



RESEARCH PAPER

Wait Until Dark? Daily Activity Patterns and Nest Predation by Snakes

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Abstract

Predation involves costs and benefits, so predators should employ tactics that reduce their risk of injury or death and that increase their success at capturing prey. One potential way that predators could decrease risk and increase benefits is by attacking prey at night when risks may be reduced and prey more vulnerable. Because some snakes are facultatively nocturnal and prey on bird nests during the day and night, they are ideal for assessing the costs and benefits of diurnal vs. nocturnal predation. We used automated radiotelemetry and cameras to investigate predation on nesting birds by two species of snakes, one diurnal and the other facultatively nocturnal. We predicted that snakes preying on nests at night should experience less parental nest defence and capture more adults and nestlings. Rat snakes (*Pantherophis obsoletus*) were relatively inactive at night (23–36% activity) but nearly always preyed on nests after dark (80% of nest predations). Conversely, racers (*Coluber constrictor*) were exclusively diurnal and preyed on nests during the times of day they were most active. These results are consistent with rat snakes strategically using their capacity for facultative nocturnal activity to prey on nests at night. The likely benefit is reduced nest defence because birds defended their nests less vigorously at night. Consistent with nocturnal predation being safer, rat snake predation events lasted three times longer at night than during the day (26 vs. 8 min). Nocturnal nest predation did not make nests more profitable by increasing the likelihood of capturing adults or removing premature fledging of nestlings. The disconnect between rat snake activity and timing of nest predation seems most consistent with rat snakes locating prey during the day using visual cues but waiting until dark to prey on nests when predation is safer, although designing a direct test of this hypothesis will be challenging.

Introduction

Predation involves both costs and benefits for predators. The benefits of predation are straightforward – acquisition of food – although many factors such as prey availability and ease of capture can affect benefits (Pyke 1984). Costs arise because being a predator can be dangerous. Predators may be vulnerable to other predators when hunting (Lima & Dill 1990) and may also risk being injured by their prey (Ellison & Ribic 2012; Mukherjee & Heithaus 2013). Predators

can also incur costs by failing to capture prey despite substantial investment of time and energy (Griffiths 1980). In response, predators should employ tactics that reduce their risk of injury or death and that increase their success at capturing prey. The costs and benefits of predation can vary on short-temporal scales (Lima & Bednekoff 1999), often with extreme differences between day and night (Fenn & Macdonald 1995). Predators capable of both diurnal and nocturnal behaviour could benefit from locating prey during one period (e.g. day) and then attacking the

prey during a different period (e.g. night) if their risk of injury is lower and prey acquisition more successful during the different periods.

Because many snake species are facultatively nocturnal (Gibbons & Semlitsch 1987; Abom et al. 2012; Sperry et al. 2013; DeGregorio et al. 2014a) and have been identified as important nest predators (Thompson et al. 1999; Weatherhead & Blouin-Demers 2004; Benson et al. 2010; Reidy & Thompson 2012; DeGregorio et al. 2014b; Visco & Sherry 2015), they make ideal model organisms to study the costs and benefits of diurnal vs. nocturnal nest predation. Parent birds often respond to snakes with vigorous nest defence (e.g. Montgomerie & Weatherhead 1988; Pietz & Granfors 2005; Staller et al. 2005; Carter et al. 2007; Ellison & Ribic 2012). This can be a direct danger to snakes when the birds are relatively large and can inflict damage (Chiavacci & Bednarz 2013) or when avian distress behaviours may alert other predators to the presence of the snake (Perrone 1980; Hogstedt 1983; Conkling et al. 2012). In our own research on rat snakes (*Pantherophis obsoletus*), we have regularly captured snakes by approaching avian alarm calls and discovering a snake at a nest. Avian alarm calls may also cause nestlings to fledge prematurely (Stake et al. 2005; Reidy et al. 2009; Ellison & Ribic 2012). Such premature fledging may reduce the likelihood that a snake captures the entire brood. Data suggest that birds do not alarm call extensively at night (Hensley & Smith 1986; Carter et al. 2007). In addition to birds not defending their nests at night, snakes might also benefit from nocturnal predation because their chances of capturing a sleeping adult bird on the nest increase (Reidy et al. 2009). For golden-cheeked warblers (*Dendroica chrysoparia*), nocturnal snake predation resulted in the predation of the incubating or brooding adult in 75% of encounters, whereas no brooding adults were lost when predation was diurnal (Reidy et al. 2009). Therefore, snakes could decrease costs (i.e. nest defence and alarm calls) and increase benefits (capture more prey) by preying on nests at night.

Seasonal snake activity has been directly linked to the timing of nest predation (Sperry et al. 2008, 2012; Weatherhead et al. 2010). If seasonal increases in snake activity result in greater nest predation, we assume that more active snakes must find more nests. If so, then we should also find an association between snake activity and nest predation at finer temporal scales. To date, no study has examined the relationship between diel activity and nest predation patterns, probably because of the difficulty of quantifying snake activity at such a fine scale and simultaneously

documenting the identity of nest predators and the timing of nest predation. Automated radiotelemetry provides researchers the ability to continuously monitor the activity of free ranging snakes (Kays et al. 2011; Ward et al. 2013). Likewise, researchers can now document nest predator identity and predation timing using miniature infrared surveillance cameras at nests (Thompson et al. 1999).

Here, we use nest cameras to document predator identity and timing of predation while also using automated radiotelemetry to determine the daily activity patterns of two snake nest predators, the rat snake and the racer (*Coluber constrictor*). We first test the prediction that if rat snakes, a facultatively nocturnal species, employ an adaptive foraging strategy, they should prey on nests predominantly at night, regardless of when they are most active. Given that nocturnal nest predation is adaptive for rat snakes, we also assess which of the hypothesized benefits favours this behaviour. If decreased predation risk resulting from reduced nest defence is important, we predict that relative to diurnal nest predation, snakes preying on nests at night should experience less nest defence from parents and be less likely to be captured by predators. Given that nest predation is safer for snakes at night, we predict that nocturnal nest predation should last longer than diurnal predation. Finally, if nocturnal predation is favoured because birds are more vulnerable at night, we predict that snakes should more often capture adult birds and nestlings at night. Conversely, the racer, a strictly diurnal snake (Ernst and Ernst 2003), should be active and prey on nests only during the day regardless of the outcome and level of nest defence.

Methods

Study Site

We conducted our research at the Ellenton Bay Set Aside Research Area on the U.S. Department of Energy Savannah River Site in Aiken County, South Carolina, an area in which both rat snakes and black racers are relatively common. The site is primarily wooded with mixed forests of laurel oak (*Quercus laurifolia*), loblolly pine (*Pinus taeda*), and slash pine (*P. elliotii*) interspersed with open shrubland areas of Chicasaw plum (*Prunus angustifolia*) and blackberry (*Rubus* sp). The site is bounded to the north by a creek and floodplain forest and to the south by a two-lane paved road. A 10-ha ephemeral wetland, Ellenton Bay, is located on the southern portion of the site.

Snake Behaviour

To investigate the daily activity patterns of rat snakes and black racers, we used conventional manual radiotelemetry during the avian nesting seasons of 2011–2013 (March–August) paired with continuous automated radiotelemetry in 2012 and 2013. We captured snakes opportunistically by hand throughout the nesting season and then transported snakes to a veterinarian who surgically implanted transmitters (model SI-2T 9 g, 11 g, or 13 g, Holohil Systems Ltd, Ontario, Canada) following Blouin-Demers & Weatherhead's (2001) modification of Reinert & Cundall's (1982) technique. All transmitters weighed <3% of the snake's mass. We released snakes at their capture location 3–5 d following surgery.

To monitor the daily activity patterns of snakes, we used automated receiving units (ARU: JDJC Corp., Fischer, IL), which provide detailed information on movement frequency of snakes, but less reliable data on movement distances (Ward et al. 2013). Each ARU was connected to an array of six, three-element Yagi antennas attached to the top of a tower. We used four ARUs on guyed 10-m television towers in a diamond configuration positioned to maximize the number of snakes within range of a tower at any given time. The azimuths of the six antennas were spaced 60° apart to give 360° coverage. Each ARU was tuned at intervals of 5–15 min (depending on the number of snakes with transmitters) to the frequency of each active transmitter and recorded the signal strengths (in dBm) and bearing from the six antennas. The search interval was programmed as a text file on a standard secure digital (SD) card using software provided by the manufacturer. Every 2 wks, we collected and downloaded data to a desktop computer. Power for each ARU was provided by a 12-volt deep cycle marine battery, which we changed monthly.

Determining a snake's activity using a single ARU involves detecting changes in the amount of energy received by the ARU from the radio transmitter (signal strength) and the bearing from the ARU to the radio-tagged snake. Most movements result in simultaneous changes in both signal strength and bearing. Based on results from a 'test' transmitter, we concluded that a snake was 'active' if its signal simultaneously changed 2° in bearing and 150 dBm signal strength between successive ARU scans. Before analysing activity, we filtered the data to remove spurious records resulting from interference with other transmissions and to eliminate signals that were too weak to reliably distinguish from background noise. Because bearings are estimated from the relative

signal strengths of the antennas that receive the strongest and second-strongest signals (using equations provided by the ARU developers), the filters focused on these two antennas for each record. We excluded records where the second-strongest signal was not received by an antenna adjacent to the antenna receiving the strongest signal and where the noise recorded on the strongest antenna was greater than -130 dBm. More details regarding analysis of ARU data are provided by Ward et al. (2013).

To complement automated radiotelemetry, we hand-tracked snakes at various times throughout the day and night at approximately 48-h intervals and recorded each location using handheld GPS. Hand tracking was conducted to ground truth data collected by automated radiotelemetry and to monitor snakes when they moved out of range of telemetry towers. Hand tracking data were also used to differentiate between inactive snakes and those that had died.

To evaluate trends in daily snake movement, we determined the frequency of movements that occurred in each hour of the day during each month of study and averaged this value across snakes. We used frequency (calculated as the number of movements detected divided by the total number of observations for each hour) because snakes occasionally moved out of range of the ARUs, meaning detections were not distributed evenly throughout the day.

Nest Monitoring and Predator Identification

To identify predators at bird nests, we located and filmed the nests of a variety of shrub and low-canopy nesting bird species from 5 May to 15 August 2011 and 15 March to 1 August 2012 and 2013. We focused primarily on locally abundant species whose nests could be easily found and monitored. We located nests using systematic searching and behavioural cues. We filmed a subset of nests with one of 15 user-built video systems (Cox et al. 2012). We placed cameras 0.5–1 m from nests and camouflaged them with nearby vegetation to reduce the likelihood of the cameras attracting predators (Richardson et al. 2009). We put cameras only on nests that were incubating or brooding to reduce the risk of nest abandonment. We checked all nests every 48 hr following the protocol described by Martin & Geupel (1993) and downloaded and switched out memory cards. Cameras were powered by deep cell marine batteries, which we replaced with charged batteries every 10 d. Following predation (full or partial) of a nest, we reviewed the video the same day to identify the predator and record the time of the predation. In

addition to determining the timing of the predation event, we watched the film from entire day (starting at sunrise) preceding nest predation to document any visits by the predator before the predation event.

Each time a nest was preyed on by a rat snake or racer, we recorded the start time of the predation event. We categorized each predation event as occurring during one of four time periods: early morning (0100–0659), late morning (0700–1259), afternoon (1300–1859) and evening (1900–0059). We used a 4×2 contingency table to compare observed proportion of predation events occurring during each time interval with that expected based on the proportion of movements for each snake species occurring during the time intervals. We performed these analyses for each month of the nesting season for both species.

Because we documented rat snakes preying on nests during both the day and night, we were able to compare snake and bird behaviour between the two situations. Because racers preyed on nests only during the day, no comparison was possible. To quantify the differences in snake and bird behaviour during diurnal and nocturnal predation attempts, we recorded all antipredatory and predatory behaviour captured on film. Parental responses were scored as 0 (no adult present or adult flushed from nest and did not reappear), 1 (moderate defence: adult remained in nest area but did not actively defend nest) and 2 (intense defence: active defence including striking and flying at snake). Our camera systems were unable to record audio so we could not incorporate distress or alarm calls into parental defence quantification. We compared overall scores between the two snake species and between diurnal and nocturnal rat snake predation events using nonparametric median tests. We also recorded how frequently racers and rat snakes struck at or captured adult birds on the nest and whether this occurred more often during the day or night. Additionally, we compared the proportion of events in which nestlings escaped from snake predators by fledging during the day vs. during the night. Given that the youngest nestlings observed fledging during our study were 8 days old, we restricted our analysis of nestling escape to nests with birds aged 8 d or older. Finally, we report the duration of snake visits to nests and the frequency with which snakes in the process of preying on nests were attacked by other predators. We determined the initiation of a predation event when the predator became visible in the field of vision of the camera and determined the termination of a predation event when the predator left the camera field of view for the final time. If an adult bird returned to the nest and resumed incubation/

brooding between successive visits by a snake, we considered these separate visits when calculating predation duration rather than the snake simply moving in and out of camera range during a single visit.

Results

Snake Activity and Nest Predation

Using ARUs from March to July 2012 and 2013, we tracked 15 rat snakes and 7 racers and obtained a total of 33 861 movements by rat snakes and 55 304 racer movements. Five of the rat snakes and 4 of the racers were tracked for 2 yrs.

Concurrently, we filmed 206 nests (from a total of 463 nests found), for a total of 3 300 exposure days. We confirmed predator identity for 137 nest failures. In total, we filmed the nests of 13 species of shrub-nesting birds, the most common of which were northern cardinals (*Cardinalis cardinalis*: 85 nests and 1 447 exposure days), blue grosbeaks (*Passerina caerulea*: 25 nests and 376 exposure days), brown thrashers (*Toxostoma rufum*: 27 nests and 409 exposure days) and indigo buntings (*P. cyanea*: 19 nests and 322 exposure days). Rat snakes were the most commonly observed nest predator accounting for 38 nest predation events (28% of total). We recorded one additional nest visit by a rat snake, although researchers in the field captured the snake for radio transmitter implantation before it attacked the nest. We identified racers as predators at 17 nests (12% of total) and documented 24 nest visits by racers because this species often made multiple trips to nests removing one nestling or egg at a time. If an adult bird returned to the nest and resumed incubation/brooding between successive visits by a racer, we considered these separate visits when calculating predation duration rather than the snake simply moving in and out of camera range during a single visit.

Rat snakes were primarily diurnal, although they increased nocturnal activity as the avian breeding season progressed. In March, only 23% of rat snake movement was nocturnal increasing to 36% in July (Fig. 1). Racers were exclusively diurnal, with most movement occurring during the warmest hours of the day (Fig. 2).

Rat snakes primarily preyed on nests after sunset (1900–0059) in all months of the nesting season (79%: 31 of 39 nest visits; Fig. 1). Rat snakes were rarely ($n = 6$) filmed preying on nests during the day (0700–1859) and even less often ($n = 2$) during the early morning (0100–0659). Contingency table analyses indicated that daily rat snake activity and timing

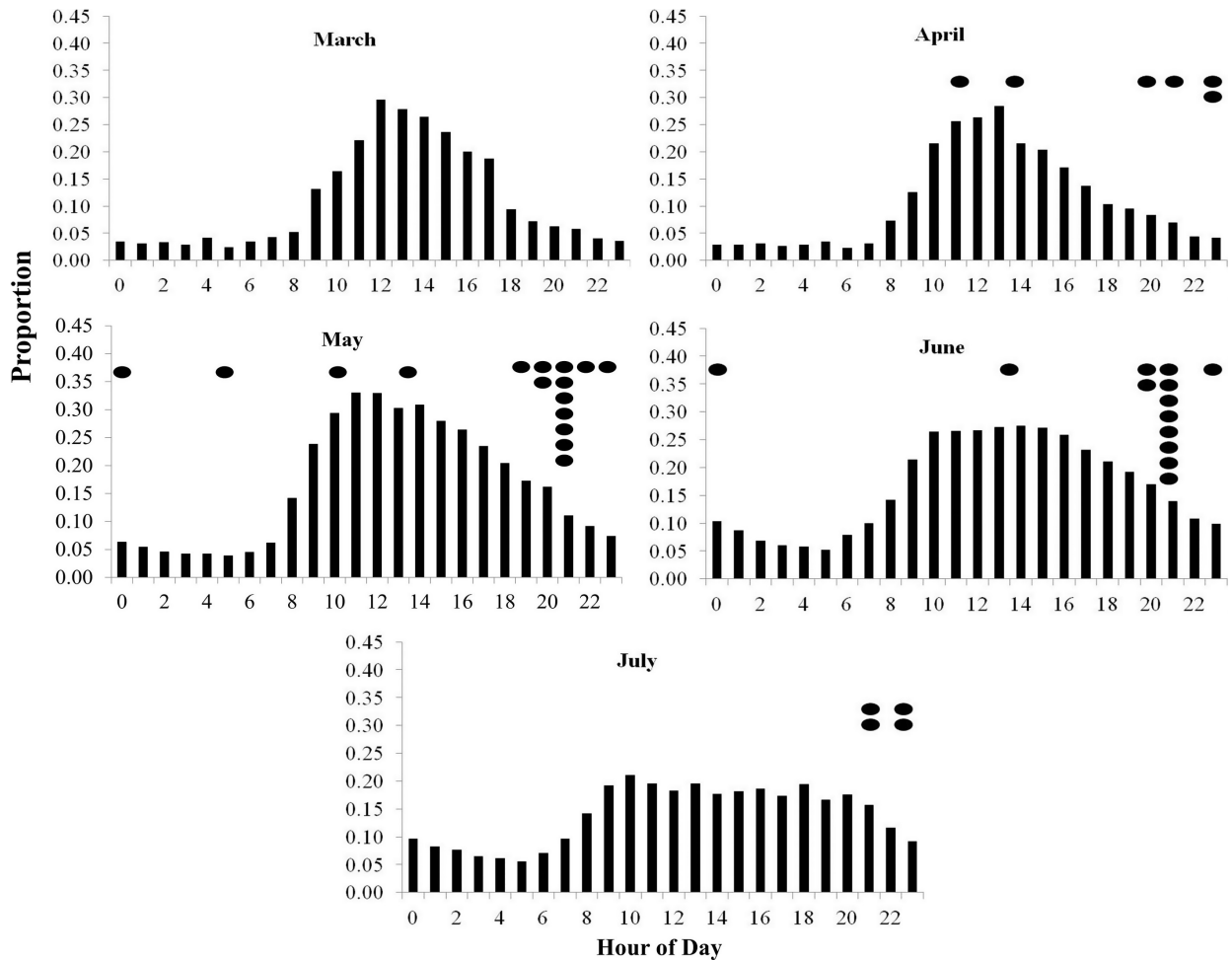


Fig. 1: Frequency of rat snake (*Pantherophis obsoletus*) movement by hour for each month during the bird nesting season based on 33 861 rat snake movements of 15 individuals recorded with automated radiotelemetry. Black ovals indicate the time of a filmed nest predation event by rat snakes in each month.

of predation by rat snakes were decoupled for April (chi-square: $\chi^2 = 60.17$, $p < 0.001$), May ($\chi^2 = 92$, $p < 0.001$), June ($\chi^2 = 110.83$, $p < 0.001$) and July ($\chi^2 = 126.2$, $p < 0.001$). Racers always preyed on nests during the day, with 37% (9 of 24) of filmed predation events occurring during the late morning and 63% (15 of 24) during early afternoon (Fig. 2). Unlike rat snakes, racers preyed on nests at the times of day they were most active (chi-square: May: $\chi^2 = 2.19$, $p = 0.53$; June: $\chi^2 = 0.08$, $p = 0.99$; July: $\chi^2 = 0.67$, $p = 0.88$). We did not record any nest predation by racers during March or April.

Safety of Snakes

Often, snakes spent considerable time exploring and tongue-flicking the nest and surrounding area after

nocturnal predation. Rat snake predation events at night lasted three times longer than predation events during the day (Mann–Whitney U -test: $U = 8.105$, $p = 0.015$; mean \pm SE: night = 26.03 ± 3.05 min; day = 8.00 ± 4.2 min). Overall, rat snake predation events lasted an average of 24.30 ± 3.09 min, which was longer than predation events by racers (13.82 min ± 1.03 min: Mann–Whitney U -test: $U = 30.277$, $p < 0.00$) (Fig. 3).

Parent birds defended their nests from racers on 8 of 14 (57%) occasions. Only twice did birds leave the area and not defend their nest from racers (once by a yellow-breasted chat (*Icteria virens*) and once by a northern cardinal). On four occasions, no adult was present during nest predation. When adults did defend their nest, they vigorously attacked the racer by flying into it and pecking it (7 of 8: 88%). Only

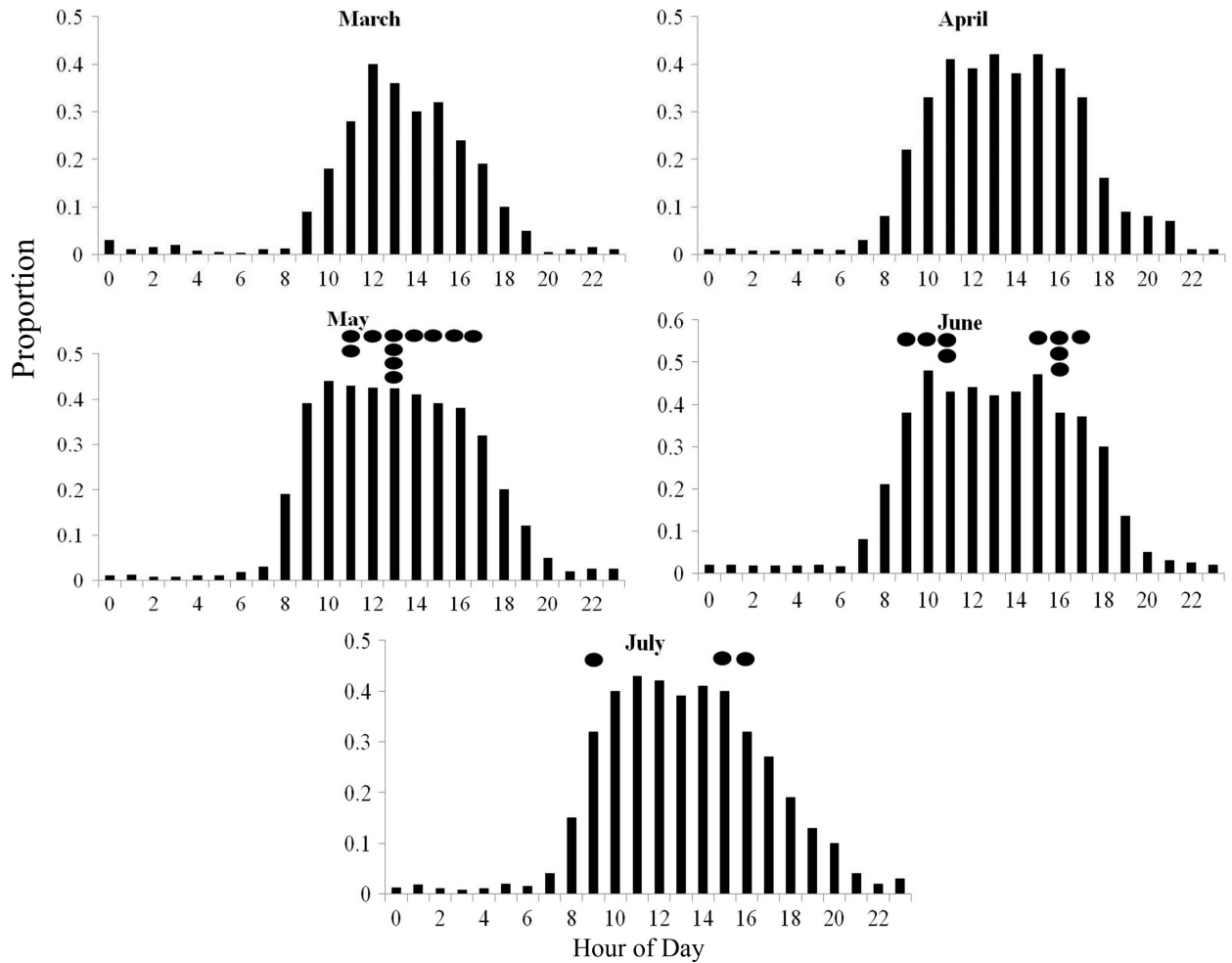


Fig. 2: Frequency of black racer (*Coluber constrictor*) movement by hour for each month during the bird nesting season based on 55 304 movements of 7 individuals recorded with automated radiotelemetry. Black ovals indicate the time of a filmed nest predation event by racers in each month.

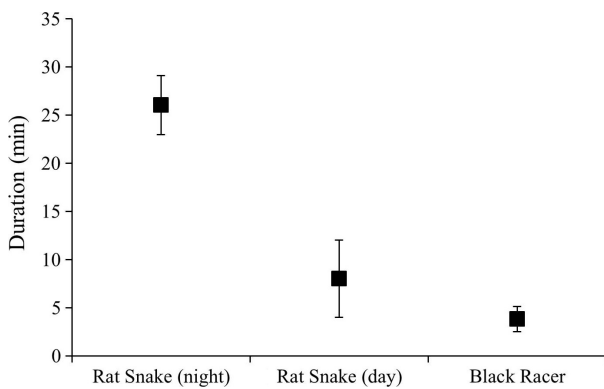


Fig. 3: Mean duration (\pm SE) of nest predation events by rat snakes (*Pantherophis obsoletus*) during the day ($n = 6$) and during the night ($n = 32$) and by black racers (*Coluber constrictor*: $n = 17$).

once did we observe a bird remain in the area but not physically attack the racer during the predation event. Despite disturbance from parental nest defence, racers were always successful in removing the contents of the nest. On 5 of 8 occasions, racers removed individual nestlings or eggs from the nest, carried them off and then returned to remove more contents. We never observed racers being attacked by other predators when preying on nests.

During the day, the intensity of parental defence in response to rat snakes did not differ from responses to racers (median test: $\chi^2 = 25.50$, $p = 0.33$) and this response was similar during both nest stages (egg: $\chi^2 = 2.00$, $p = 0.26$; nestling: $\chi^2 = 0.26$, $p = 0.61$). Parent birds always attempted to defend nests from rat snakes during the day (5 of 5: 100%). On a sixth occasion, our camera had shifted off the nest and we

were unable to observe parental behaviour. Nest defence against rat snakes during the day was characterized by aggressive defence on three occasions and moderate defence in two cases. Intensity of nest defence against rat snakes was greater during the day than at night (median test: $\chi^2 = 23.33$, $p < 0.001$). We observed adult nest defence on only 2 of 30 (7%) nocturnal nest predations, and in both cases, defence intensity was moderate. We never observed rat snakes attacked by predators when preying on nests during the day or at night, although the field of vision of nest cameras was limited.

Predation Success

We never observed either species of snake capturing adult birds, although racers did strike at adult birds in 5 of 6 (83%) nest predation events in which the adult was on the nest when the snake first approached. Rat snakes struck at adults in only 3 of 17 (18%) events in which adult birds were on the nest when the snake arrived and each of these events occurred at night. Only once did we record a rat snake visiting a nest with adults present during the day and not striking at the adult bird.

Adult nest defence never prevented rat snakes or racers from obtaining most or all of the contents of nests. Premature fledging associated with nest predation may have prevented some fledglings from being eaten, although we are unable to address this with our camera data. We had no daytime observations of rat snakes preying on nests with nestlings at least 8 d old (old enough to jump from the nest). At night, nestlings leaped from the nest during 3 of 5 predation events by rat snakes where nestlings were at least 8 d old. Stake et al. (2005) reported that rat snakes pinned nestlings using coils of their body to prevent escape. We observed this behaviour for five predation events, although the nestlings were old enough to have fledged on only one of those occasions. On two occasions, nestlings leaped from the nest while the rat snake was swallowing the first nestling it had captured. On another occasion, all three 8- to 9-d-old cardinal nestlings leaped from the nest as a rat snake approached. The snake investigated the nest, left and returned to the nest 42 min later with a large bolus. It is unclear how many nestlings the snake tracked down but the bolus suggests that at least one of the nestlings was captured outside the nest.

Black racers caused nestlings to fledge 33% of the time (2 of 6) when nestlings were old enough. On one occasion, a racer struck violently at the flushing adult bird and landed on the 8- to 10-d-old blue

grosbeak nestlings. The nestlings appeared to be injured and the snake remained on the nest as it swallowed each of the three nestlings. On a different occasion, as a racer arrived at a blue grosbeak nest, all three nestlings leaped out and the snake struck and captured one nestling in the air. The snake returned to the nest 45 min later with a large bolus.

Discussion

We found that rat snakes at our site were relatively inactive after sunset (23–36% of activity) but nearly always preyed on nests after dark (80% of nest predation). Conversely, racers were exclusively diurnal and preyed on nests during the times of day when they were most active. We also found that rat snakes that preyed on nests after dark spent longer at nests than rat snakes preying on nests during the day. These results are consistent with rat snakes strategically using their capacity for facultative nocturnal activity to prey on nests at a time when parental nest defence and risk of injury are lowest.

We identified one clear advantage for snakes that preyed on nests at night. Presumably because many birds do not see well enough at night to defend their nest from predators (Fendley 1980; Hensley & Smith 1986; Carter et al. 2007), the same species of birds that defended nests against snakes vigorously during the day did not do so at night. Although none of the birds we studied were large enough to kill adult snakes, many of the species (e.g. brown thrasher, northern cardinal) should be able to injure even large snakes. The lack of nest defence by adult birds at night may explain why rat snakes spent three times longer at nests at night than during the day. It is also possible that snakes spend longer at nests at night because reduced vision requires more time to confirm that all nest contents have been taken. It is unlikely that avoiding heat stress favours nocturnal predation because most nests were in the shade.

Although we did not observe any predation on snakes by predators attracted by parental nest defence during the day, there are several reasons to think this hypothesis is relevant. First, our cameras were narrowly focused on nests, so any predation on snakes close to but not at the nest would not have been seen. Second, we expect this predation risk of snakes to be relatively low because if snakes commonly died during nest predation, they should switch to alternative prey. Third, snakes behaved as though diurnal nest predation was risky. Racers, which preyed on nests only during the day, often removed eggs or nestlings individually and swallowed them away from the nest.

When rat snakes preyed on nests during the day they spent only a third as much time at the nest as they did during nocturnal predation. However, despite reduced time spent at nests, rat snakes always removed all nest contents during diurnal nest predation. Fourth, there is one published case of a rat snake being captured by a coyote during nest predation (Conkling et al. 2012). Also, because we (and other researchers: Graeter et al. 2013) have captured rat snakes using avian alarm calls to locate the snakes, we assume that animals that eat rat snakes could use the same strategy to find them. Testing this hypothesis adequately may require using nest cameras with a wider field of view and filming a more substantial number of nest predation events.

We found no evidence that nocturnal nest predation was more profitable for snakes. Although we observed snakes attempt to capture adult birds at the nest, none of those attempts was successful. Reidy et al.'s (2009) observed that rat snakes regularly capture adult golden-cheeked warblers during nocturnal nest predation. Thus, it seems likely there is something unique about the behaviour of golden-cheeked warblers or the placement of their nests that makes adults vulnerable to snake predation at night. Snakes probably capture more adult birds when the opportunity for escape is limited (e.g. cavities or nest boxes: Fendley 1980) or when nests are on solid branches that do not move under the weight of approaching snakes. Additionally, most of the bird species we studied were considerably larger and presumably more difficult to capture than golden-cheeked warblers.

Nocturnal nest predation also did not appear to make preying on nests more profitable by reducing the likelihood of nestlings fledging prematurely, although it is possible that snakes are better able to capture prematurely fledged nestlings outside of the nest at night. Data from nest cameras did not allow us to assess this possibility. Based on the small number of nests observed with nestlings old enough to fledge prematurely, premature fledging occurred during both nocturnal and diurnal predation.

Our results have some broader implications for both birds and rat snakes. One objective in studying nest predation by snakes is to understand what options are available to birds for lowering their risk of nest predation (Weatherhead & Blouin-Demers 2004). Where nocturnal predation by rat snakes is a substantial risk, options for birds to reduce their risk is quite limited once a snake has detected a nest. It is not apparent how birds could reduce risks to their nests, although by building nests in ways that allow the birds to detect an approaching snake could at least reduce risks of

the parents. Predation by rat snakes in Missouri is diurnal, whereas in Texas and South Carolina, it is predominantly nocturnal (Stake et al. 2005). Perhaps species with a breeding range encompassing this continuum of snake behaviour adjust their nest substrate choices to avoid nocturnal capture by snakes. Because diurnal nest predation by rat snakes appears to be risky, perhaps mortality rates of rat snakes are higher in areas where snakes are primarily diurnal relative to areas where snakes are primarily nocturnal, although Sperry et al. (2010) found that rat snakes at lower latitudes (Texas) had higher active season mortality than snakes at higher latitudes (Ontario, CA).

The hypothesis that seems most compelling to explain the disconnect between rat snake activity and timing of nest predation is that rat snakes locate nests during the day using visual cues (Mullin & Cooper 1998) but wait until after dark to prey on the nests (e.g. the wait-until-dark hypothesis). The disconnect between activity and predation did not appear to be a consequence of some non-hunting-related activity (e.g. mate searching), because the disconnect was similar in every month of the snakes' active season. Consistent with wait-until-dark hypothesis, on three occasions, Stake et al. (2005) observed rat snakes near black-capped vireo nests during the day, with those nests subsequently being preyed on by rat snakes that night, suggesting the same snakes may have been involved. Additionally, we observed one instance of a rat snake approaching a nest during the day and retreating without removing the contents (white-eyed vireo nestlings (*Vireo griseus*)). Researchers in the field, drawn to the distress calls of the adults, captured the snake for radio implantation, so it is unknown whether the snake would have returned to the nest that night. Šalek & Zamecnik (2014) recently proposed that other predators may also delay nest predation until the parents are away from the nest to avoid nest defence, which, if true, suggests that delayed predation may be common. Unfortunately, designing a direct test of the wait-until-dark hypothesis seems likely to be difficult. More generally, however, experimental studies of foraging behaviour in rat snakes may be an effective way to assess the extent to which these snakes can trade off costs and benefits when making foraging decisions.

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