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Source: Journal of Herpetology, 40(2):285-289. 2006.
Published By: The Society for the Study of Amphibians and Reptiles
DOI: http://dx.doi.org/10.1670/92-05N.1
URL: http://www.bioone.org/doi/full/10.1670/92-05N.1

Journal of Herpetology, Vol. 40, No. 2, pp. 285–289, 2006

Thermal Biology of Reproduction in Female Eastern Foxsnakes (*Elaphe gloydi*)

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ABSTRACT.—**Although females of oviparous snake species presumably would benefit by modifying their thermoregulatory behavior while gravid, few studies have investigated whether gravid females actually thermoregulate differently than nongravid conspecifics in the field. To this end, we recorded body temperatures (T_bs) from female Eastern Foxsnakes (*Elaphe gloydi*) housed in a large seminatural enclosure using temperature-sensitive radio-transmitters. Contrary to our expectations, gravid females did not maintain higher or less variable T_bs than nongravid females. We suspect that the thermal environment available to gravid females at our site may render further increases in thermoregulatory effort, beyond that of nongravid females, unnecessary and potentially detrimental, given possible costs of thermoregulation.**

Reproductive condition can have profound effects on the thermoregulatory behavior of female snakes (Peterson et al., 1993). Whereas changes in thermoregulatory behavior attributable to reproductive condition have been well documented for viviparous snake species (e.g., Graves and Duvall, 1993; Charland, 1995; Dorcas and Peterson, 1998; Brown and Weatherhead, 2000), the subject has been investigated to a lesser extent in oviparous taxa (e.g., Blouin-Demers and Weatherhead, 2001a; Isaac and Gregory, 2004). This disparity is due at least partly to the relatively shorter period of egg retention in oviparous species, with the consequent effect of making changes in thermoregulatory behavior (e.g., increased basking) less amenable to casual observation or quantification. The primary way a female can be expected to change her thermoregulatory behavior while gravid is to make a greater effort to maintain body temperatures (T_bs) optimal for embryogenesis (rate and function); that is, to thermoregulate more "carefully." Of course, maintaining T_bs optimal for embryogenesis could impose additional costs on females, as a result of, for example, depletion of energy reserves (Charland, 1995; Lourdais et al., 2004), increased exposure to predators (Madsen and Shine, 2000), and a reduction in foraging opportunities (Aubret et al., 2005). Presumably, this cost–benefit ratio will vary with site-specific biotic and abiotic factors; thus, it may be adaptive for gravid females to increase thermoregulatory effort in some environments, but not others.

To explore effects of reproductive status on female thermoregulatory behavior in oviparous snakes, we recorded T_bs from Eastern Foxsnakes (*Elaphe gloydi*) housed in a seminatural enclosure using temperature-sensitive radio-transmitters. We hypothesized that despite the relatively short period of egg retention in oviparous snakes, the benefits of thermoregulating carefully would outweigh the associated costs; thus, we predicted that gravid females would maintain higher and less variable T_bs than nongravid females.

MATERIALS AND METHODS

Study Area and Species.—We conducted the study on Pelee Island, situated in the western basin of Lake Erie (41°47′N, 82°40′W). *Elaphe gloydi* is a relatively large (91–137 cm snout–vent length [SVL]), oviparous colubrid (Powell, 1990). In this population, emergence from hibernation occurs from mid-April to mid-May, mating occurs from late May to mid-June, and oviposition occurs from early to mid-July (R. Willson, unpubl. data).

Field-captured snakes were measured, weighed, and sexed. Reproductive condition of females was determined by gentle palpation, visible distension of the abdomen, and confirmed by pre- and postoviposition body mass. We surgically implanted radio-transmitters into 26 female foxsnakes in 1998 and 1999 (mean SVL = 107.6 ± 10.62 cm [SD]; range = 93–130 cm) under isoflurane anesthesia delivered via a precision vaporizer following Reinert and Cundall (1982). Transmitter mass was always less than 3% of snake body mass. Snakes were released 24–48 h postoperative. Transmitter removal procedures were similar except that snakes were often retained an additional 24 h to ensure recovery.

Two temperature-sensitive radio-transmitter models (SI-2T, 8.95–9.6 g; BD-2GT, 1.9 g; Holohil Systems Ltd.) were used for this study. Manufacturer-supplied calibration data were used for new transmitters, whereas for refurbished units, we generated calibration data by placing each transmitter in a swirling water bath (0.3–40°C) against a standardized thermometer. In both cases, we generated third-order regression equations for each transmitter and used them to convert pulse intervals to temperatures.

Seminatural Enclosure.—Because of limited radio-reception range from radio-tagged, free-ranging foxsnakes on Pelee Island, we constructed a seminatural enclosure to keep snakes in a location amenable to continuous radiotelemetric monitoring of T_b. We erected walls of 1-m high flexible sheet metal within a regenerating old field where non–radio-tagged foxsnakes were commonly encountered. The following microhabitats, commonly used as cover by free-ranging foxsnakes, were found within the enclosure: a limestone rock pile, numerous clumps of dead grass, and large patches of herbaceous shrubs. In addition to satisfying the thermal preferences of gravid and nongravid foxsnakes within the enclosure, we also sought to provide the former with an adequate choice of potential nest sites. To that end, nine "nest logs" and five "nest

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piles" were placed within the enclosure, and were modeled after natural foxsnake nests found on Pelee Island (Porchuk, 1996; Porchuk and Brooks, 1995). To supplement natural food sources already available (e.g., rodents and small passerines; R. Willson, pers. obs.), one to three white-footed mice (*Peromyscus leucopus*) were released into the enclosure each morning. The circular enclosure encompassed an area of approximately 1,018 m^2 (36-m diameter); this was significantly larger than other enclosures constructed to investigate snake thermal ecology (e.g., the next largest that we are aware of was 600 m^2; Lee and Mills, 2000).

Temperature Monitoring System.—To assess the thermal environment available to snakes, operative temperatures (T_e; Bakken and Gates, 1975) were measured with copper models following Peterson et al. (1993). Model reliability was gauged by placing models in an exposed location adjacent to a road-killed foxsnake that had a thermistor inserted cloacally to mid-body. The dead snake and models were cooled to the same ambient temperature and measurements were taken at 3-min intervals for 8 h starting at noon. To assess the range of environmental temperatures within the enclosure, two models were placed in areas fully exposed to sunlight, one model was placed within a large shrub, and a "free" transmitter was placed at the bottom of a rock pile. To document the thermal properties of potential foxsnake retreat sites, one model was placed under dead grass, and another model was placed under an overhanging limestone slab. Model temperatures were recorded at 15-min intervals by HOBO data loggers (Onset Computer Corp.); temperatures from the free transmitter were recorded as per the snake T_bs (see below).

Although an automated data acquisition system was not available, we employed a relatively efficient method to record pulse intervals from multiple snakes. A three-element Yagi antenna was mounted adjacent to the enclosure and connected to a single channel receiver (Wildlife Materials Inc., TRX-2000S) in our research cabin via coaxial cable. The receiver's audio output was then connected via a conductor cable to the audio line-in port of a notebook computer. Frequencies were tuned manually and pulse intervals were computed using audio editing software. With this monitoring system, three to four pulses from each frequency could be recorded quickly; hence, time between first and last snake T_b sampled at hourly intervals (see Thermal Profiles) was $\leq$ 10 min.

Although we recognized the utility of deriving preferred T_bs using a controlled laboratory thermal gradient (Hertz et al., 1993), power limitations at our field station (solar power generation) prevented us from setting up a suitable thermoregulatory chamber.

Thermal Profiles.—Six gravid and eight nongravid radio-tagged foxsnakes were released into the enclosure between 18 and 27 June 1999; individuals were given seven days to acclimate to the new surroundings before their T_b measurements were used in analyses. Body temperatures of snakes within the enclosure were recorded at hourly intervals from 29 June to 7 July. Apart from daily structural integrity checks of the enclosure wall, snakes within were minimally disturbed during the thermal profiling. However, gravid females that had spent a day or more in one of the potential nests, and then moved, were radio-located to verify visually their reproductive status; those that appeared to have oviposited were weighed to confirm condition. Two individuals oviposited before the thermal profiles concluded; thus, only T_bs recorded prior to our best approximation of time of oviposition for these individuals were used in analyses. Snakes used in the enclosure experiment were released at their capture locations.

Data Analysis.—To account for the possibility that environmental conditions corresponding to T_b observations may have varied among individuals, we used the mean maximum T_e ($T_e$max) for each individual as a covariate in analysis of covariance (ANCOVA). Because gaps in the dataset (due to loss of transmitter signals) precluded repeated-measures analyses, we used the mean, standard error, minimum, maximum, and range of T_bs calculated for each snake (i.e., each individual contributed only one datum per statistic) in analyses. Reproductive groups were compared during the entire period of monitoring, and also only when T_es were $\geq$ 30°C. This latter analysis was conducted to ensure snake T_bs were not being constrained by environmental temperatures (Dorcas and Peterson, 1998). Finally, to assess possible differences in nocturnal thermoregulation, we also compared the reproductive groups using T_b data collected at night only (arbitrarily, 2100–0700 h). Because some snakes had fewer T_b observations (due to signal loss or early oviposition), values were weighted by the number of T_b observations for each snake in ANCOVA analyses. Statistical analyses were conducted with JMP ver. 5 (SAS Institute). Data were checked for significant deviations from normality and homoscedasticity by inspecting histograms and box plots; no significant departures were detected. Means ± 1 standard error (SE) are reported unless otherwise indicated. Statistical significance was set at $\alpha = 0.05$.

RESULTS

Operative Temperatures.—Our thermal models accurately tracked the internal temperature of a dead foxsnake (T_d; $N = 159$); however, they did lag approximately 3°C behind during rapid heating and cooling phases. The maximum difference between T_d and any of the model T_es for any measurement was 3.8°C (maximum mean difference between T_d and any model was 1.0°C[0]); however, this disparity decreased quickly when rates of temperature change declined and model T_es approached equilibrium. We therefore considered the models to be reliable estimators of foxsnake T_b.

Operative temperatures measured within the enclosure indicated that snakes had ample opportunity to maintain T_bs within the range available to free-ranging individuals. The maximum T_e was at least 32°C on each day of the sampling period, and was > 36.1°C (the maximum T_b selected by *E. gloydi* in this study) on six of the days. Sufficiently cool retreat sites were also available at all times within the enclosure, as evidenced by the range of hourly minimum T_es (14.1–26.3°C; $N = 146$).

Thermal Profiles.—Hourly T_bs were recorded from 14 snakes during the 8-day period (29 June to 7 July; 146 h). Of the 2,098 T_b measurements collected during the thermal profile, 1,729 were used in analyses. Visual inspection of T_b plots suggested that gravid females

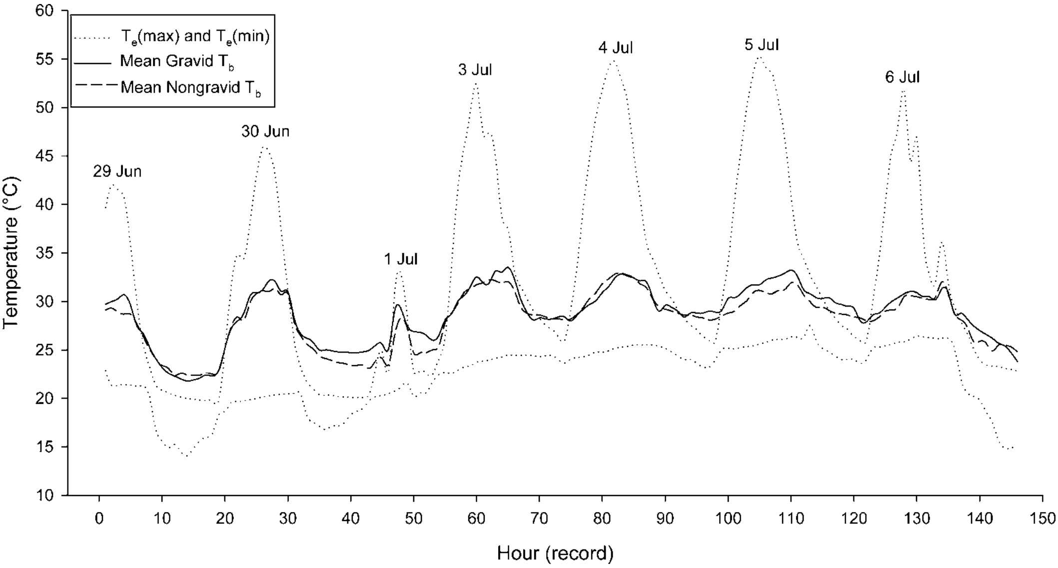

FIG. 1. Thermal profile of gravid (N = 6) and nongravid (N = 8) *E. gloydi* housed within a seminatural enclosure (29 June to 7 July 1999). Mean hourly T_bs are illustrated.

selected T_bs similar to those of nongravid females (Fig. 1), and one-way ANCOVA with reproductive condition as the factor confirmed this observation: no significant differences were found between the reproductive groups for any of the T_b statistics (Table 1). One-way ANCOVA also showed that T_b statistics of gravid and nongravid females were not significantly different when $T_e$max was ≥ 30°C (Table 1). Finally, although examination of Fig. 1 suggests there may have been nocturnal T_b differences between reproductive groups, one-way ANCOVA (reproductive condition as the factor) indicated these differences were nonsignificant (Table 1).

DISCUSSION

Our data did not support the hypothesis that gravid foxsnakes thermoregulate differently than nongravid individuals. Gravid females did not maintain higher or less variable T_bs than nongravid females, and this was true across the entire range of environmental temperatures and diel cycle, and also when analyses were restricted to specific temperature and time ranges. In addition, qualitative behavioral observations of both free-ranging and enclosure-bound females suggested that gravid and nongravid females were thermoregulating similarly (i.e., we did not observe pronounced differences in basking or microhabitat use).

Although the emerging pattern among viviparous snakes is that of significant differences in thermoregulatory behavior between females of dissimilar reproductive status (Charland and Gregory, 1990; Graves and Duvall, 1993; Charland, 1995; Dorcas and Peterson, 1998; Brown and Weatherhead, 2000), the pattern for oviparous taxa is less clear because of the paucity of comprehensive studies (but see Blouin-Demers and Weatherhead, 2001a). It is possible that the period of egg retention in oviparous snakes is too short, as suggested by Tu and Hutchinson (1994), for a female to enhance embryogenesis to a level where the benefits of

TABLE 1. Body temperature statistics and one-way ANCOVA results comparing T_bs of gravid (N = 6) and nongravid (N = 8) *E. gloydi* within a seminatural enclosure on Pelee Island, 29 June to 7 July 1999. Means ± 1 SE (°C) are presented.

	Entire profile (146 h)			$T_e$max ≥ 30°C (66 h)			2100–0700 h (67 h)		
Statistic	Mean ± SE	$F_{1,11}$	P	Mean ± SE	$F_{1,11}$	P	Mean ± SE	$F_{1,11}$	P
Gravid mean	28.6 ± 0.26	4.37 $\exp^{-01}$	0.522	31.0 ± 0.46	0.692	0.423	26.8 ± 1.03	0.075	0.789
Nongravid mean	28.2 ± 0.52			30.5 ± 0.30			26.5 ± 0.85		
Gravid SE	0.3 ± 0.05	2.50 $\exp^{-05}$	0.996	0.2 ± 0.02	0.110	0.746	0.4 ± 0.08	0.058	0.814
Nongravid SE	0.3 ± 0.05			0.3 ± 0.04			0.4 ± 0.05		
Gravid minimum	20.3 ± 1.61	4.00 $\exp^{-04}$	0.985	26.7 ± 0.43	1.561	0.238	20.3 ± 1.66	1.00E^{-04}	0.992
Nongravid minimum	20.3 ± 1.34			25.5 ± 0.66			20.4 ± 1.36		
Gravid maximum	34.2 ± 0.27	1.19 $\exp^{-02}$	0.915	34.3 ± 0.28	0.028	0.869	31.5 ± 0.32	0.564	0.468
Nongravid maximum	34.3 ± 0.48			34.3 ± 0.48			31.0 ± 0.51		
Gravid range	14.0 ± 1.73	2.20 $\exp^{-03}$	0.963	7.6 ± 0.24	0.971	0.346	11.2 ± 1.96	0.050	0.828
Nongravid range	14.1 ± 1.78			8.8 ± 0.96			10.7 ± 1.31		

earlier oviposition dates (e.g., increased maternal and/or offspring survivorship) or optimal offspring phenotypes (Downes and Shine, 1999) outweigh the costs of increased thermoregulatory effort. Nevertheless, Blouin-Demers and Weatherhead (2001a) found that gravid *Elaphe obsoleta* maintained higher T_bs, thermoregulated more effectively, and exploited the available thermal environment to a greater extent than nongravid females. Therefore, in at least some oviparous snake species or populations, gravid females thermoregulate more carefully than conspecifics.

Three potential limitations generated by our study design need to be addressed. First, some studies using enclosures have reported female snakes failing to give birth (Charland and Gregory, 1990) or failing to oviposit at normal times (Shewchuk, 1996). Our efforts to minimize this possibility, however, via the provision of suitable environmental temperatures and potential nests, appear to have been largely successful: oviposition dates were within the range demonstrated by free-ranging individuals; all gravid, enclosure-bound snakes oviposited in artificial nests; and incubation was successful in five of the six clutches. In addition, the ranges of T_bs selected by three free-ranging females (two gravid, one nongravid) during a 24-h thermal profile (Willson, 2000) were similar to the T_bs selected by females in the enclosure. Second, because snakes in the enclosure were provided with opportunities to feed, some individuals may have exhibited postprandial thermophily, potentially obscuring thermoregulatory differences attributable to reproductive condition. However, although studies have documented this phenomenon in snakes inhabiting thermally limiting environments (e.g., Blouin-Demers and Weatherhead, 2001b), other studies have failed to find a postfeeding effect on T_b in the field (Brown and Weatherhead, 2000). Interestingly, Brown and Weatherhead's (2000) results were obtained from snakes inhabiting a relatively favorable thermal environment. This finding is relevant to results presented here because our study was also conducted during a time when the thermal environment available to snakes was nonconstraining. Third, some free-ranging, radio-tagged females in our study population showed considerable annual fidelity to microhabitats. Although thermally suitable retreat sites were available within the enclosure, and females were allowed a week to acclimate to the new environment, preferred "hot spots" (e.g., a structurally and thermally ideal log or brush pile) used by some females during reproductive years would have been absent. Therefore, some gravid females within the enclosure may have accepted lower T_bs rather than search for new sites.

Our observations of foxsnakes on Pelee Island suggest that gravid females can produce viable offspring without increasing their thermoregulatory effort beyond that of nongravid females. Shine and Madsen (1996) also found little evidence of overt thermoregulatory behavior in water pythons (*Liasis fuscus*) throughout much of the active season; they attributed these observations to northern Australia's benign thermal environment, as well as to the range of thermally suitable microhabitats available. Although we do not suggest that Pelee Island's climate offers female foxsnakes a thermal environment similar to northern Australia, we do suspect that thermal conditions during the period of egg retention (mid-June to mid-July) are highly conducive to the timely completion of embryogenesis (prelaying). In addition to favorable ambient temperatures, most of the free-ranging foxsnakes we radio-tracked had access to thermally suitable microhabitats (e.g., brush piles, rodent runways below clumps of dead grass). In conclusion, we hypothesize that the favorable thermal conditions (ambient and microhabitat mediated) during the period of egg retention reduce the benefits of increased thermoregulatory effort by gravid females to a level where they are outweighed by potential costs.

Acknowledgements.—Jeremy Rouse, Ben Porchuk, Carrie MacKinnon, and Mike Ethier provided invaluable assistance in the field. Ben Porchuk graciously allowed us to build the enclosure on his property. Gabriel Blouin-Demers provided help with initial surgical setup. Reviews by Gabriel Blouin-Demers and several anonymous reviewers substantially improved the manuscript. Our research was carried out under the guidelines of the Canadian Council on Animal Care and University of Guelph Animal Care Protocol 98R037. This research was supported by grants from the Endangered Species Recovery Fund (ESRF) of World Wildlife Fund Canada and Environment Canada, the Canadian Wildlife Federation, and from a Natural Sciences and Engineering Research Council of Canada operating grant to R. Brooks.

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Accepted: 17 March 2006.