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Female Eastern Hog-nosed Snakes (*Heterodon platirhinos*) choose nest sites that produce offspring with phenotypes likely to improve fitness

C.A. Peet-Paré and G. Blouin-Demers

Abstract: Nest-site selection is an important behaviour in oviparous reptiles because incubation conditions affect offspring phenotype, with favourable conditions leading to higher offspring fitness. We aimed to identify the habitat characteristics involved in nest-site selection in Eastern Hog-nosed Snakes (*Heterodon platirhinos* Latreille, 1801) and to determine whether females select nest sites that result in offspring with phenotypes likely to improve fitness. We compared the habitat characteristics and temperature profiles of 21 nests with 21 randomly selected sites. Eastern Hog-nosed Snakes selected open, grassy sites with less herbs and shrubs than random sites, and nests were significantly warmer than random sites during the 2 years of the study. In the second year of the study, we incubated 215 eggs from eight nests in a split-clutch design at mean nest (24 °C) and random site (22 °C) temperatures approximating those of the first year of the study. Eggs incubated at 24 °C resulted in neonates that hatched earlier, had fewer scale anomalies, were larger, and swam faster than neonates from eggs incubated at 22 °C. Our results indicate that Eastern Hog-nosed Snakes select nest sites that lead to offspring with phenotypes likely to improve fitness.

Key words: Eastern Hog-nosed Snake, *Heterodon platirhinos*, nest-site selection, incubation, split-clutch design, oviparity.

Résumé : Le choix du site de nidification est un comportement important chez les reptiles ovipares puisque les conditions d'incubation ont une incidence sur le phénotype de la progéniture, des conditions favorables se traduisant par une plus grande aptitude de celle-ci. Notre objectif était de cerner les caractéristiques de l'habitat qui entrent en ligne de compte dans le choix du site de nidification chez les couleuvres à nez plat (*Heterodon platirhinos* Latreille, 1801) et de déterminer si les femelles choisissent des sites de nidification qui se traduisent par une progéniture dont les phénotypes peuvent vraisemblablement améliorer leur aptitude. Nous avons comparé les caractéristiques de l'habitat et les profils de température de 21 sites de nidification et de 21 sites choisis au hasard. Les couleuvres à nez plat ont choisi des sites herbeux et ouverts présentant moins de plantes herbacées et d'arbustes que les sites choisis au hasard, et la température des nids était significativement plus élevée que celles des sites aléatoires durant les deux années de l'étude. Pendant la deuxième année, nous avons incubé 215 œufs provenant de huit nids selon un schéma de nichée fractionnée à des températures moyennes des nids (24 °C) et des sites choisis au hasard (22 °C) reflétant les températures mesurées durant la première année de l'étude. Les œufs incubés à 24 °C ont donné des nouveau-nés qui ont éclos plus tôt, présentaient moins d'anomalies d'écailles, étaient plus grands et nageaient plus vite que les nouveau-nés provenant d'œufs incubés à 22 °C. Nos résultats indiquent que les couleuvres à nez plat choisissent des sites de nidification qui se traduisent par une progéniture dont les phénotypes améliorent vraisemblablement leur aptitude.

Mots-clés : couleuvre à nez plat, *Heterodon platirhinos*, choix du site de nidification, incubation, schéma de nichée fractionnée, oviparité.

[Traduit par la Rédaction]

Introduction

Most oviparous reptiles abandon their eggs after laying them. This means that the only form of parental care is the selection of the site in which the eggs will develop. Nest-site selection has thus been studied extensively in reptiles (Burger and Zappalorti 1986; Doody et al. 2006; Escalona et al. 2009; Pike et al. 2010; Refsnider et al. 2010). The physical conditions an egg experiences during incubation affect offspring phenotype and survival (Shine 2003; Brown and Shine 2004). One of the most important factors that affect offspring

development during incubation is temperature (Booth 2006). Incubation temperatures can determine neonate sex and can influence offspring morphology and behaviour (Shine 2003; Booth 2006). Experimental studies on the effects of incubation temperature on snake neonate development have found evidence that mean incubation temperature, and temperature variance, have implications for offspring fitness (Burger 1989, 1990, 1998; Blouin-Demers et al. 2004; Patterson and Blouin-Demers 2008). These findings show that female snakes can potentially increase the fitness of their offspring by selecting nest sites with optimal incubation temperatures

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(Webb et al. 2001; Blouin-Demers et al. 2004; Booth 2006). Despite the growing evidence of incubation mediated phenotypic plasticity, however, few studies to date have put this phenomenon in an ecologically relevant context (but see Huang and Pike 2011, 2012). Studies of incubation effects often lack information on female nest-site selection and on factors that affect the success of nest sites that are selected in the wild. Without information on natural variation in incubation temperature, one cannot be certain that laboratory incubation treatments actually represent variation that natural selection could act upon.

The habitat characteristics of a nest site are important because they determine the temperature within it, and may influence whether a female chooses to use a site (Burger and Zappalorti 1986). Although descriptions of snake nest sites exist for a number of species (Sexton and Claypool 1978; James and Henderson 2004; Cunningham and Cebek 2005), few studies actually quantify nest-site microhabitat selection (Burger and Zappalorti 1986). By comparing nest sites to available but unused surrounding sites, the habitat characteristics that are important in nest-site selection can be identified (Burger and Zappalorti 1986).

In this study, we compared the temperature profiles and habitat characteristics of nest sites excavated by Eastern Hog-nosed Snakes (*Heterodon platirhinos* Latreille, 1801) with randomly selected sites. We also incubated eggs of Eastern Hog-nosed Snakes at mean nest and mean random site temperatures typical of the first year of the study to determine the effects of temperature on neonate morphology and behaviour. We tested the hypothesis that female Hog-nosed Snakes select particular nest sites because these nest sites produce offspring with phenotypes likely to improve fitness.

Materials and methods

Study species

Eastern Hog-nosed Snakes are heavy-bodied snakes that lay 25 eggs, on average (Cunnington and Cebek 2005; current study). Eastern Hog-nosed Snakes are an ideal species for this study due to their nesting behaviour. Female Hog-nosed Snakes excavate sandy soil to create a burrow in which to lay their eggs (Cunnington and Cebek 2005). Because the snakes excavate the nests themselves, rather than locating nest sites opportunistically, they are a good choice for a study on nest-site selection (Burger and Zappalorti 1986). A pile of sand at the opening of the nest also makes nest sites easy to identify (Cunnington and Cebek 2005).

Study site

We conducted the study from June 2009 to September 2010 in two areas of Norfolk County, Ontario, Canada. Over the 2 years of the study, we found 21 nests of Eastern Hog-nosed Snakes. We identified nests by the distinctive sand pile at their entrance. We excavated each nest to confirm the presence of eggs. The nest depths ranged from 7.0 to 20.1 cm, and each consisted of a long, partially sand-filled tunnel ending in an egg chamber. The tunnels were up to 1 m long.

Temperature profiles

We placed temperature logging iButtons (DS1921 and DS1922; Dallas Semiconductor, Sunnyvale, California, USA)

in the nests and then refilled the nests. We selected a random site for each nest site. We chose random sites by walking 50 m from the nest in a random direction selected by blindly spinning the bearing dial of a magnetic compass (see Blouin-Demers and Weatherhead 2001). The 50 m distance ensured that all random sites fell within the open sandy habitat that is used for nesting by Hog-nosed Snakes. We placed temperature loggers within random sites at the same depth as their corresponding nest site. We programmed the temperature loggers to record temperature every 30 min. We used temperature data from 8 July to 19 August in both 2009 and 2010 in the analyses.

Microhabitat selection

We measured several habitat characteristics at the sites (Table 1) following the protocol used by Blouin-Demers and Weatherhead (2001). Grass was defined as any grass or grass-like sedge species. Shrubs were defined as perennial species with woody stems, while herbs were defined as annual plant species. Ground cover was measured using a plastic sighting tube (2.5 cm diameter, 25 cm long) with cross-hairs at one end. The tube was randomly pointed at the ground 20 times within a 1 m radius area that was centred on the nest, and the type of vegetative ground cover that intersected the cross-hairs was recorded. The results were then multiplied by five to get a percentage of ground cover for each cover type. Canopy cover was recorded in the same way. The observer lay next to the site and pointed the tube randomly within a 45° cone. Only canopy cover from trees with a diameter at breast height larger than 7.5 cm was recorded. Edge was deemed to be the beginning of a continuous stretch of forest. Habitat characterisations were performed before sites were excavated to ensure that the habitat was undisturbed.

Egg collection and incubation

In 2010, we removed and incubated eggs from eight nests. Clutch size ranged from 17 to 40 eggs, with a mean of 28.3 eggs. We based incubation temperatures on the nest- and random-site temperatures measured in 2009. The mean (\pm SD) temperature of the nests in 2009 was 24.6 ± 3.3 °C, while the random-site mean temperature was 22.2 ± 2.1 °C. We randomly divided clutches with half the eggs of each clutch incubated at 22 °C and the other half at 24 °C. The incubator consisted of two attached compartments and was made of foam insulated plastic. Each compartment had a thermostat attached to a 100 W bulb to control the temperature and a small fan to circulate air. We placed eggs in plastic containers with a 2:1 (by mass) mixture of water and vermiculite and half buried them in the substrate. We placed a temperature logging iButton (DS1922; Dallas Semiconductor, Sunnyvale, California, USA) in each compartment to record the temperature during incubation. We weighed containers at the beginning of the incubation and reweighed them every second day throughout incubation. This allowed us to replace water that had evaporated and to change the positions of the containers in the incubator (to avoid positional effects).

Phenotypic measurements

We checked eggs twice daily towards the end of the incubation period. We removed any neonates that had emerged

Table 1. Habitat variables (mean \pm SD) measured at Eastern Hog-nosed Snake (*Heterodon platirhinos*) nest sites and random sites in 2009 and 2010 with associated abbreviations.

Variable	Description	Nest site	Random site
%grass	Grass coverage (%) in 1 m radius	54.1 \pm 15.8	19.8 \pm 20.2
%leaves	Leaf coverage (%) in 1 m radius	3.4 \pm 4.5	5.1 \pm 8.9
%sticks	Stick coverage (%) in 1 m radius	0.1 \pm 0.4	3.0 \pm 6.1
%moss	Moss coverage (%) in 1 m radius	7.4 \pm 15.2	8.7 \pm 13.8
%sand	Sand coverage (%) in 1 m radius	31.5 \pm 11.3	32.4 \pm 34.9
%shrub	Shrub coverage (%) in 1 m radius	1.3 \pm 4.9	17.1 \pm 18.9
%herb	Herb coverage (%) in 1 m radius	2.1 \pm 2.8	13.9 \pm 13.8
slope	Slope (%) in 1 m radius	4.4 \pm 5.7	2.3 \pm 3.6
slopeasp	Slope aspect (°) in 1 m radius	109.1 \pm 137.0	95.6 \pm 129.5
cancover	Canopy coverage (%) in a 45° cone	3.0 \pm 4.2	13.0 \pm 20.0
canheight	Mean height (m) of canopy in a 45° cone	6.7 \pm 8.2	8.6 \pm 7.0
distedge	Distance (m) to nearest edge	17.8 \pm 7.4	13.8 \pm 8.1

from their eggs and recorded their response to first handling (being picked up from the incubation container). We scored behaviours as follows: 0, no response; 1, hissing; 2, flattening their body; 3, attempting to escape; 4, striking; 5, playing dead. If more than one behaviour was displayed, the snake received a total score based on the sum of all responses. Therefore, possible scores ranged from 0 to 15. Our scoring system reflected the natural escalation of antipredator responses in Hog-nosed Snakes.

We took further measurements within 3 days of hatching. We sexed neonates using a small probe to detect the presence of hemipenes. We measured snout–vent length (SVL) and tail length to the nearest millimetre by placing neonates beside a taped-down wooden ruler. SVL was based on a mean of two measurements, although measurements never varied by more than 1 mm. We weighed neonates using a spring scale accurate to 0.5 g. We also recorded the number of split ventral scales (Forsman et al. 1994; Blouin-Demers et al. 2004; Löwenborg et al. 2011). We recorded neonate swimming speed in a swim trough with 2.5 cm deep of 24 °C water (based upon Blouin-Demers et al. 2004). Neonates swam a distance of 2 m with the swim time over the middle 1.5 m recorded with a stopwatch. We encouraged neonates to swim rapidly by gently tapping their tails, and the fastest time out of two trials was recorded. Although Eastern Hog-nosed Snakes are terrestrial, we chose to measure swimming speed instead of crawling speed because of the death feigning response of this snake (when handled they often respond by playing dead), and because previous studies documented that neonates react defensively when on land (Blouin-Demers et al. 2004). Forcing them to swim, as opposed to crawl, did not elicit defensive strikes or death feigning and allowed us to measure locomotion speed.

The procedures used in this study were approved by the Animal Care Committee of the University of Ottawa (protocol BL-244) and are in accordance with the guidelines of the Canadian Council on Animal Care.

Analyses

We located 21 nests and measured 12 habitat variables at these nests and at the 21 paired random locations. Given our modest sample of nests, we were unable to enter all 12 habitat variables in a MANOVA. We therefore ran preliminary

univariate analyses (ANOVAs for the effect of nest type on each variable) and retained the five variables (%grass, %sticks, %shrub, %herb, and cancover) that had P values < 0.10 in these univariate analyses.

Because neonate SVL and mass were highly correlated ($r = 0.76$), we only used SVL as our measure of neonate size. Because there are major genetic influences on morphology and performance (Blouin-Demers et al. 2004; Patterson and Blouin-Demers 2008), we included clutch ID as a control variable in our analyses dealing with morphology and performance. In addition, ANOVA with clutch ID included as a control variable revealed that there was sexual size dimorphism in both tail length ($F_{[1,176]} = 133.4$, $P < 0.001$) and SVL ($F_{[1,176]} = 40.9$, $P < 0.001$) in our neonates with, on average, males having tails 3.8 mm longer, but females being 6.1 mm longer. We therefore also included sex as a control variable in subsequent analyses of morphology and performance. All statistical analyses were conducted on JMP version 8.0 (SAS Institute Inc., Cary, North Carolina, USA) and we accepted significance at $\alpha = 0.05$.

Results

MANOVA with the five retained habitat variables (%grass, %sticks, %shrub, %herb, and cancover) as response variables and location type (nest or random site) as the predictor variable revealed a significant multivariate habitat difference between nests and random sites ($F_{[5,36]} = 50.46$, $P < 0.001$). Nests had more grass, but less shrub, herb, and canopy cover than random sites. Thus, nests were in more open microhabitats than random sites, which explains why they were, on average, warmer than random sites. In 2009, the mean (\pm SD) temperature of the nine nests was 24.6 ± 3.3 °C, while the mean temperature of the nine random sites was 22.2 ± 2.1 °C. In 2010, an unusually warm year in our study area, the mean (\pm SD) temperature of the 12 nests was 27.4 ± 2.6 °C, while the mean temperature of the 12 random sites was 26.2 ± 2.8 °C. Importantly, the mean hourly temperature in nests was higher than the mean hourly temperature in random sites in both 2009 (paired $t_{[2015]} = 75.90$, $P < 0.001$, mean difference 2.4 °C) and 2010 (paired $t_{[2015]} = 88.03$, $P < 0.001$, mean difference 1.2 °C).

The 22 °C incubator had a mean (\pm SD) temperature of 22.7 ± 0.04 °C, while the 24 °C incubator had a mean tem-

perature of 24.5 ± 0.04 °C, which are very close to the mean temperatures recorded in random sites and nests, respectively, in 2009. We incubated 215 eggs and 185 hatched (hatching success per clutch averaged $82.6\% \pm 7.1\%$). A paired t test revealed that hatching success was not different between the two incubation treatments ($t_{171} = 0.27$, $P = 0.79$). Sex ratios were not significantly biased at 22 °C (53 females and 41 males, $\chi^2_{[1]} = 1.54$, $P = 0.22$) or at 24 °C (43 females and 48 males, $\chi^2_{[1]} = 0.27$, $P = 0.60$). ANOVA with incubation temperature and clutch ID as predictors and hatch date as a response variable indicated that, on average, eggs incubated at 22 °C hatched 13 days later than those incubated at 24 °C ($F_{[1,6]} = 960.98$, $P < 0.001$). ANOVAs with clutch ID, sex, and incubation treatment entered as predictor variables revealed that neonates arising from eggs incubated at 24 °C were longer ($F_{[1,175]} = 50.46$, $P < 0.001$, mean difference = 3.2 mm; Fig. 1), were less likely to have split ventral scales ($F_{[1,175]} = 50.46$, $P = 0.003$, 14.9% of individuals at 22 °C versus 2.2% of individuals at 24 °C), swam faster ($F_{[1,174]} = 162.54$, $P < 0.001$, mean difference = 0.045 m/s; Fig. 1), but were not different in their response to handling ($F_{[1,174]} = 1.91$, $P = 0.17$).

Discussion

Microhabitat selection

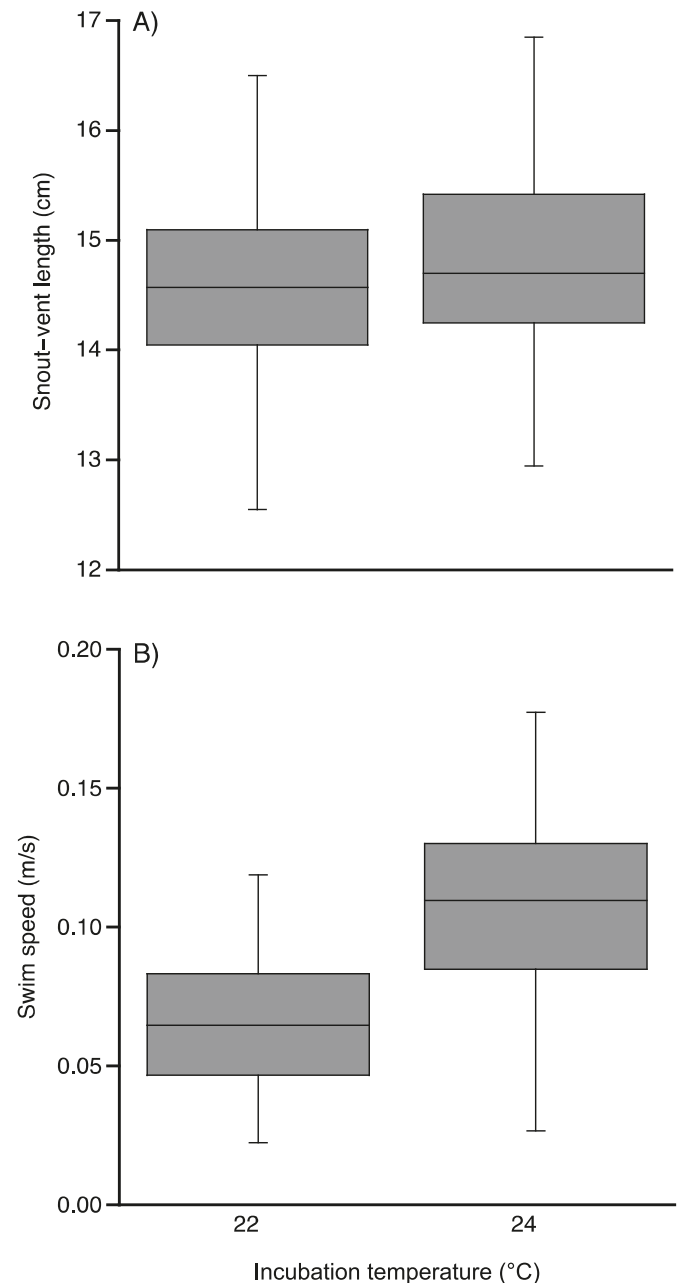
Female Eastern Hog-nosed Snakes selected open, grassy sites with few herbs and shrubs to nest. These results mirror those of Burger and Zappalorti (1986) in their study of nest-site selection of Pine Snakes (*Pituophis melanoleucus* (Daudin, 1803)), which is probably due to the similarity in nesting behaviour between Eastern Hog-nosed Snakes and Pine Snakes (Burger and Zappalorti 1986; Cunnington and Cebek 2005). Sites with more herbs and shrubs likely have more roots and therefore may be more difficult to excavate (Burger and Zappalorti 1986). Increased ground cover could also reflect and absorb sunlight and so reduce the amount of radiant energy reaching the nest itself. Grass may be more common at nest sites simply because it is found where shrubs and herbs are not. Sites with grass could also be chosen because they provide some roots which help prevent nests from collapsing during excavation (Burger and Zappalorti 1986). Moisture levels have also been shown to affect neonate fitness (Plummer and Snell 1988; Brown and Shine 2004, 2006), so it is possible that increased vegetation has an effect on the amount of water able to reach the eggs.

Open sites were most likely selected because of the increased sunlight penetration, which led to higher temperatures in nests than in random sites. Because temperature is so important in neonate development, it is possible that the snakes choose sites based solely on canopy cover (and therefore temperature) (Shine 2003; Booth 2006). This means that the type of ground cover may be a result of the amount of canopy cover and, therefore, incidental. Indeed, in our sample of nests and random sites, locations with closed canopies tended to have more shrubs ($r = 0.50$ between cancover and %shrub).

Temperature profiles

Nests were, on average, approximately 2 °C warmer than random sites. Nest temperatures were similar to Eastern

Fig. 1. Neonate Eastern Hog-nosed Snakes (*Heterodon platirhinos*) ($n = 91$) emerging from eggs incubated at temperatures typical of nest sites selected by females are longer (A) and swim faster (B) than those emerging from eggs incubated at temperatures typical of sites selected at random ($n = 94$). Box plots indicate the range, median, 25% quartile, and 75% quartile.



Hog-nosed Snake nest temperatures recorded by Cunnington and Cebek (2005) at the same latitude. A study on nests of Black Ratsnakes (*Elaphe obsoleta* (Say in James, 1823)) at the same latitude, however, recorded higher temperatures (Blouin-Demers et al. 2004). Mean temperatures of nests of Black Ratsnakes ranged from 22.2 to 31.8 °C, with a communal nest mean temperature of 27.9 °C (Blouin-Demers et al. 2004). The lower temperatures of nests of Eastern Hog-nosed Snakes are likely due to their location within sandy soil as opposed to decomposing organic debris. Black Rat-

snakes and many other snake species lay eggs in leaves, wood, and other organic litter that releases heat as it decomposes, warming the eggs (Burger and Zappalorti 1986; Blouin-Demers et al. 2004; Löwenborg et al. 2010). Eggs laid in sand gain heat from solar radiation warming the ground only, and so nests are cooler. In sand, shallow nests would be warmer, but may come with added risks such as increased predation and the risk of egg exposure by weather. Deeper nests may also have a more stable environment with less thermal and hydric variation.

Phenotypic measurements

Eggs incubated at 24 °C resulted in neonates that were longer, faster, and had fewer scale anomalies compared with those incubated at 22 °C. Eggs incubated at 24 °C also hatched, on average, 13 days before those incubated at 22 °C. There were no significant differences in hatching success or response to handling between treatments. The shorter incubation period of the 24 °C eggs is an advantage because a reduced incubation period provides neonates with extra time to feed and to find a place to hibernate before winter. This is especially important at the northern extreme of the range, as snakes have to begin hibernation soon after hatching. Adult snakes in this population begin hibernation from early September to early October (Robson 2011). If neonates begin hibernation at similar dates, late-hatching snakes would have only a few weeks before hibernation. Early hatching also provides a head start in neonate growth, which is an advantage because larger snakes have a higher survival rate (Brown and Shine 2004; Kissner and Weatherhead 2005).

In addition to the earlier hatching date, neonates from the 24 °C treatment were already significantly larger at hatching and therefore more likely to survive (Brown and Shine 2004; Kissner and Weatherhead 2005). Because hatchling snakes are easy prey and because neonate Eastern Hog-nosed Snakes emerge in open sandy habitat, faster neonates can find cover more quickly to avoid predation. Newly hatched snakes also need to dig their way out of the nest through packed sand and plant roots and so increased size and strength are an advantage. Scale anomalies are known to be indicators of developmental issues such as fused vertebrae (Forsman et al. 1994; Blouin-Demers et al. 2004; Löwenborg et al. 2011). Löwenborg et al. (2011) found evidence that scale anomalies lead to a lower survival rate.

Although no significant difference was found between treatments in response to first handling, this behaviour may be less important early on because neonates are too small to intimidate predators with defensive displays. Therefore, escape from predators may be mostly dependant on neonate speed. It is intriguing that similar studies involving other snake species have found significant differences in neonate behaviour at different incubation temperatures (Burger 1990, 1998b; Blouin-Demers et al. 2004; Patterson and Blouin-Demers 2008).

In conclusion, because eggs incubated at nest temperatures resulted in neonates with phenotypes likely to lead to higher fitness than those incubated at random-site temperatures, we provide support for the hypothesis that female Eastern Hog-nosed Snakes select particular nest sites because they produce offspring phenotypes that likely improve fitness.

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References

- Blouin-Demers, G., and Weatherhead, P.J. 2001. Habitat use by black rat snakes (*Elaphe obsoleta obsoleta*) in fragmented forests. *Ecology*, **82**: 2882–2896. doi:10.1890/0012-9658(2001)082[3025:TEOBRS]2.0.CO;2.
- Blouin-Demers, G., Weatherhead, P.J., and Row, J.R. 2004. Phenotypic consequences of nest-site selection in black rat snakes (*Elaphe obsoleta*). *Can. J. Zool.* **82**(3): 449–456. doi:10.1139/z04-014.
- Booth, D.T. 2006. Influence of incubation temperature on hatchling phenotype in reptiles. *Physiol. Biochem. Zool.* **79**(2): 274–281. doi:10.1086/499988. PMID:16555187.
- Brown, G.P., and Shine, R. 2004. Maternal nest-site choice and offspring fitness in a tropical snake (*Tropidonophis mairii*, Colubridae). *Ecology*, **85**(6): 1627–1634. doi:10.1890/03-0107.
- Brown, G.P., and Shine, R. 2006. Effects of nest temperature and moisture on phenotypic traits of hatchling snakes (*Tropidonophis mairii*, Colubridae) from tropical Australia. *Biol. J. Linn. Soc.* **89**(1): 159–168. doi:10.1111/j.1095-8312.2006.00669.x.
- Burger, J. 1989. Incubation temperature has long-term effects on behavior of young pine snakes (*Pituophis melanoleucus*). *Behav. Ecol. Sociobiol.* **24**(4): 201–207. doi:10.1007/BF00295199.
- Burger, J. 1990. Effects of incubation temperature on behavior of young black racers (*Coluber constrictor*) and kingsnakes (*Lampropeltis getulus*). *J. Herpetol.* **24**(2): 158–163. doi:10.2307/1564223.
- Burger, J. 1998. Effects of incubation temperature on hatchling pine snakes: implications for survival. *Behav. Ecol. Sociobiol.* **43**(1): 11–18. doi:10.1007/s002650050461.
- Burger, J. 1998b. Antipredator behaviour of hatchling snakes: effects of incubation temperature and simulated predators. *Anim. Behav.* **56**(3): 547–553. doi:10.1006/anbe.1998.0809. PMID:9784202.
- Burger, J., and Zappalorti, R.T. 1986. Nest site selection by pine snakes, *Pituophis melanoleucus*, in the New Jersey pine barrens. *Copeia*, **1986**(1): 116–121. doi:10.2307/1444896.
- Cunnington, G.M., and Cebek, J.E. 2005. Mating and nesting behavior of the eastern hognose snake (*Heterodon platirhinos*) in the northern portion of its range. *Am. Midl. Nat.* **154**(2): 474–478. doi:10.1674/0003-0031(2005)154[0474:MANBOT]2.0.CO;2.
- Doody, J.S., Guarino, E., Georges, A., Corey, B., Murray, G., and Ewert, M. 2006. Nest site choice compensates for climate effects on sex ratios in a lizard with environmental sex determination. *Evol. Ecol.* **20**(4): 307–330. doi:10.1007/s10682-006-0003-2.
- Escalona, T., Valenzuela, N., and Adams, D.C. 2009. Nesting ecology in the freshwater turtle *Podocnemis unifilis*: spatiotemporal patterns and inferred explanations. *Funct. Ecol.* **23**(4): 826–835. doi:10.1111/j.1365-2435.2009.01562.x.
- Forsman, A., Merila, J., and Lindell, L.E. 1994. Do scale anomalies cause differential survival in *Vipera berus*? *J. Herpetol.* **28**(4): 435–440. doi:10.2307/1564955.
- Huang, W.-S., and Pike, D.A. 2011. Climate change impacts on

- fitness depend on nesting habitat in lizards. *Funct. Ecol.* **25**(5): 1125–1136. doi:10.1111/j.1365-2435.2011.01855.x.
- Huang, W.-S., and Pike, D.A. 2012. Effects of intraguild predators on nest-site selection by prey. *Oecologia (Berl.)*, **168**(1): 35–42. doi:10.1007/s00442-011-2060-7. PMID:21739239.
- James, A., and Henderson, R.W. 2004. Communal nesting site in the snake *Liophis juliae* in Dominica, West Indies. *Caribb. J. Sci.* **40**: 263–265.
- Kissner, K.J., and Weatherhead, P.J. 2005. Phenotypic effects on survival of neonatal northern watersnakes *Nerodia sipedon*. *J. Anim. Ecol.* **74**(2): 259–265. doi:10.1111/j.1365-2656.2005.00919.x.
- Löwenborg, K., Shine, R., Kärvmemo, S., and Hagman, M. 2010. Grass snakes exploit anthropogenic heat sources to overcome distributional limits imposed by oviparity. *Funct. Ecol.* **24**(5): 1095–1102. doi:10.1111/j.1365-2435.2010.01730.x.
- Löwenborg, K., Shine, R., and Hagman, M. 2011. Fitness disadvantages to disrupted embryogenesis impose selection against suboptimal nest-site choice by female grass snakes, *Natrix natrix* (Colubridae). *J. Evol. Biol.* **24**(1): 177–183. doi:10.1111/j.1420-9101.2010.02153.x. PMID:20964787.
- Patterson, L.D., and Blouin-Demers, G. 2008. The effect of constant and fluctuating incubation temperatures on the phenotype of black rat snakes (*Elaphe obsoleta*). *Can. J. Zool.* **86**(8): 882–889. doi:10.1139/Z08-067.
- Pike, D.A., Webb, J.K., and Shine, R. 2010. Nesting in a thermally challenging environment: nest-site selection in a rock-dwelling gecko, *Oedura lesueurii* (Reptilia: Gekkonidae). *Biol. J. Linn. Soc.* **99**(2): 250–259. doi:10.1111/j.1095-8312.2009.01353.x.
- Plummer, M.V., and Snell, H.L. 1988. Nest site selection and water relations of eggs in the snake, *Opheodrys aestivus*. *Copeia*, **1988**(1): 58–64. doi:10.2307/1445922.
- Refsnider, J.M., Daugherty, C.H., Keall, S.N., and Nelson, N.J. 2010. Nest-site choice and fidelity in tuatara on Stephens Island. *N.Z. J. Zool.* **280**: 396–402.
- Robson, L.E. 2011. The spatial ecology of eastern hognose snakes (*Heterodon platirhinos*): habitat selection, home range size, and the effects of roads on movement patterns. M.Sc. thesis, Department of Biology, University of Ottawa, Ottawa, Ont.
- Sexton, O.J., and Claypool, L. 1978. Nest sites of a northern population of an oviparous snake, *Opheodrys vernalis* (Serpentes, Colubridae). *J. Nat. Hist.* **12**(4): 365–370. doi:10.1080/00222937800770231.
- Shine, R. 2003. Reproductive strategies in snakes. *Proc. R. Soc. Lond. B Biol. Sci.* **270**(1519): 995–1004. doi:10.1098/rspb.2002.2307. PMID:12803888.
- Webb, J.K., Brown, G.P., and Shine, R. 2001. Body size, locomotor speed and antipredator behaviour in a tropical snake (*Tropidonophis mairii*, Colubridae): the influence of incubation environments and genetic factors. *Funct. Ecol.* **15**(5): 561–568. doi:10.1046/j.0269-8463.2001.00570.x.