nest was empty and relatively undisturbed during the nest check closest to the estimated fledge time for the species. We then confirmed fledging by reviewing the photographs. For each depredated nest, we reviewed the photographs to determine predator identity, the time and date that predation occurred, the duration of the predation event, as well as any additional details that could be ascertained from photographs. Following depredation events in which birds were killed, we swept the carcasses of birds from nest boxes but otherwise did not clean out nest boxes between seasons. All field work was done under Auburn University animal care and use protocol #2016-2036.

Data analysis

We identified 6 variables of interest for use in our analysis of nest survival. Because predators may detect different cues or find more value in depredating nests at different stages (egg or nestling), we included the stage of the nest in our analysis. We included day of year as one of the variables in our analysis because predators often have seasonal activity patterns (Sperry et al. 2008). Relative to those placed on garden poles, we hypothesized that boxes mounted on natural trees might be easier for some predators (e.g., snakes, Flying Squirrels) to access, or might be more often encountered by chance as the predators used trees to move between the ground and the canopy, so we included the effect of mount type on daily survival. The different avian species which nested in our boxes could experience different daily survival rates, so we also included nesting species identity as a variable. We examined the effect of year to account for potential yearly

differences (e.g., weather) and plot ID to account for potential patch-level differences in survival between study sites.

We first modeled overall daily nest survival as a function of these 6 variables, using logistic exposure methods (Shaffer 2004) in R 3.3.2 (R Core Team 2016). We examined 6 models, each including 1 of the above variables, and used AIC_C and model weights (Burnham and Anderson 2002) to compare them with a global model containing all variables, and an intercept-only (constant survival) model. For models with considerable support ($> 35\%$ weight of evidence and $\sim 2 \Delta AIC_C$ units from next competing model), we examined predictions and 95% confidence intervals.

As the data were collected in the field, it became increasingly clear that Flying Squirrels were by far the most frequent nest predator in our study. We conducted further analyses on predator class-specific predation probability on a subset of nests for which the predator was known. We used a 1-way goodness-of-fit test (in R 3.3.2) to confirm that a disproportionate number of the predation events we observed were caused by Flying Squirrels. To explore what factors potentially made predation by squirrels more likely, we examined a multinomial model in SAS 9.4 (Cary, NC) using PROC LOGISTIC. In this model, we classified the outcome of each daily exposure period as either survive, depredated by Flying Squirrel, or depredated by another predator. We used nest outcome as the response variable, with “survive” as the reference category. We included egg or nestling stage and nest-box mount type (tree or pole) as predictor variables. Because we had relatively few observations of predators other than Flying Squirrels depredating nests, we limited our model to just these 2 variables, which we hypothesized had the most potential to differentiate what causes predation by different species. We present estimated daily predation probabilities for the different groups of the predictor variables.

Results

We monitored 26 active avian nests (11 in 2016 and 15 in 2017), belonging to 4 species including Eastern Bluebird, *Poecile carolinensis* Audubon (Carolina Chickadee), *Baeolophus bicolor* L. (Tufted Titmouse), and *Thryothorus ludovicianus* Latham (Carolina Wren) (Table 1). Twenty-one of the active bird nests were in boxes mounted on trees, and 5 were in boxes mounted on poles. Of the 26 monitored nests, 5 successfully fledged young and 21 were completely depredated

Table 1. Summary of avian nests monitored with trail cameras at Conecuh National Forest, AL, during the 2015 and 2016 nesting seasons. We filmed a total of 26 avian nests in artificial nest boxes for a total of 390 exposure days. Overall, 21 nests were depredated and 5 successfully fledged young.

Species	No. nests	Exposure days	No. fledged	No. failed	Daily survival rate
Carolina Wren	7	61	0	7	0.885
Carolina Chickadee	4	105	2	2	0.981
Eastern Bluebird	10	118	2	8	0.937
Tufted Titmouse	5	106	1	4	0.959
Total	26	390	5	21	0.946

(Table 1). We identified Flying Squirrels (Fig. 1) as the predator responsible for 16 nest failures. We also determined ants, an unidentified bird of prey, and an unknown rodent as being responsible for 1 nest failure each. We failed to identify the nest predator responsible for 2 additional depredation events due to camera malfunction. However, the condition of 1 of these nests (lid of box removed, nest heavily damaged) suggested it was likely depredated by a Flying Squirrel.

In our analysis of nest survival using logistic exposure models (26 nests, $n = 390$ exposure days), the identity of the nesting species was the only model with more weight than constant survival (Table 2). The estimated daily survival rate for Carolina Chickadees was highest (0.981), while Carolina Wren daily survival was lowest (0.885). Confidence intervals for all species overlapped (Fig. 2A), and the difference between Carolina Chickadee and Carolina Wren nests was not significant when adjusted for multiple comparisons (Tukey-adjusted $P = 0.094$).

We were able to use data from 24 nests ($n = 379$ exposure days), which were either successful or depredated by known-identity predators, in our analyses of predator class. Flying Squirrels were by far the most frequent nest predator, depredating 84% of nests where the predator identity was known ($\chi^2 = 8.89$, $P = 0.003$). The effects of mount type and nesting stage were non-significant ($P = 0.38$ and $P = 0.46$, respectively) and confidence intervals overlapped broadly (Fig. 2B).



Figure 1. *Glaucomys volans* (Southern Flying Squirrel) was a major predator of bird nests in nest boxes during the 2015 and 2016 avian nesting seasons.

Flying Squirrels exclusively preyed on nests at night, with the earliest event initiating at 2033 hrs and the latest beginning at 0209 hrs. Once a predation event began, squirrels were always successful in accessing and destroying the contents of nests; nest-defense behavior by adult birds was not documented (although we cannot be assured it did not occur). Squirrels were responsible for the failure of 7 nests containing eggs and 9 nests containing nestlings. During 2 of the nest-predation events, the Flying Squirrel killed the adult female bird (Eastern Bluebird and Tufted Titmouse) in the nest box. Neither of the killed adults was eaten or partially eaten by the squirrel. We found no evidence that nestlings killed by squirrels were eaten either. However, eggs appeared to be eaten as only eggshells remained after

Table 2. Logistic exposure models of nest survival for cavity-nesting birds using artificial nest boxes in Alabama, 2015–2016. Analysis includes all nest data (26 nests, $n = 390$ exposure days) from successful nests and nests depredated by Southern Flying Squirrels, other identified predators, and unknown predators.

Model	k	AIC _C	Δ AIC _C	w_i
Nesting species	4	163.95	0.00	0.41
Constant survival	1	165.57	1.62	0.19
Mount type	2	166.28	2.33	0.13
Day of year	2	166.94	2.99	0.09
Nest stage	2	167.51	3.56	0.07
Year	2	167.54	3.59	0.07
Plot ID	3	168.72	4.77	0.04
Global	11	174.60	10.65	<0.01

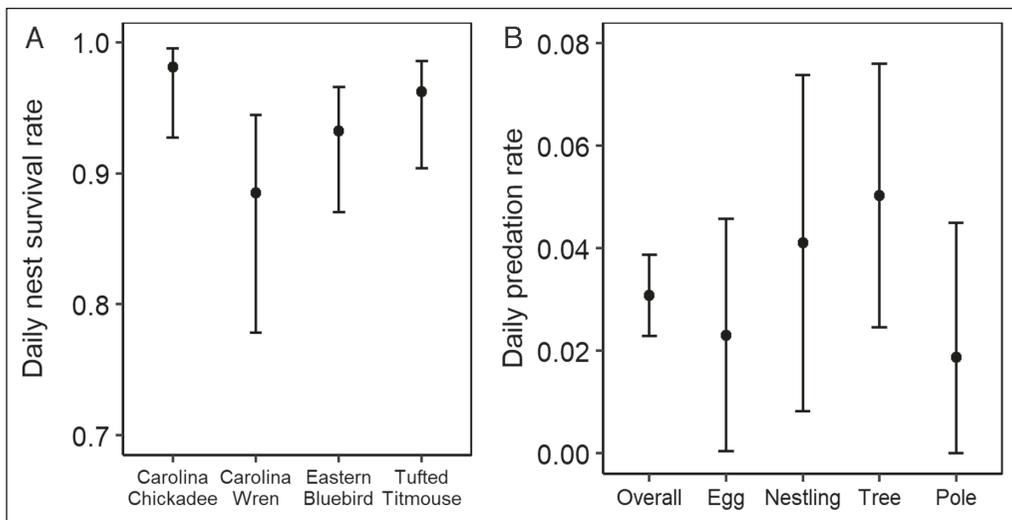


Figure 2. (A) Estimated daily survival rate of bird nests in nest boxes by species in Conecuh National Forest, AL, in 2015 and 2016. (B) Predicted daily predation rates from *Glaucomys volans* (Southern Flying Squirrel) estimated from a multinomial model. Estimates were generated for all nests (overall) as well as each level of the nest stage and box mount type variables, while holding the other variable at its mean level.

depredation. All predation events by squirrels resulted in complete loss of the brood (when nestlings were present) or clutch (when eggs were present). Nest-predation events varied from 1 min in duration to 144 min, with a mean of 37 min. Although Flying Squirrels are social animals, we never saw more than 1 squirrel visit a bird nest at the same time.

Discussion

Our results revealed that Flying Squirrels were major nest predators in artificial nest boxes in this Longleaf Pine forest, accounting for 16 of 19 (84%) nest failures where the predator identity was known. Flying squirrels have been identified as potential predators of avian cavity nests (Laves and Loeb 1999, Miller 2002), but the empirical data that exist suggests this species (typically considered to feed on mast and seeds; Harlow and Doyle 1990) rarely prey upon nests (15 out of 1900 documented nest failures; DeGregorio et al. 2016). Specifically, Flying Squirrels have been documented preying on *Mimus polyglottos* L. (Northern Mockingbird) nests in Florida ($n = 4$; Stracey 2011), *Hylocichla mustelina* Gmelin (Wood Thrush) nests ($n = 8$; Williams and Bohall Wood 2002) in West Virginia, and the open-cup nests of common shrubland and suburban birds in Ohio ($n = 1$; Rodewald and Kearns 2011) and Missouri ($n = 2$; Cox et al. 2012b). Furthermore, there has been little evidence connecting Flying Squirrels to decreased avian nest success (Conner et al. 1996, Mitchell et al. 1999). In fact, experiments have shown that removal of Flying Squirrels has relatively little influence on Red-cockaded Woodpecker nesting success, with some birds successfully fledging young when they used cavities in the same tree as active squirrel cavities (Conner et al. 1996, but see Laves and Loeb 1999). Given the high proportion of nest failures in our study attributed to Flying Squirrels, it seems likely that this species has a measurable effect on avian breeding success in this ecosystem.

The lack of diversity in the nest-predator assemblage we observed was also surprising. Typically, nest-predator assemblages are highly diverse with even the most common nest predators accounting for less than half of all observed nest predation (DeGregorio et al. 2016, Reidy and Thompson 2012, Thompson and Burhans 2003). There are some exceptions, but they generally occur in climatic extremes where biological diversity is relatively low. For example, 80% of observed bird nest failure in Alaska was attributed to *Alopex lagopus* L. (Arctic Fox; Liebezeit and Zack 2008), and *Tamiasciurus hudsonicus* Erxleben (Red Squirrel) caused 45% and 85% of nest failure, respectively, in Northwest Territories and Alberta, Canada (Ball et al. 2008).

Given that other studies in neighboring Georgia and Florida have shown relatively high diversity of predator species (including raptors, snakes, and mammals; e.g., Conner et al. 2010, Ellis-Felege et al. 2012, Stracey 2011), the high proportion of nest failure due to Flying Squirrels documented here suggests they may be a particularly important nest predator in managed southern pine forests, although our inferential power is limited because we monitored nests in artificial cavities, our absolute sample size was relatively low, and the complex ecology of the natural

system (e.g., Blanc and Walters 2008) may result in surprising patterns. For example, it has been suggested that Flying Squirrels may develop a search image for artificial nest boxes and find them relatively easily (Miller 2002). The relatively high density of nest boxes that we deployed may have made them even easier for Flying Squirrels to detect. Further study of the ecology of the system is warranted to better understand potential effects on avian assemblages and population demographics; these studies may be particularly worthwhile given ongoing Eastern Indigo Snake reintroductions in Conecuh National Forest. Although we did not document differences among sites, the presence of Eastern Indigo Snakes (which prey on snakes that eat Flying Squirrels; Rudolph et al. 2009), may eventually initiate a trophic cascade with consequences for both Flying Squirrels and cavity-nesting birds.

Typically, nest boxes experience lower predation rates and higher survival than natural cavities (Møller 1989, Nilsson 1984, Purcell et al. 1997). Consequently, the nest survival rates we observed (~20% overall survival) were surprisingly low. It remains unclear why Flying Squirrels were responsible for the failure of so many nests. Although Flying Squirrels killed nestlings and adult birds, they rarely consumed them, suggesting that the predatory behavior was not primarily motivated by food. However, Flying Squirrels did consume eggs when they raided nests containing them and so it is possible that adults and nestlings are simply killed as Flying Squirrels search for eggs. Alternatively, the lack of natural cavities in managed Longleaf Pine ecosystems (Newton 1994, Waters et al. 1990) may have forced Flying Squirrels to usurp birds and take over the boxes. We added over 250 boxes to the landscape at once, and relatively few of them were colonized by birds (< 6% per year) or squirrels (3% on average occupied at any given day), so there should have been no shortage of artificial cavities for squirrels to use. However, Flying Squirrels often use multiple tree cavities for different purposes including nesting, roosting (individually or communally), food storage, or as latrines (Brady et al. 2000, Layne and Mendi 1994). Additionally, Flying Squirrels will often switch between multiple boxes to reduce their ectoparasite risk (Hanski et al. 2000), which could lead to squirrels using more nest boxes than would be anticipated based upon their abundance. Several studies have demonstrated the dangers and costs of artificial nest boxes for birds and suggested that in some situations these nesting structures may act as ecological traps (Eadie et al. 1998, Gowaty and Bridges 1991, Klein et al. 2007). Unfortunately, we were unable to concurrently monitor bird nests in natural cavities within the study plots to serve as controls to assess a baseline nest-predation rate.

Nocturnal nest predation, such as by Flying Squirrels, can be dangerous to incubating or brooding adult birds. Reidy et al. (2009) estimated that 14.6% of breeding female *Setophaga chrysosparia* P.L. Sclater & Salvin (Golden-cheeked Warbler) were killed on nests by nocturnal snakes. Cavity-nesting birds are thought to be especially vulnerable to nocturnal nest predators (Fendley 1980, Hensley and Smith 1986), and we observed Flying Squirrels killing at least 2 brooding adult female birds (Eastern Bluebird and Tufted Titmouse) while depredating nests. Flying Squirrels always preyed on nests at night, likely reducing the ability of birds

to defend their nest or escape. Although not closely related to Flying Squirrels, *Petaurus breviceps* Waterhouse (Australasian Sugar Gliders) are morphologically and ecologically similar and have been documented depredating cavity nests of several rare birds, including the critically endangered *Lathamus discolor* Shaw (Swift Parrot; Stojanovic et al. 2014). Nest predation pressure by Sugar Gliders, during which adult females are often killed, has been identified as a severe threat to Swift Parrot populations, potentially causing collapse within 3 generations (Heinsohn et al. 2015). While the 4 avian species we studied are not generally considered of conservation concern and unlikely to experience range-wide population declines due to nocturnal predation, predators that remove reproductive females from a population have the potential to cause devastating effects on small or declining populations such as the Red-cockaded Woodpecker (Heinsohn et al. 2015, Reidy et al. 2009), and their effects should be considered by biologists tasked with managing imperiled species, especially when artificial nest cavities are being considered as a conservation action. Additionally, before nest boxes are placed into systems, researchers and managers should consider the potential unintended consequences of boxes.

Our identification of Flying Squirrels as major nest predators of birds using artificial nest boxes in this system was surprising and highlights the need for a better understanding of Flying Squirrel ecology to determine what brings them into contact with nests, as part of the larger goal of developing a clearer picture of the identity of nest predators at cavity nests across North America. Predators of cavity nests are likely quite different from those of open-cup nests. Because of the vulnerability of birds in cavities to predators, understanding predator identity will likely be an important step in conserving cavity-nesting birds.

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14. ABSTRACT Bird population dynamics are strongly affected by the ability to successfully reproduce, and nest predation is the primary cause of reproductive failure for most birds. Efforts to understand nest predation and manage its effects on species of conservation concern require knowledge of the ecology of associated predator assemblages. Recently, studies using cameras to record events at nests have illuminated this previously under-studied avian life stage, but such studies have been largely limited to open-cup nests. Cavity nests may be depredated by a different suite of predators and incubating or brooding females occupying such nests may be more vulnerable to predation relative to open-cup nests. Here, we used motion-activated, infrared trail cameras to record predators of artificial nest boxes in a <i>Pinus palustris</i> Mill. (Longleaf Pine) forest in southern Alabama. Although <i>Glaucomys Volans</i> L. (Southern Flying Squirrel) have only rarely been captured on film preying on nests, we found them to be responsible for the vast majority (84%) of bird-nest depredations at nest boxes, and these depredations contributed to a surprisingly low overall rate of nest success (~20%). These results may have implications for the conservation of birds that nest in artificial cavities in Longleaf Pine forests and highlight the importance of further studies on predator assemblages and their effects on nesting birds.					
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