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Facultative nocturnal behaviour in snakes: experimental examination of why and how with Ratsnakes (*Elaphe obsoleta*) and Racers (*Coluber constrictor*)

Brett A. DeGregorio, Jinelle H. Sperry, Daniel P. Valente, and Patrick J. Weatherhead

Abstract: Diel activity patterns are often fixed within species such that most animals can be classified as diurnal, crepuscular, or nocturnal, and have sensory abilities that reflect when they are active. However, many snake species appear capable of switching between diurnal and nocturnal activity. Here, we evaluate the hypothesis that some species are constrained in their activity by the sensory cues used for foraging. We experimentally assessed differences between two sympatric snake species in their ability to alter diel activity patterns, to address why those snakes that switch do so (do thermal constraints force them to be active in otherwise nonpreferred conditions?), and to explore how sensory abilities to locate prey facilitate or constrain this shift. Ratsnakes (*Elaphe obsoleta* (Say in James, 1823)) were active when temperature was optimal, regardless of light level, suggesting their activity pattern is genuinely plastic. Consistent with our predictions, Ratsnakes successfully detected prey in low and high light using visual or chemical cues, and were most successful when cues were coupled. Racers (*Coluber constrictor* L., 1758) were almost exclusively diurnal, regardless of temperature, and became less active when daytime temperatures were suboptimal. The ability of Ratsnakes to shift activity may confer a foraging advantage and should buffer Ratsnakes and similarly flexible species from climate change, whereas climate change may pose a more serious threat to inflexible species such as Racers.

Key words: activity patterns, climate change, *Coluber constrictor*, *Elaphe obsoleta*, foraging, Racer, Ratsnake, sensory modality, thermal ecology.

Résumé : Les motifs d'activité circadienne sont généralement figés au sein d'une espèce donnée, de sorte que la plupart des animaux peuvent être classés comme étant diurnes, crépusculaires ou nocturnes, leurs capacités sensorielles reflétant la période du jour durant laquelle ils sont actifs. De nombreuses espèces de serpents semblent toutefois capables de passer d'une activité diurne à une activité nocturne. Nous évaluons l'hypothèse voulant que l'activité de certaines espèces soit modulée par des signaux sensoriels utilisés pour la quête de nourriture. Nous avons évalué expérimentalement les différences entre deux espèces de serpents sympatriques en ce qui concerne leur capacité de modifier leurs motifs d'activité circadienne afin d'examiner les raisons qui font que ces motifs changent chez certains serpents (est-ce que des facteurs thermiques les forcent à être actifs dans des conditions autres que celles qu'ils préfèrent?) et comment les capacités sensorielles de recherche de proies facilitent ou limitent ce changement. Des couleuvres obscures (*Elaphe obsoleta* (Say dans James, 1823)) étaient actives quand la température était optimale, peu importe le niveau de lumière, ce que laisse penser que leur motif d'activité est réellement plastique. Conformément à nos prédictions, les couleuvres obscures réussissaient à détecter des proies dans des conditions de lumière faible ou forte à l'aide de signaux visuels ou chimiques, y parvenant le mieux quand ces deux types de signaux étaient jumelés. Des couleuvres agiles (*Coluber constrictor* L., 1758) étaient presque exclusivement diurnes, peu importe la température, et devenaient moins actives quand les températures diurnes n'étaient pas optimales. La capacité des couleuvres obscures à modifier le moment où elles sont actives pourrait leur conférer un avantage pour la quête de nourriture et les protéger, ainsi que d'autres espèces versatiles, contre les changements climatiques, alors que ces derniers pourraient constituer une menace plus grave pour les espèces non versatiles comme les couleuvres agiles. [Traduit par la Rédaction]

Mots-clés : motifs d'activité, changements climatiques, *Coluber constrictor*, *Elaphe obsoleta*, approvisionnement, couleuvre agile, couleuvre obscure, modalité sensorielle, écologie thermique.

Introduction

Diel activity patterns are often fixed within species such that most animals can be classified as diurnal, crepuscular, or nocturnal (Metcalfe et al. 1998). The sensory systems and hormonal cycles of most species constrain their activity to times when they perform best (Snyder and Weathers 1976; Thorpe and Morgan 1978; Lutterschmidt et al. 2002, Lutterschmidt and Mason 2010). Deviations from these patterns have been viewed as minor, such as modest shifts between diurnal and crepuscular activities rather than overall shifts between diurnal and nocturnal activities (Ashby 1972; Metcalfe et al. 1998). For certain taxa, such as snakes, this behaviour appears to be more plastic (Gibbons and Semlitsch 1987; Oishi et al. 2004). Here, we use experiments to investigate the differences between two sympatric snake species in their abil-

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B.A. DeGregorio and P.J. Weatherhead. Department of Natural Resources and Environmental Sciences, University of Illinois at Urbana – Champaign, 1102 South Goodwin Avenue, IL 61801, USA.
J.H. Sperry. Department of Natural Resources and Environmental Sciences, University of Illinois at Urbana – Champaign, 1102 South Goodwin Avenue, IL 61801, USA; Engineer Research and Development Center, 2902 Newmark Drive, Champaign, IL 61826, USA.
D.P. Valente. Engineer Research and Development Center, 2902 Newmark Drive, Champaign, IL 61826, USA.
Corresponding author: Brett A. DeGregorio (e-mail: bdegrego@illinois.edu).

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ity to alter their diel activity patterns, examine why those snakes that switch do so (do thermal constraints force them to be active in otherwise nonpreferred conditions?), and explore how sensory abilities to locate prey facilitate or constrain this shift.

Facultatively nocturnal species may shift their activity in response to a number of mechanisms including predation risk (Fraser et al. 2004), competition (Cloudsley-Thompson 1970), body condition, (Metcalfe et al. 1998), habitat (Fox and Bellwood 2011), age (Krysko 2002), or season (Abom et al. 2012). For instance, black bears (*Ursus americanus* Pallas, 1780) may shift from diurnal to nocturnal activity to avoid grizzly bears (*Ursus arctos horribilis* Ord, 1815) or humans (Schwartz et al. 2010). Changes in activity may not only reduce predation risk but may also confer advantages to flexible predators. Black bears foraging at night may be more successful because their salmonid prey is less evasive (Reimchen 1998). Ratsnakes (*Elaphe obsoleta* (Say in James, 1823)) that prey on bird nests at night are more likely to consume both the nest contents and the attending female, the latter being rarely captured by diurnally foraging snakes (Reidy et al. 2009).

The relatively common occurrence of diel activity shifts among snakes (Gibbons and Semlitsch 1987; Krysko 2002; Oishi et al. 2004; Sperry et al. 2010) is often assumed to be associated with ectothermy, such that snakes shift activity in response to temperature variability, although only a few studies have explored this phenomenon systematically (e.g., Heckrotte 1975; Weatherhead et al. 2012). Our interest here is in two general questions about plasticity in timing of activity in snakes. First, why do shifts occur? For example, do snakes capable of being active under either light or dark conditions prefer to be active under one of those conditions but shift activity to the other only when environmental temperatures favor doing so? Second, given that being active both day and night requires detection and acquisition of prey in very different light conditions, how do the snakes' sensory abilities allow them to hunt in both light and dark conditions? To date, no study has investigated which sensory cues snakes use to detect prey in both high and low light and whether plasticity in which sensory cues are used is associated with plasticity in timing of activity.

Information on the sensory cues nonviperid snake species use to find prey is available primarily for Garter Snakes (genus *Thamnophis* Fitzinger, 1843) and Water Snakes (genus *Nerodia* Baird and Girard, 1853). Chemical cues (Gove and Burghardt 1975; Saviola et al. 2012), visual cues (Drummond 1985; Mullin and Cooper 1998), or a combination of both (Heinen 1995; Shivik 1998) have been documented. All of these studies tested snakes under only one light condition (either day or night), however, and only Shivik (1998) studied snakes at night. To understand how snakes can forage in both light and dark, it is necessary to study the same snakes under both conditions. Furthermore, many of these studies presented snakes with a prey cue (a scented cotton swab or a skewered chunk of earthworm) to record tongue flicking rates, rather than studying actual foraging behaviour. Within the confines of laboratory experiments, more realistic foraging situations and prey cues would be more informative.

In this study, we evaluate the hypothesis that facultative nocturnal activity of ectotherms is constrained by the sensory cues used for foraging and not temperature. To test this hypothesis, we determine experimentally whether the timing of activity of two sympatric snake species is a function of preference for particular light conditions, ambient temperatures, or both, and how sensory ability allows effective foraging both diurnally and nocturnally. Ratsnakes are active year-round in parts of their range, with individuals seasonally switching between diurnal and nocturnal behaviours (Weatherhead et al. 2012). Racers (*Coluber constrictor* L., 1758) are sympatric with Ratsnakes across much of the eastern United States and are considered strictly diurnal (Ernst and Ernst 2003). Thus, we first predicted that Ratsnakes would shift their activity to take advantage of optimal temperatures whether they occur at night or day, whereas Racers would be constrained to diurnal activity, regardless of temperature. Associated with being active both diurnally and nocturnally, Ratsnakes have been documented capturing avian prey during the day and at night (Thompson and Burhans 2003; Reidy et al. 2009). Conversely, Racers appear to be exclusively diurnal hunters. To test the hypothesis that timing of activity is constrained by the sensory cues used for foraging, we presented both species with a prey-location task under different light levels. The specific predictions we test are that Ratsnakes will locate food using visual cues during the day and olfactory cues at night, whereas Racers will rely on visual cues and thus be able to locate prey only during the day.

Materials and methods

Study animals

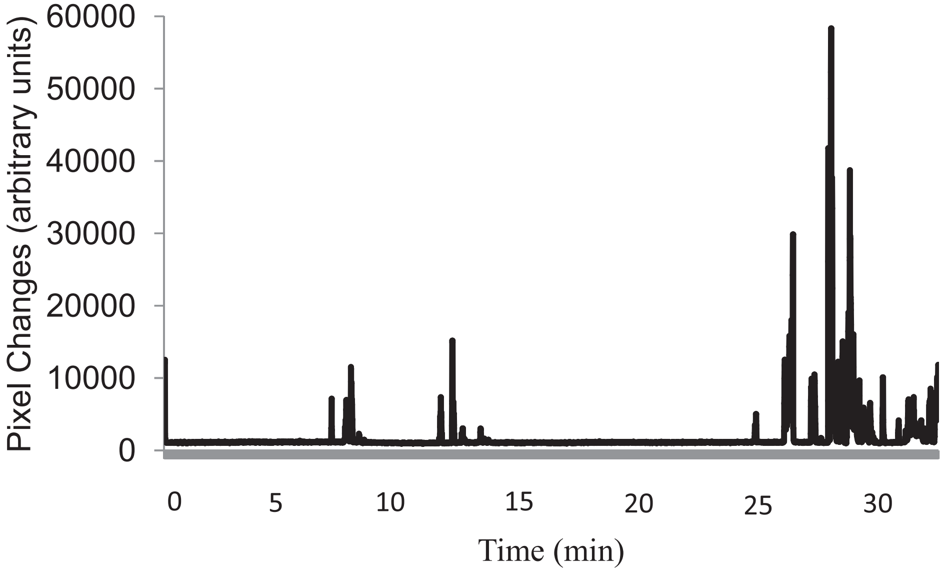
Ratsnakes and Racers were captured opportunistically by hand in Aiken and Barnwell counties, South Carolina, USA. We probed the cloaca of each individual to determine its sex, assessed the reproductive condition of females by palpation. We excluded gravid females because they may be less vagile and less food-motivated than their nongravid counterparts. We held any snake with a visible food bolus until the item was digested and excreted. All other snakes were held for between 2 and 5 days for activity trials and for 1 week prior to foraging trials. Only adults (>70 cm) were used in trials. Captured animals were housed individually at the Savannah River Ecology Laboratory animal care facility in either 38 or 75 L aquaria. Each aquarium had a substrate of aspen shavings, a water bowl, and an overturned bowl under which a snake could hide. A 60 W bulb at the end of each aquarium created a thermal gradient within the enclosure. All animals were kept on a 12 h light : 12 h dark photoperiod at a constant ambient temperature of 30 °C. Different snakes were used for each experiment to minimize time in captivity and were subsequently released at their capture locations. All snakes were collected under South Carolina Department of Natural Resources permits Nos. G-11-03 and 23-2012A and all procedures conformed to permits approved by the University of Illinois (IACUC No. 11054) and University of Georgia (AUP No. A2011 04-007-Y2-A0).

Snake activity

To assess the influence of temperature on snake activity, we filmed snakes under three temperature treatments in a wooden-frame enclosure (2.25 m long × 1.5 m wide × 0.46 m high) with nylon screen walls. The enclosure had aspen bedding and was otherwise empty except for a water bowl. At one end of the enclosure, we installed a camera with infrared diodes to film snake activity continuously. Video was recorded at 6 frames/s and downloaded every 24 h. The enclosure was in a room that allowed control of temperature and light. Snakes were placed individually in the enclosure and exposed to each of following three treatments in a randomly determined order: (1) optimal day (30 °C; Blouin-Demers and Weatherhead 2001) and night (30 °C) temperatures; (2) optimal day (30 °C) and suboptimal night (22 °C) temperatures; (3) suboptimal day (22 °C) and optimal night (30 °C) temperatures. Each of the three treatments lasted 24 h and was conducted under a 12 h light : 12 h dark photoperiod. All trials took place between 1 May and 25 July 2012 and 2013.

Movement on video recordings can best be quantified by detecting pixel changes (Radke et al. 2005). Similar to pixel-difference methods presented in Valente et al. (2007), we created software to detect and quantify snake activity. Because the camera was static and the snake was the only moving object, simple pixel-difference measures could reasonably approximate snake motion, including postural changes. By summing the number of frames for which pixel differences were greater than the background level, we could calculate the amount of time a snake was moving (Fig. 1). We wrote the software in PYTHON using the OpenCV library.

Fig. 1. Example of output from our custom software. The *y* axis indicates the sum of squared pixel differences from one frame to the next (in arbitrary units) as the snake moved. The flat line above the *x* axis indicates no movement, with each spike indicating that pixels are changing and the snake is moving. We summed the number of frames for which pixel differences were above the baseline to calculate the amount of time a snake was moving. In this example, the Ratsnake (*Elaphe obsoleta*) moved in 2580 frames or 7 min and 10 s in the 30 min period.



To ensure the accuracy of this method, we randomly selected 30 min segments of video and manually determined the amount of time a snake was actively moving. We then used linear regression to compare the amount of activity detected by our software and by observation. Additionally, when watching video, we categorized each snake movement as either slight or substantial and either under or above substrate, or stationary other than the head moving. We used these categories to test for differences between the species in particular behaviours (i.e., movement under substrate) that might bias results from our software. We assigned each behaviour a nominal score and compared the amount of time each species was engaged in each behaviour using a Student's *t* test.

To analyse differences in snake activity relative to the three temperature treatments, we quantified the amount of time each snake was moving during each 12 h period of each treatment. We log-transformed the data to better meet the assumptions of normality. We analysed data using a repeated measures generalized linear mixed model. We evaluated the influence of the fixed factors (species and treatment) and their interaction on snake activity, using individual as a random factor. If we found either fixed factor to be significant at $\alpha < 0.05$, we analysed the trials separately by species and treatment using pairwise *t* tests.

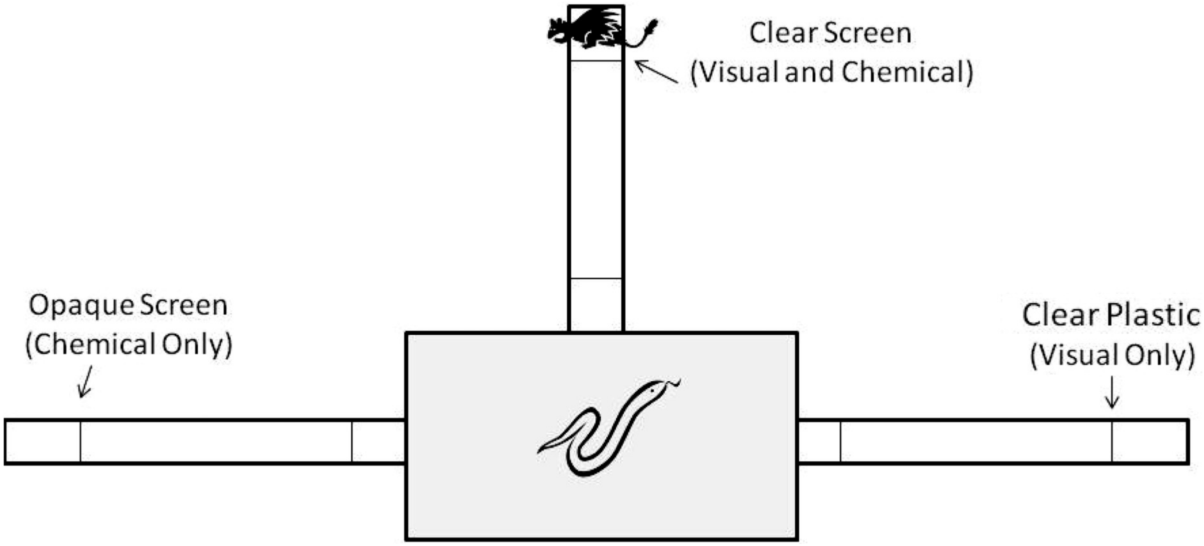
Prey detection

To assess how Ratsnakes and Racers locate prey in different light conditions, we presented snakes with a discrimination task that required them to locate prey using a visual stimulus, a chemical stimulus, or both stimuli together, in both light and dark conditions. Within their first 2 days in captivity, each snake was offered a dead mouse (*Mus musculus* L., 1758) (purchased frozen but thawed in warm water prior to presentation) weighing less than 2% of their body mass. All snakes accepted the mouse, establishing the sight and smell of dead mice as desirable food. After consumption of the mouse, we held snakes for a minimum of 7 days (range 7–14 days; 8.3 ± 2.8 days, mean ± SD) before trials to ensure a strong appetitive response.

We performed all trials in a room with a constant temperature of 30 °C and one of two light levels: high light provided by overhead fluorescent lighting or low light (1 lx) to approximate light conditions on a cloudy night. We placed snakes individually in a plastic holding container (33.8 cm long × 21.6 cm wide × 11.9 cm high) with three clear tubes (10.2 cm diameter × 120 cm long) radiating out (one on each of three sides; Fig. 2). At the end of each tube was a compartment, one of which was baited with prey during each trial. The snake was initially prevented from entering any of the tubes by clear screen gates (aluminum window screen) placed between the holding container and the tube entrances. In each trial, both a dead, thawed mouse and a life-like toy mouse on a string were placed together at the end of one tube, either behind opaque screen made from six layers of charcoal fiberglass window screen (chemical stimulus only), a clear plastic barrier (visual stimulus only), or a clear barrier made from aluminum window screen (visual and chemical stimuli). The barriers used in each of these treatments also prevented snakes that chose the baited tube from accessing the prey. Snakes were allowed access to all three tubes in each trial, but only one tube (randomly determined) contained prey. Thus, in each trial there was one baited tube and two unbaited tubes. After allowing the snake 30 min to acclimate (to cease escape behaviour and to react to the prey), we removed the gates, allowing the snake simultaneous access to all three tubes. We interpreted the snake entering one of the tubes as having reacted to the prey (or lack thereof) in that tube. A trial ended when a snake had entered a tube or after 30 min, whichever came first. After each trial, we cleaned tubes thoroughly with paper towels and an odourless disinfectant and then rearranged them in a randomly determined order.

We recorded a snake's response as a multinomial variable, with snakes entering the baited tube designated as having "reacted to prey", snakes entering one of the unbaited tubes as "failed to react to prey", and snakes that remained in the holding container for the entire 30 min as "failed to respond". One of the authors (B.A.D.) watching from behind a blind (and making the mouse on a string move in a life-like fashion) determined that a snake had "selected" a tube when its head was 25 cm from the holding container (marked by a piece of black tape around each tube). Note that under low light conditions during trials, it was still (just) possible to detect the dark snakes in the clear plastic tubes. We also recorded the time from removal of the barriers to when a snake's head was 25 cm from the container (defined as latency). We tested snakes either three (night trials only) or six (day and night trials) times with the stimulus treatments presented in

Fig. 2. A schematic representation of the experimental apparatus. A snake was held in the container for 30 min, after which it was given simultaneous access to all three tubes, two of which were unbaited controls in any given trial, while the third lead to a dead mouse (odour cue) and a life-like mouse on a string (visual cue). By varying which tube had the mouse stimuli (both were always presented together), each trial consisted of one of three treatments: visual cues only, chemical cues only, or both cues together.



random order. All tests for a given snake were conducted on the same day and we used "trial order" as a variable in our analyses to control for a snake's ability to learn between trials. All trials took place between 1 June and 15 August 2011 or 1 May and 5 June 2012 between the hours of 0900 and 1400. Only one author (B.A.D.) performed trials to eliminate interobserver variability.

We compared the number of snakes that detected prey with that expected by chance (33.3%) using χ^2 analysis. Because reaction to prey was recorded as a multinomial variable (reacted to prey vs. failed to react to prey vs. no choice), we then used a generalized linear mixed model with multinomial logistic regression to compare the effect of stimulus type on reaction to prey. We used species (Ratsnake vs. Racer), stimulus type (visual, chemical, or both), light level (day or night), an interaction effect between stimulus type and light, time since last meal, and trial order as fixed factors, with snake identity as a random factor. We analysed latency to reaction using a univariate generalized linear model with the fixed factors of stimulus type, light level, an interaction effect between stimulus type and light, time since last meal, and trial order, with snake identity as a random factor. We used a Tukey's post hoc test to assess differences in latency between stimulus types.

Results

Snake activity

We tested 14 Ratsnakes and 10 Racers for a total of 69 trials and accumulated 1656 h of video. We scored thirty-seven 30-min video segments manually and using our automated scoring software. The two methods agreed reasonably well ($r^2 = 0.68$, $P = 0.01$), although the software underestimated activity, on average, by 30%. This was primarily due to the program missing movement when the snake was under the substrate or making slight movements at the far end of the arena. We detected no difference in these behaviours between the two snake species (Student's t test, $t = 0.44$, $P = 0.33$). All subsequent results are based on data obtained using the automated software.

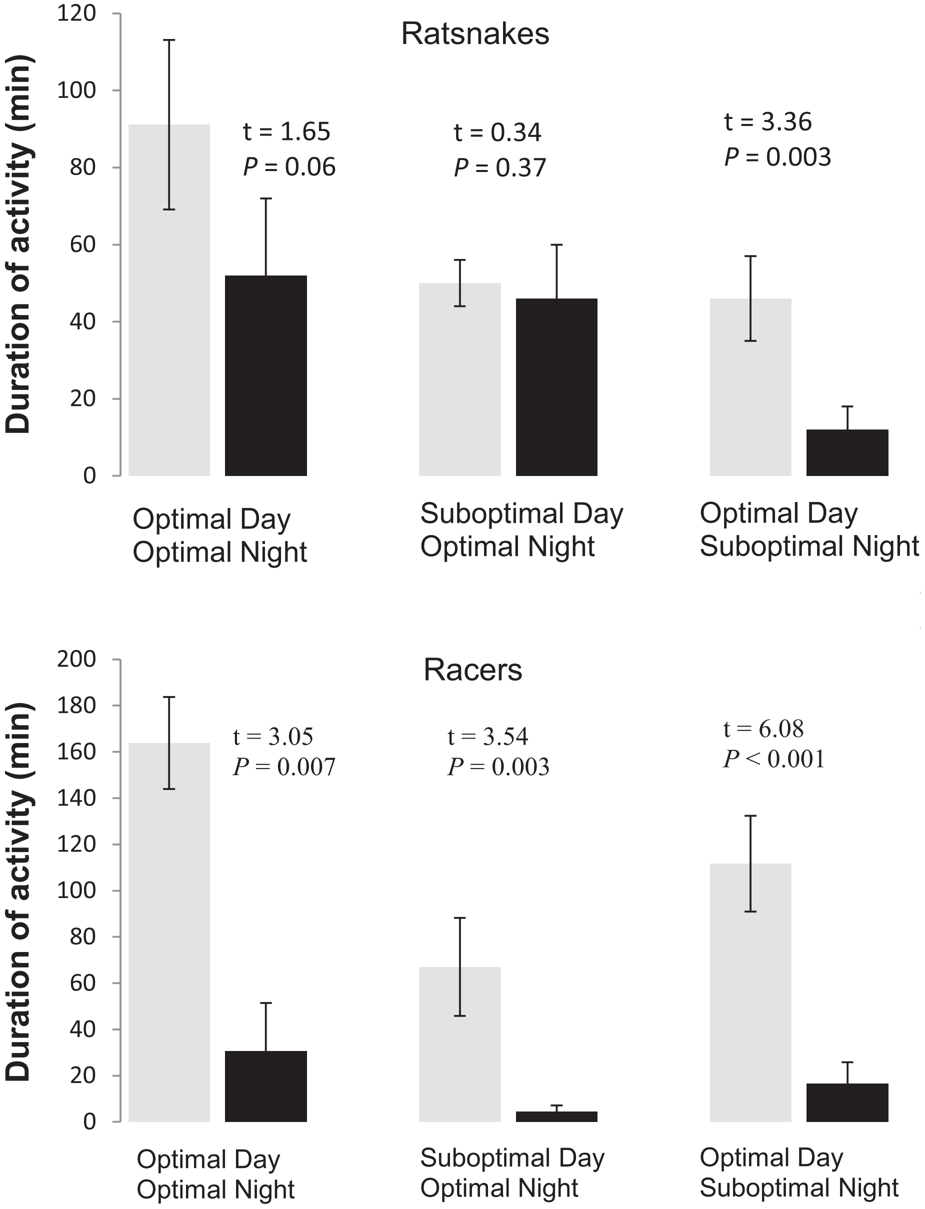
Racers were generally more active than Ratsnakes and nearly all Racer activity was diurnal. Treatment and the interaction between treatment and species had significant effects on activity ($F_{[3,65]} = 3.65$, $P = 0.002$; Fig. 3). When temperatures were optimal for a full 24 h period, Racers were active almost exclusively during the day (84% of movement: pairwise t test, $t = 3.05$, $P = 0.007$). Ratsnakes were active both day and night, with a tendency to be more active during the day (67% of movement: pairwise t test, $t = 1.65$, $P = 0.06$). When daytime temperature was decreased to 22° C, Racers halved their mean diurnal activity compared with when temperatures were optimal, but still moved only during the day (94% of movement: pairwise t test, $t = 3.54$, $P = 0.003$). Ratsnakes also substantially decreased their diurnal activity when daytime temperatures were suboptimal (51% of movement), while maintaining high nocturnal activity (pairwise t test, $t = 0.34$, $P = 0.37$). The largest discrepancy in movement between day and night for both species occurred when day temperatures were optimal and night temperatures were suboptimal. Both species showed high levels of diurnal activity and little or no nocturnal activity (79% diurnal movement for Ratsnakes: pairwise t test, $t = 3.36$, $P = 0.003$; 87% diurnal movements for Racers: pairwise t test, $t = 6.08$, $P = 0.001$). Although Racers were expected to be exclusively diurnal, we did detect some nocturnal activity. This activity primarily occurred soon after the lights were dimmed (32% of movement within 60 min of light change).

Prey detection

We tested 16 Ratsnakes for a total of 48 night trials and 33 day trials, and 9 Racers for a total of 24 night and 24 day trials. Ratsnakes successfully reacted to prey at greater than chance (i.e., 33%) rates in day (57%: $\chi^2_{[10]} = 12.3$, $P = 0.02$) and night (60%: $\chi^2_{[15]} = 8.9$, $P < 0.01$: Fig. 3) trials. Racers reacted to prey at rates expected by chance in both light and dark conditions (29% light and dark: $\chi^2_{[11]} = 2.60$, $P = 0.99$; Fig. 3). Ratsnakes were more successful than Racers at reacting to prey ($F_{[1,68]} = 6.94$, $P = 0.001$). Because species had such a strong effect, we analysed species separately.

For Ratsnakes, stimulus type had a significant effect on successfully reacting to prey ($F_{[2,69]} = 3.07$, $P = 0.05$). Success was highest in both light treatments when chemical and visual stimuli were coupled (>70% success). Success was lowest in both light levels when only a visual stimulus was presented (50% night, 30% day). Although Ratsnakes were slightly more successful at night (60% vs. 57%), the effect of light was not significant ($P = 0.50$). The interaction of stimulus type and light, time since last meal, and trial order were all not significant ($P = 0.21$). Ratsnakes did not leave the holding container in seven trials, four during night and three

Fig. 3. Differences in time (mean ± SE) that Ratsnakes (*Elaphe obsoleta*) and Racers (*Coluber constrictor*) moved in a laboratory enclosure under three temperature treatments: optimal day and night temperatures (30 °C); suboptimal night (22 °C) and optimal day temperatures; optimal night and suboptimal day temperatures.



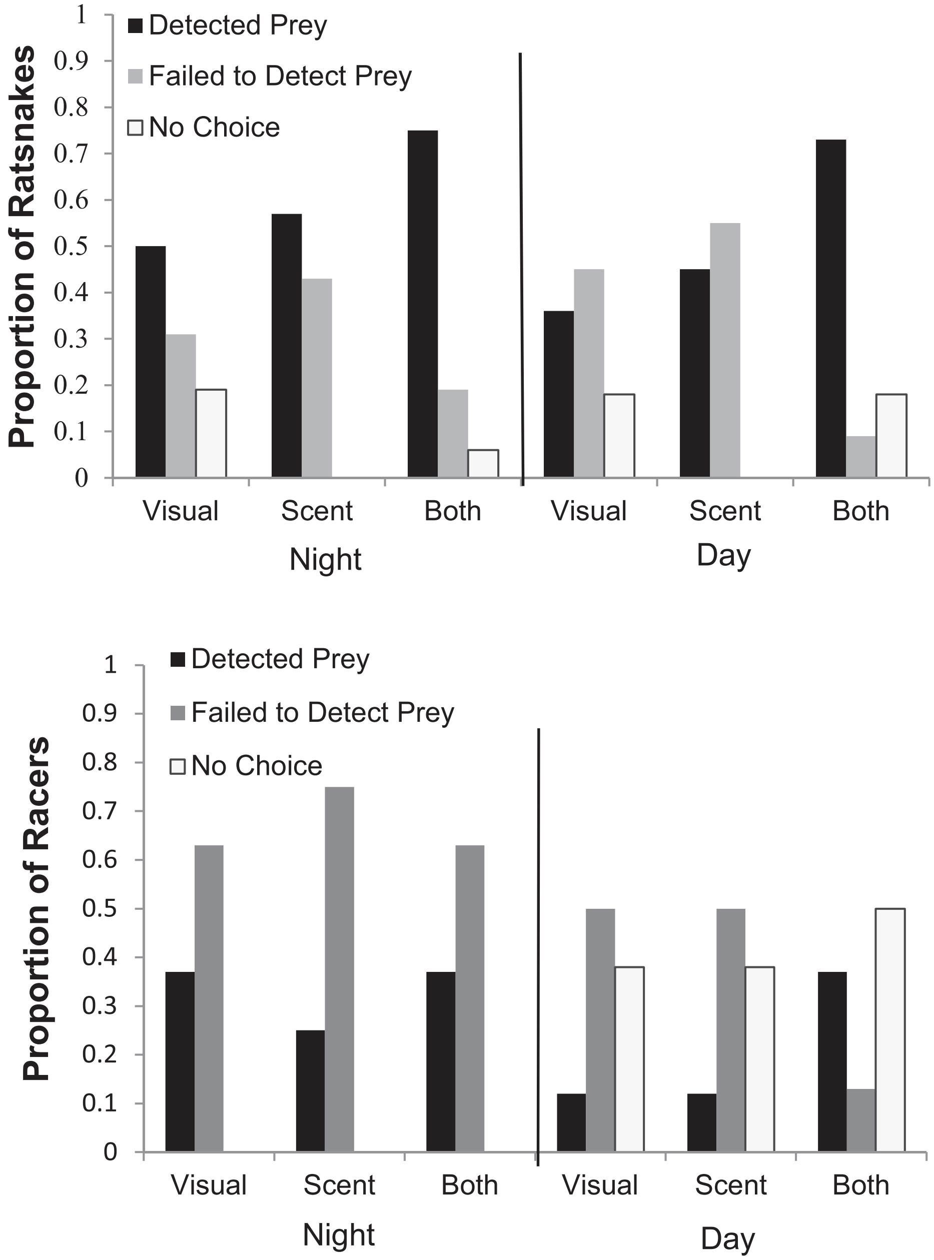
during day. Four of the "no choice" results occurred when only a visual stimulus was presented and the other three when visual and chemical cues were presented together. When only a chemical stimulus was presented, Ratsnakes always made a choice. For Racers, none of the variables had a significant effect on an animal's ability to react to prey ($P = 0.50$). Additionally, Racers did not leave the holding container in 40% of day trials and always left the container in night trials.

For Ratsnakes, stimulus type also had the greatest impact on latency to react to prey ($F_{[2,69]} = 3.76$, $P = 0.03$). When presented with only a chemical stimulus, Ratsnakes reacted to and approached prey more quickly than when a visual stimulus ($P = 0.03$) or both stimuli ($P = 0.07$) were present (Fig. 3). Light treatment, the interaction effect of light and stimulus type, trial order, and time since last meal were all not significant ($P = 0.60$). Racers tended to react to prey more quickly during the day ($P = 0.08$; Fig. 4). Stimulus type, the interaction between stimulus type and light, time since last meal, and trial order all had no significant effects on latency to react to prey for Racers ($P = 0.25$; Fig. 5).

Discussion

Ratsnakes were more active when temperature was optimal, regardless of whether it was light or dark, suggesting their ability to switch between diurnal and nocturnal activities is genuinely plastic. Interestingly, Ratsnakes appeared capable of altering activity patterns in response to short-term proximate cues (temperature and light). Ratsnakes in the wild shift from diurnal to nocturnal behaviour gradually over periods of weeks or months (Sperry et al. 2013). Although relatively little is known about reptilian circadian rhythms (Oishi et al. 2004), many species appear to have internal, entrained clocks that operate in the absence of light or temperature cues (Klein et al. 2006; Ellis et al. 2006). The rapid shifts in timing of activity by

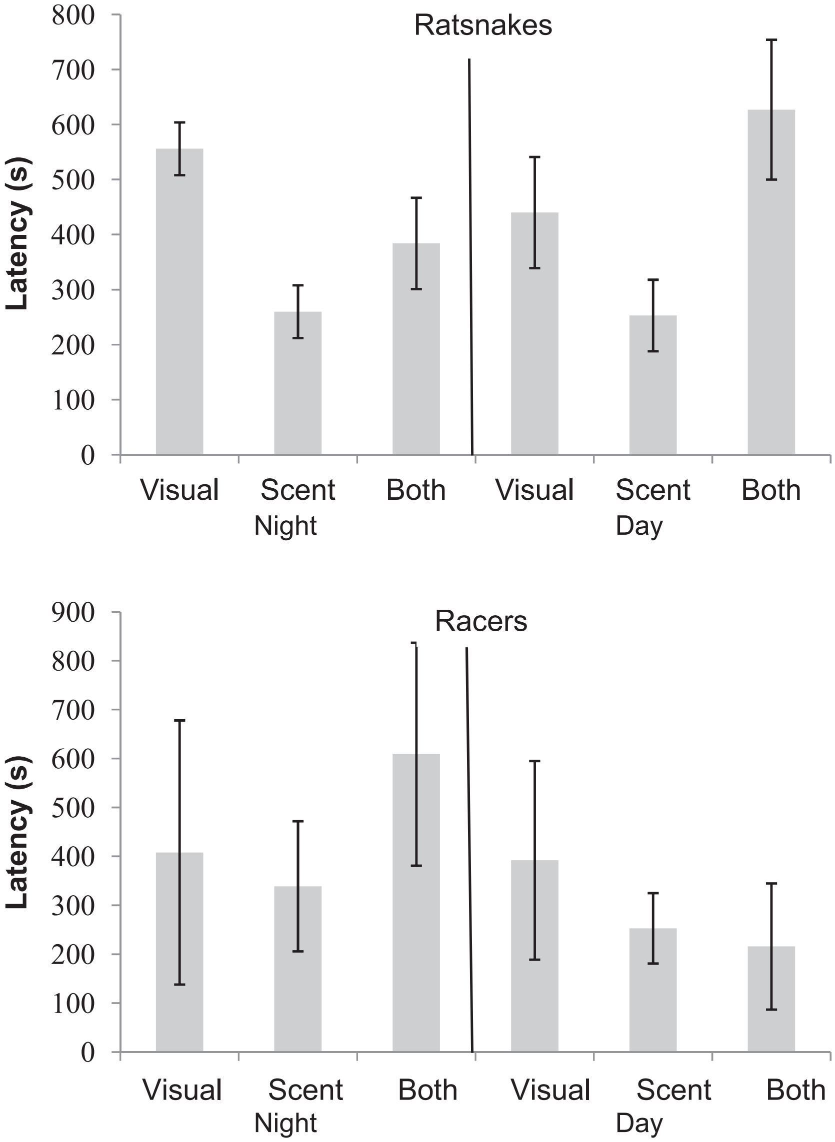
Fig. 4. Proportion of Ratsnakes (*Elaphe obsoleta*) and Racers (*Coluber constrictor*) that reacted to prey in either high or low light conditions.



Ratsnakes indicate that whatever circadian rhythms they possess do not prevent these snakes from responding to short-term changes in environmental factors. Consistent with this flexibility, Ratsnakes successfully reacted to prey in both low and high light. Contrary to our prediction that they would switch sensory modalities, regardless of light conditions Ratsnakes were most successful reacting to prey when both visual and chemical cues were provided, but also reacted to prey when either cue was available alone. Racers were almost exclusively diurnal, regardless of temperature. When daytime temperatures were suboptimal, Racers simply became less active. Unfortunately, the foraging experiments were not informative regarding whether Racers are exclusively diurnal due to an inability to forage at night. Under both light conditions, Racers "located" prey at chance levels, although their behaviour suggested that they were primarily motivated either to hide or to escape from the apparatus. Thus, we restrict most of the discussion to the implications of our results for Ratsnakes.

Ratsnakes are major avian nest predators (Weatherhead and Blouin-Demers 2004) and prey on nests during the day and at night (Thompson and Burhans 2003), with potentially severe consequences for birds whose nests are located at night. Reidy et al. (2009) reported that in 75% of cases when Ratsnakes find nests at night, the attending female is eaten by the snake with the contents of the nest. Despite their importance as nest predators, however, we know little about how Ratsnakes find nests. We hypothesized that Ratsnakes would be visually oriented hunters during the day and olfactory hunters at night. Mullin and Cooper (1998) showed that Ratsnakes in captivity used the visual cue of an animated bird on a string to locate a nest cavity more quickly. Although those results indicate that Ratsnakes can use vision, the experiment was conducted only in daylight and used only visual

Fig. 5. Latency (mean ± SE) of Ratsnakes (*Elaphe obsoleta*) and Racers (*Coluber constrictor*) to react to prey in either day or night conditions. Trials for which snakes did not leave the holding container in the 30 min period are excluded.



cues. Our results indicate that Ratsnakes do not change sensory modalities between day and night, but rather use coupled stimuli during both periods. Synergy between visual and olfactory cues has been identified as an important foraging stimulus for other snake species (Heinen 1995; Shivik et al. 2000). Complicating our understanding of Ratsnake foraging strategies are observations suggesting that snakes may sometimes locate nests during the day and wait until nightfall to prey on them (Stake et al. 2005), although confirmation that this actually occurs, and if so, how frequently, has not been obtained.

Many snake species switch from diurnal to nocturnal behaviour seasonally (Gibbons and Semlitsch 1987). Presumably, this shift occurs in response to changing temperatures. However, other factors influence the seasonal rhythms of snakes including photoperiods (Ellis et al. 2006) and hormones (Lutterschmidt et al. 2002, Lutterschmidt and Mason 2010). Ratsnakes display some nocturnal activity even near the northern extent of their geographic range (Sperry et al. 2013). At northern latitudes it is unlikely that extreme temperatures force snakes to switch to nocturnal activity, but rather releases them from strict diurnal activity. If nocturnal activity confers foraging benefits to flexible predators (e.g., the capture of adult birds), plasticity in timing of activity could provide substantial advantages. This raises the question of why some snake species (e.g., Racers) have not evolved the ability to switch between diurnal and nocturnal activities. Despite the perspective that snakes are generally quite flexible in when they are active (Gibbons and Semlitsch 1987), little is known about the activity patterns of most snake species and even less about their foraging ecology. Further investigations into interactions between snakes and their prey are needed. Additionally, studies are needed on more snake species relating sensory modalities to foraging ecology. Very little is known regarding the visual acuity of most snake species and how this may vary between species. Limited evidence indicates North American colubrids have keen eyesight (Baker et al. 2007), but we do not know how visual acuity varies with light levels and among species.

In addition to temperature, photoperiods, and hormones influence reptile circadian rhythms (Oishi et al. 2004; Ellis et al. 2006; Klein et al. 2006). Performance of diurnal or nocturnal species may be adversely affected if tested during times when they are not typically active (Llewelyn et al. 2006). Because we conducted all of our foraging tests during the day, Racers should not have been at a performance disadvantage relative to Ratsnakes, so constraints associated with underlying circadian rhythms cannot explain the inability of Racers to locate prey. Additionally, Ratsnakes should not have been at a disadvantage because they never entirely abandon diurnal activity for strict nocturnality even at the southern portions of their range (Sperry et al. 2013).

As climates change, many animals adjust their phenology (e.g., Visser and Both 2005), including diel and seasonal changes in activity (Parmesan 2007). Animals with more plastic traits may survive better in a changing world. Ectotherms may need to mediate the effects of climate warming behaviourally by shifting their activity and spending more time inactive or in retreats (Huey et al. 2009; Kearney et al. 2009). Rising temperatures throughout the geographic range of both Ratsnakes and Racers (IPCC 2007) will result in more frequent inhospitable daytime temperatures. Our results indicate that Ratsnakes should be able to respond to such temperatures by increasing nocturnal activity, supporting Weatherhead et al.'s (2012) suggestion that shifts in diel activity rather than seasonal activity should be sufficient for Ratsnakes to respond successfully to warmer climates. The less flexible Racer may not be able to respond to climate change behaviourally (Huey and Tewksbury 2009; Sears and Angilletta 2011) and may face the same deleterious consequences of warming currently facing diurnal lizards (Sinervo et al. 2010). Again, the dearth of detailed studies of snake activity and sensory ecology limit our ability to generalize how climate warming will affect most snakes.

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