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Patterns of Habitat Use and Behaviors by Gray Ratsnakes (*Pantherophis obsoletus alleghaniensis*) Occupying an Abandoned Building

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Abstract.—**We used time-lapse cameras to monitor Gray Ratsnake (*Pantherophis obsoletus alleghaniensis*) activity at an abandoned building in central Mississippi, USA. Snake activity was high in spring and waned in summer before snakes abandoned the building in autumn. Snakes arrived and departed both on the ground and by climbing or descending trees adjacent to the building. Climbing predominated in spring, whereas ground activity was more frequent later in the year. In early spring, snakes made frequent or daily ascents into the canopy but usually returned to the building each evening. During rainstorms snakes often partially emerged from within the walls to drink from the surfaces of the building. We compared the phenology of observed climbing behavior to the nesting phenology of birds in the region. Climbing behavior adjacent to the structure decreased earlier than predicted, during the time when bird eggs and nestlings should have been abundant. We attributed the observed decline in arboreal activity at the building to dispersal as the snakes switched from post-dormancy basking to foraging widely. We observed a correlation of moon phase to nocturnal movements that has not been reported in other studies. Ecdysis occurred throughout the active season but was most common in September even though total activity was relatively low then. We documented interactions between snakes that warrant further study.**

Key Words.—camera traps; climbing behavior; drinking; ecdysis; habitat use; moon phase; time-lapse photography; seasonal activity

***Resumen*.—Usamos cámaras de lapso de tiempo para documentar la actividad de la Culebra Ratonera Gris (*Pantherophis obsoletus alleghaniensis*) en un edificio abandonado en Mississippi central, USA. Las culebras mostraron actividades altas en la primavera, pero la actividad disminuyó en el verano antes de que las culebras abandonaron el edificio en el otoño. Las culebras entraron y salieron del edificio reptando por el suelo, y trepando arboles aledaños. El trepar predominó en la primavera, mientras que el uso del suelo fue más frecuente más tarde en el año. Temprano en la primavera las culebras hicieron frecuentes o diarios ascensos al dosel de los** árboles, **pero en general regresaron al edificio cada atardecer. Durante tormentas de lluvia, las culebras con frecuencia emergieron de dentro de las paredes para beber de las superficies del edificio. Examinamos la relación entre la frecuencia de trepado y la actividad de anidación de aves. Encontramos que el comportamiento de trepado en las cercanías del edificio decreció antes de lo predicho, durante un tiempo en el que huevos y polluelos debieron haber sido abundantes. Atribuimos el decremento en actividad arborícola en la estructura a la dispersión, debido a que las culebras cambiaron de actividad de tomar el sol después de salir de inactividad a forrajear más ampliamente. Observamos influencia de fases de la luna en las actividades nocturnas de las culebras que no ha sido reportado en otros estudios. La ecdisis ocurrió durante la temporada activa, pero fue más común en septiembre, aunque la actividad total era relativamente baja en ese momento. Documentamos entre culebras y está observación justifica estudios posteriores.**

Palabras Clave.—actividad estacional; bebiendo; comportamiento de trepado; ecdisis; fase lunar; fotografía de lapso de tiempo; trampas cámaras; uso del hábitat

Introduction

Cryptic organisms, such as snakes, can have behavior patterns that are difficult to quantify because of the challenges of species detection (Durso et al. 2011) and repeatedly observing individuals without disrupting their behavior (Stickel et al. 1980). For ratsnakes of the *Pantherophis obsoletus* species complex, the study methods that have been most productive at revealing their natural history are long-term mark-recapture (Fitch 1963; Stickel et al. 1980; Ferguson et al. 2020), radiotelemetry (Durner and Gates 1993;

Sperry et al. 2013), and the use of remote cameras (e.g., Thompson et al.1999; Clark 2006; DeGregorio et al. 2015). Such techniques reveal habitat preferences, activity timing, diet, predatory behavior, growth, degree of arboreality, and some reproductive patterns. Geographic comparisons have shown effects of latitude on the timing of spring onset of activity and the lengths of active season and dormancy.

One aspect of ratsnake habitat use that remains little studied is their tendency to occupy human-built structures (Durner and Gates 1993; George et al. 2022). Ratsnakes frequent structures, particularly in agricultural areas, where the snakes may be attracted by abundant rodents or the presence of poultry (Ditmars 1922; Bartlett and Bartlett 2005). In addition to food, structures can provide necessary resources such as refuge from predators, thermoregulatory opportunities, and contact with conspecifics for courtship and mating. The extent to which human-built structures meet snake needs has not been systematically compared with snake use of unaltered habitats.

Here we report a study of seasonal changes in activity and use of habitat by Gray Ratsnakes (*Pantherophis obsoletus alleghaniensis*). Our observations were possible because of aggregation of adult ratsnakes at an abandoned building (Fig. 1) that apparently created appropriate microhabitat (Zappalorti and Reinert 1994). Snakes used the structure, which we call The Snake Shed (TSS hereafter), through their active season.

Time-lapse photography using trail cameras of TSS and adjacent trees enabled us to quantify climbing behavior. Reasons for ratsnakes to ascend to the tree canopy could include foraging, thermoregulation, seeking mates, safety during skin shedding, and use of tree cavities for shelter from predators, oviposition (Pierce et al. 2008), or hydration (DeGregorio et al. 2021). Our goal was to quantify the use of TSS and trees for comparison to established knowledge of ratsnake habitat use and the ecology of snakes in general. A detailed knowledge of snake habitat use and behavior has potential conservation applications. For example, ratsnakes are predators of endangered birds such as Black-capped Vireos (*Vireo atricapilla*; Sperry et al. 2008) and Red-cockaded Woodpeckers (*Dryobates borealis*; RCW; Jackson 1974). Predation rates on bird nests are known to be influenced by season, temperature, and humidity (George et al. 2015), so risks to endangered birds can vary over time. Our study site lacked RCWs but was within 100 km of RCW breeding habitat, so changing behaviors and activity patterns at our site could provide useful comparisons to locations where ratsnakes prey on RCWs.

Figure 1. (Left) The Snake Shed (TSS) at our study site in Mississippi, USA, was 2.8 m long × 2.8 m wide, with a height of 2.5 m (yellow scale bar = 1 m at the northwest corner, but scale varies in this perspective). It was constructed of structural clay tile (hollow blocks), with a concrete veneer on both exterior and interior surfaces of the walls. The roof and foundation were concrete slabs. (Right) TSS doorway where exposed voids in the ceramic blocks allowed snakes access to wall interiors. Some voids in the blocks were partially occluded by mortar, but if not blocked they were 4.5 cm tall × 10 cm wide and extend to the corners of the structure. Four Gray Ratsnakes (*Pantherophis obsoletus alleghaniensis*) are visible in this view, and their activities can be interpreted from a sequence of photographs. Snake 1 is partially visible moving from the roof up the diagonal cedar trunk, beginning to ascend to the canopy. The entire body of snake 2 is visible as it descends from the canopy on the cedar trunk. Snake 3 occupies a void in the wall; its head is just visible protruding into the doorway. Snake 4 is entering a low void from the diagonal cedar tree. At the time this photograph was taken, two additional snakes were visible on the Window camera. (Photographed by Frank R. Hensley).

Table 1. Time-lapse camera monitoring summary for Gray Ratsnakes (*Pantherophis obsoletus alleghaniensis*) in central Mississippi, USA. An asterisk (*) indicates that the number of snakes were photographed simultaneously. In 2019, the earliest activity may have been missed due to camera malfunction. In 2020, 11 is the number of snakes estimated by tracking arrivals, departures, and movements between voids.

Year	Number of Cameras	Interval of Photographs	Monitoring dates	Number of Photographs	Date of First snake	Date of Last snake	Number of Snakes
2017	2	60 s	November-December	80,000	–	18 November	–
2018	2	60 s	1 February to 29 December	720,000	19 February	26 November	3*
2019	5	60 s	13 February to 30 December	1,810,000	23 February	11 November	6*
2020	5	40 s	4 January to 12 December	3,260,000	18 February	3 December	3* 11

We examined the relationship between ratsnake activity and abiotic factors, including testing the hypothesis that activity at TSS was affected by moon phase, because previous studies have varied in their conclusions about nocturnal snake behaviors and moon phases (Clarke et al. 1996; Spence-Bailey et a. 2010; Lillywhite and Brischoux 2012). Because biotic factors can also be important, we examined the relationship between climbing phenology and bird activity. Although ratsnakes may eat more mammals than birds, even during bird nesting season (Weatherhead et al. 2003), bird nests might still have an important influence on when snakes climb trees. We thus predicted that climbing frequency would remain high throughout the egg laying and nestling season and potentially decline only after most nests had fledged.

Materials and Methods

Study species.—Our subject snakes are members of the *Pantherophis obsoletus* species complex, the taxonomy of which has been controversial. Formerly the epithet *spiloides* was applied to Mississippi ratsnakes in the complex, but consensus now holds this was incorrect (Burbrink et al. 2021; Hillis and Wüster 2021) and that *alleghaniensis* is the correct name in Mississippi. Hillis (2022) argues that the case for splitting *P. obsoletus* into separate species is not well established, so we refer to our study organisms with the trinomial *P. obsoletus alleghaniensis*. For comparison to other studies, we limit our use of the term ratsnake to taxa within the *P. obsoletus* complex, including various current and historical epithets (*alleghaniensis*, *lindheimeri*, *obsoletus, quadrivittatus,* or *spiloides*).

Study site.—We conducted this research on land that lies within the historic boundaries of the Chahta Yakni (Choctaw), Natchez, and O-ga-xpa Ma-zho^{n} (O-ga-xpa) Nations of North America. The study site is a 125-hectare property in Jackson, Hinds County, Mississippi, USA, which functioned during 1942–1946 as a prisoner of war camp, Camp Clinton (Allard 1994), and subsequently as the location of the Waterways Experiment Station of the U.S. Army Corps of Engineers including the Mississippi River Basin Model. Historical aerial photographs show sparse trees, but since 1971, succession has largely reclaimed the property with a mix of second-growth hardwoods and pines, including more than 50 tree species. Among the most abundant trees are Loblolly Pine (*Pinus taeda*), Sweetgum (*Liquidambar styraciflua*), Eastern Red Cedar (*Juniperus virginiana*), Winged Elm (*Ulmus alata*), Cherrybark Oak (*Quercus pagoda*), and Green Ash (*Fraxinus pennsylvanica*). Much of the original infrastructure of both the camp and the river model is gone, but concrete ruins persist. We focused our snake observations at the site on TSS, a disused 7.85 m^2 masonry structure with voids in the walls that are accessible to snakes in the doorway and around the single window (Fig. 1). Trees within 1 m of TSS allow ratsnakes access to the roof and serve as routes to and from the forest canopy.

Monitoring.—We monitored snake activity using StealthCam™ (GSM Outdoors, Irving, Texas, USA) model STG-G42NG and STG-G45NG cameras set to take photographs at 1-min intervals (2017–2019) or 40-s intervals (2020; Table 1). Cameras operated 24 h/d, and automatically switched to infrared mode in dim light. Initially we chose a 1-min interval to balance the workload of photograph review against the probability of failing to detect behaviors of brief duration. We initially detected snake use of the building by discovering three decaying shed skins at the building in October 2017. We began our study with the assumption that TSS served as a communal site of winter dormancy. In 2018, to quantify variation in spring emergence from TSS (Carpenter 1953; Fitch 1963; Blouin-Demers et al. 2000), we positioned two cameras near the building (Dorcas and Willson 2009; DeGregorio et al. 2016). Our initial assumption that in spring snakes would emerge from dormancy within the walls proved incorrect. Instead, snakes did not occupy the structure during winter but used it during the active season. Also, we learned that we needed more than two cameras to accurately document arrivals and departures. In addition to activity at the doorway and window, snakes frequently ascended and descended two cedar trees adjacent to TSS that were not in view of the cameras in 2018. Therefore, we considered 2018 observations to be preliminary and on 13 February 2019, began using five cameras, positioning them so that the door frame and both frequently climbed trees were each visible by at least two cameras. In 2020 we reduced the photographic interval to 40 s to increase detection of brief behaviors. This interval was the shortest possible with the data storage capacity of the cameras.

We collected photographs from cameras weekly. We reviewed all photographs from two primary cameras and then used the other three cameras selectively to help complete documentation of snake activity sequences. We reviewed photographs using IrfanView64 (https://www.irfanview.net/) at approximately seven frames per second, often with two observers. For each observation we recorded temperature, date, and time as stamped on the photograph by the camera. We classified snake activities into five major categories for analysis: (1) ascent to the canopy; (2) descent from the canopy; (3) departure on the ground; (4) arrival on the ground; and (5) activities in and on the walls (which we subcategorized as basking, moving between voids, shedding, drinking, and touching conspecifics).

In December 2019, we deployed two Govee H5075 temperature and humidity loggers (Govee Moments Ltd., Hong Kong, China) at TSS. We set one logger in a shady outdoor location 10 m from TSS under a rain hood. We placed the second one inside one of the voids in a TSS wall, away from direct sunlight. These loggers allowed for monitoring of overall seasonal temperature and humidity patterns and for comparison of conditions inside the voids in the TSS walls to ambient conditions outside of TSS.

Estimation of snake numbers.—During winters (January 2019 and January 2020) we used a fiberoptic camera to thoroughly inspect the voids in the walls to census overwintering snakes. During the active season of 2020, we estimated the number of snakes present by keeping track of snake arrivals and departures and by tracking the positions of individual snakes moving among voids in the walls. Even with time-lapse intervals of just 40 s, rapid arrivals or departures could occasionally be missed. We attempted to correct missed arrivals by subsequent observations of snake activity, confirming the presence of a snake. Missed departures, however, imply that a snake remained in the walls unobserved, causing overestimates of snake numbers. By re-setting our count to zero each week, we corrected for any bias caused by missed departures.

Behavior patterns.—We tested for a relationship between moon phase and nocturnal activity at TSS. For this test we categorized observations by location (ground, wall, or canopy). We used a unit circle to represent the lunar cycle, and for each observation we used days since the most recent full moon to calculate an angle (full moon = 0°). We calculated circular means for each category of behavior. By using angle from the most recent full moon, cosine of the angle becomes a measure of expected lunar brightness and sine indicates whether moon phase is waxing or waning. Landler et al. (2021) found Multivariate Analysis of Variance (MANOVA) to be the most powerful detector of concentration differences in von Mises (circular random) distributions for data sets with small sample sizes. Our data failed to meet the assumptions of MANOVA, however, so we employed two nonparametric Kruskal-Wallis tests on brightness and waxing-waning with Bonferroni corrections of $\alpha = 0.025$. We used JASP version 0.17.2.1 software for statistical tests (https://jasp-stats.org/).

We recorded observations of snakes shedding their skins in photographs, and collected any shed skins encountered at weekly visits to TSS from October 2017 through December 2022. We plotted monthly counts of shed skins to detect any seasonality of ecdysis. We compared ratsnake climbing behavior to regional avian nesting phenology to examine whether ratsnake climbing frequency might be associated with foraging for eggs and nestlings. For this comparison we obtained bird nesting data ($n = 950$ records for 62 species of tree, shrub, and nest box nesters) for 2009–2019 for Louisiana, Mississippi, and Alabama, USA, from the NestWatch program at the Laboratory of Ornithology at Cornell University. We then graphed together avian nesting phenology (oviposition, hatching, and fledging) and ratsnake climbing frequency for visual comparison.

Results

Detection and estimates of snake numbers.—We detected most snake arrivals and departures on multiple cameras, and typically an arrival or departure was visible in two or more sequential photographs from each camera. Our ability to detect snakes in photographs varied with changing light in the environment; neither visible nor infrared photography was consistently better. Detecting a snake in a single photograph can be challenging but reviewing photographs in rapid succession facilitates detection of the movement of snakes between subsequent exposures. Multiple camera angles of the same scene also improved snake detection.

Table 2. Summary of activities documented for Gray Ratsnakes (*Pantherophis obsoletus alleghaniensis*) in central Mississippi, USA. An asterisk (*) indicates that two snakes were in continuous contact for 5 d prior to shedding. In May 2020, two snakes were in contact with each other intermittently on 3 d prior to shedding.

	Climbing (ascents)		Drinking		
Year	Date range	Temperature range	Date range	Temperature range	Shed skins collected (n)
2019	n = 93	n = 93	n = 8	n = 8	April (2) June (2)
	23 February- 22 September	16° C–32° C	1 March-26 April	6° C–20° C	August (3) September (4)*
	Median: 30 March	X̄ = 25.0° C	Median: 30 March	X̄ = 12.6° C	
2020	n = 63	n = 63	n = 14	n = 14	March (1) April (1)
	1 March- 18 October	18° C–36° C	4 March- 27 November	8° C–31° C	May (2) July (2) August (1)
	Median: 25 March	X̄ = 26.8° C	Median: 11 May	X̄ = 19.9° C	September (5)

The window on the north wall of TSS was the location of much activity. Gray Ratsnakes (*P. o. alleghaniensis*) always accessed this window from the roof (n = 149 arrivals or departures). We never observed snakes descending from the window to the ground (103 cm below), nor ascending from the ground to the window. We observed a maximum of six snakes using the window on a single day, but the maximum in a single photograph was four, on 24 March 2019. The highest number of snakes detected in a single photograph of the front door area was four on 23 March 2019 (Fig. 1). Within one minute of these two photographs, other snakes were visible from other camera angles, yielding minimum counts of five and six snakes, respectively. Weekly counts of arrivals and departures and tracking of individual movements among voids resulted in a high estimate of 11 snakes during the week of 11 March 2020 (Table 1).

Seasonality of snake numbers and climbing activity.— We detected the onset of snake activity at TSS in February each year, with the last activity in November or December (Tables 1 and 2). Our fiberoptic inspections of the voids during January of 2019 and 2020 revealed no evidence of snakes overwintering in TSS. Weekly tracking of individual movements in 2020 confirmed the departure of all snakes from TSS in November and early December.

Snakes arrived at TSS from unknown winter dormancy locations in late February and early March each year and then began frequent diurnal arboreal activity (Figs. 2 and 3). We observed frequent ascents to and descents from the tree canopy in both March and April, but frequency declined steadily beginning in late March. Terrestrial activity was also highest in March

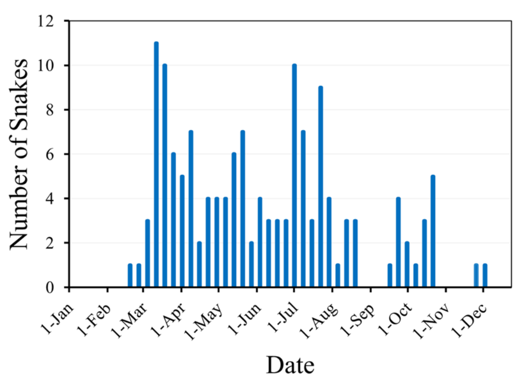

Figure 2. Gray Ratsnake (*Pantherophis obsoletus alleghaniensis*) numbers in The Snake Shed during 2020, estimated by monitoring movements of individual snakes. We detected no snake activity from 1 January to 18 February. The first six snakes observed all arrived on the ground between 18 February and 11 March. The next four snakes to arrive, 11–13 March, arrived by descending from the canopy.

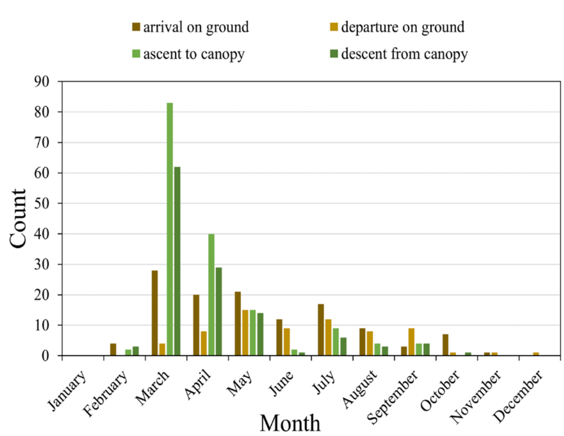

Figure 3. Monthly arrivals and departures of Gray Ratsnakes (*Pantherophis obsoletus alleghaniensis*) at The Snake Shed during 2019–2020. In February and early March snakes arrived mostly on the ground, but post-dormancy basking in the tree canopy dominated in later March and April. From May through the end of the active season most activity was on the ground, but some climbing occurred through September.

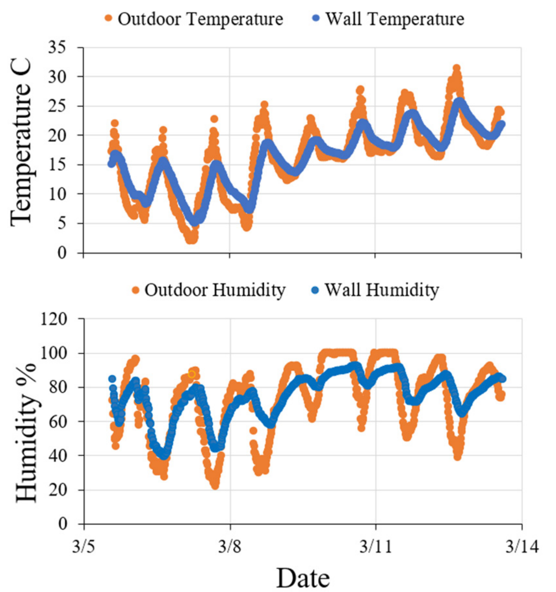

Figure 4. Temperature and humidity in voids in The Snake Shed walls compared to outdoors during March 2020, the month during which ratsnake activity occurred over the widest range of temperatures.

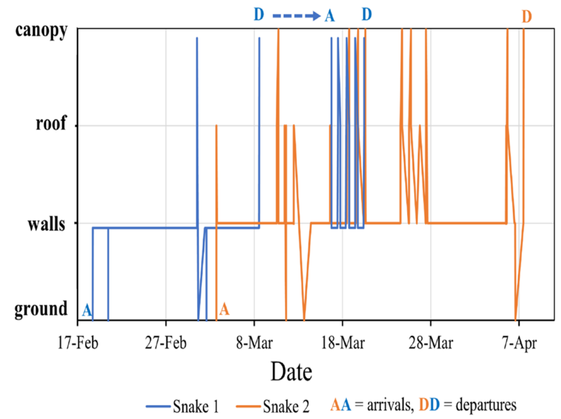

Figure 5. Daily activity in spring 2020 of two Gray Ratsnakes (*Pantherophis obsoletus alleghaniensis*) that could be individually identified by size and color pattern, showing frequent brief ascents to the canopy. Plots are offset slightly for clarity. Snake 1 (blue) arrived on the ground on 18 February (Feb), basked aloft on 1 March (Mar), and departed to the canopy 9 March. After a 7-d absence (dashed arrow) Snake 1 returned via the canopy on 16 March, and then basked aloft each afternoon until it departed via the canopy on 20 March. Snake 2 (orange) arrived on the ground on 3 March and departed to the canopy 8 April (Apr), basking on the roof five times, and making nine afternoon excursions to the canopy. During the time interval shown, we estimate eight other snakes arrived and made excursions to the canopy, but individual identification was not possible from our photographs.

and declined as the season progressed, but the decline in arboreal activity was faster, so that by May terrestrial activity dominated and remained most common for the rest of the active season (Fig. 3). With a single exception, snake activity at TSS in October and November was not arboreal (Figs. 2 and 3).

Temperatures and humidity measured within the walls of TSS were less variable than ambient conditions (Fig. 4). On warmer, sunnier days snakes often ascended to the tree canopy about midday and stayed aloft for 5–6 h, descending before sunset. We cannot recognize most individuals from photographs, but in 2019 and 2020 two individual snakes that could be identified based on size, markings, and habits exemplified this general pattern (Fig. 5), ascending then returning to the same two voids within the wall of TSS each afternoon. For these two snakes, between 1 March and 3 May 2020, we recorded 15 bouts of ascent/descent with an average departure time of 1154 (range from 1007–1349) and average descent time of 1642 (range from 1349–1821). The average duration of these canopy visits was 4 h 48 m (range from 35 min to 7 h 42 m). Although Fig. 5 displays the activity of only those two snakes, 2–4 other snakes were active over that same interval, frequently making afternoon ascents to the canopy, and possibly returning to the same voids in the walls. Snakes did not necessarily ascend every day, nor did they all ascend on the same days. Canopy activity in March was correlated with temperature, with climbing generally initiated at temperatures above the monthly average of daily high temperature (Fig. 6). General snake activity was also more frequent at higher temperatures (Fig. 6), particularly in spring. During our weekly visits to TSS in spring we could often observe one or more snakes basking on the branches of the two cedar trees.

Approximately 96% of all our observations occurred during daylight hours. The infrequent nocturnal activity appeared evenly distributed across May-September (Fig. 6). Seventy-six of 100 observations of nocturnal activity occurred during the brighter half of the lunar cycle (Fig. 7). The brightness effect was significant (H = 16.55, df = 2, P < 0.001, η^2 = 0.167). Arboreal movements were significantly more likely to occur during the darker half of the moon phase cycle (Dunn's *post hoc* test, P = 0.002; Fig. 7) compared to nocturnal activity on TSS walls and on the ground, which did not differ from each other (Dunn's *post hoc* test, P = 0.218). Whether the moon was waxing or waning did not show a significant relationship to nocturnal activity (H = 4.22, df = 2, P = 0.121, η^2 = 0.043).

Behaviors.—At TSS we observed a variety of behaviors, intraspecific interactions, and encounters with other vertebrate species that are potential predators, prey, or competitors with ratsnakes. Unfortunately, photographic intervals of 40–60 s limited the amount of behavioral detail recorded. Our most frequent observation was of snakes spending up

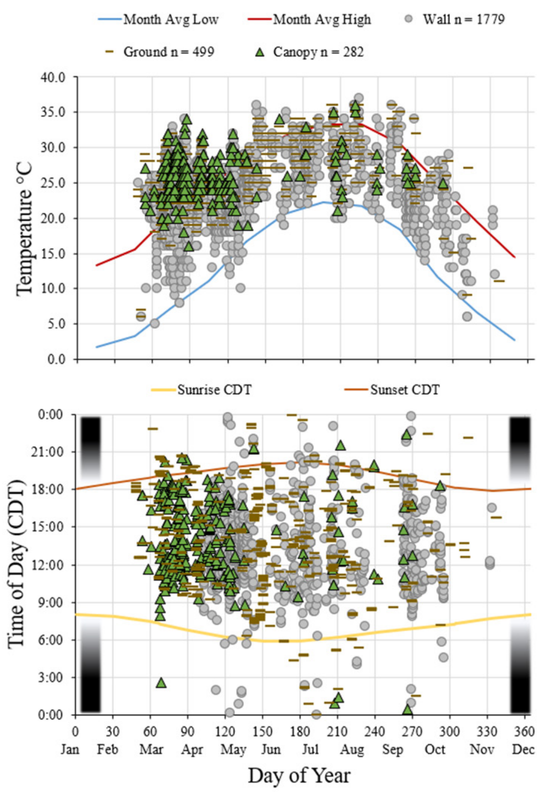

Figure 6. (Top) Seasonal pattern during 2019–2020 of Gray Ratsnake (*Pantherophis obsoletus alleghaniensis*) activity (n = 2,560 observations). (Top) With respect to temperature, canopy activity occurs mostly in March and April, mostly above the monthly average of daily high temperatures. Snake activity temperatures are from camera infrared detection and are therefore surface temperatures. The monthly average of daily high and low temperatures are air temperatures in shade. (Bottom) With respect to time of day, most activity occurred between sunrise and sunset. Nocturnal activity was evenly distributed across the months of May-September and occurred at all hours of the dark phase.

to several continuous hours with their heads protruding from voids in the walls but keeping most of their body inside the structure.

Our time-lapse photographs documented 122 descents on trees in 2019–2020, always headfirst and generally slowly enough to be recorded by multiple photographs. Still photographs cannot distinguish between a fall to the ground directly from the canopy and an arrival over ground after descending an off-camera tree. We have no direct evidence that snakes ever fell from trees, but we documented abundant evidence of slow, headfirst descents.

We occasionally saw evidence of snakes sharing a void in the walls, but levels of snake activity and their ability to move between voids undetected during intervals between photographs meant it was impossible to quantify how frequently this occurred. On a few occasions we saw one snake enter an occupied void, and almost immediately one snake would exit. We could not determine if the initial resident was displaced or if the intruding snake exited. We also noted that snakes rarely made physical contact with each other, and when one snake would make a major move (such as climbing to the roof of the building), other snakes would usually withdraw from the moving snake. Limited camera angles and photograph intervals meant that quantifying the frequency of contact or lack thereof was not possible.

We rarely observed prolonged physical contact between individuals. On 8 September 2019, a snake attempted to enter the space at the bottom of the TSS window, which was already occupied. Over the next 29 h it remained partially visible but gradually forced its way deeper into the space, where it stayed for 5 d, possibly blocking the exit of the other snake. Both snakes exited on 13 September, just 13 min apart, shedding their skins as they ascended to the roof of the building (Table 2). On 11, 12, and 13 May 2020, two snakes made physical contact while basking on the bars of the window. On 11 and 13 May, the larger snake initiated the contact by bringing its head beneath the head of the smaller snake. On 12 May, the smaller snake-initiated contact by moving its head atop the head of the larger snake. Contact lasted 19, 13, and 78 min, respectively, on the three days. After contact ended the snakes retreated into separate voids in the wall. The smaller snake in these observed interactions shed its skin on 17 May 2020, and the larger snake shed its skin on 21 May. In both cases shedding was simultaneous with departure from TSS via the roof

In 2019 and 2020, we collected 23 shed skins at TSS (Table 2). We observed ecdysis on camera 11 times, and we saw no pattern in times of day when shedding occurred. On six of those occasions, we confirmed that snakes immediately departed TSS, but on two occasions snakes completed ecdysis and then returned to a void in the walls until at least the next day. In 2017-2022 we collected 41 shed skins, providing a larger sample for visualizing seasonal patterns (Fig. 8). Ecdysis is apparently common in spring but infrequent in July, before peaking in September.

On 29 occasions during rainfall, we observed snakes partially emerging from within the walls of TSS and drinking from exterior surfaces of the building. At the window, snakes primarily drank by positioning their heads beneath the horizontal iron bars to collect droplets. At the front door, snakes typically extended their bodies downward, then turned their heads upward and drank water flowing down the walls of the building.

We observed interactions with other species but did not quantify details for the most common species. Photographs showed potential prey species almost daily. These included many Gray Squirrels (*Sciurus carolinensis*) and Carolina Wrens (*Thryothorus

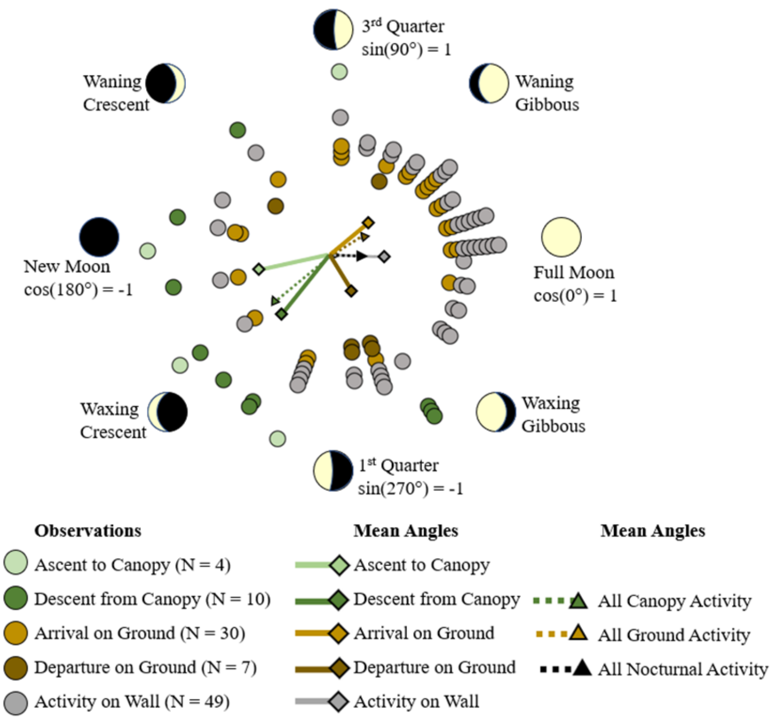

Figure 7. Nocturnal activity of Gray Ratsnakes (*Pantherophis obsoletus alleghaniensis*) with respect to moon phase. Small circles are individual observations (n = 100) color coded by location and direction of movement. Shades of brown denote ground-level activity, shades of green denote canopy, and shades of gray indicate activity on The Snake Shed walls. Vectors in the center use the same color scheme to show the circular mean angle of moon phase for each category of movement. Circular mean vector lengths indicate the dispersion of the moon phase angles for each category. Most nocturnal activity was in the brighter half of the lunar cycle (76 of 100 observations). In contrast 10 of 14 nocturnal movements to or from the tree canopy occurred in the darker half of the moon phase.

ludovicianus) in daytime photographs and small- or medium-sized rodents such as deer mice (*Peromyscus* sp.) and Eastern Woodrats (*Neotoma floridana*) at night. On occasion photographs showed snakes face to face with Gray Squirrels or Eastern Chipmunks (*Tamias striatus*), but we never observed predation by snakes.

We have photographed Coyotes (*Canis latrans*), Bobcats (*Lynx rufus*), feral Domestic Dogs (*Canis lupus familiaris*), Raccoons (*Procyon lotor*), Barred Owls (*Strix varia*), and Red-shouldered Hawks (*Buteo lineatus*) at TSS, and they are potential predators of ratsnakes. We found one possible predation event

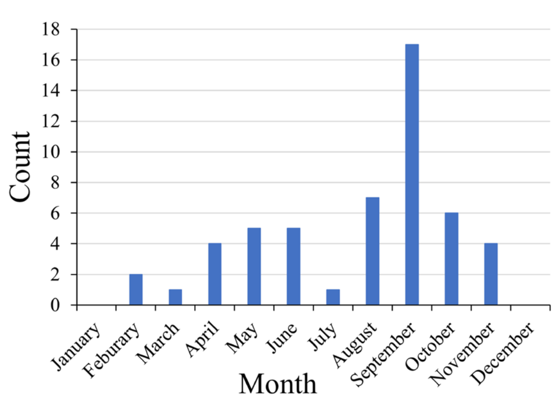

Figure 8. The seasonal pattern of ecdysis of 41 Gray Ratsnakes (*Pantherophis obsoletus alleghaniensis*) during 2017–2022 at The Snake Shed showing shedding in spring, a decline in frequency in July, and a peak in September.

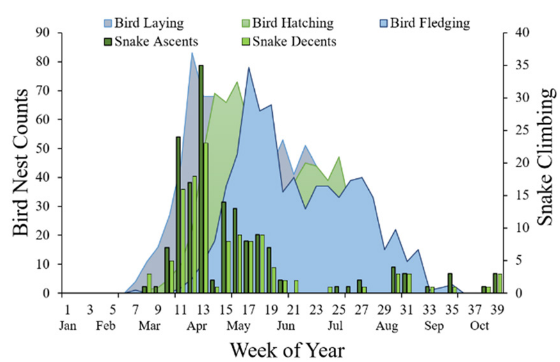

Figure 9. Climbing behavior of Gray Ratsnakes (*Pantherophis obsoletus alleghaniensis*) observed in 2019–2020 compared to regional data on bird nesting behaviors for 2009–2019. The seasonal onset of climbing behavior cooccurs with regional bird egg laying but observed climbing behavior declined earlier than we expected if climbing is associated with foraging on eggs and hatchlings.

of a snake. In one photographic sequence, a ratsnake emerged from the front door of TSS, and in the next photograph no snake was visible, but a Red-tailed Hawk (*Buteo jamaicensis*) was about 1 m from where the snake had been and had its wings spread, possibly mantling over its prey.

Our cameras sometimes photographed small snakes, but limited camera resolution prevented identification of species. Litter-dwelling species known from the immediate vicinity (pers. observ.) include Ringnecked Snakes (*Diadophis punctatus*), Eastern Wormsnakes (*Carphophis amoenus*), Midland Brownsnakes (*Storeria dekayi*) and Smooth Earthsnakes (*Virginia valeriae*). On rare occasions larger snakes appeared in photographs; these included two Black Racers (*Coluber constrictor*), one Speckled Kingsnake (*Lampropeltis holbrooki*), and one Southern Copperhead (*Agkistrodon contortrix*). On two occasions Cornsnakes (*Pantherophis guttatus*) appeared on the ground at TSS but disappeared after just two photographs.

We found that climbing behavior of ratsnakes varied over time. In comparison to the NestWatch data on avian nesting, the frequency of climbing behavior at TSS peaked at the 13th week of the year, one week after the expected peak of avian egg laying in the region (Fig. 9). Climbing frequency at TSS, however, declined steeply while bird eggs and nestlings were likely still abundant (and might have remained so for several more weeks).

Discussion

Time-lapse photography can help answer questions about when, and perhaps why, ratsnakes use habitats as they do. Activities like climbing, basking, drinking, and foraging are likely correlated with physical habitat such as temperature, moisture, or moon phase. Such activities are probably also affected by biotic factors such as prey presence, predators, or intraspecific social interactions.

***Annual patterns*.**—Seasonal activity patterns of ratsnakes are well documented (Stickel et al. 1980; Gibbons and Semlitsch 1987; Sperry and Weatherhead 2009; Sperry et al. 2010; George et al. 2015). In cooler climates ratsnakes overwinter in subterranean retreats (Fitch 1963), but possibly also within tree cavities (Stickel et al. 1980). Dormancy sites are often disjunct from active-season home ranges (Fitch 1963). After spring emergence, a period of daily basking is typical (Fitch 1963; Stickel et al. 1980; Graham 2018) and might be a response to skin or respiratory infections (Fitch 1963) or might promote egg development (Stickel et al. 1980). Mating occurs in late spring, with oviposition in summer and hatching in late summer or early autumn (Fitch 1963; DeGregorio et al. 2016). In a comparison of *P. obsoletus*-complex snakes in six study areas from Texas, USA, to Ontario, Canada, Ferguson et al. (2020) found a correlation between length of the active season and latitude, with Texas snakes active for 9 mo and Ontario snakes for 5 mo. At TSS snakes were absent from the structure, which is entirely above ground, during winter. They were subsequently active for about 8.5 mo.

When not dormant, ratsnakes have home ranges of about 9.7 ha (Fitch 1963) to 25 ha (Ward et al. 2013) but occasionally make long forays away from their core areas (Stickel et al. 1980; Ward et al. 2013). Ward et al. (2013) suggested that these forays might represent cases of central-place foraging (Orians and Pearson 1979), which is a pattern consistent with infrequent large meals followed by prolonged digestion in low-risk sites. Stickel et al. (1980) described focal hollow trees that are shared by multiple adult snakes, many of which return year after year. Ratsnakes spend substantial time in trees, apparently ascending to forage for arboreal prey after observing visual cues such as bird activity (Mullin and Cooper 1998, 2000). Ratsnake activity is primarily diurnal, but much predation on bird eggs and nestlings can be after dark (Stake et al. 2005; DeGregorio et al. 2015). This is consistent with our observation at TSS that most nocturnal arboreal activity occurred during the darker phases of the moon. The seasonal peak of avian nesting generally overlaps with peak *P. obsoletus*-complex activity (Carfagno and Weatherhead 2008; Sperry et al. 2008; Weatherhead et al. 2010; Sperry et al. 2012), as did peak exploitation of arboreal prey in Kansas, USA, (Fitch 1963) and in Ontario (Weatherhead et al. 2003). We interpret the seasonal decline in arboreal activity at TSS as indicating a transition from spring basking to summer foraging, consistent with well-established seasonal patterns (Fitch 1963; Pierce et al. 2008; George et al. 2022).

Another potential reason for ratsnakes to use TSS is for protection prior to ecdysis. For several days prior to shedding its skin, the eyes of a snake become cloudy, and snakes are often more reclusive during this phase (Greene 1997; Graham 2018), possibly because occluded vision limits their ability to forage or evade predators. Over 2 y of camera surveillance and 4 y of collecting shed skins at TSS, we found most shedding occurred in September each year. This frequency of ecdysis was out of proportion to overall snake activity, which is lower in September than in spring. Ecdysis, therefore, is perhaps the most important reason snakes use TSS in late summer and autumn.

***Estimates of snake numbers*.**—Whether directly counting snakes or using estimates based on tracking movements between wall voids, we documented a seasonal rise and fall in snake numbers. The observed decline of snake numbers from spring into summer that we saw agrees with the idea of spring aggregation at

TSS prior to wider dispersal in summer for foraging, with occasional returns between foraging bouts (Orians and Person 1979; Ward et al. 2013; George et al. 2022). The fact that we could recognize two individuals and that they returned several times over both years supports this interpretation.

Physical environment.—Changes in activity levels of ectotherms are often seasonal because of direct effects of temperature and moisture or indirect effects such as seasonality of food availability or reproduction. For ratsnakes, complex interactions between temperature, humidity and season can affect activity levels including predation rates on bird nests (George et al. 2015). At TSS the thermal inertia of a concrete structure adjacent to basking sites probably allowed snakes to thermoregulate better than other nearby options (e.g., Huey et al. 1989). Temperatures and humidity measured within the walls of TSS were less variable than ambient conditions. Similarly, at the Dallas Zoo (Texas, USA) a honey-combed concrete wall provided a focal ratsnake habitat (Ferguson et al. 2020).

Additional insights about the physical environment at TSS can be gained by comparison to another abandoned masonry structure (designated Paint Storage on historic Corps of Engineers maps) located 27 m northeast of TSS. The Paint Shed (TPS) is built of hollow cinder blocks and its roof is entirely missing. There are many voids in the walls of TPS, and a tree touching the north wall affords access to the forest canopy. We checked TPS irregularly in 2018 and 2019 and weekly during 2020. We never saw any snakes at TPS, nor found any shed skins there. Yet on multiple occasions snakes departed TSS on the ground headed generally toward TPS. We are not sure why one structure was a focal area (Stickel et al. 1980) of ratsnake activity and the other apparently was avoided entirely. Like TSS, TPS could provide a thermally insulated, predator-resistant retreat but unlike TSS, TPS has vertical voids, and because TPS has no roof, rainfall can freely enter the voids. The fact that TSS provides a dry retreat, but TPS does not could explain the lack of snake use of TPS, particularly if spring basking and a dry environment help snakes overcome respiratory or skin infections acquired during dormancy at high humidity (Fitch 1963).

DeGregorio et al. (2021) demonstrated that ratsnakes experienced less temperature variation when using water-filled tree cavities and used such cavities more frequently in the hottest months studied. We saw snakes drinking any time that rain fell throughout the active season. Cliburn (1977) reported that Gray Ratsnakes were frequently encountered in wetlands, and he observed diurnal drinking behavior on three occasions. Drinking can impose costs such as increased risk of predation (Bonnet and Brischoux 2008). The Snake Shed provided an opportunity for snakes to drink while remaining partially concealed from predators and thermally buffered, and it may thus alleviate the need to seek water.

During a 2-y experiment, DeGregorio et al. (2021) documented 42 incidents where ratsnakes used naturally occurring water-filled cavities but only a single instance of a ratsnake using a newly provided artificial cavity. This suggests that detecting new cavities is uncommon. Their snakes using natural cavities as a water source and our snakes using TSS as a drinking site may share a common long history of snakes following the scent trails of other snakes (Lillywhite 2014) to detect such valuable but cryptic microhabitats.

Diel cycle and moon phase.—Other influential aspects of the physical environment include changes in sunlight and moonlight. Many snake species can be considered facultatively nocturnal (Gibbons and Semlitsch 1987; Abom et al. 2012; Sperry et al. 2013; DeGregorio et al. 2014). Although snake observations at TSS were primarily diurnal (96% of observations), studies elsewhere show frequent nocturnal activity in ratsnakes. Glorioso and Waddle (2017) found that for 50–75% of nocturnal encounters, ratsnakes were in trees. DeGregorio et al. (2015) found that radio-telemetered *P. obsoletus* were relatively inactive at night (23–36% activity) but usually preyed on bird nests after dark (80% of nest predations). A late summer shift to greater nocturnal activity was reported in Texas (Sperry et al. 2013; Ferguson et al. 2020) and Stake et al. (2005) reported regional differences in nocturnal vs. diurnal predation by ratsnakes on bird nests. A mismatch between activity level and timing of nest predation suggests that ratsnakes actively hunt for prey by visual cues during daylight but wait until dark to depredate nests, when foraging can be safer (DeGregorio et al. 2015). If nocturnal activities at TSS are associated with movement to or from more distant foraging areas rather than hunting near TSS, this could explain the very low level of nocturnal activity compared to other field studies.

Moon brightness significantly correlated with arboreal arrivals at and departures from TSS. This contrasts with the results of Sperry et al. (2013) who found no effect of moon phase on total nocturnal activity levels in ratsnakes in Texas nor Illinois, USA, although they did not subcategorize movements. Snake activity during brighter moon phases might be associated with visual prey detection, whereas activity during darker phases could provide protection from predators (Lillywhite and Brischoux 2012) or avoidance of mobbing by defensive birds (DeGregorio et al. 2015).

Climbing and foraging.—Lillywhite (2014) noted that descent behaviors of climbing snakes are poorly known and pondered the possibility that snakes sometimes fall voluntarily as a means of descent. We saw only controlled head-first descents, but the sudden appearance of a snake on the ground in a photograph could be due to a terrestrial arrival or a voluntary fall from above. Seasonal and diel patterns of climbing by ratsnakes vary considerably among studies. In Texas (Fitch 1963) and Ontario (Weatherhead et al. 2003), the highest frequency of arboreal prey capture co-occurred with the peak in avian nesting. In contrast, Pierce et al. (2008) found that arboreal activity of snakes peaked well after avian nesting. At TSS, climbing peaked very early in the avian nesting period, then declined rapidly just when bird eggs and chicks were probably abundant. The timing of this decline was not what we predicted based on the idea that climbing at TSS would be influenced by bird nesting phenology. Instead, climbing at TSS seems primarily about basking rather than foraging, and is consistent with the observation by Weatherhead et al. (2003) that mammals make up the majority of ratsnake diets, even during avian nesting season.

The habitat use of ratsnakes is also influenced by potential interactions with predators, prey, competitors, and conspecifics. Although we observed a variety of potential prey at TSS, we never observed predation attempts or feeding by snakes at TSS. Thus, we saw no evidence that the use of TSS was directly related to prey availability at TSS. Reduced summer tree climbing at TSS and reduced overall snake activity at TSS are consistent with a switch from basking at TSS in favor of more dispersed foraging, rather than effects of avian or mammalian prey abundance at TSS.

Social behavior.—Social interaction could also influence habitat use (Gardner et al. 2015). Historically snakes have been considered solitary organisms with social interactions limited mostly to courtship, mating, sharing of hibernacula (Noble and Clausen 1936), and in the case of some viviparous species, attendance to offspring (Greene 1997; Lillywhite 2014). Infrequently reported snake social behaviors might be rare, or just be rarely detected.

Snakes are known to sometimes share hibernacula, cover objects (Gregory 2004), basking locations (Noble and Clauson 1936; Gregory 1984), ecdysis sites (Stickel et al. 1980; Zappalorti and Reinert 1994; Loughran et al. 2015), or other physical resources. They might share without regard to the presence of conspecifics. For example, in cool climates ratsnakes are known to share hibernacula, but social behaviors such as courtship, mating, or communal nesting have not been documented at these winter dens. This suggests that aggregation at dens is driven by habitat requirements rather than social interactions. Ratsnakes are known to sometimes court and mate in trees (Stickel et al. 1980; George et al. 2022), and Stickel et al. (1980) speculated that these trees could also serve as communal hibernacula. Gardner et al. (2015) did not mention ratsnakes among species of squamates reported to demonstrate stable social aggregations characterized by stable membership or by the presence of juveniles in aggregations of adults. Yet Stickel et al. (1980) reported that some individual snakes used the same shared focal trees in multiple (though not necessarily consecutive) years, and thus were present in aggregations in multiple years. The degree of stability in aggregations of ratsnakes is, however, unknown. One possible indication of social organization in snakes is co-occurrence of individuals at the same times and locations, as demonstrated by Shine et al. (2005) using mark-recapture synchrony to detect social grouping in sea snakes. Being able to recognize all individual snakes at TSS would help us understand whether social organization might be occurring.

It is possible that ratsnakes are attracted to TSS in part because they are attracted to each other. Some snake species are substantially more social than previously thought, such as rattlesnakes (*Crotalus* spp.; Schuett et al. 2017) and Eastern Gartersnakes (*Thamnophis sirtalis*; Skinner and Miller 2020). Our only observations that imply reproductive activity at TSS were two cases of close following of one snake by another, and the 3 d of body contact described previously. Social and non-social attraction to habitats might interact. For example, DeSantis et al. (2020) found that male rattlesnakes invested less effort and energy searching for females when associated with earthen stock tanks, which were richer in prey than unaltered habitats. Similarly, ratsnakes could be attracted to TSS for non-social benefits, but then encounter potential mates. Lillywhite (2014) noted that courtship is sometimes associated with ecdysis, as cutaneous pheromones of freshly shed females are most attractive to males. The simplest inference is that interactions we observed were pre-courtship behaviors, but that courtship did not proceed, possibly because ecdysis had not yet occurred. The location of such interactions at TSS could have been due to the shared need for a safe site for ecdysis, but we might not detect the subsequent social interaction if courtship and mating occur outside of the fields of view of our cameras.

If aggregation at TSS occurred mostly because of the physical environment, we might expect that other snake species of comparable size and climbing ability would also be attracted to the structure. In fact, the co-occurrence of multiple species of snake under the same cover object is well known to herpetologists (Gregory 2004). On five occasions we observed brief visits to TSS by comparable species (two Black Racers, two Cornsnakes, and one Speckled Kingsnake) but they did not enter voids in the block walls, even though they are competent climbers and frequent predators of many of the same species eaten by ratsnakes. It is possible that these other species have different microhabitat preferences, or that the presence of a ratsnake aggregation deterred these three species from remaining, but such explanations would be difficult to test.

Future questions.—Many questions remain unanswered regarding seasonal habitat use by ratsnakes. The importance of spring basking for physiological recovery from winter dormancy and preparation for seasonal reproduction and foraging requires further study. Spring basking locations might generally be important locations for drinking to rehydrate after dormancy, or for dry conditions to aid in recovery from infections acquired during dormancy. In addition, the importance of spring basking locations for social interactions such as mate selection are unknown. The frequency and significance of pre-ecdysis interactions between males and females is an open question, and for each of these issues, comparisons of natural retreats versus human-built structures could clarify why snakes choose different microhabitats. Advanced tracking and recording technologies would provide continuous monitoring, identification of individuals, and more details about use of shared focal habitats vs. widely dispersed activity. A more detailed understanding of ratsnake behavior and habitat use could lead to better predictions about their impacts on other species.

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Literature Cited

Abom, R., K. Bell, L. Hodgson, and L. Schwarzkopf. 2012. Moving day and night: highly labile diel activity patterns in a tropical snake. Biotropica 44:554–559.

Allard, M.A. 1994. A history of the Clinton prisoner of war camp, 1942–1946. M.A. Thesis, Mississippi College, Clinton, Mississippi, USA. 144 p.

Bartlett, R.D., and P.P. Bartlett. 2005. Guide and Reference to The Snakes of Eastern and Central North America (North of Mexico). University Press of Florida, Gainesville, Florida, USA.

Blouin-Demers, G., K.A. Prior, and P.J. Weatherhead. 2000. Patterns of variation in spring emergence by Black Rat Snakes (*Elaphe obsoleta obsoleta*). Herpetologica 56:175–188.

Bonnet, X., and F. Brischoux. 2008. Thirsty sea snakes forsake refuge during rainfall. Austral Ecology 33:911–921.

Burbrink, F.T., R.A. Pyron, M. Gehara, A.D. McKelvy, and E.A. Myers. 2021. The corrected taxonomic history of the North American ratsnakes (*Pantherophis obsoletus* complex). Herpetological Review 52:537–547.

Carfagno, G.L., and P.J. Weatherhead. 2008. Energetics and space use: intraspecific and interspecific comparisons of movements and home ranges of two colubrid snakes. Journal of Animal Ecology 77:416–424.

Carpenter, C.C. 1953. A study of hibernacula and hibernating associations of snakes and amphibians in Michigan. Ecology 34:74–80.

Clark, R.W. 2006. Fixed videography to study predation behavior of an ambush foraging snake, *Crotalus horridus*. Copeia 2006:181–187.

Clarke, J.A., J.T. Chopko, and S.P. Mackessy. 1996. The effect of moonlight on activity patterns of adult and juvenile Prairie Rattlesnakes (*Crotalus viridis viridis*). Journal of Herpetology 30:192–197.

Cliburn, J.W. 1977. *Elaphe obsoleta spiloides* (Gray Rat Snake) in aquatic habitats. Journal of the Mississippi Academy of Sciences 22:89–90.

DeGregorio, B.A., J.H. Sperry, D.P. Valente, and P.J. Weatherhead. 2014. Facultative nocturnal behaviour in snakes: experimental examination of why and how with Ratsnakes (*Elaphe obsoleta*) and Racers (*Coluber constrictor*). Canadian Journal of Zoology 92:229–237.

DeGregorio, B.A., J.H. Sperry. M.P. Ward, and P.J. Weatherhead. 2015. Wait until dark? Daily activity patterns and nest predation by snakes. Ethology 121:1225–1234.

DeGregorio, B.A., J.H. Sperry, and P.J. Weatherhead. 2021. Factors influencing the use of water-filled tree cavities by Eastern Ratsnakes (*Pantherophis alleghaniensis*). Herpetological Conservation and Biology 16:173–182.

DeGregorio, B.A., P.J. Weatherhead, M.P. Ward, and J.H. Sperry. 2016. Do seasonal patterns of Rat Snake (*Pantherophis obsoletus*) and Black Racer (*Coluber constrictor*) activity predict avian nest predation? Ecology and Evolution 6:2034–2043.

DeSantis, D.L., V. Mata-Silva, J.D. Johnson, and A.E. Wagler. 2020. Integrative framework for long-term activity monitoring of small and secretive animals: validation with a cryptic pitviper. Frontiers in Ecology and Evolution 8:169–183.

Ditmars, R.L. 1922. Reptiles of The World: Tortoises and Turtles, Crocodilians, Lizards and Snakes of The Eastern and Western Hemispheres. Macmillan, New York, New York, USA.

Dorcas, M.E., and J.D. Willson. 2009. Innovative methods for studies of snake ecology and conservation. Pp. 5–37 *In* Snakes: Ecology and Conservation. Mullin, S.J., and R.A. Seigel, (Eds.). Cornell University Press, Ithaca, New York, USA.

Durner, G.M., and J.E. Gates. 1993. Spatial ecology of Black Rat Snakes on Remington Farms, Maryland. Journal of Wildlife Management 57:812–826.

Durso, A.M., J.D. Willson, and C.T. Winne. 2011. Needles in haystacks: estimating detection probability and occupancy of rare and cryptic snakes. Biological Conservation 144:1508–1515.

Ferguson, G.W., D.T. Roberts, R. Hartdegen, W.H. Gehrmann, L.A. Mitchell, and B. Lawrence. 2020. Seasonal activity and population fluctuations of a free-ranging population of the Rat Snake *Pantherophis obsoletus* inhabiting the Dallas Zoo, Texas. Southwestern Naturalist 64:173–179.

Fitch, H.S. 1963. Natural history of the Black Rat Snake (*Elaphe o. obsoleta*) in Kansas. Copeia 1963:649–658.

Gardner, M.G., S.K. Pearson, G.R. Johnston, and M.P. Schwarz. 2015. Group living in squamate reptiles: a review of evidence for stable aggregations. Biological Reviews 91:925–936.

George, A.D., F.R. Thompson, III, and J. Faaborg. 2015. Isolating weather effects from seasonal activity patterns of a temperate North American colubrid. Oecologia 178:1251–1259.

George, A.D., F.R. Thompson III, and J. Faaborg. 2022. Movements and habitat use by Western Ratsnakes (*Pantherophis obsoletus*) in a fragmented midwestern landscape. Herpetological Conservation and Biology 17:306–315.

Gibbons, J.W., and R.D. Semlitsch. 1987. Activity patterns. Pp. 396–415 *In* Snakes: Ecology and Evolutionary Biology. Seigel, R.A., J.T. Collins, and S.S. Novak (Eds.). McGraw Hill, New York, New York, USA.

Glorioso, B.M., and J.H. Waddle. 2017. Nocturnal arboreality in snakes in the swamplands of the Atchafalaya Basin of south-central Louisiana and Big Thicket National Preserve of southeast Texas. Journal of North American Herpetology 2017:11–18.

Graham, S.P. 2018. American Snakes. Johns Hopkins University Press, Baltimore, Maryland, USA.

Greene, H.W. 1997. Snakes: The Evolution of Mystery in Nature. University of California Press, Berkeley, California, USA.

Gregory, P.T. 1984. Communal denning in snakes. Pp. 57–75 *In* Vertebrate Ecology and Systematics: A Tribute to Henry S. Fitch. Seigel, R.A., L.E. Hunt, J.L. Knight, L. Malaret, and N.L. Zuschlag (Eds.). University of Kansas Museum of Natural History Miscellaneous Publications 10, Lawrence, Kansas, USA.

Gregory, P.T. 2004. Analysis of patterns of aggregation under cover objects in an assemblage of six species of snakes. Herpetologica 60:178–186.

Hillis, D.M. 2022. Species, clades, and their relationship to paraphyly and monophyly: examples from the *Pantherophis obsoletus* complex. Herpetological Review 53:47–53.

Hillis, D.M., and W. Wüster. 2021. Taxonomy and nomenclature of the *Pantherophis obsoletus* complex. Herpetological Review 52:51–52.

Huey, R.B., C.R. Peterson, S.J. Arnold, and W.P. Porter. 1989. Hot rocks and not-so-hot rocks: retreat-site selection by garter snakes and its thermal consequences. Ecology 70:931–944.

Jackson, J.A. 1974. Gray Rat Snakes versus Red-cockaded Woodpeckers: predator-prey adaptations. Auk 91:342–347.

Landler, L., G.D. Ruxton, and E.P. Malkemper. 2021. Advice on comparing two independent samples of circular data in biology. Scientific Reports 11:1–10. https://www.nature.com/articles/s41598-021-99299-5

Lillywhite, H.B. 2014. How Snakes Work: Structure, Function and Behavior of the World's Snakes. Oxford University Press, Oxford, UK.

Lillywhite, H.B., and Brischoux, F. 2012. Is it better in the moonlight? Nocturnal activity of insular Cottonmouth snakes increases with lunar light levels. Journal of Zoology 286:194–199.

Loughran, C.L., D.B. Beck, and R.E. Weaver. 2015. Use of communal shedding sites by the Northern Pacific Rattlesnake (*Crotalus oreganus oreganus*) in central Washington state. Northwestern Naturalist 96:156–160.

Mullin, S.J., and R.J. Cooper. 1998. The foraging ecology of the Gray Rat Snake (*Elaphe obsoleta spiloides*)-visual stimuli facilitate location of arboreal prey. American Midland Naturalist 140:397–401.

Mullin, S.J., and R.J. Cooper. 2000. The foraging ecology of the Gray Rat Snake (*Elaphe obsoleta spiloides*). II. Influence of habitat structural complexity when searching for arboreal avian prey. Amphibia-Reptilia 21:211–222.

Noble, G.K., and H.T. Clausen. 1936. The aggregation behavior of *Storeria dekayi* and other snakes, with especial reference to the sense organs involved. Ecological Monographs 6:269–316.

Orians, G.H., and N.E. Pearson. 1979. On the theory of central place foraging. Pp. 154–177 *In* Analysis of Ecological Systems. Horn, D.J., R.D. Mitchell, and G.R. Stairs (Eds.). Ohio State University Press, Columbus, Ohio, USA.

Pierce, J.B., R.R. Fleet, L. McBrayer, and D.C. Rudolph. 2008. Use of trees by the Texas Ratsnake (*Elaphe obsoleta*) in eastern Texas. Southeastern Naturalist 7:359–367.

Schuett, G.W., R.W. Clark, R.A. Repp, M. Amarello, C.F. Smith, and H.W. Greene. 2017. Social behavior of rattlesnakes: a shifting paradigm. Pp. 61–244 *In* Rattlesnakes of Arizona, Volume 2. Schuett, G.W., M.J. Feldner, C.F Smith, and R.S. Reiserer (Eds.). Eco Publishers, Rodeo, New Mexico, USA.

Shine, R., T. Shine, J.M. Shine, and B.G. Shine. 2005. Synchrony in capture dates suggests cryptic social organization in sea snakes (*Emydocephalus annulatus,* Hydrophiidae). Austral Ecology 30:805–811.

Skinner, M., and N. Miller. 2020. Aggregation and social interaction in garter snakes (*Thamnophis sirtalis sirtalis*). Behavioral Ecology and Sociobiology 74:1–13.

Spence-Bailey, L.M., D.G. Nimmo, L.T. Kelly, A.F. Bennett, and M.F. Clarke. 2010. Maximising trapping efficiency in reptile surveys: the role of seasonality, weather conditions and moon phase on capture success. Wildlife Research 37:104–115.

Sperry, J.H., and P.J. Weatherhead. 2009. Does prey availability determine seasonal patterns of habitat selection in Texas Ratsnakes? Journal of Herpetology 43:55–65.

Sperry, J.H., D.G. Barron, and P.J. Weatherhead. 2012. Snake behavior and seasonal variation in nest survival of Northern Cardinals, *Cardinalis cardinalis*. Journal of Avian Biology 43:496–502.

Sperry, J.H., G. Blouin-Demers, G.L. Carfagno, and P.J. Weatherhead. 2010. Latitudinal variation in seasonal activity and mortality in Ratsnakes (*Elaphe obsoleta*). Ecology 91:1860–1866.

Sperry, J.H., R.G. Peak, D.A. Cimprich, and P.J. Weatherhead. 2008. Snake activity affects seasonal variation in nest predation risk for birds. Journal of Avian Biology 39:379–383.

Sperry, J.H., M.P. Ward, and P.J. Weatherhead. 2013. Effects of temperature, moon phase, and prey on nocturnal activity in ratsnakes: an automated telemetry study. Journal of Herpetology 47:105–111.

Stake, M.M., F.R. Thompson, III, J. Faaborg, and D.E. Burhans. 2005. Patterns of snake predation at songbird nests in Missouri and Texas. Journal of Herpetology 39:215–222.

Stickel, L.F., W.H. Stickel, and F.C. Schmid. 1980. Ecology of a Maryland population of Black Rat Snakes (*Elaphe o. obsoleta*). American Midland Naturalist 104:1–14.

Thompson, III, F.R., W. Dijak, and D.E. Burhans. 1999. Video identification of predators at songbird nests in old fields. Auk 1999:259–264.

Ward, M.P., J.H. Sperry, and P.J. Weatherhead. 2013. Evaluation of automated radio telemetry for quantifying movements and home ranges of snakes. Journal of Herpetology 47:337–345.

Weatherhead, P.J., G. Blouin-Demers, and K.M. Cavey. 2003. Seasonal and prey-size dietary patterns of Black Ratsnakes (*Elaphe obsoleta obsoleta*). American Midland Naturalist 150:275–282.

Weatherhead, P.J., G.L. Carfagno, J.H. Sperry, J.D. Brawn, and S.K. Robinson. 2010. Linking snake behavior to nest predation in a Midwestern bird community. Ecological Applications 20:234–241.

Zappalorti, R.T., and H.K. Reinert. 1994. Artificial refugia as a habitat-improvement strategy for snake conservation. Captive management and conservation of amphibians and reptiles. Contributions to Herpetology 11:369–375.

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