



Contents lists available at ScienceDirect

Journal of Thermal Biology

journal homepage: www.elsevier.com/locate/jtherbio

Latitudinal variation in thermal ecology of North American ratsnakes and its implications for the effect of climate warming on snakes

Patrick J. Weatherhead^{a,*}, Jinelle H. Sperry^{a,1}, Gerardo L.F. Carfagno^{a,2}, Gabriel Blouin-Demers^b

^a Program in Ecology, Evolution and Conservation Biology, University of Illinois, 606 E. Healey Street, Champaign, IL 61820, USA

^b Department of Biology, University of Ottawa, 30 Marie-Curie, Ottawa, Canada, ON K1N 6N5

ARTICLE INFO

Available online 21 March 2011

Keywords:

Thermoregulation
Latitude
Snakes
Climate change

ABSTRACT

Behavioral thermoregulation is expected to be critical in determining the capacity of reptiles to respond to climate warming and how that response will vary with latitude. We used radio-telemetry to compare behavioral thermoregulation among ratsnake (*Elaphe obsoleta*) populations in Texas, Illinois, and Ontario, a latitudinal distance of > 1500 km. Despite numerous specific differences among populations, overall the thermal ecology was surprisingly similar during the months that snakes in all three populations were active. Preferred temperatures varied only slightly across the snakes' range, the extent of thermoregulation was similar, and by varying when during the day and season they thermoregulated, snakes in all three populations realized body temperatures within their preferred temperature range 15–20% of the time. The ability to use fine-scale behavioral thermoregulation (i.e., selective use of habitats and microclimates) to a similar extent and achieve similar outcomes across such a wide latitudinal and climatic gradient is made possible by large-scale differences in timing of activity (ratsnakes in Texas switch to nocturnal activity during summer, whereas in Illinois and Ontario activity is exclusively diurnal and hibernation lasts 5–7 months). Modeling indicated that a 3 °C increase in ambient temperature will generally improve thermal conditions for all three populations. Our empirical analyses suggest that the snakes' ability to respond to climate warming will be determined more by their capacity to adjust when they are active than by changes in the extent of fine-scale behavioral thermoregulation. The ability to adjust timing of activity appears to make many snakes fundamentally different from lizards. As such, the consequences of climate warming may be very different for these two groups of reptiles.

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1. Introduction

Biologists have long been interested in patterns associated with latitude (e.g. Bergmann, 1847; Darwin, 1859). Latitudinal variation in temperature is the principal abiotic factor that underlies the biological patterns. Because the biology of ectotherms is strongly influenced by temperature (Huey, 1982), the life history, ecology, and behavior of ectotherms should be strongly influenced by latitude. Studies of squamate reptiles support that expectation. For example, there is a transition from

oviparity in the tropics to viviparity at higher latitudes (Shine and Bull, 1979), and growth rates decline with increasing latitude (Blouin-Demers et al., 2002). An important gap in our knowledge, however, is how behavior varies with latitude, given that behavior is the mechanism by which reptiles maintain relatively stable body temperatures in the face of thermally variable environments (e.g. Huey, 1982; Huey and Kingsolver, 1989; Peterson et al., 1993). Behavioral thermoregulation will be critical in determining the capacity for ectotherms to respond to climate warming and how that response will vary with latitude (Deutsch et al., 2008; Kearney et al., 2009). Here we compare behavioral thermoregulation in populations of ratsnakes (*Elaphe obsoleta*) at the southern (Texas), central (Illinois), and northern (Ontario) parts of their distribution and use those results to assess likely consequences of climate warming for these snakes.

The thermal quality of a reptile's environment should influence its thermoregulatory strategy (Huey and Slatkin, 1976) because the availability of preferred temperatures should affect the time and energy that must be expended to maintain optimal body temperatures. Those costs must be balanced against the

* Corresponding author. Tel.: +2172440319; fax: +2172650056.

E-mail addresses: pweather@illinois.edu (P.J. Weatherhead), Jinelle.Sperry@usace.army.mil (J.H. Sperry), gcarfagn@gettysburg.edu (G.L.F. Carfagno), gblouindemers@mac.com (G. Blouin-Demers).

¹ Present address: Engineer Research and Development Center, PO Box 9005, Champaign, IL 61826, USA.

² Present address: Department of Biology, Gettysburg College, 300 North Washington Street, Gettysburg, PA 17325, USA.

fitness costs that would result from not thermoregulating (Blouin-Demers and Weatherhead, 2001a; Row and Blouin-Demers, 2006). Tropical snakes may thermoregulate less than cool temperate-zone snakes (Shine and Madsen, 1996; Brown and Weatherhead, 2000; Blouin-Demers and Weatherhead, 2001a; Row and Blouin-Demers, 2006), suggesting that as the thermal environment becomes more challenging, the benefits of thermoregulation exceed the costs (Blouin-Demers and Weatherhead, 2001a). This latitudinal comparison is based on a small number of taxonomically diverse species and, therefore, could be confounded by ecological differences among species. The approach that we use here is to compare the thermal ecology of populations of the same snake species at different latitudes.

Among snake species, thermal preferences vary between about 28 and 34 °C, with most being close to 30 °C (Lillywhite, 1987), so among ratsnake populations we did not expect thermal preferences to vary substantially. Therefore, the main difference in thermal ecology among populations should be how much time snakes realize body temperatures within their preferred range, and how much those temperatures result from behavioral thermoregulation. We consider two alternative possibilities. First, given that snakes at low latitudes may often realize preferred temperatures with little thermoregulatory effort (Shine and Madsen, 1996), ratsnakes in Texas should realize preferred temperatures more with less thermoregulatory effort than ratsnakes in Ontario, with snakes in Illinois intermediate. Alternatively, if conditions are most suitable for a given species at the center of its range because that is where local conditions meet the species' needs along most axes of their niche (Brown, 1984), thermal conditions may be most benign for ratsnakes in the center of their range. Cold temperatures are the main challenge for ratsnakes in Canada (Blouin-Demers and Weatherhead, 2001a), whereas our own observations and video camera evidence of ratsnake predation on birds' nests (Stake and Cimprich, 2003; Stake et al., 2004) indicate that ratsnakes in Texas switch from diurnal to nocturnal activity in the hottest part of the year. In Illinois and Ontario ratsnakes are exclusively diurnally active. Therefore, ratsnakes in Texas may have to work to avoid temperatures that are too hot in the same way that ratsnakes in Ontario have to work to avoid cold temperatures.

Our broader goal is to consider the implications of latitudinal variation in thermoregulation for how snakes might be affected by climate warming. Knowledge of latitudinal differences in thermal biology among related taxa can be used to predict the relative impact of climate change at different latitudes. For example, narrower thermal tolerance could make tropical ectotherms more vulnerable to climate warming despite a lower projected rate of warming in the tropics (Deutsch et al., 2008; Tewksbury et al., 2008). We use our thermal ecology data from ratsnakes at lower latitudes to predict how snakes at higher latitudes are likely to respond to a warmer climate. We also model the effect of increasing mean temperatures for all three populations. The general prediction we test is that higher temperatures will be detrimental to ratsnakes in Texas but beneficial to ratsnakes in Ontario, given that the major thermal challenge for ectotherms is avoiding high body temperatures at low latitudes and low body temperatures at higher latitudes (Kearney et al., 2009).

2. Materials and methods

2.1. Study sites and species

Research was conducted in southern Illinois from 2002–2004 at the Cache River State Natural Area (37° 23' N, 88° 54' W) and in

central Texas from 2004–2007 at Fort Hood (30° 10' N, 97° 45' W). Research in eastern Ontario was conducted from 1997–1999 at the Queen's University Biological Station (44° 34' N, 76° 19' W). Although results from Ontario have already been published (Blouin-Demers and Weatherhead, 2001a), we present some of those results here to facilitate comparison among populations. In other cases explained below (2.4), we re-analyzed the Ontario data so the results we present here differ from those published previously.

At all three sites the habitat consisted of forest interspersed with more open habitats. Although patch sizes varied among sites, all habitat types at a site were accessible to all snakes at that site using their normal range of movement. Forest was principally eastern deciduous in Ontario and Illinois (with some differences in component species), and oak-juniper in Texas. An important difference between sites was that in both Texas and Ontario, open habitats were often completely exposed (e.g. bare rock or ground), whereas in Illinois open habitats were fields in various stages of succession, with little bare ground.

The span of approximately 14° of latitude between the Texas and Ontario study sites (a N–S distance of > 1500 km) encompasses almost the full latitudinal range of ratsnakes. Based on data from weather stations near each study site, mean annual temperatures for Texas, Illinois, and Ontario are 19.5, 14.4, and 6.6 °C, respectively, and there are 240, 190, and 142 frost-free days, respectively. The snakes' active season extends from May through September in Ontario, April through October in Illinois, and in Texas the snakes do not hibernate and can be active in any month of the year if the weather is warm (Sperry et al., 2010). From May to September when snakes in all three populations are active, mean monthly high and low temperatures in Texas are, respectively, approximately 5 and 10 °C warmer than in Illinois and 10 and 20 °C warmer than in Ontario.

Although *Elaphe obsoleta* was historically considered a single species, mitochondrial DNA analyses (Burbrink et al., 2000) revealed three distinct clades that Burbrink (2001) proposed to be considered as separate species. However, Gibbs et al. (2006) found that the Ontario population studied here was a hybrid of the eastern and central clades. Regardless of how the taxonomy is resolved, what is important for our study is that our "populations" are closely related and ecologically similar based on both diet (Weatherhead et al., 2003; Carfagno et al., 2006; Sperry and Weatherhead, 2009) and habitat use (Blouin-Demers and Weatherhead, 2001b; Carfagno and Weatherhead, 2006; Sperry et al., 2009).

2.2. Radio-telemetry

To ensure that results were comparable between studies, we followed the methods of Blouin-Demers and Weatherhead (2001a) to the extent possible. In Illinois we captured ratsnakes as they emerged from hibernacula each spring and opportunistically through the season. Because ratsnakes in Texas do not hibernate, all captures were opportunistic. Snakes for which transmitters weighed < 3% of their body mass had temperature-sensitive transmitters (Model SI-2T, Holohil Systems Ltd., Ontario) implanted surgically (Weatherhead and Blouin-Demers, 2004a). We relocated snakes approximately every 48 h using hand-held telemetry and recorded their body temperatures (T_b) using transmitter pulse rates, which accurately predicted transmitter temperatures (all $R^2 > 0.99$). We also used four–six automated radio-telemetry data loggers at each site (SRX 400, Lotek Wireless, Ontario) to record T_b every 10 min around the clock through the active season. By regularly repositioning data loggers we maximized the number of snakes within transmission range, although no snake produced continuous records.

2.3. Preferred temperature range (T_{set})

We used a thermal gradient (~ 15 to ~ 40 °C) to determine snakes' preferred temperature range (T_{set}), i.e., T_b s selected in the absence of competing interests. Chambers (250 cm \times 60 cm \times 60 cm) had constant, homogeneous illumination. Heating and cooling sources were switched between trials. Snakes from the field studies were placed individually in the chamber after fasting for several days. Following 24 h of acclimation, we recorded T_b every 10 min for 24 h using an automated data logger. We used the bounds of the central 50% of observed T_b s for each individual as the lower and upper set points of its T_{set} (Hertz et al., 1993).

2.4. Operative environmental temperature (T_e)

Operative environmental temperatures (T_e) are the T_b s available to an ectotherm in thermal equilibrium with its environment, in the absence of metabolic heating or cooling (Bakken and Gates, 1975). By placing physical models that have the same thermal characteristics as the species of interest within all commonly available habitats, one can estimate the T_b s an animal would realize by using habitats randomly (Brown and Weatherhead, 2000). The models we used were water-filled copper pipes (40 cm \times 4 cm) containing a thermocouple attached to a data logger (HOBO Temp, ONSET Computer Corporation, Massachusetts) that recorded temperatures every 10 min, which we averaged for each hour. These models accurately reflect the thermal properties of ratsnakes (Blouin-Demers and Weatherhead, 2001a) without requiring adjustments for thermal inertia (Seebacher and Shine, 2004) because ratsnakes move infrequently (Carfagno and Weatherhead, 2008).

We used models to collect temperature data from 5 to 11 microhabitats within each major habitat (Texas: forested mesa slopes, savannah oak clumps, open savannah; Illinois: upland forest, bottomland forest, successional field, old field). We chose microhabitats that were available to and used by the snakes (e.g. on the ground, within vegetation, on tree branches, inside logs). Models were left in each microhabitat for up to 6 weeks to ensure sampling over a broad range of ambient conditions.

Determining T_e s was a two-step process. We first used backward stepwise regression (up to degree 3) to derive equations that best predicted model temperatures in each habitat based on solar radiation, air temperature, precipitation, and wind speed from nearby weather stations recorded coincident with the time that data from the models were collected. With these equations (Table 1) and weather records we then predicted hourly T_e values for each habitat around the clock throughout the active season. We modified the methods used by Blouin-Demers and Weatherhead (2001a) to calculate T_e and applied these changes to all three populations. All changes made T_e better reflect the T_b s a snake would realize if it moved randomly with respect to temperature. Blouin-Demers and Weatherhead (2001a) assumed that snakes in edges had access to both habitats that created the edge at no cost. We did not classify edges as a separate habitat and assumed that a randomly moving snake would spend time in the habitats on either side of an edge in proportion to their availability. Also, Blouin-Demers and Weatherhead (2001a) did not weight habitats by their availability when estimating T_e . By weighting habitats we better reflect the thermal conditions a randomly moving snake would encounter, and take into account differences in habitat availability among study sites. Details of how habitats were quantified are provided by Blouin-Demers and Weatherhead (2001b), Carfagno and Weatherhead (2006) and Sperry and Weatherhead (2009). Third, we excluded retreat sites from the calculation of T_e . In Ontario retreat sites were rock piles, large logs, old barns and flat rocks and in Texas these were brush piles. There were no habitat features similar to these in Illinois.

Table 1

Multiple regression equations used to predict model snake temperature in the different habitats available to ratsnakes in Texas, Illinois, and Ontario. The variables included in the models were air temperature (T) in °C, solar radiation (R) in kW/m², wind speed (W) in m/s, and rainfall (RA) in mm/h. Ontario equations taken from Blouin-Demers and Weatherhead (2001a).

Location	Habitat	Equation	R^2
Texas	Grassland Savannah	$1.00T + 0.02R - 0.95W + 0.14RA + 0.33$	0.80
	Oak Savannah	$0.80T + 0.01R - 1.04W + 0.09RA + 4.52$	0.72
	Forested slope	$0.66T + 0.01R - 0.53W + 0.13RA + 6.00$	0.66
Illinois	Old field	$0.99T + 8.11R - 0.42W + 0.18RA + 0.65$	0.76
	Successional field	$0.85T + 4.66R + 0.10W + 0.06RA + 2.06$	0.83
	Upland forest	$0.74T - 1.93R + 0.05W + 0.10RA + 4.09$	0.75
	Bottomland forest	$0.67T - 1.82R - 0.16W + 0.03RA + 6.74$	0.84
Ontario	Rock outcrop	$1.42T + 24.39R + 0.18W - 7.60$	0.89
	Field	$1.25T + 31.12R - 9.44$	0.94
	Forest	$1.16T + 0.66R - 0.02W - 4.07$	0.86

Although important to the snakes, retreat sites were small in area and therefore would be encountered rarely by a randomly moving snake.

2.5. Quantifying thermoregulation

We quantified thermoregulation using several standard indices. First, the accuracy of body temperature (d_b) measures how close body temperatures are to preferred temperatures, calculated as the absolute value of the difference between T_b and T_{set} (Hertz et al., 1993). Similarly, the thermal quality of the environment (d_e) measures how close environmental temperatures in each habitat are to preferred temperatures, calculated as the absolute value of the difference between T_e and T_{set} .

We used $d_e - d_b$ (Blouin-Demers and Weatherhead, 2001a) to quantify the effectiveness of thermoregulation, i.e., the extent to which snakes experience T_b s close to T_{set} given available environmental temperatures. High values of $d_e - d_b$ represent effective thermoregulation, values near zero thermoconformity, and negative values avoidance of thermally preferable sites.

The thermal exploitation index (E_x) quantifies how often preferred temperatures were realized when conditions allowed (Christian and Weavers, 1996), i.e., the proportion of T_b values within T_{set} when preferred temperatures were available in at least one habitat. The larger the E_x , the more a snake realizes preferred temperatures when conditions allow. We also determined the proportion of T_b values below and above T_{set} when preferred temperatures were available, to determine the direction of deviation of T_b from T_{set} (Brown and Weatherhead, 2000).

2.6. Modeling climate warming

To model climate warming we incorporated a 3 °C increase in ambient temperatures in the regression equations derived from our snake model analyses (Table 1). We chose a 3 °C increase for consistency with Kearney et al.'s, (2009) analysis of the global impact of climate warming on ectotherms and because 3 °C is well within the range of temperature increases projected for central and eastern North America this century (Solomon et al., 2007). We kept all other weather variables unchanged. We used the equations to predict hourly T_e values through the active season in each habitat at each study location. Our goal was to assess the effect of the same temperature increase on each population (e.g. Kearney et al., 2009). In doing so we acknowledge that temperature increases are not expected to be uniform

geographically (Deutsch et al., 2008) and that changes in climate variables other than temperature might also affect snakes.

2.7. Statistical analyses

All analyses were performed on data averaged for each individual over the appropriate time period. We grouped males and females because separate analyses indicated that both sexes exhibited similar patterns of thermal preference and thermoregulation. Also, although gravid females thermoregulated differently from non-gravid females in Ontario (Blouin-Demers and Weatherhead, 2001a), the unknown reproductive status of many females in Illinois and Texas precluded separate analysis. We required a minimum of 10 observations for an individual to be included in calculations of mean monthly and hourly values. We limited analyses to May through September. This excludes the early and late parts of the active season for Illinois and Texas, but focuses on the time those snakes are most active (Sperry et al., 2010) and when warmer temperatures would have the greatest impact. For comparisons among populations, we used general linear models with individuals nested within population of origin to account for multiple measurements taken from the same individuals.

Analyses were conducted using JMP Version 4.0 (SAS Institute 2000), SYSTAT Version 10.2 (SYSTAT Software 2002) and NCSS (Hintze, 2006). We inspected box plots to determine if assumptions of normality and homogeneity of variance were upheld, and detected no significant violations. Means are reported ± 1 SE.

3. Results

We radio-tracked 22 ratsnakes in Illinois (12 males, 10 females) and 63 in Texas (38 males, 25 females). Blouin-Demers and Weatherhead (2001a) tracked 53 ratsnakes (17 males, 36 females) in Ontario. Over three years in Illinois we recorded

59,390 T_b s in the field from May through September that we condensed to 15,348 hourly means. Over three years in Texas we recorded 154,684 T_b s between May and September that we condensed to 20,471 hourly means. Blouin-Demers and Weatherhead (2001a) recorded 150,368 T_b s that were condensed to 34,211 hourly means, so totals across the three populations are 364,442 T_b s (70,030 hourly means) from 138 snakes.

3.1. Preferred temperature range (T_{set})

Temperature preference data came from 3 male and 6 female snakes in Texas and 10 male and 9 female snakes in Illinois. Although results were similar across the three populations ($F_{2,66}=0.84$, $P=0.44$), mean preferred temperature declined from Texas (29.2 ± 0.35 °C) to Illinois (28.7 ± 0.67 °C) to Ontario (28.1 °C). The 25% quartiles also declined from Texas to Ontario ($F_{2,66}=2.45$, $P=0.09$), whereas 75% quartiles remained constant across populations ($F_{2,66}=0.02$, $P=0.98$). Thus, the breadth of T_{set} tended to decrease from north to south (Fig. 1).

To determine whether snakes preferred the same temperatures in the field, for all individuals tracked we calculated mean T_b and its 25% and 75% quartiles when T_e allowed the lower bound of T_{set} to be reached in at least one habitat. Values again declined from Texas to Ontario (Fig. 1). Relative to the respective lab estimates for each population, in the field the means (Texas: $t_{68}=2.07$, $P=0.04$, Illinois: $t_{39}=2.57$, $P<0.02$, Ontario: $t_{93}=5.71$, $P<0.001$) and lower bounds (Texas: $t_{68}=2.46$, $P=0.02$, Illinois: $t_{39}=4.22$, $P<0.001$, Ontario: $t_{93}=7.44$, $P<0.001$) of snake temperatures were significantly lower, whereas upper bounds differed only for Ontario (Texas: $t_{68}=0.92$, $P=0.36$, Illinois: $t_{39}=0.43$, $P=0.68$, Ontario: $t_{93}=2.84$, $P=0.01$). In the field, therefore, ratsnakes generally realized lower T_b s than in the lab when conditions allowed preferred temperatures to be reached, and this tendency was most pronounced in the north.

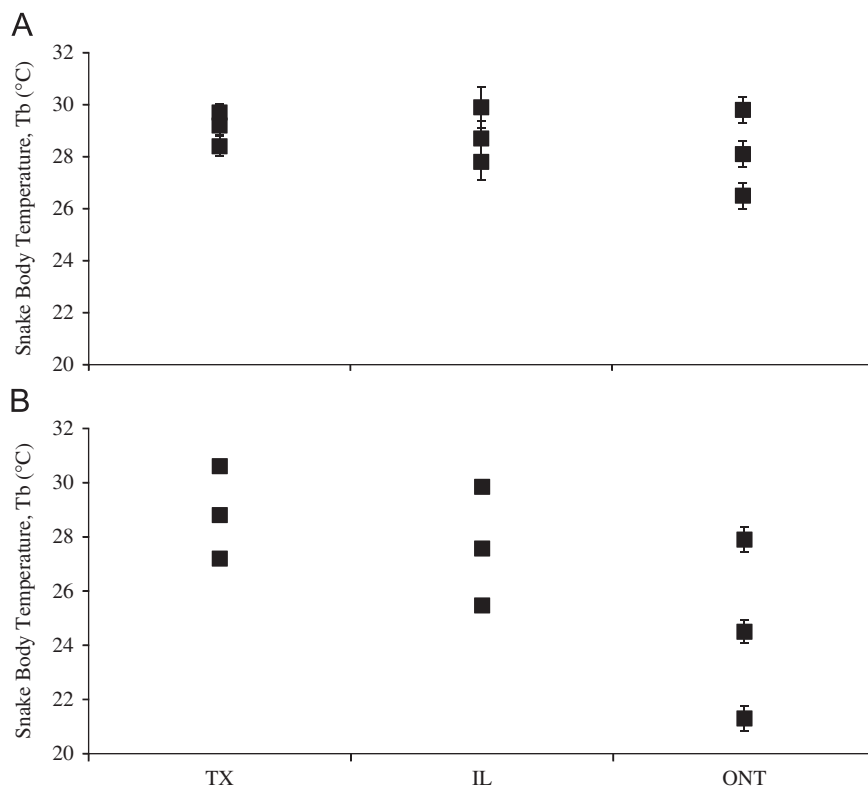


Fig. 1. Mean, 25% and 75% quartiles of body temperatures (T_b) of ratsnakes (A) in a laboratory thermal chamber and (B) in the field when the operative environmental temperatures (T_e) allowed the lower bound of T_{set} to be reached in at least one habitat in Texas, Illinois, and Ontario. Ontario data taken from Blouin-Demers and Weatherhead (2001a).

3.2. Thermal quality of the environment

Mean d_e values calculated across the active season provide a measure of the magnitude of the deviation of environmental temperatures from preferred temperatures. Mean d_e values indicated that Texas was thermally relatively benign, whereas

Ontario was clearly the most challenging environment. The overall mean d_e for the three years, averaged across habitat types in each of the studies was 5.6 ± 0.31 °C in Texas, 6.9 ± 0.97 °C in Illinois, and 10.2 ± 0.89 °C in Ontario ($F_{2,7} = 17.66$, $P < 0.01$). Tukey–Kramer analysis indicates that Ontario d_e differed from both Texas and Illinois. Mean d_e in different habitats ranged from 5.0 to 6.1 °C in Texas, 6.3 to 7.9 °C in Illinois, and from 9.2 to 12.0 °C in Ontario.

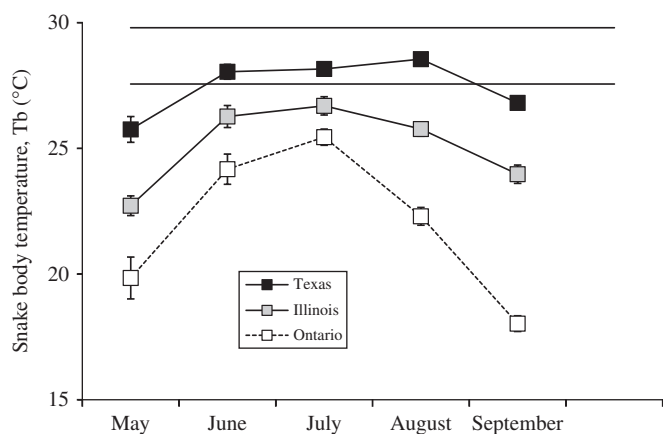


Fig. 2. Mean (\pm SE) monthly body temperatures (T_b) of ratsnakes in Texas, Illinois, and Ontario, in relation to the average upper and lower bounds of the preferred temperature ranges (T_{set}) of all three populations, indicated by parallel horizontal lines. Ontario data taken from Blouin-Demers and Weatherhead (2001a).

3.3. Snake body temperatures (T_b)

Averaged by individual, overall mean T_b s differed significantly between the three study sites over the active season, with snakes being warmest in Texas (27.5 ± 0.31 °C), followed by Illinois (25.6 ± 0.48 °C) and Ontario (22.2 ± 0.32 °C; nested ANOVA $F_{2,75} = 72.03$, $P < 0.001$). A Tukey–Kramer multiple-comparison test indicated that all populations differed. Snake hourly T_b s were within T_{set} 20.6% of the time in Texas, 15.4% of the time in Illinois and 17.5% of the time in Ontario. Based on mean monthly values, ratsnakes in Texas realized consistently warmer T_b s through the season, followed by Illinois and Ontario (Fig. 2).

Mean hourly T_b s indicated that ratsnakes in all populations exhibited similar thermal profiles over the course of the day, although there were some differences among populations (Fig. 3). Generally, snakes warmed through the morning, reached their highest mean T_b s in the afternoon (Texas: 29.5 ± 0.21 °C, Illinois: 26.1 ± 0.35 °C, and Ontario: 25.2 ± 0.44 °C), and then gradually cooled until the following morning. Texas snakes maintained warm temperatures through the

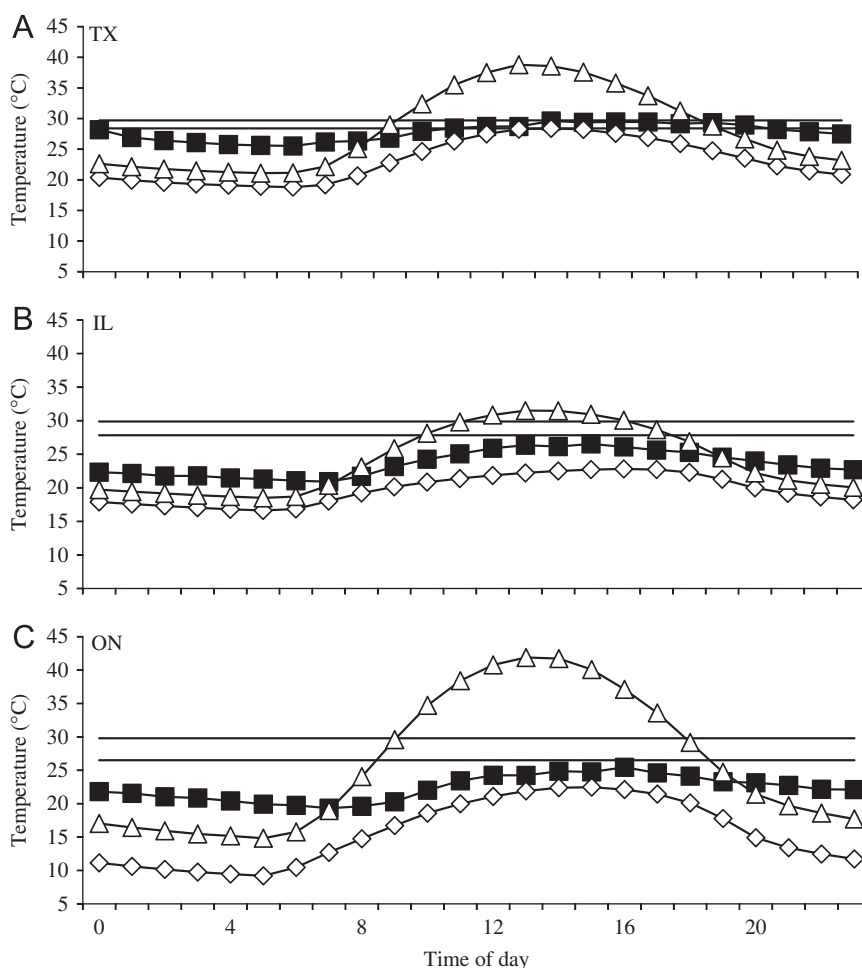


Fig. 3. Daily variation in hourly (mean \pm SE) snake body temperatures (T_b – solid squares) and minimum (open diamonds) and maximum (open triangles) operative environmental temperatures (T_e), in relation to the upper and lower bounds of the preferred temperature range (T_{set}) for Texas (A), Illinois (B), and Ontario (C) ratsnakes in May through September, indicated by parallel horizontal lines.

evening, with mean T_b s remaining within T_{set} for 10 h, whereas snakes in Illinois and Ontario exhibited more obvious peaks in T_b during the afternoon and never experienced mean T_b s within T_{set} (Fig. 3). During the day, snake T_b s in all three populations remained well below maximum T_e s, even though exploiting those temperatures would have allowed Ontario and Illinois snakes to increase T_b s so they reached T_{set} (Fig. 3). At night, snakes in Illinois were as warm as their environment allowed, whereas snakes in both Texas and Ontario were actually warmer than the environment appeared to allow (Fig. 3). This is probably explained by the use of retreat sites in Texas and Ontario that were not included in the analysis of T_e . If this explanation is correct, then even though Texas ratsnakes were active at night during the summer, they were still using retreat sites to maintain T_b s.

3.4. Effectiveness of thermoregulation ($d_e - d_b$)

Population means, calculated as the average of the mean d_b s for each individual in each year, indicated that snakes in Texas deviated least from T_{set} (2.10 ± 0.26 °C), snakes in Ontario deviated the most (5.33 ± 0.27 °C), with Illinois snakes intermediate (3.58 ± 0.40 °C; nested ANOVA: $F_{2,76}=37.77$, $P < 0.01$).

Mean deviation of T_b s from T_{set} relative to the deviation of environmental temperatures from T_{set} (i.e., $d_e - d_b$) indicated that ratsnakes in Ontario thermoregulated most (3.66 ± 0.29 °C), Illinois snakes the least (3.08 ± 0.38 °C), with Texas snakes intermediate (3.24 ± 0.25 °C), although differences among populations were not significant (nested ANOVA: $F_{2,76}=1.06$, $P=0.35$). By month, however, there were clear differences in thermoregulation among populations. Ontario snakes thermoregulated less as the active season progressed, whereas Texas snakes thermoregulated more, with snakes in Illinois not exhibiting a clear seasonal pattern (Fig. 4).

Hourly values revealed the clearest differences in thermoregulation among populations. Snakes in both Ontario and Illinois thermoregulated at night, although Ontario snakes were much more effective than snakes in Illinois (Fig. 5). During the day when snakes in both Ontario and Illinois are active, they became essentially thermal conformers (i.e., $d_e - d_b \approx 0$). Texas ratsnakes thermoregulated at night and again during the day, but exhibited sharp drops in thermoregulation in the morning and evening (Fig. 5). This pattern suggests that rather than being truly nocturnally active Texas ratsnakes may actually be crepuscular.

3.5. Thermal exploitation (E_x)

Averaged over the season, snakes in all three populations appeared to behave similarly, in that T_b s were within T_{set} a similar

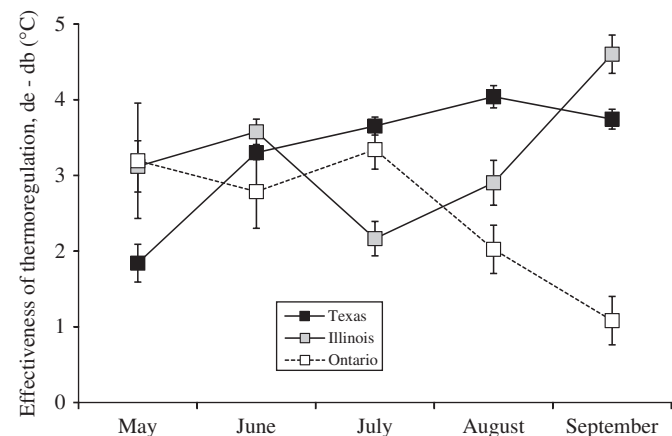


Fig. 4. Monthly variation (mean ± SE) in measures of the effectiveness of thermoregulation ($d_e - d_b$) for ratsnakes in Texas, Illinois, and Ontario.

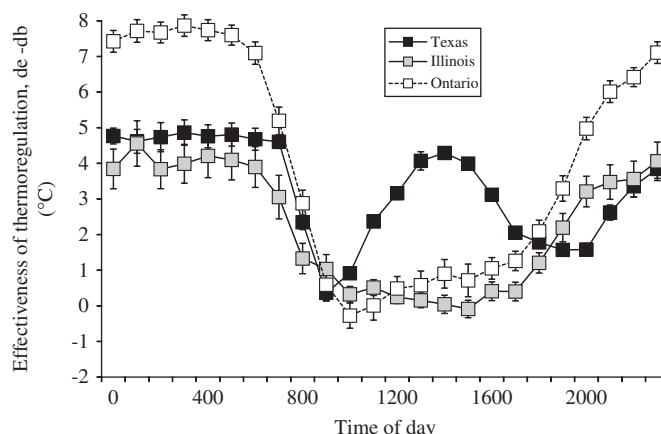


Fig. 5. Daily variation in hourly (mean ± SE) measures of the effectiveness of thermoregulation ($d_e - d_b$) for ratsnakes in Texas, Illinois, and Ontario.

Table 2

Percentage of hourly observations ratsnake body temperatures (T_b), averaged by individual snake, fell within, below or above ratsnake preferred temperature ranges (T_{set}) when it was possible (E_x) during May through September for Texas, Illinois, and Ontario ratsnake populations.

Location	$T_b = T_{set}$ (%)	$T_b < T_{set}$ (%)	$T_b > T_{set}$ (%)
Texas	23.9 ± 1.5	39.3 ± 2.5	36.7 ± 2.1
Illinois	26.7 ± 2.3	47.5 ± 3.8	25.7 ± 3.3
Ontario	21.6 ± 1.5	61.6 ± 2.5	16.7 ± 2.2

Table 3

Percentage of hourly observations that operative environmental temperature (T_e) averaged across all habitats fall within, below or above ratsnake preferred temperature ranges (T_{set}) currently, and given a 3 °C increase in ambient temperatures, for Texas, Illinois, and Ontario.

Location	$T_e = T_{set}$		$T_e < T_{set}$		$T_e > T_{set}$	
	Current	+3 °C	Current	+3 °C	Current	+3 °C
Texas	4.4	6.1	65.6	54.5	29.7	39.5
Illinois	6.2	11.1	91.3	79.1	2.5	9.8
Ontario	7.5	9.7	82.2	72.1	10.2	18.6

amount of time when it was possible (Texas: 23.91% ± 1.46; Illinois: 26.74% ± 2.26; Ontario: 21.59% ± 1.49; nested ANOVA: $F_{2,75}=1.88$, $P=0.16$). Where the populations differed, however, was in the distribution of T_b s that were outside T_{set} . The proportion of T_b s above T_{set} was much higher in Texas than in Ontario, with Illinois intermediate (nested ANOVA: $F_{2,75}=22.06$, $P < 0.001$), with the opposite pattern for T_b s below T_{set} (Table 2; nested ANOVA: $F_{2,75}=20.01$, $P < 0.001$). Tukey–Kramer analysis indicated that Texas significantly differed from other populations for the T_b s above T_{set} analysis and Ontario significantly differed from the other populations for the T_b s below T_{set} analysis.

3.6. Climate change model

For all populations, a 3 °C increase in ambient temperature would result in an increase in the length of time mean T_e for all the habitats would fall within and above T_{set} , and thus a decrease in the time T_e would fall below T_{set} (Table 3). From this analysis Illinois appears to have a cooler climate than Ontario, both now and with a rise in temperature. This results from the relative scarcity of open habitat (i.e., the bare ground or rock that was common in open habitat in Texas and Ontario). That meant that most of the thermal models (data from which were used to

Table 4

Mean hourly values of d_e [i.e., differences ($^{\circ}\text{C}$) between environmental temperatures (T_e) and snake preferred temperature range (T_{set})] in each habitat (arranged by increasing amount of canopy) for Texas, Illinois, and Ontario, given ambient temperatures and a 3°C increase in ambient temperatures. Percent change indicates the difference in mean d_e from ambient to elevated temperatures.

Location	Habitat	d_e	$d_e (+3^{\circ})$	% Change
Texas	Grassland Savannah	6.1 ± 0.04	5.7 ± 0.05	-6.5
	Oak Savannah	5.0 ± 0.03	3.7 ± 0.04	-25.3
	Forested slope	5.6 ± 0.03	4.3 ± 0.04	-22.7
Illinois	Old field	6.3 ± 0.05	5.1 ± 0.04	-18.1
	Successional field	6.3 ± 0.05	4.9 ± 0.04	-22.3
	Upland forest	7.9 ± 0.04	5.7 ± 0.04	-27.5
	Bottomland forest	7.1 ± 0.03	5.1 ± 0.03	-28.0
Ontario	Rock outcrop	9.5 ± 0.07	8.8 ± 0.08	-6.9
	Field	12.0 ± 0.07	10.5 ± 0.07	-12.7
	Forest	9.2 ± 0.06	6.3 ± 0.05	-31.4

develop the statistical models) in Illinois were placed in at least partially shaded locations even in open habitat, which resulted in few extremely high temperatures that are typically recorded when models are in constant direct sunlight. This effect of shade is apparent in the analysis of mean d_e values by habitat (Table 4). A 3°C increase in temperature will reduce d_e in all habitats at all three sites. The magnitude of the change, however, varies substantially by habitat. In open habitats in Texas and Ontario, where model temperature is affected primarily by the extent of solar radiation, the magnitude of the change in d_e was relatively small. In shaded habitats, however, where ambient temperature has the greatest effect on model temperature, the relative change predicted in d_e is high (Table 4).

The focus on mean temperatures in the previous analysis potentially misses important changes in extreme temperatures. For example, although a 3°C increase in ambient temperature appears to improve the thermal environment for ratsnakes in Texas, it is possible that occasional extreme temperatures could be dangerously hot for snakes. To examine this possibility we first determined how a 3°C increase in ambient temperature would affect T_e during the hottest hour of the day at each site. The warmest hour of the day was 13:00–14:00 for Texas, 16:00–17:00 for Illinois, and 14:00–15:00 for Ontario. Over the active season the predicted mean hourly temperatures were substantially above T_{set} in Texas, whereas in Illinois and Ontario they fell within or near T_{set} (Fig. 6). We then identified the highest predicted hourly value of T_e in any habitat at each location to determine the thermal extreme that ratsnakes might confront. Although most of these extremes were above 40°C , at the same time that these extremes occurred there would be temperatures below 35°C available to the snakes in at least one other habitat (Fig. 6). Note that apparent anomalies in the predicted extreme temperatures are again a consequence of specific habitat differences among study locations. Snake models placed in full sunlight on bare rock produced the high extreme values for Ontario, whereas the partial shading in open habitat in Illinois resulted in more moderate extreme temperatures.

4. Discussion

There are two general ways to view the patterns of body temperature and thermoregulation that we documented for ratsnakes from Texas to Ontario. One view is that, as expected, there were many differences among populations. The alternative

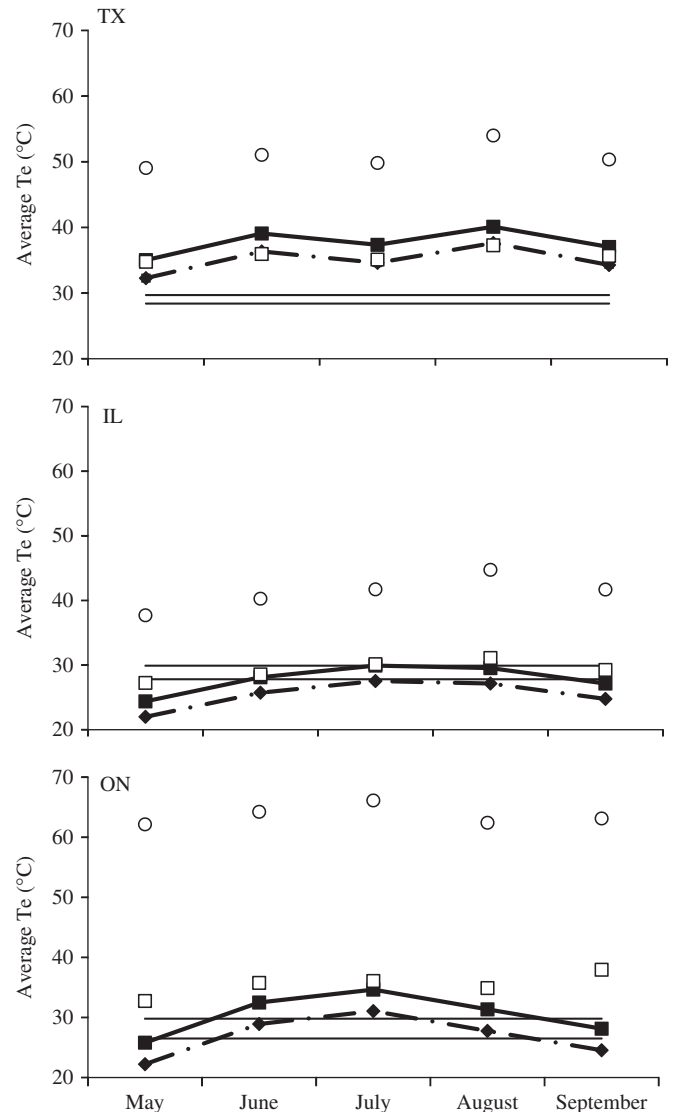


Fig. 6. Monthly variation in hourly mean operative environmental temperatures (T_e) during the warmest hour of the day under current ambient conditions (dashed line) and with a 3°C increase in ambient temperatures (solid line), in relation to the average upper and lower bounds of the preferred temperature ranges (T_{set}) of ratsnakes in Texas, Illinois, and Ontario, indicated by parallel horizontal lines. SE bars were plotted for each mean but are too small to be apparent. Open circles represent the hottest hourly temperature recorded in any habitat for that month and open squares represent the coolest hourly temperature recorded at that same time. The warmest hour of the day began at 13:00 for Texas, 16:00 for Illinois, and 14:00 for Ontario.

view is that the differences were surprisingly small given the broad latitudinal range over which the data were collected and the associated large differences in ambient temperatures between study locations. We consider both perspectives to have merit. We address each interpretation in turn before considering the implications of both our empirical data and the modeling results for how climate warming is likely to affect ratsnakes.

4.1. Population differences

Across their range, ratsnakes appear to prefer similar body temperatures, although moving from south to north, T_{set} became broader as a result of a decrease in the lower bound of T_{set} . The overall similarity in T_{set} is consistent with thermal preferences being conserved among snake species (Lillywhite, 1987), whereas the broadening of T_{set} with latitude is consistent with the general

pattern among ectotherms of decreased thermal specialization with latitude (Janzen, 1967; Tewksbury et al., 2008). Despite the thermal environment becoming increasingly challenging with latitude, snakes in all three populations realized body temperatures within their preferred temperature range 15–20% of the time.

We had predicted that during the active season, preferred temperatures would either be realized most often and with less effort in Texas and least often with more effort in Ontario, or alternatively, that Illinois would be superior to both Texas and Ontario. Neither hypothesis received clear support. Texas snakes did realize preferred temperatures most often and had the highest mean body temperatures. However, there were no significant differences in the extent of thermoregulation among populations.

The failure of the two hypotheses to predict general latitudinal patterns of body temperature and thermoregulation appears to result at least in part from the snakes in different populations using different temporal patterns of thermoregulation. Seasonally, snakes in Ontario thermoregulate most in spring when temperatures are cool, whereas snakes in Texas thermoregulate most in summer when temperatures are hot. On a daily basis, thermoregulation appears to reflect activity patterns. Snakes in Ontario and Illinois thermoregulate at night when inactive and are thermoconformers during the day when they are active. Snakes in Texas thermoregulate most of the day and night but become thermoconformers in the evening and early morning. We know that Texas ratsnakes are active at night during summer, and this pattern of thermoregulation suggests that their nocturnal activity may be primarily crepuscular. By modifying seasonal and daily patterns of thermoregulation to match local thermal conditions, ratsnakes in different populations are able to realize similar overall body temperatures with similar thermoregulatory effort.

Given the temporal flexibility in behavioral thermoregulation, the overall similarity in thermal ecology of the three ratsnake populations is striking. The explanation for how this is achieved involves the large-scale component of behavioral thermoregulation. Our focus in this study was on fine-scale thermoregulation, whereby snakes exploit thermal heterogeneity among macro and microhabitats to control their body temperatures. The other way in which ectotherms respond behaviorally to environmental temperature variation is by varying when they are active. This includes the time of day, such as the switch to nocturnal activity by Texas ratsnakes during the summer, and the time of year. In both Ontario and Illinois, ratsnakes hibernate for a substantial part of the year. Ratsnakes in Texas do not hibernate, but greatly reduce their activity through the winter (Sperry et al., 2010). Therefore, the primary thermoregulatory strategy of ratsnakes for adjusting to latitudinal variation in climate is to vary when their active season occurs during the year and within the active season, when during the day they are actually active. These large-scale behavioral responses then allow the snakes to expend a similar effort in fine-scale behavioral thermoregulation and realize similar thermal outcomes, regardless of latitude. Thus, just as seasonal activity patterns of ratsnakes appear to be highly conserved across their range (Sperry et al., 2010), so is the extent of conventional (i.e., fine-scale) thermoregulatory behavior.

4.2. Response to climate warming

Climate warming may be less detrimental for temperate-zone than tropical ectotherms despite greater predicted increases in temperature because ectotherms at higher latitudes have broader thermal tolerances (Deutsch et al., 2008; Tewksbury et al., 2008) and because low rather than high temperatures are a more important constraint at high latitudes (Kearney et al., 2009). Consistent with the latter point, our modeling of the effects of

climate warming indicated that a 3 °C increase in temperature generally improved thermal conditions for all three populations. Our results also confirmed the importance of habitat features such as the availability of shade and retreat sites for mitigating the effects of higher temperatures (Kearney et al., 2009). In some of our analyses, Ontario actually appeared to be warmer than Illinois from a snake's perspective because open habitat in Illinois was vegetated and thus shaded, whereas open habitats in Ontario were exposed to direct sun.

Given our conclusions from the analyses of thermoregulatory behavior, we expect that the likely response of ratsnakes to climate warming will be adjustments in the timing of activity more than changes in the extent of fine-scale behavioral thermoregulation. The ease with which ratsnakes can make these changes depends on the extent to which differences observed among populations are genetically determined (i.e., will changes in timing of activity require an evolutionary response or is the behavior highly plastic?). Genetic differentiation among ratsnake populations over short distances suggests that gene flow is restricted (Lougheed et al., 1999), making it likely that behavioral differences among populations will have some genetic basis. Conversely, the fact that timing of spring emergence from hibernation varies with temperature in Ontario (Blouin-Demers et al., 2000) indicates some plasticity in one of the behaviors that determines the duration of the active season. Ultimately a common-garden experiment will be necessary to assess the extent to which differences in thermoregulatory behavior among populations are environmentally determined.

Switching to nocturnal activity during summer is a behavior that might require an evolutionary change because it would also seem to involve changes in how the snakes find prey or in the type of prey hunted. Again, however, there is evidence from several ratsnake populations that suggests that nocturnal foraging is a facultative behavior. Occasional nocturnal predation on bird nests by ratsnakes has been reported from Arkansas (Hensley and Smith, 1986; Benson et al., 2010), Florida (Carter et al., 2007), and Missouri (Stake et al., 2005). Available evidence suggests ratsnakes are visual predators (Weatherhead and Blouin-Demers, 2004b), which raises interesting questions about how a facultative switch to nocturnal foraging is achieved. Nonetheless, from the perspective of how ratsnakes will respond to warmer climates, this flexibility should be advantageous.

Although some snakes species appear to be active exclusively either during the day or at night, facultative switching between diurnal and nocturnal activity in response to temperature has been documented in a number of species (Gibbons and Semlitsch, 1987). Therefore, this flexibility in the timing of activity may allow many snake species to adjust easily to warmer climates. More and better data on the timing of activity for more snake species are required to help identify which species have the flexibility to respond behaviorally to climate warming and which do not. Such data could also be used to identify the ecological factors associated with flexible timing of activity, allowing predictions to be made about snakes generally. Given what is known about snake activity, it seems likely that the consequences of climate warming for snakes may be quite different from the consequences for lizards. Most lizards are active diurnally and at high temperatures, which substantially restricts when they can be active (Huey et al., 2010). Climate warming is already narrowing that activity window sufficiently to imperil many populations and species, with more dire prospects predicted as climates get warmer (Sinervo et al., 2010). Although the ability to regulate their body temperatures behaviorally provides all ectotherms some flexibility to respond to climate warming, the interaction between ecology, physiology and how temperature is regulated behaviorally will determine how particular species will be affected.

Acknowledgement

For the Texas portion of this project, we thank the US Army and the Army Corps of Engineers, Engineer Research and Development Center for funding and J. Cornelius, T. Hayden, C. Pekins, G. Eckrich, T. Buchanan and The Nature Conservancy for logistical support. For the Illinois portion we thank the University of Illinois and The Nature Conservancy for funding and L. Jones and the US Fish and Wildlife Service and J. Waycullis and the Illinois Department of Natural Resources for logistical support. Funding for the Ontario portion of this project was provided by NSERC, Parks Canada, and the Ontario Ministry of Natural Resources. None of these organizations or individuals was involved in study design; in the collection, analysis and interpretation of data; in the writing of the report; or in the decision to submit the paper for publication.

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