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Effects of Temperature, Moon Phase, and Prey on Nocturnal Activity in Ratsnakes: An Automated Telemetry Study

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ABSTRACT.—Nocturnal activity is important for many animals, but difficulty in documenting that activity has hampered efforts to understand factors that influence when animals are active at night. We used automated radiotelemetry to provide the first detailed tests of the hypothesis that the nocturnal activity of free-ranging snakes should be influenced by temperature, moon phase, and prey abundance by using data for Ratsnakes (*Pantherophis* spp.) from Texas and Illinois. Ratsnakes exhibited some nocturnal behavior throughout their active season in both Texas and Illinois, although snakes were much more active at night in Texas than in Illinois. Texas snakes transitioned from primarily diurnal activity to primarily nocturnal activity over this snake's active season, whereas Illinois snakes were always most active in the middle of the day. For both populations, nocturnal activity was positively related to temperature but unrelated to moon phase. Ratsnakes in Texas exhibited a stepwise increase in nocturnal activity in mid-summer, independent of temperature and coincident with the shift in their diet to almost exclusively mammals active at night. Given the ability of snakes in both populations to be active at night when temperatures allow, warming climates could lead to an increase in nocturnal activity, with consequences for both the snakes and the species on which they prey.

Although nocturnal behavior can be a critical aspect of a species biology (e.g., McNeil et al., 1992), documenting nocturnal behavior poses logistic difficulties for many wildlife species. Commonly available methods such as night-viewing technologies (Allison and Destefano, 2006), nocturnal capture rates, and radiotelemetry using conventional hand-tracking (e.g., Greenwood, 1982; Grindler and Krausman, 2001) usually provide incomplete data on nocturnal behavior and are challenging logistically. Satellite radiotelemetry allows continuous monitoring of behavior, including at night (Tucker, 2010), but is available only for species large enough to carry a GPS-enabled transmitter (Cooke et al., 2004). Advances in automated radiotelemetry have allowed detailed examination of the nocturnal behavior of a small number of species (Lambert et al., 2009) but has been largely absent from snake research. Here we document nocturnal activity patterns of Ratsnakes (*Elaphe obsoleta*) using automated radiotelemetry and test several hypotheses about the factors predicted to affect variation in nocturnal behavior.

The limited research to date that has examined nocturnal activity of snakes has relied on capture rates (Shine, 1979; Brown and Shine, 2002; Maciel et al., 2003), observations of captive snakes (Moore, 1978), or occasional nocturnal radio tracking using conventional methods (Durner and Gates, 1993). Although these methods have limitations, this research has shown that nocturnal activity appears important for some snake species and highlights the need for more-detailed examination. Automated telemetry has been used extensively to continuously monitor body temperature of free-living snakes (e.g., Brown and Weatherhead, 2000). The use of automated telemetry to quantify activity patterns of free-ranging snakes, however, has been used rarely (Slip and Shine, 1988a,b; Davis et al. 2008), and identification of the factors affecting nocturnal activity using continuously collected data has yet to be undertaken for any snake species.

Many snake species vary diel patterns of activity through the active season (e.g., Moore, 1978; Slip and Shine, 1998a). Snakes may shift to nocturnal activity to take advantage of more suitable nighttime temperatures or to avoid dangerously hot

daytime temperatures. Nocturnal capture rates have been shown to vary with temperature for several species (Brown and Shine, 2002; Maciel et al., 2003). Also, videography has documented more-extensive predation on birds' nests at night by Ratsnakes in Texas (Stake and Cimprich, 2003) than in Missouri (Stake et al., 2005), which may be related to latitudinal differences in nocturnal temperatures. A recent analysis of thermoregulation by Ratsnakes also suggested that nocturnal activity increased with temperature and decreased with latitude (Weatherhead et al., 2012). Here we use data collected from Ratsnakes in Texas and Illinois to test the hypothesis that variation in nocturnal behavior is a function of temperature. This hypothesis predicts that Ratsnake activity at night should increase with daytime and nighttime temperatures which, in turn, should lead to more nighttime activity in mid-summer than early and late in the active season. In addition, Ratsnakes should be more active at night in Texas than in Illinois.

Factors other than, or in addition to, temperature could also affect nocturnal activity. For example, thermal profiles suggest that Rubber Boas (*Charina bottae*) may occasionally be active at night when temperatures are suboptimal (Dorcas and Peterson, 1998). A potential nonthermal reason for snakes to be active at night is to synchronize their activity with that of their prey (Marques and Puerto, 1998) or, alternatively, for snakes to reduce their own risk of predation by being active when their predators are less active (Dorcas and Peterson, 1998). We used two indirect approaches to assess the possibility that predator-prey relationships affect nocturnal activity of Ratsnakes. The first approach took advantage of the seasonal change in Ratsnakes' diet and focused on our data from Texas, where the snakes' active season is longer. Ratsnakes prey on small mammals throughout their active season but also prey extensively on songbirds when the birds are nesting (Weatherhead et al., 2003; Carfagno et al., 2006; Sperry and Weatherhead, 2009). Nesting songbirds are active primarily during the day, and nesting season in Texas is primarily concentrated between April and July. The four species detected most commonly at our study sites were the Blue-grey Gnatcatcher (*Poliophtila caerulea*), White-eyed Vireo (*Vireo griseus*), Northern Cardinal (*Cardinalis cardinalis*), and Painted Bunting (*Passerina ciris*) (Sperry and Weatherhead 2009), and all have either ceased or have much-reduced breeding effort by August (Ellison, 1992; Hopp et al.,

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1995; Halkin and Linville, 1999; Lowther et al., 1999). The three small mammals on which Ratsnakes prey most extensively in Texas (*Peromyscus* spp., *Sigmodon hispidus* and *Baiomys taylori*; Sperry and Weatherhead, 2009) are active primarily at night (Marten, 1973; Cameron and Spencer, 1981; Eshelman and Cameron, 1987). Because the nesting season ends in the middle of the snakes' active season in Texas, we tested the hypothesis that, if the timing of prey activity affects when the snakes are active, a change in the timing of activity should coincide with when the snakes transition from a mixed diet of birds and mammals to a diet that is comprised largely of mammals. Specifically, the snakes should become more active at night following the end of the bird nesting season.

The second indirect approach we used to assess whether predator or prey activity could affect when snakes are active relied on extensive evidence that many small mammal species are less active on moonlit nights (Wolfe and Summerlin, 1989; Daly et al., 1992), whereas some predators are more active on nights with a full moon (Fernandez-Duque, 2003; Jetz et al., 2003). Given that Ratsnakes prey extensively on small mammals, variation in prey availability could lead to increased activity on moonlit nights, particularly given evidence that Ratsnakes are visual predators (Mullin and Cooper, 1998). Alternatively, snakes could be more vulnerable to visual predators on moonlit nights, favoring reduced activity. Several studies have documented increased (Lillywhite and Brischoux, 2011) or decreased (Madsen and Osterkamp, 1982; Clarke et al., 1996; Weaver, 2011) capture or encounter rates of snakes on nights with more moonlight. Therefore, we sought to determine whether Ratsnake nocturnal activity varies with moonlight.

METHODS

We conducted this study from 2006–2007 at Fort Hood, Texas and from 2009–2011 at Kennekuk County Park, Illinois. The vegetation at Fort Hood, an 87,890-ha military installation in central Texas, is predominantly oak–juniper (*Quercus* spp. and *Juniperus ashei*) woodland and oak savannah habitats. The topography of Fort Hood is characterized by flat-top mesas and oak savannahs. Detailed information on snake habitat use at Fort Hood is provided in Sperry and Weatherhead (2009). The vegetation at Kennekuk County Park, a 3,000-acre park in central Illinois, is primarily oak–hickory (*Quercus* spp. and *Carya* spp.) forest and native tallgrass prairie.

Our study organism, the Ratsnake (*Elaphe obsoleta*), was historically considered a single species with multiple subspecies. Although genetic analyses indicate that the taxonomy of Ratsnakes needs to be revised (see Burbrink et al. 2000, Burbrink 2001, and Gibbs et al. 2006), we have retained the original name in this paper. What is important for this study is that Ratsnakes in Texas and Illinois are closely related and ecologically similar. Ratsnakes were caught opportunistically by hand throughout the field season and, in Illinois, by fencing known hibernation sites. Radio transmitters were implanted surgically and snakes were released at the location of capture. Transmitter weight was <3% of body weight (Weatherhead and Blouin-Demers, 2004). Transmitters weighed 9 or 13 g, with batteries lasting 12 months and 24 months, respectively (Model SI-2T, Holohil Systems Incorporated, Ontario, Canada).

Snake activity was monitored using automated receiving units (ARU; JBJC Corp., Fisher, IL). Each ARU is associated with a radio tower topped with a circular array of six antennas. The height of towers varied from 3 m in Texas to 10–15 m in Illinois.

The ARUs were set to scan the radio frequencies of the snake transmitters at intervals of 3 and 5 min in Illinois and Texas, respectively. In Texas, we used single ARUs that we periodically relocated as snakes with transmitters moved out of range. In Illinois we used a fixed array of ARUs. In many instances, the signal from an individual snake's transmitter was received by more than one ARU in the array, but in these instances we used only the signal from the closest ARU (i.e., the strongest signal) in our analyses. Therefore, in both Texas and Illinois, our analysis of activity is based on signals received by a single ARU and, thus, the analytical methods are the same for both locations.

We identified movements based on the strength of signals for a given transmitter received by the ARU's six antennas. We used the general principle that a movement had to involve simultaneous changes in signal strength and bearing. In the circumstance that a snake moved directly toward or away from the ARU, so that only signal strength would change, this would not be recorded as a movement. Similarly, if a snake moved in a circular path around the ARU, such that only the bearing changed, again no movement would be recorded. We assumed that both of these circumstances would be rare. Before analyzing activity, it was necessary to filter 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 by 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 (Crofoot et al., 2008) and where the noise (the background signal between transmitter pulses) recorded on the strongest antenna was greater than -130 dBm, indicating that the strength of the "signal" itself may have been an artifact of high noise (threshold determined by the ARU developers). Postural changes by a snake (e.g., coiling or uncoiling) that alter the orientation of the transmitter antenna relative to the ARU antennas can also change signal strength without the snake having changed locations. We used field tests with both real and artificial snakes to determine that changes in bearing of up to 2° , and in signal strength of up to 8 dBm, could occur just from postural changes (M. P. Ward, pers. obs.). We then applied these values as thresholds for filtering data. When bearing and signal strength changed over the course of successive recording periods, we considered them to be a single movement; thus, not all movements were of the same duration. These methods likely produced conservative estimates of movement and may underestimate activity. More details on ARUs can be found in Kays et al. (2011) and at <http://www.sparrowsystems.biz>.

Daily temperatures were obtained from weather station data collected at Fort Hood, Texas (<20 km from field site) and Champaign, Illinois (<60 km from field site). Moon phase data were obtained from the U.S. Naval Meteorology and Oceanography Command website (<http://aa.usno.navy.mil/data/docs/MoonFraction.php>). We classified "nocturnal" as nighttime hours in which there was no solar radiation detected by local weather stations. Using this approach, rather than using arbitrary times to define day and night, allowed us to accommodate changes in day length over the season.

We examined nocturnal activity in three ways. First, to provide a graphical representation of diel patterns of activity,

we determined the frequency of movements that occurred in each hour of the day. 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 could be distributed unevenly throughout the day.

Second, we examined the relationship between abiotic factors (mean nighttime temperature, mean daytime temperature, and moon phase) and whether or not a snake exhibited nocturnal activity on a given night; this was done with mixed models (Proc GLIMMIX) using logit link and binomial distribution in Program SAS (SAS Enterprise Guide Version 4.3, SAS Institute, Cary, NC). For this analysis, nocturnal activity was considered a binary variable such that each snake either did or did not exhibit nocturnal activity on a particular date. To control for pseudo-replication, we included individual snake identity as a random effect.

Finally, because snake activity is so erratic (long periods of inactivity followed by bursts of movement), and because snake activity was much higher in early summer than late fall, we examined the percentage of daily movements that were nocturnal for each snake averaged across each month. Unlike the previous analyses, this analysis did not consider the absolute amount of movement in any given month but rather the percentage of each snake's movements that were nocturnal.

RESULTS

We monitored snake activity in Texas from May–November 2006 and April–November 2007. We tracked a total of 21 (six female and 15 male) snakes over this time which, after data filtering, resulted in 151,341 observations (mean = 7,206.7 ± 1,555.0 observations per snake). In Illinois, we monitored snake activity from June–August 2009 and 2010 and May–August 2011. Logistical constraints limited the duration of study in Illinois, although snakes likely exhibited a longer active season than we were able to monitor with automated telemetry (Sperry et al. 2010). Twelve (five female, five male, and two unknown sex) snakes were tracked, resulting in 267,158 observations (mean = 22,263.1 ± 4,920.0 observations per snake) after filtering. Because the number of individuals tracked was relatively small, and the reproductive status of females was unknown, we combined sexes for all analyses.

Overall patterns of diel activity indicate that snakes in both Texas and Illinois exhibited some nocturnal behavior in every month that we monitored them (Fig. 1). Texas snakes transitioned from being most active during the day in spring to primarily crepuscular in early summer and then primarily nocturnal later in the summer (Fig. 1). In the fall, snakes in Texas were uniformly active throughout the day and night, although overall activity levels in the fall were much lower than earlier in the year. Ratsnakes in Illinois were most active in the middle of the day in every month we monitored them and exhibited low levels of nocturnal activity in each of those months (Fig. 1).

The percentage of each snake's movements that occurred at night in Texas remained relatively constant for the first half of the summer (25.4–31.0%) and then exhibited a sharp increase to >50% in August, where the percentage remained through November (Fig. 2). The timing of this stepwise increase was consistent with the prediction that snakes should become more active at night once the nesting season for birds was complete. The high proportion of nocturnal activity in the fall occurred despite a decline in nighttime temperatures (Fig. 2). Ratsnakes

in Illinois were much less active at night than were Ratsnakes in Texas for the 4 months we monitored them, and the proportion of activity that was nocturnal remained relatively constant, never rising above 17.2% ± 2.2 of movements in August (Fig. 2). Mean nighttime temperatures during this time in Illinois also remained relatively constant (Fig. 2).

In both Texas and Illinois, nocturnal activity of Ratsnakes was related positively to mean temperatures at night ($F = 20.60$ and $F = 13.68$, respectively; $P < 0.001$ for both; Fig. 3) and during the day ($F = 14.55$ and $F = 7.62$; $P < 0.001$ and $P < 0.01$, respectively) on that date. The proportion of snakes active at night (on nights when at least three snakes were tracked) generally increased with increasing nighttime temperatures (Fig. 4). Because we documented some nocturnal activity in all months (even on some of the coldest nights: a 10.0°C night in Texas and a 12.6°C in Illinois), there was little evidence of a thermal threshold below which snakes were not active at night. Nocturnal activity was not related to moon phase for Texas or Illinois snakes ($F = 0.00$ and $F = 1.57$; $P = 0.99$ and $P = 0.21$, respectively). Given the lack of evidence for an effect of moon phase, we did not attempt to refine the analysis by controlling for cloud cover, particularly because heavy overcast at night at this time of year is rare, especially in Texas. There was little evidence for individual variation in nocturnal activity in any of the models ($P > 0.06$ for all solutions for random effects).

DISCUSSION

Our data revealed that Ratsnakes in both Texas and Illinois exhibited some nocturnal activity in all months in which we tracked snakes, although nocturnal movement was much more prevalent in Texas. Snakes in Texas transitioned from being primarily diurnal in the early summer, to crepuscular, and then to primarily nocturnal in late summer, whereas in Illinois peak snake activity occurred in mid-day throughout the summer. Nocturnal activity was positively related to both night and day temperatures, but there was no relationship with moon phase; this suggests that, for nocturnal behavior, temperature may be more important than nocturnal visual prey detection or predator avoidance. Automated radiotelemetry proved to be very effective at documenting fine-scaled temporal patterns of Ratsnake activity. It is noteworthy that general seasonal patterns of movement documented using conventional telemetry, where snakes were located every 48 h (Sperry et al., 2010), were similar to the seasonal patterns we documented here. However, fine-scale patterns of movement inferred from patterns of thermoregulation incorrectly suggested that nocturnal activity by Texas Ratsnakes is primarily crepuscular and that Illinois Ratsnakes were not active at night (Weatherhead et al., 2012). We consider direct measurements of movement from ARUs to be more reliable.

Although the number of snakes tracked and the duration of tracking was more extensive in Texas, we can draw general conclusions about latitudinal differences in nocturnal behavior. During the summer months when snakes were tracked in both locations, Texas Ratsnakes were much more active at night than the Illinois snakes. Ratsnakes in Illinois have been assumed to be exclusively diurnal (Carfagno and Weatherhead, 2008; Weatherhead et al., 2012), so the extent of nocturnal behavior we recorded was unexpected. For both populations, nocturnal activity was related strongly to temperature but not to moon phase, suggesting that similar mechanisms control nocturnal

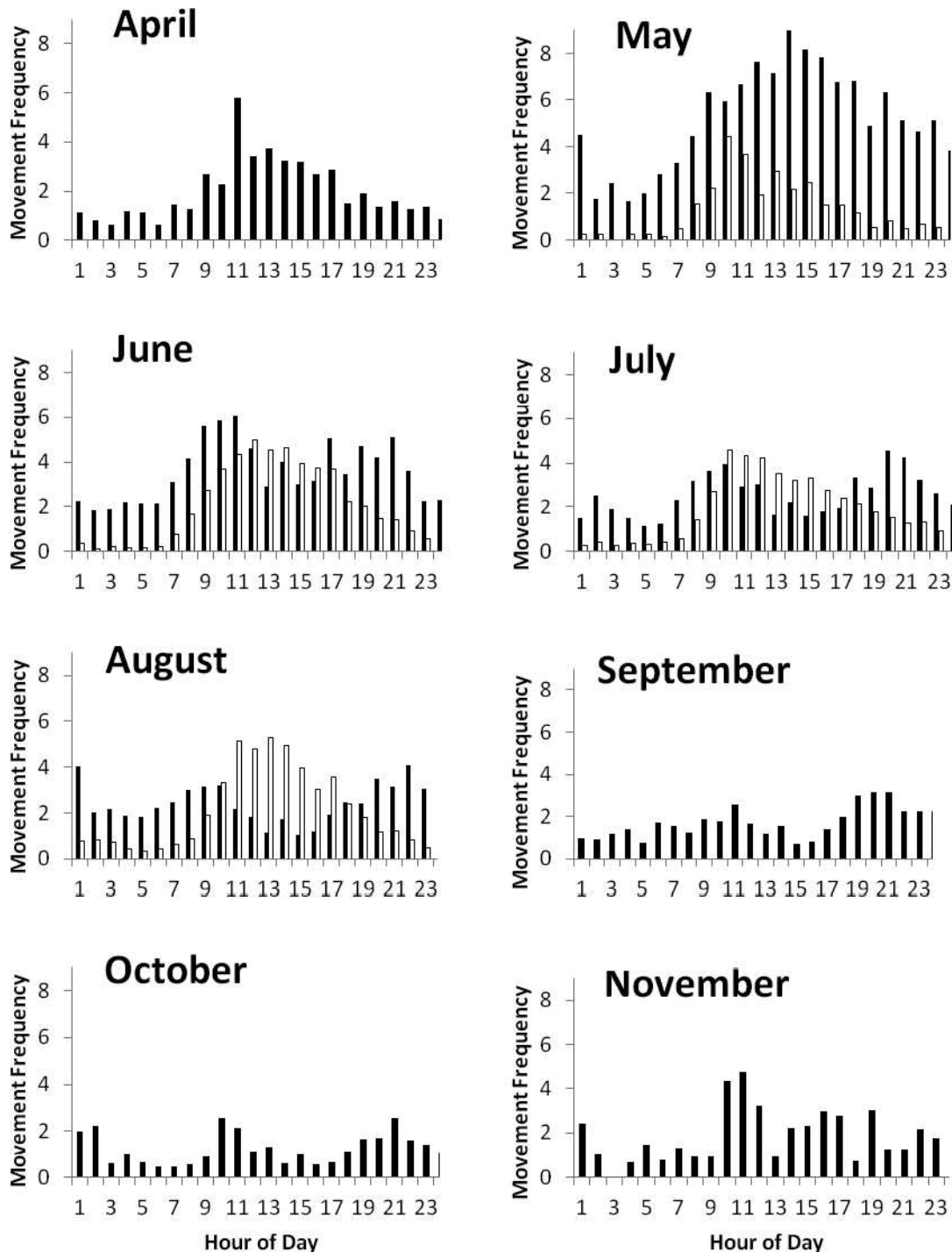


FIG. 1. Frequency of movements (calculated as percentage of observations each hour in which a movement was detected) for Ratsnakes in Texas and Illinois for each hour of the day and for each month that snakes were monitored. Black bars indicate Texas snakes and white bars indicate Illinois snakes. Data collected May–November, 2006 and April–November 2007 in Texas and from June–August 2009 and May–August 2011 in Illinois. Sunrise time ranged between approximately 0630 h (June)–0800 h (November) in Texas and 0530 h (June)–0615 h (August) in Illinois. Sunset time ranged between approximately 1830 h (November)–2040 h (June) in Texas and 1930 h (August)–2030 h (June) in Illinois.

behavior in both populations, with thermal differences accounting for lower nocturnal activity in Illinois.

Despite the importance of temperature in influencing when Ratsnakes were active at night, our results also indicate that the effects of temperature are far from absolute. Although snakes moved more at night in the warmest summer months and on warmer nights, we recorded some nocturnal activity in all months and on some of the coldest nights. We documented

nocturnal movements at minimum ambient temperatures of 10.0°C in Texas and 12.6°C in Illinois, well below the preferred body temperature of approximately 29°C for Ratsnakes in both Texas and Illinois (Weatherhead et al., 2012). On those particular days, daytime temperatures reached 14°C and 26°C, respectively, indicating that the snakes could have moved diurnally under more-favorable thermal conditions. Dorcas and Peterson (1998) found evidence that Rubber Boas move primarily at night, even

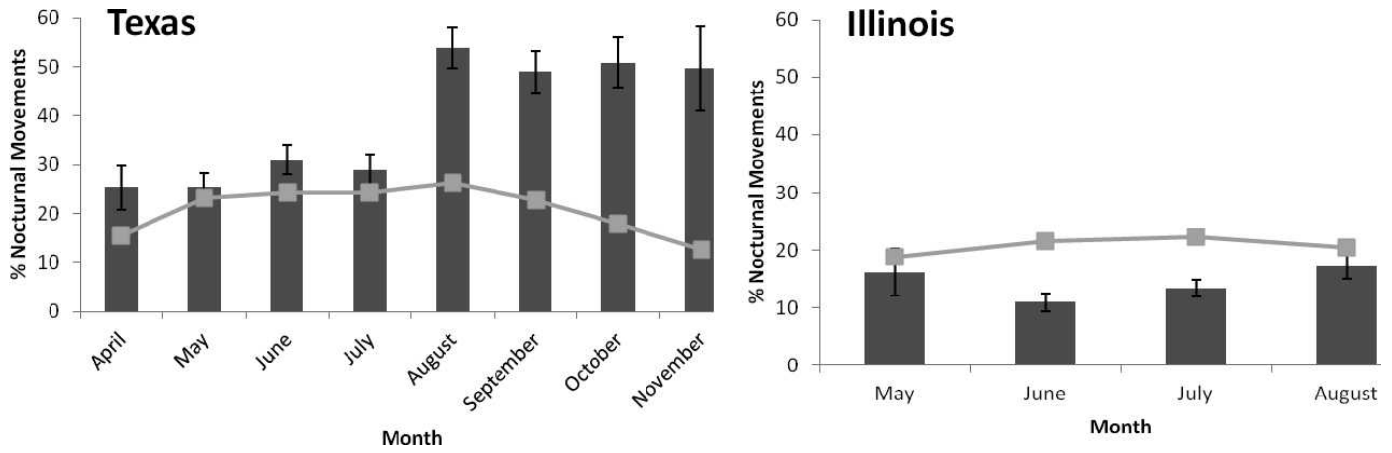


FIG. 2. Monthly mean (\pm SE) percentage of daily movements that occurred during nocturnal hours for Ratsnakes (columns) and mean (\pm SE) daily nocturnal temperatures (line) in Texas and Illinois. Data collected May–November, 2006 and April–November 2007 in Texas and from June–August 2009 and May–August 2011 in Illinois.

when temperatures were far below optimal, and hypothesized that nocturnal activity may allow the snakes to avoid diurnally active predators. Nocturnal behavior may also allow snakes to synchronize their activity with that of their prey (Marques and Puerto, 1998). If the snakes' principal predators or prey are endotherms, and thus relatively unconstrained by temperature, both of these factors could cause snakes to be active at times that are not always thermally optimal for themselves.

Our results for Texas Ratsnakes suggest that the activity patterns of their prey could contribute to shaping the snakes' activity patterns. Consistent with our prediction that a transition to increased nocturnal activity should coincide with the seasonal transition from a mixed diet of birds and mammals to a diet comprised largely of mammals, we found a stepwise increase in nocturnal activity at the end of July when most avian nesting activity ends. A potential difficulty with our interpretation is that predation on bird nests by Texas Ratsnakes occurs primarily at night (Stake and Cimprich, 2003). However, it has been hypothesized that snakes locate nests during the day using visual cues (e.g., provisioning adults; Mullin and Cooper, 1998) and then prey on nests at night when parental defenses are lowered (Stake et al., 2005). If that is the case, Ratsnakes may maintain a combination of diurnal and nocturnal activity during

the bird breeding season and then shift to more nocturnal activity, and exclusively mammalian prey, once avian nesting ceases. The evidence in support of this hypothesis is indirect but warrants further testing.

Unlike many previous studies of other snake species (Madsen and Osterkamp, 1982; Clarke et al., 1996; Lillywhite and Brischoux, 2011; Weaver, 2011), we did not find a relationship between moon phase and snake nocturnal activity. A trade-off between visual foraging ability and safety from predators would predict that prey species would be more likely to avoid moonlit nights, whereas visual predators would prefer well-lit nights. Lillywhite and Brischoux (2011) found an increase in Cottonmouth (*Agkistrodon piscivorus conanti*) activity on moonlit nights and suggested that this was a result of increased prey (carrion) detectability. They further hypothesized that the decreased activity documented in other predators may be a function of reduced prey availability on well-illuminated nights as opposed to being a safety trade-off. However, just as the type of prey may influence the foraging-safety trade-off, the predators present in a community also likely influences this relationship. If mortality was primarily from nocturnal predators that rely on visual cues (such as owls or mesocarnivores), it could be expected that snakes would avoid moonlit nights in an

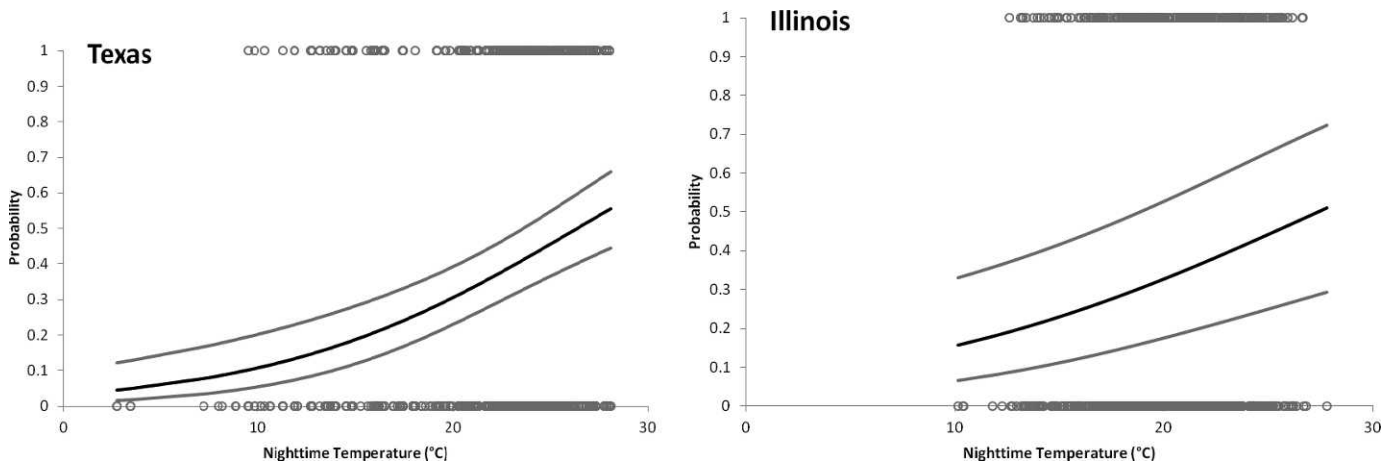


FIG. 3. Relationship between probability of nocturnal movement and nighttime temperature for Ratsnakes in Texas and Illinois. Probabilities were calculated using mixed models. Circles indicate observed values with "1" indicating nocturnal movement and "0" indicating no nocturnal movement. Because observations occurred only during the summer months in Illinois, we did not record nighttime temperatures below 10°C.

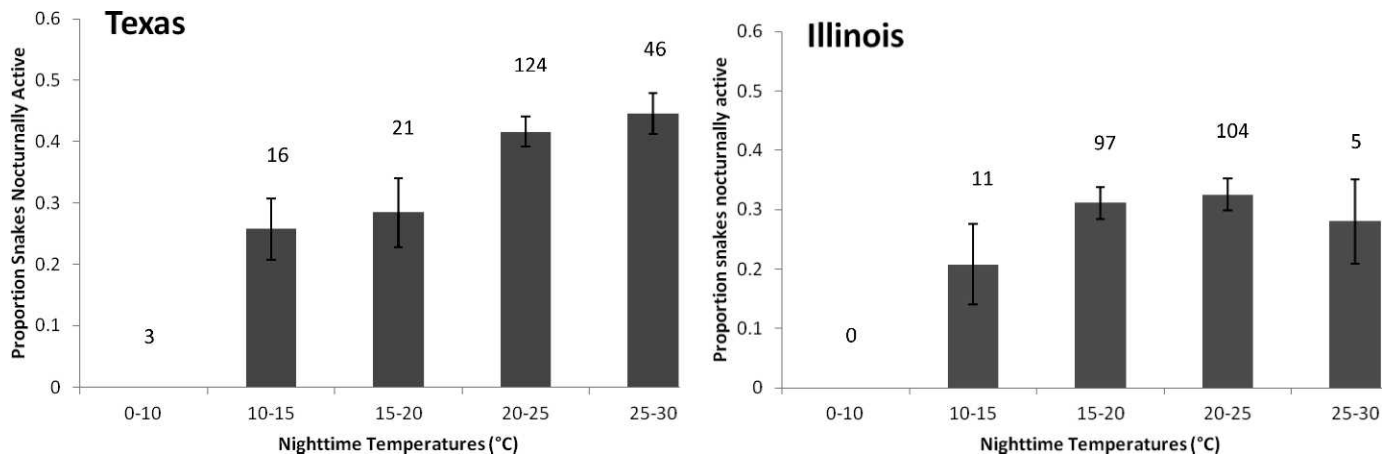


FIG. 4. Mean (\pm SE) proportion of snakes each night that exhibited nocturnal behavior and the temperatures associated with those movements for Ratsnakes in Texas and Illinois. Numbers above each column indicate the number of nights with mean temperatures within each temperature range.

attempt to minimize predation risk. In Texas, confirmed causes of mortality include road mortality and diurnal raptor predation (Sperry and Weatherhead 2008), neither of which would be affected by moon phase. Little is known about the cause of mortality of snakes in Illinois. Addressing this question will require detailed study of the predator community as well as the type and timing of snake predation.

Understanding the factors that affect snake nocturnal activity has important implications for predicting the effects of climate change. Given that temperature appears to be an important determinant of nocturnal activity, we expect that an increase in temperature would lead to an increase in nocturnal activity. This expansion could be seen both seasonally, for populations that currently exhibit some nocturnal behavior, as well as latitudinally, with higher-latitude populations experiencing novel opportunities for nocturnal activity. An increase in nocturnal activity would likely affect not only the snakes but the species upon which the snakes prey. For example, nocturnal predation by snakes on birds' nests at lower latitudes has been implicated as an important cause for conservation concern because avian parents are less able to defend their nests at night and also because the parents themselves become much more vulnerable to snakes (Carter et al., 2007; Reidy et al., 2009). An increase in nocturnal activity by snakes at lower latitudes, and an expansion of nocturnal activity at higher latitudes, could negatively affect nesting birds, particularly populations that are currently naïve to nocturnal snake predation.

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