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ECOLOGY AND PREDATION BEHAVIOR OF CORN SNAKES (*PANTHEROPHIS GUTTATUS*) ON AVIAN NESTS

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Abstract.—**Relatively little is known about the ecology of free-ranging Corn Snakes (*Pantherophis guttatus*), although they have been implicated as regionally important avian nest predators. We used nest camera data from 97 snake predation events, 25% of which were attributable to Corn Snakes, to assess how the ecology and behavior of nest predation by Corn Snakes compares to that of sympatric snakes that predate nests. Unlike Ratsnakes (*P. alleghaniensis*) and Racers (*Coluber constrictor*), Corn Snakes more frequently preyed on nests located away from forest edges. Nest predation by Corn Snakes, like that by Ratsnakes and Racers, increased over the nesting season. Of the four snake species documented preying on nests at our site, Corn Snakes were the only exclusively nocturnal nest predator, arriving at nests between 2024 and 0220. Corn Snakes were nearly five times more likely to prey on nestlings than eggs, suggesting that they may locate nests visually during the day. On four occasions Corn Snakes arrived at nests shortly after or while other snakes preyed on nestlings, indicating that Corn Snakes may use cues provided by other snakes to locate prey. Unlike other snake species, Corn Snakes never struck at adult birds on the nest and often actually pushed sleeping adults off the nest or pushed under them to access nestlings. Although Corn Snakes do not appear to present nesting birds with unique challenges for avoiding predation, Corn Snakes do present researchers with intriguing questions about their foraging behavior.**

Key Words.—activity patterns; behavior; Black Racers; Corn Snakes; edge effects; nest predation; Ratsnakes

INTRODUCTION

Growing evidence from video cameras placed at avian nests (Cox et al. 2012a) implicates snakes as major nest predators (Weatherhead and Blouin-Demers 2004; DeGregorio et al. 2014a). The importance of nest predation to breeding birds has therefore led to growing research on the ecology of nest predation by snakes (e.g., Weatherhead and Blouin-Demers 2004; Robinson et al. 2005; Stake et al. 2005; Klug et al. 2010; Visco and Sherry 2015). In North America, Eastern and Texas Ratsnakes (*Pantherophis alleghaniensis and P. obsoletus*) have been a focus of much of that research, as both species are major predators of avian nests (e.g., Thompson et al. 1999; Stake and Cimprich 2003; Stake et al. 2004, 2005; DeGregorio et al. 2014a). Other snake species that are regionally significant nest predators, such as the Corn Snake (*P. guttatus:* Fig. 1) in the southeastern US and the Fox Snake (*P. gloydi and P. vulpinus*) in the Great Lakes region of North America, have received less attention despite their importance to the birds on whose nests they prey. Determining how patterns of predation between species of snakes is necessary to assess whether different snake species present nesting birds with unique challenges for reducing the risk of predation.

Avian nest predation risk can be influenced by the location of nests within the landscape. For example, the influence of forest edges on nest predation risk by snakes has been well documented. Snakes often use forest edges (e.g., Blouin-Demers and Weatherhead 2001; Carfagno and Weatherhead 2006), which leads to increased nest predation by snakes near edges (Sperry et al. 2009; Cox et al. 2012b; DeGregorio et al. 2014b). Snakes may also prey more frequently on nests in shrub habitats than in forests (Thompson and Burhans 2003). Similarly, Klug et al. (2010) showed that snakes in grasslands were often found in shrubby patches and that nest predation was highest in these patches. However, because no study to date has focused on the Corn Snake, it is not known whether this species also exhibits similar foraging patterns.

Nest predation risk by snakes can be temporally variable. For instance, at some but not all locations, nest predation by Eastern and Texas Ratsnakes increases during the times of the season when they are most active (Sperry et al. 2008, 2012; Weatherhead et al. 2010). Likewise, nest predation by Racers (*Coluber constrictor*) increases through the nesting season as Racers become more active (Weatherhead et al. 2010; DeGregorio et al. 2016). Differences in daily foraging patterns at varying

FIGURE 1. A Corn Snake (*Pantherophis guttatus*) leaving a Brown Thrasher (*Toxostoma rufum*) nest after eating the nestlings at the Savannah River Site, South Carolina, USA, 2011. (Photographed by user-built miniature video camera).

latitudes and between species can also be observed. Video evidence shows that Eastern and Texas Ratsnakes prey on nests during the day at northern latitudes but nocturnally at southern locations (Stake et al. 2005; Carter et al. 2007). Nest predation by Racers is strictly diurnal (Stake et al. 2005; Carter et al. 2007; DeGregorio et al. 2015) and predation by Corn Snakes at a site in Florida was strictly nocturnal (Carter et al. 2007).

Finally, video recordings of snake predation provide insight into both the behavior of the snakes and implications for the birds on whose nests they prey. Texas Ratsnakes and Great Plains Ratsnakes (*P. emoryi*) have been documented capturing sleeping adult female birds on the nest (Stake 2001; Reidy et al. 2009), which potentially has demographic implications for bird populations. Stake et al. (2005) reported that Eastern and Texas Ratsnakes often use the coils of their body to pin nestlings and prevent escape. It is unknown if Corn Snakes also employ this sophisticated behavior when preying on nestlings. Interestingly, Carter et al. (2007) reported that Corn Snakes often arrived at nests as other snakes preyed on the nest. In two instances, Corn Snakes arrived at nests shortly after another Corn Snake or Eastern Ratsnake had found the nest and in another instance an Eastern Ratsnake arrived at a nest as a Corn Snake was swallowing nestlings and used its body to prevent the Corn Snake from accessing the remaining nestlings. Whether these observations are evidence of social foraging by Corn Snakes is currently unknown.

We used miniature surveillance cameras at bird nests to better understand the foraging behavior of Corn Snakes in relation to other snake species. The objectives of our research were to (1) determine if nest predation by Corn Snakes was greater on edges as would be expected if Corn Snakes are edge specialists like Texas and Eastern Ratsnakes, (2) assess seasonal and daily patterns in nest predation by Corn Snakes, and (3) document the behavior of Corn Snakes at avian nests. We studied the success of snakes at capturing adult birds, frequency with which they pin nestlings during predation, the duration of nest visits, and the frequency with which Corn Snakes visit nests with other snakes.

MATERIALS AND METHODS

Study site and study species.—We studied snakes at the Savannah River Site, which encompasses 900 km^2 in Aiken and Barnwell counties, South Carolina, USA. The site consists of diverse upland and lowland habitats and there is no public access. Our study took place at the Ellenton Bay Set Aside Research area located in the east-central portion of the Savannah River Site. The set aside area is a roughly 200-ha area centered around Ellenton Bay, a 10-ha ephemeral wetland surrounded by mixed and highly fragmented forests interspersed with open shrubby areas, and dirt roads and power line right-of-ways. Although the boundaries of the set aside area encompass a 200-ha area, our study expanded beyond these boundaries to the surroundings areas to encompass approximately 900 ha.

The Corn Snake is medium-sized (to 180 cm total length) constrictor found in many habitat types throughout the Southeastern US (Ernst and Ernst 2003). Encounters of most Corn Snakes occur from April to June and their daily activity appears to be primarily nocturnal (Ernst and Ernst 2003). Mating extends from

March into June and females lay eggs in June and July in mammal burrows and rotting logs and stumps. Although reported as a common predator of avian eggs and nestlings (e.g., Carter et al. 2007), Corn Snakes eat a variety of warm-blooded prey, and mammals likely constitute the largest proportion of their diet (Hamilton and Pollack 1956).

Nest videography.—To assess the effects of temporal and nest-site characteristics on predation by Corn Snakes, we located and monitored nests of a variety of shrub and low-canopy nesting bird species during the avian nesting seasons of 2011–2013. Because our goals were to monitor and film the contents of nests, we restricted our nest monitoring to nests < 3 m off the ground. We located nests by intensively searching suitable nesting habitat and by noting behavioral cues provided by nesting birds. We filmed nests using 15 user-built miniature video systems (Cox et al. 2012a). We placed cameras 0.5–1 m from nests and camouflaged them with vegetation to reduce the likelihood of the cameras attracting predators. Research suggests that nest cameras do not increase the rate of predation for filmed nests and in many cases may decrease predation rates (Richardson et al. 2009). We put cameras only at nests that were incubating or brooding to reduce the risk of nest abandonment. We checked nests every 48 h to confirm they were still active and to change the memory cards in the DVRs. Cameras were powered by deep-cycle marine batteries, which we changed every 7–10 d.

Following predation of a nest, we reviewed the video to identify the predator, the behaviors exhibited by the predator and the nesting bird, and to document the time of the predation event. Because some snakes locate nests during the day but wait until night to prey on them (Stake et al. 2005; DeGregorio et al. 2015), we also reviewed all of the video starting at sunrise of the day of the predation event and watched until sunrise of the following day to document any visits to the nest by snakes prior to or following the predation event. We recorded details of any interactions between predators at nests and events in which more than one snake species visited the same nest. We identified all predators to species (when possible) and recorded the start and end time of each nest visit by a predator. We determined start of a nest predation event by recording when the predator was first visible to the camera and determined the end of the event to be when the predator left the view of the camera and did not return for at least 5 min. All nests were filmed until they either fledged or were preyed on and then we moved the camera to another nest to film as many nests as possible each season.

For analyses of factors influencing predation by Corn Snakes, we considered multiple visits to a nest from the same predator species as one predation event, even if they occurred on different days, because we did not know whether this was more than one individual. For quantification of predator behavior (i.e., timing of visits), we extracted behavioral data from each visit. If more than one predator species removed contents from the same nest, we considered these independent events.

Nest site characteristics.—After avian nesting had concluded each year (late July to early August), we measured a suite of nest site variables that we *a priori* hypothesized could influence nest vulnerability to Corn Snakes. These variables included nest height, distance to nearest potential snake retreat structure (snag, brush pile, stump, or log), distance to nearest forest edge, distance to nearest overstory tree, diameter of the supporting branch, and canopy cover. We measured nest height to the nearest cm from the ground to the bottom of each nest using a measuring tape. We also measured distance to the nearest overstory tree, forest edge, and snake retreat structure with a measuring tape to the nearest cm. Overstory trees were defined as trees taller than 7 m. We considered forest edge to be the interface between any forested habitat patch and any open habitat patch or road. If the nearest forest edge was further than 100 m, we used a GPS unit (Garmin Rino 610, Garmin Ltd., Olathe, Kansas, USA) to measure the distance. We defined a potential snake retreat structure as any structure large enough for an adult Corn Snake to completely conceal itself in or under and that would prevent an observer from capturing the snake. Thus, a log or a snag had to be substantial enough to conceal and protect a large snake from capture. We measured the diameter of the branch that most supported each nest using a measuring tape. Canopy cover was visually estimated to the nearest 10% immediately above each nest.

Statistical analysis.—To assess the influence of these nest-site variables on predation by Corn Snakes, we used a multinomial logistic regression model with Proc GLIMMIX in SAS 9.2 (SAS Institute, Cary, North Carolina, USA). The data consisted of each 24-h interval a nest was filmed and the response of each nest at the end of the interval. Responses were predation by Corn Snake, Eastern Ratsnake, Racer, other predator (mammalian, avian, or arthropod), or survived (our reference group). We excluded nests for which predator identity could not be determined as a result of camera failure and nests that failed for reasons unrelated to predation (e.g., weather). We evaluated support for each of the following independent variables: canopy cover, nest height, distance to nearest edge, distance to nearest snake retreat structure, distance to nearest overstory tree, diameter of the supporting branch, nesting guild, nest stage, day of season (Julian date), and maximum daily temperature.

Because we were unable to film enough nests of different bird species to analyze separately, we combined all bird species. However, we did include a variable for nesting guild to look for differences in predator identity at ground nests, open shrub nests (those located in shrubs within open habitats such as power line right-of-ways or shrublands), closed shrub nests (those located in dense shrubs), and tree nests. Although this variable does not account for individual species behaviors, it does capture the nesting heterogeneity displayed by the species we monitored. We obtained max daily temperature from a nearby (7 km) weather station and chose this weather variable among many available because it has been shown to influence nest predation by snakes (Cox et al. 2013). We categorized each nest according to the stage of the contents such that each nest was either incubating (contained eggs but laying had ceased) or had nestlings (contained young birds).

To assess differences in the timing of nest predation by Corn Snakes relative to other snake species, we recorded the time that snakes arrived at each nest for each predation event (not including return visits). To normalize these data for analyses, we took the difference in minutes between snake arrival time and sunset for that date (civil twilight times using http://www.sunrisesunset.com). We assessed the effects of species, month, and a month by species interaction term using a generalized linear model (Proc GLM). We then used Tukey's post-hoc tests to make pair-wise comparisons between Corn Snakes and Eastern Ratsnakes and Corn Snakes and Racers. Although data were normalized for analyses, when we discuss raw time data, we present medians and quartiles.

We explored differences between the duration of nest predation by different snake species using a Kruskal-Wallis test. We have previously reported on the differences in duration between predation by Racers and Eastern Ratsnakes and between Eastern Ratsnake predation during the day and night (DeGregorio et al. 2015), but present this information again here for comparative purposes with Corn Snakes. We made pair-wise comparisons of predation duration between species (including diurnal vs. nocturnal Eastern Ratsnake predation) using Wilcoxon Rank Sum tests. All analyses were performed with either SAS 9.1 (SAS Institute Inc., Cary, North Carolina) or SPSS 22.0 (IBM Corp., Chicago, Illinois) using an α = 0.05.

Results

We deployed nest cameras at 206 nests of 13 species of birds. These were primarily the Northern Cardinal (*Cardinalis cardinalis*; nests: 85, exposure days: 1,447), Blue Grosbeak (*Passerina caerulea*; nests: 25, exposure days: 376), Brown Thrasher (*Toxostoma rufum*; nests: 27, exposure days: 409), and Indigo Bunting (*Passerina cyanea*; nests: 19, exposure days: 322). We confirmed predator identity for 137 predation events (DeGregorio et al. 2014b). These include 10 occasions in which more than one predator preyed on the same nest. Snakes collectively were the most frequent nest predators, accounting for 80 predation events. Eastern Ratsnakes (hereafter Ratsnake) were the most frequent snake nest predator species (38 nest failures; 28% of all nest failures), followed by Corn Snakes (20 nest failures; 15%), Black Racers (17 nest failures; 12%), and Coachwhips (*Masticophis flagellum*: five nest failures; 4%). Including return visits and predation events with more than one snake at a nest, we collected data for 39 nest visits by Ratsnakes, 24 visits by Corn Snakes, 24 by Racers, and 10 by Coachwhips. Because Coachwhips accounted for so few nest failures (n = 5), we restricted formal comparisons of Corn Snakes to Ratsnakes and Racers. In addition to the 137 confirmed nest predation events, we failed to identify predators at 12 events and documented 67 successful fledging events.

Table 1. Contents of songbird nests preyed on by Corn Snakes (*Pantherophis guttatus*), Eastern Ratsnakes (*P. alleghaniensis*), and Black Racers (*Coluber constrictor*) at the Savannah River Site, South Carolina, USA, 2011-2013.

Nest Stage	Corn Snake	Ratsnake	Black Racer
Eggs	4	6	4
Nestlings	16	32	11
Post-Predation or Fledglings	4	0	2

Influence of nest characteristics on predation.— Snakes were more likely to prey on nestlings than eggs ($F_{8,1819}$ = 4.13, P < 0.001), although the effect size varied by snake species. Corn Snakes and Ratsnakes were 4.5–5 times more likely to prey on nestlings than eggs (β = -1.510; 85% CI: -1.600 to -1.420, β = -1.647; 85% CI: -1.724 to -1.570, respectively; Table 1). Racers were also more likely to prey on nestlings than eggs although the effect size was smaller (β = 0.979; 85% CI: -1.078 to -0.881).

Predation rate by Corn Snakes increased the further that nests were from forest edges (β = 0.009; 85% CI: 0.008–0.035). This effect was most apparent at large distances from forest edge. We recorded Corn Snakes preying on nests both in shrublands and deep in forest patches. Conversely, Ratsnakes and Racers were more likely to prey on nests located near forest edges (Ratsnake: β = -0.005; 85% CI: -0.006 to -0.004; Racer: β = -0.011; 85% CI: -0.013 to -0.010; Fig. 2).

Distance to nearest retreat structure also influenced daily predation rate by snakes overall ($F_{5,1824}$ = 2.81, P =

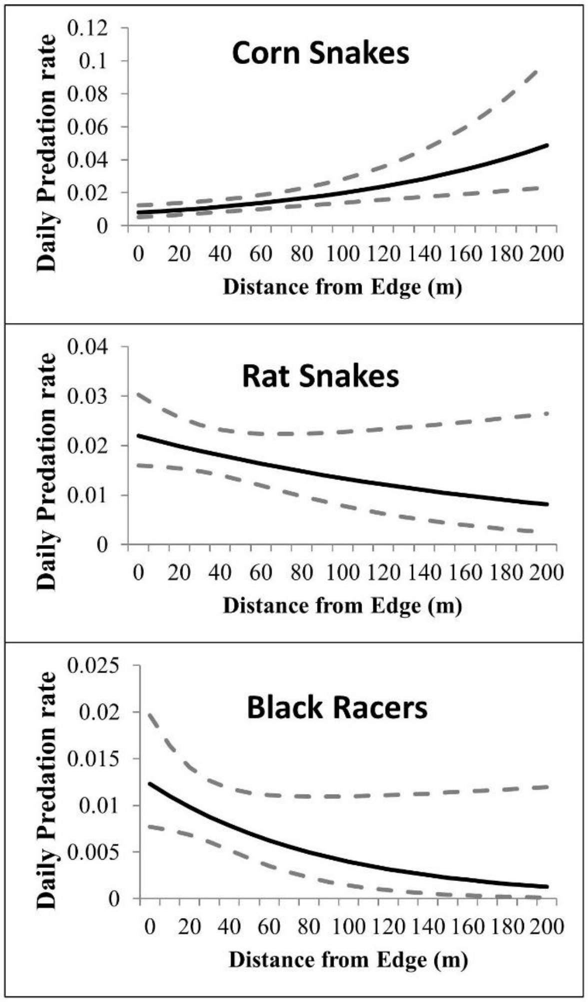

FIGURE 2. Influence of distance from nearest forest edge on daily nest predation rate (85% confidence intervals) by Corn Snakes (*Pantherophis guttatus*), Eastern Ratsnakes (*P. alleghaniensis*), and Black Racers (*Coluber constrictor*) at the Savannah River Site, South Carolina, USA, 2011–2013.

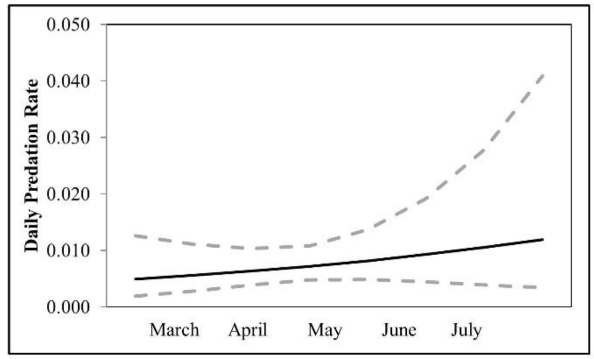

FIGURE 3. Seasonal trends in daily nest predation rate (85% confidence intervals) by Corn Snakes (*Pantherophis guttatus*), at the Savannah River Site determined via nest videography 2011–2013.

0.015), but differently by species. Predation by Corn Snakes was not related to distance to retreat structure (β = 0.006; 85% CI: 0.003, 0.008) but increased with proximity to retreat structures for Ratsnakes (β = -0.022; 85% CI: -0.024, -0.019) and decreased with proximity to retreat structures for Racers (β = 0.0334; 85% CI: 0.031–0.035). Predation rate by snakes was not influenced by macrohabitat type ($F_{5,1824}$ = 2.81, P = 0.150), canopy cover ($F_{5,1824}$ = 1.57, P = 0.167), nest height ($F_{5,1824}$ = 1.00, P = 0.416), diameter of the supporting branch ($F_{5,1824}$ = 1.05, P = 0.385), distance to the nearest tree ($F_{5,1824}$ = 1.03, P = 0.397), nesting guild ($F_{14,1814}$ = 1.39, P = 0.151), or maximum daily temperature ($F_{5,1824}$ = 1.81, P = 0.108). Although day of year was not significant ($F_{5,1824}$ = 1.00, P = 0.414), daily predation rate by Corn Snakes did increase throughout the nesting season (Fig. 3).

Timing and duration of nest predation.—Different snake species depredated nests at different times of the day ($F_{2,80}$ = 39.33, P = 0.001). However, month and the month by species interaction term did not affect when snake species preyed on nests ($F_{3,80}$ = 1.19, P = 0.320 and $F_{8,80}$ = 1.29, P = 0.260, respectively; Fig. 4). Corn Snakes were the only exclusively nocturnal predator and nests between 2024 and 0220 with a median time preyed on of 2145 (2122–2216: first-third quartiles). Ratsnakes were the only species to prey on nests during both day and night, but most Ratsnake nest visits occurred shortly after sunset (mean = 12 min after sunset, range: 2000 and 2200; median = 2058: 2025–2134). Although Corn Snakes generally depredated nests later at night than Ratsnakes, the difference between the median times of nest predation by the two species was not significant when considering only nocturnal nest visits by Ratsnakes (P = 0.188). Black Racers were exclusively diurnal and visited nests between 0936 and 1734 (median = 1352: 1145–1616). Corn Snakes and Ratsnakes each visited nests later in the day than Racers (P = 0.001 and P = 0.004, respectively).

The duration of nest visits varied by species, primarily driven by the large difference in duration between Corn Snakes and Racers (χ^2 = 30.75, df = 3, P < 0.001; Fig. 5). On average, nest visits by Corn Snakes lasted 35.8 min ± 8.9 (mean ± SE). Nest visits by Ratsnakes and Racers lasted 24.30 min ± 3.09 and 3.82 min ± 1.03, respectively. There was no significant difference between the duration of Corn Snake and Ratsnake visits (all Ratsnake visits combined: χ^2 = 0.06, df = 2, P = 0.806). As reported in DeGregorio et al. (2015), nocturnal Ratsnake visits lasted three times longer than diurnal predations (χ^2 = 8.105, df = 2, P = 0.015; mean night = 26.03 ± 3.05 min vs. mean day: 8.00 ± 4.2 min).

Predatory behavior.—We observed pinning of nestlings in the nest by Ratsnakes only five times (6%) and only once (6%) by a Corn Snake. We did not

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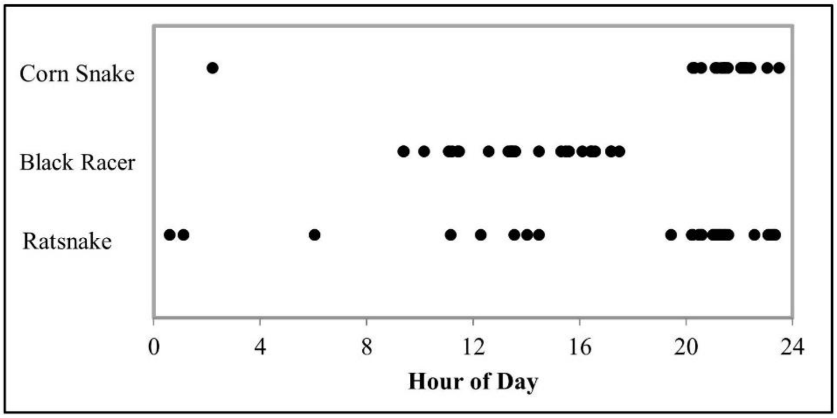

FIGURE 4. Time of day that Corn Snakes (*Pantherophis guttatus*), Eastern Ratsnakes (*P. alleghaniensis*), and Black Racers (*Coluber constrictor*) preyed on songbird nests at the Savannah River Site determined via nest videography 2011–2013.

observe Racers using this tactic. Racers frequently carried prey items away from the nest (36%) to swallow them, presumably to minimize risk of adult nest defense or exposure to other predators. Ratsnakes and Corn Snakes almost always consumed prey at the nest (96% and 93% of the time, respectively) and on the occasions when they did not, it appeared that snakes fell from the nest while manipulating nestlings.

During our study, snakes were never observed capturing an adult bird. Corn Snakes came within striking distance of adult birds on the nest 11 times. On six of these occasions Corn Snakes used their head to push adult birds off the nest or attempted to access nest contents by forcing their way under the bird and into the nest. On most of these occasions, snakes appeared large enough to capture and eat the adult bird (e.g., adult Corn Snake and Painted Bunting, *Passerina ciris*) but showed no aggression towards them. During the other five

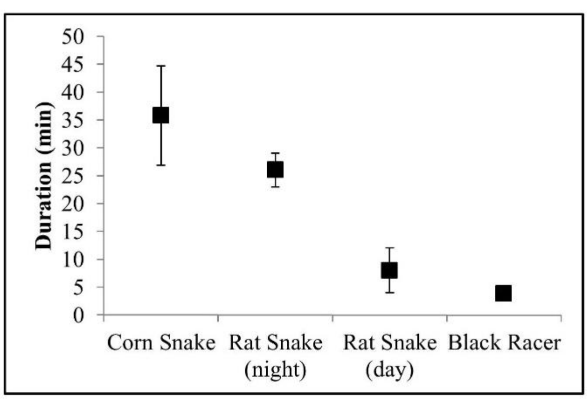

FIGURE 5. Duration of nest visits by Corn Snakes (*Pantherophis guttatus*), Eastern Ratsnakes (*P. alleghaniensis*), and Black Racers (*Coluber constrictor*) at the Savannah River Site 2011–2013.

occasions, adult birds were either not present (n = 1) or flushed before the snake was within striking distance (n = 4). Ratsnakes visibly struck at adult birds in only three of 17 cases when the adult was present, but we never documented Ratsnakes approaching close enough to adults to make contact with them like Corn Snakes routinely did. Conversely, Racers struck at adult birds, but never successfully, in five of six nest predation events in which the adult was present.

Inter and intraspecific interactions at nests.—On seven occasions we documented multiple snakes visiting the same nest and Corn Snakes were involved in four of these events. The first occasion entailed a Corn Snake attempting to gain access to a Brown Thrasher nest as a Ratsnake swallowed one of two nestlings. The Ratsnake tightly coiled its body over the nest, and prevented the Corn Snake from gaining access to the uneaten nestling. When the Corn Snake retreated, the Ratsnake swallowed the second nestling. The Corn Snake returned to the nest 44 min later and spent 28 min actively tongue flicking and moving about the nest and left without eating an unhatched egg. On another occasion two Corn Snakes arrived at a Blue Grosbeak nest at the same time. Due to heavy rain, we cannot provide further details other than that both snakes were in the nest from 2142–2153 and all of the nestlings were eaten. On two other occasions, we observed Corn Snakes arriving at nests after other snakes had depredated them (3 h 59 min after a Racer and 48 min after a Ratsnake).

We recorded three occurrences of other snake species preying on nests following predation by a different snake. In one case a Coachwhip flushed an incubating female Northern Cardinal off its nest containing three eggs. The Coachwhip made two trips to the nest and swallowed one egg each time. Six hours and nine minutes later a Racer arrived and ate the final egg. In the second example a Ratsnake visited a Northern

Cardinal nest and ate two nestlings 9 h and 40 min after a Racer had visited the nest and eaten the first of the three nestlings. The final incident involved two Ratsnakes visiting the same White-eyed Vireo (*Vireo griseus*) nest. On 25 April 2012, we heard the distress calls of adult White-eyed Vireos and discovered a Ratsnake moving away from the nest and being vigorously attacked by the adult birds. We captured the Ratsnake as part of a radio-telemetry study. Our video indicated that the snake had made contact with the nest containing four nestlings (5–6 d old) and retreated from the nest. That night (2025) a different Ratsnake depredated the nestlings.

Discussion

At the Savannah River Site in South Carolina, we documented four species of snakes depredating avian nests. Corn Snakes accounted for 25% of predation by snakes, confirming a previous report from Florida (Carter et al. 2007) that Corn Snakes can be locally important nest predators in the southeastern US. Similar to the report from Florida (Carter et al. 2007), Corn Snakes at our site were exclusively nocturnal nest predators and more frequently preyed on nestlings than eggs. Corn Snakes exhibited different nest depredation behavior than the other sympatric snake species in the region, but not in ways that seem likely to favor different avian nesting strategies to reduce predation risk.

Many species of snake preferentially use forest edges, a pattern that corresponds with higher rates of nest predation by snakes (e.g., Sperry et al. 2009; Cox et al. 2012b; DeGregorio et al. 2014b). However, unlike other snakes at our site, predation risk by Corn Snakes was greater away from forest edges. Despite the statistical differences in edge association between Corn Snakes, Ratsnakes, and Racers, there was still considerable overlap in habitat. Corn Snakes were documented preying on nests in both shrub habitats and forest interior, so the breadth of habitat use appears similar among the snakes that prey on avian nests within our study area. Similarly, our results indicated that with minor differences, Corn Snakes did not prey on nests associated with different microhabitat features from those preyed on by other sympatric snake species (e.g., Ratsnake predation associated with retreat sites). These results suggest that where Corn Snakes are abundant, the risk of nest predation by snakes does not substantially alter where in the habitat of the bird that the risk occurs. Thus, the opportunity for birds to alter predation risk from snakes by changing where they nest does not change with the addition of Corn Snakes to the snake fauna.

Similar to Ratsnakes and Racers, nest predation by Corn Snakes increased throughout the bird nesting season and occurred much more frequently during the nestling stage than during incubation. Corn Snakes differed from the other species, however, in daily timing of predation, being exclusively nocturnal nest predators. Greater incidence of nest predation during the nestling period has been interpreted as snakes observing parental feeding visits to locate nests (Mullin and Cooper 1998). If this interpretation is correct, then snakes that are nocturnal nest predators, such as Corn Snakes and Ratsnakes, must locate nests during the day when birds are feeding nestlings, but wait until dark to depredate these nests. We recently presented indirect evidence for Ratsnakes consistent with this hypothesis: Ratsnakes are most active during the day but prey on nests most at night (Degregorio et al. 2015). We do not know when Corn Snakes are active, but anecdotally, we rarely encountered Corn Snakes during the day while in the field, whereas we encounter Ratsnakes and Racers regularly.

Although Stake et al. (2005) reported Ratsnakes and Eastern King Snakes (*Lampropeltis getula*) covering the top of nests and pinning nestlings with their bodies during 41% of predation events during the nestling period, we observed this behavior by Ratsnakes only five times (6%) and only once (6%) by a Corn Snake during the nestling period. Ratsnakes may employ this technique more frequently during the day when nestlings may be better able to elude capture outside of the nest. At our site, most nest predation by Ratsnakes and Corn Snakes occurred primarily after dark (85 and 100% of nest predation events) when nestlings forced to fledge from the nest would be unlikely to elude capture by nocturnal snakes.

A seemingly paradoxical aspect of Corn Snake nest predation was the absence of any attempt to capture adult birds on the nest, despite regular opportunities to do so. Adult birds on the nest can be vulnerable to predation by nocturnal snakes (Reidy et al. 2009), and Ratsnakes and Racers both made unsuccessful strikes at adults they encountered as they approached nests. By contrast, Corn Snakes often reached nests without disturbing the adult, but then either pushed the adult off the nest or pushed under the adult to access the nestlings. Limited gape size cannot explain why Corn Snakes did not attempt to capture adults of at least smaller prey species, given that those adults were smaller than some of the nestlings of larger species that Corn Snakes consumed over the course of the study (e.g., adult Indigo or Painted Buntings compared to Brown Thrasher nestlings). It is possible that the commotion associated with subduing an adult bird could cause premature fledging of the nestlings, resulting in the Corn Snake getting a lower return from a nest than when it focuses exclusively on capturing nestlings. Our observations suggest that Corn Snakes are unlikely to be responsible for the death of many adult birds on the nest, unlike what has been reported for Ratsnakes and Great Plains

Ratsnakes in some locations (Stake 2001; Reidy et al. 2009).

We documented several instances of interactions between two snakes at a nest or of a snake arriving at nests following predation by another snake. Corn Snakes were common participants, but not the only species involved in these interactions. Carter et al. (2007) previously documented three instances of Corn Snakes interacting with other snakes at nests. This type of interaction appears to occur more often than would be expected if the participating snakes were finding nests independently. We filmed nests for an average of 16 (± 7 SD) d and only 58% were preyed on by snakes, so for two snakes to arrive at the same nest at or close to the same time would be a rare event if it occurred by chance. The most likely explanation for this behavior is that snakes (Corn Snakes in particular) sometimes actively follow other snakes. Often snakes do not consume the entire contents of nests, so by following another snake the follower may occasionally benefit from scavenging what is left by the other snake. Scavenging could include capturing nestlings that eluded capture by other snakes by leaping out of the nest. We have documented snakes capturing nestlings outside the nest and we have evidence of nestlings eluding capture and surviving until the following day by jumping from the nest, so it is unclear how vulnerable nestlings are to snakes after leaving the nest. Snakes have been documented following scent trails of other snakes to hibernation sites (e.g., Costanzo 1989), but we are unaware of any previous evidence of scent trailing being used as part of a foraging strategy, although Timber Rattlesnakes (*Crotalus horridus*) may use cues from conspecifics to select successful ambush sites (Clark 2004).

Our study has raised a number of questions about Corn Snake behavior, particularly regarding how they find avian nests and the potential role of social foraging. Further studies are required to address these questions to better understand Corn Snake foraging ecology and behavior. It may also be important to study these questions across the range of a species if their foraging behavior varies regionally as it does for the Eastern Ratsnake.

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