

Habitat selection as the mechanism for thermoregulation in a northern population of massasauga rattlesnakes (*Sistrurus catenatus*)¹

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Abstract: Although temperature is recognized as an important barrier to reptile distribution, the mechanisms of this limitation are poorly understood. We investigated the association between temperature, habitat selection, and thermoregulation in a population of massasauga rattlesnakes (*Sistrurus catenatus*) near their northern range limit, where low temperatures are likely an important constraint. Movement data indicated that the lower limit of the massasauga's performance range (*i.e.*, $\geq 50\%$ of optimal) was 19.9 °C. Operative environmental temperatures were almost always below the massasauga's preferred range (30.0–33.6 °C) and frequently below its performance range in spring and fall. Massasaugas differed from other northern snakes by thermoregulating primarily by microhabitat selection and not by macrohabitat selection. Massasaugas thermoregulated more effectively as their visibility increased and forest cover decreased. Gravid females increased thermoregulatory behaviour in response to low temperatures in spring and summer. Male and non gravid female massasaugas did not take full advantage of thermoregulatory opportunities in the spring and fall, and as a consequence were often too cool to perform essential functions such as prey capture. Our results are consistent with the hypothesis that temperature limits massasauga distribution primarily via effects on gestation and hence juvenile recruitment.

Keywords: cold climate, macrohabitat selection, microhabitat selection, radiotelemetry, thermal constraints, thermoregulation.

Résumé : Bien que la température soit reconnue comme une barrière importante à la distribution des reptiles, les mécanismes de cette limitation sont mal compris. Nous avons examiné les liens entre la température, la sélection d'habitats et la thermorégulation dans une population de serpents à sonnettes massasaugas (*Sistrurus catenatus*) près de leur limite nordique de distribution, où les basses températures constituent probablement une contrainte importante. Les données de mouvement indiquaient que la limite inférieure de l'étendue des températures permettant au massasauga de bien fonctionner (c'est-à-dire $\geq 50\%$ de celle optimale) était 19,9 °C. Les températures opérantes de l'environnement étaient presque toujours inférieures à l'étendue des températures préférées du massasauga (30,0–33,6 °C), et au printemps et à l'automne, fréquemment inférieures à celles lui permettant de bien fonctionner. La thermorégulation des massasaugas différait de celle des autres serpents nordiques en s'effectuant principalement par la sélection au niveau du microhabitat et non pas au niveau du macrohabitat. La thermorégulation des massasaugas devenait plus efficace lorsque leur visibilité augmentait et que le couvert forestier diminuait. Les femelles gravides augmentaient leur comportement de thermorégulation en réponse aux basses températures au printemps et l'été. Les mâles et les femelles non gravides massasaugas n'utilisaient pas les opportunités de thermorégulation à leur plein potentiel au printemps et l'automne, et par conséquent, ils étaient souvent trop froids pour exécuter des fonctions essentielles comme la capture de proies. Nos résultats sont compatibles avec l'hypothèse que la température limite la distribution des massasaugas principalement par des effets sur la gestation et le recrutement juvénile.

Mots-clés : climat froid, contraintes thermiques, sélection de macrohabitat, sélection de microhabitat, télémétrie radio, thermorégulation.

Nomenclature: Fisher, Joynt & Brooks, 2007.

Introduction

The inability of most reptiles to generate substantial metabolic heat means that environmental temperatures largely determine where and how they live. Body temperatures of reptiles, however, are not simply a passive function of environmental temperatures. Rather, reptiles that live in thermally heterogeneous environments actively exploit that heterogeneity to achieve body temperatures conducive to optimal physiological performance (Cowles & Bogert,

1944; Huey, 1991), thus broadening the geographic range they can occupy (Lillywhite, 1987). Most studies of thermal constraints on reptiles have focused on how squamates (snakes and lizards) respond to environmental temperatures above tolerance limits (Grant & Dunham, 1988; Beaupre, 1995; Bashey & Dunham, 1997; Beck & Jennings, 2003). Many snakes and lizards occur in extremely hot environments (*e.g.*, deserts) whereas few occur as far north as the Arctic Circle (Zug, Vitt & Caldwell, 2001), suggesting that the ability to keep warm, rather than the ability to stay cool, is the more important barrier to reptile distribution (Shine & Madsen, 1996). Here we investigate the association between temperature, habitat selection, and thermoregulation in a population of massasauga rattlesnakes (*Sistrurus catenatus*,

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Viperidae) near their northern range limit, where low temperature is likely to be an important constraint.

It is common practice to interpret thermoregulatory behaviour in reference to a temperature range within which most bodily functions are maximized (Hare *et al.*, 2009; Monasterio *et al.*, 2009; Smolinsky & Gvozdk, 2009; Thierry *et al.*, 2009). Many reptiles are capable of functioning at temperatures remote from their optimal range, however, and may actually spend most of their time in suboptimal thermal environments (Stevenson, Peterson & Tsuji, 1985; Lillywhite, 1987; Huey *et al.*, 1989a; Blouin-Demers, Weatherhead & McCracken, 2003; Isaac & Gregory, 2004). Therefore, the more ecologically relevant basis for assessing thermoregulation for reptiles living in thermally challenging environments may be the temperature range within which reptiles are capable of performing reasonably well, rather than the temperature range that optimizes performance. This is especially likely to be the case in highly variable thermal environments such as those occurring near northern range limits, because reptiles are expected to perform well over a broad range of temperatures in these areas (Huey & Kingsolver, 1993; Angilletta, Niewiarowski & Navas, 2002). Therefore, our first goal in evaluating thermoregulatory behaviour in massasaugas was to identify the range of body temperatures within which massasaugas perform most functions reasonably well. We define this as the range of temperatures in which snakes in the field regularly move between locations. Because snakes are generally capable of locomotion over a broader range of body temperatures than the range required for other activities (Lillywhite, 1987), environmental temperatures that constrain movement should also be unsuitable for other processes (digestion, ecdysis, gestation).

Although many studies have documented an association between habitat selection and thermoregulation in reptiles (Huey *et al.*, 1989b; Diaz, 1997), some fundamental gaps remain in our understanding of this relationship. For example, we know that snakes selectively use both macrohabitats (Blouin-Demers & Weatherhead, 2001a,b) and microhabitats (Huey *et al.*, 1989b; Robertson & Weatherhead, 1992; Webb, Pringle & Shine, 2004) to regulate body temperatures, but we do not know the relative importance of these 2 types of habitat selection for thermoregulation. Our primary goal in this study was to determine the relative importance of macro- and microhabitat selection for thermoregulation by massasaugas. Previously, we documented that massasaugas use their habitat non-randomly at both scales, but we did not assess the role of thermoregulation in that behaviour (Harvey & Weatherhead, 2006a).

Related to the issue of the relative importance of macro- and microhabitat selection for thermoregulation is whether snakes thermoregulate equally in macrohabitats of different thermal quality. Only 2 studies have addressed this question; those studies found that both ratsnakes (*Elaphe obsoleta*) and milksnakes (*Lampropeltis triangulum*) realized more favourable body temperatures with less additional investment in thermoregulation in thermally superior habitats (Blouin-Demers & Weatherhead, 2002; Row & Blouin-Demers, 2006). Therefore, our second objective

was to determine whether massasaugas also vary their thermoregulation with the thermal quality of their habitat. In principle, the mechanism for differential thermoregulation could involve differences in both microhabitat selection and basking behaviour. At the finest scale, however, microhabitat selection sometimes cannot be distinguished from basking behaviour (*e.g.*, selecting the underside or top of a rock). When assessing whether massasaugas thermoregulate differently by habitat, therefore, we also determine the influence of basking behaviour on thermoregulation.

If low environmental temperature is an important constraint for the northern population of massasaugas that we studied, we expect the snakes to select habitat that allows them to maintain body temperatures within the performance range whenever possible. Alternatively, snakes may modify their behaviour and actively select thermally superior habitat only at particular times. For example, females may thermoregulate more when they are gravid in mid-summer or males may thermoregulate more while undergoing spermatogenesis in the spring (Herczeg *et al.*, 2007; Crane & Greene, 2008; Gardner-Santana & Beaupre, 2009). Gravid massasaugas maintain higher body temperatures than males or nongravid females, suggesting that gestation is the element of the life cycle most sensitive to temperature (Harvey & Weatherhead, forthcoming), so if snakes vary in the extent to which they use habitat selection to thermoregulate, we expect that gravid females would be more selective than males and nongravid females. Therefore, when addressing our objectives regarding habitat selection and thermoregulation we consider the influence of sex and reproductive status on this behaviour.

Methods

STUDY SITE AND RADIODIOMETRY

We conducted our research on the Upper Bruce Peninsula (45° 10' N, 81° 29' W), Ontario, Canada, approximately 50 km from the northern limit of the massasauga's distribution. We used 2 study sites 12.5 km apart, collectively containing a mix of the principal local habitats (sand dunes, alvars, wetlands, coniferous and deciduous forests, and successional old fields) (Harvey & Weatherhead, 2006a). We initially found snakes opportunistically by searching both study sites, with most subsequent captures resulting from finding snakes temporarily associated with those we were tracking. We sexed snakes using probes; the reproductive condition of females was based on direct observations of whether or not they gave birth that season. From 2001 to 2003, we implanted temperature-sensitive radio transmitters (Model SI-2T, Holohil Systems Inc., Carp, Ontario, Canada) in 19 males and 15 females (9 gravid and 6 nongravid). Five females were gravid in one year and nongravid the next year, and 1 female went from nongravid to gravid between years. Surgical procedures generally followed Reinert and Cundall (1982), with transmitters implanted in snakes' body cavities. Following surgery snakes were held for 3 d and then released at the point of capture.

We located snakes on average every 2 d until they entered hibernation and again when they re-emerged

the following spring. Hibernation typically lasted from November through April (Harvey & Weatherhead, 2006b). Snake locations were classified by season as “spring” (May and June), “summer” (July and August), or “fall” (September and October). Exact positions were recorded in Universal Transverse Mercator (UTM) coordinates (North American Datum of 1983) using a handheld global positioning system unit (GPS 12XL) with a mean precision of 4.6 m. Upon location of each snake we recorded the pulse rate of the implanted transmitter. We used pulse rate to calculate the temperature of the transmitter (thus, the snake’s internal body temperature) using calibration equations derived from calibration curves supplied by the manufacturer. The calibration equations were calculated for each transmitter using polynomial regression (including all terms up to degree four) with 8 calibration points to determine the relationship between pulse rate and temperature ($R^2 > 0.99$ for all equations). Although we also used data loggers to collect more extensive temperature data for other purposes (Harvey & Weatherhead, forthcoming), here we use only temperature data collected when snakes were located so that each body temperature observation could be associated directly with observations of habitat use.

HABITAT USE

We determined the macrohabitat of each snake location using a satellite image classified into 4 broad categories (open, wetland, sparse forest, and dense forest; see Harvey & Weatherhead, 2006a for details). We used a two-step process to determine the relative contribution of macro- and microhabitat selection to thermoregulatory effectiveness. First, we compared the thermal quality of a snake’s chosen macrohabitat to the mean thermal quality of all macrohabitats (*i.e.*, the effectiveness of macrohabitat selection). Second, we compared the body temperature of the snake to the mean thermal quality of the macrohabitat where it was located at the time (*i.e.*, the effectiveness of microhabitat selection).

In using this indirect approach to determine the importance of microhabitat selection for thermoregulation we are assuming that differences in body and environmental temperatures reflect the snake’s choice of microhabitat. Because basking could also contribute to those differences, however, we documented basking by estimating the proportion (to the nearest 25%) of the snake that was visible each time we located it. We did not estimate visibility in the few instances that a snake was moving when observed in case our approach had caused the movement and thus affected visibility. The effectiveness of basking for thermoregulation is likely to be affected by the amount of forest canopy above a snake. Therefore, at each snake location we also estimated the percentage of forest cover (no nearby trees = 0%, many trees with complete canopy closure = 100%).

OPERATIVE ENVIRONMENTAL TEMPERATURE (T_e)

Operative environmental temperature (T_e) is the temperature an ectotherm would experience if behaving without regard to the thermal environment. T_e is commonly estimated using models with the same thermal properties as the animal of interest (Dzialowski, 2005). We quantified the

thermal environment available to massasaugas by placing 5 to 15 copper snake models in each of the 4 major habitat types (open, wetland, sparse forest, and dense forest) and used data loggers (SRX 400, Lotek Engineering, Newmarket, Ontario, Canada) to record model temperatures continuously for up to 3 weeks. To determine the mean T_e within each habitat at all times throughout the active season, we developed multiple regression equations linking the model temperatures to weather variables (solar radiation, air temperature, relative humidity, and wind speed) recorded at a nearby weather station.

We used 3 temperature ranges to interpret the impact of the thermal environment on massasauga performance: the activity range, the preferred range, and the performance range. The activity range is the range of temperatures within which snakes are able to sustain aboveground activity, determined by the lowest and highest T_b observed from a field-active snake (Huey, 1982). The activity range for massasaugas on the Upper Bruce Peninsula is 1.1 °C to 44.0 °C (Harvey & Weatherhead, forthcoming). The preferred temperature range (T_{set}) is the range of temperatures within which snakes maintain body temperatures in the absence of external factors that influence temperature selection (*e.g.*, predators; Huey, 1982). Most physiological and whole-animal functions are optimized within T_{set} (Bennett, 1980; Huey, 1982; Huey & Bennett, 1987). Operationally, T_{set} is determined as the lower and upper values of the median 50% of temperatures selected by snakes in a thermal gradient (Hertz, Huey & Stevenson, 1993). T_{set} for our population of massasaugas is 30.0 °C to 33.6 °C (Harvey & Weatherhead, forthcoming). We defined the performance range as the range of temperatures within which most functions are performed reasonably well. We set the lower limit of the performance range as the temperature below which snakes had less than a 50% probability of moving between successive locations. We did not set an upper limit to the performance range because temperatures low enough to permit movement were always available. A snake was considered immobile if it did not move > 10 m between observations. We compared the probability of movement to the highest T_e (averaged among all habitats) documented between successive snake observations, assuming massasauga movement was limited by the highest temperatures generally available. We excluded gravid females from calculation of the performance range because they rarely moved regardless of T_e .

THERMOREGULATION INDICES

Following Hertz, Huey, and Stevenson (1993), we quantified the thermal quality of the environment (d_e) as the deviation of environment temperature from the preferred range, calculated as the absolute value of the difference between T_e and T_{set} . Accuracy of body temperature (d_b) is the deviation of body temperature from the preferred range, calculated as the absolute value of the difference between T_b and T_{set} . The difference between d_e and d_b is a measure of thermoregulatory effectiveness (Blouin-Demers & Weatherhead, 2001b), with high values of $d_e - d_b$ indicating disproportionate use of thermally favourable habitat. In contrast, low values of

$d_c - d_b$ indicate thermoconformity, and negative values suggest avoidance of thermally favourable sites.

STATISTICAL ANALYSES

We pooled observations from individual snakes to conduct analyses (no individual snake represented > 7% of observations). We performed polynomial regression (including terms up to the 3rd degree) to determine the relationship between movement probability and environmental temperature. We rounded d_c values to the nearest integer, and for each 1 °C increment of d_c we used the proportion of snakes observed that moved as the movement probability.

We used multiple linear regression to determine the effects of habitat use and basking on thermoregulatory effectiveness. The snake visibility and forest cover estimates were log-transformed prior to analysis. We used *t*-tests and ANOVA to compare group means and Tukey’s test for *post hoc* comparisons. Statistical analyses were performed using JMP 4.0.0 (SAS Institute Inc., Cary, North Carolina).

Results

PERFORMANCE RANGE

We recorded 2487 snake locations from 34 individuals. Snakes changed locations between successive tracking episodes approximately 70% of the time when environmental temperatures were close to T_{set} , although when temperatures were within T_{set} the snakes actually became less active (Figure 1). Once d_c increased beyond 9 °C the probability of snakes moving dropped steadily (Figure 1). The estimated temperature below which movement probability was less than 50% was 19.9 °C. Hereafter we refer to environmental temperatures within the snakes’ preferred range as “favourable”, outside the snakes’ preferred range (*i.e.*, < 30.0 °C) but above or equal to 19.9 °C as “challenging”, and below 19.9 °C as “constraining”.

THERMAL QUALITY OF THE ENVIRONMENT

During the massasauga’s aboveground months (May through October), the thermal environment was always

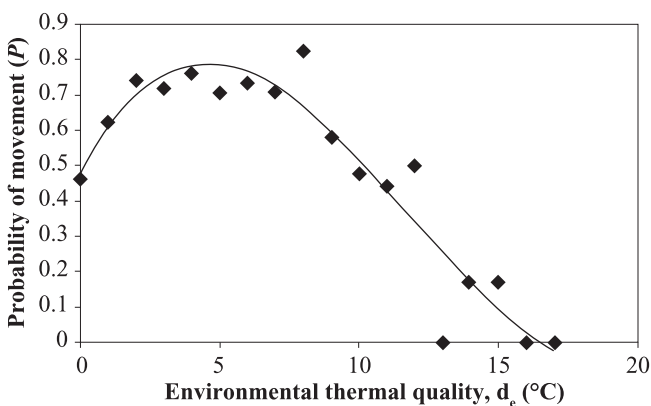


FIGURE 1. The probability of *Sistrurus catenatus* movement ($n = 504$) in relation to the thermal quality of the environment (d_c) on the Upper Bruce Peninsula, Ontario. Each point represents the proportion of snakes that moved at a given temperature. A third-order polynomial equation is fit to the points ($y = 0.48 + 0.15x - 0.21 \cdot 10^{-1}x + 0.59 \cdot 10^{-3}x$, $R^2 = 0.90$).

suitable for activity (> 1.1 °C) within at least 1 habitat, and was within the massasauga’s activity range > 99.9% of the time ($n = 13\,248$), averaged across habitats. On average, environmental temperatures were constraining during May and September and at night in all seasons, and challenging otherwise (Figure 2). Of our 2487 observations of snake locations, 13 were recorded when environmental temperatures were favourable, 1381 (56%) when temperatures were challenging, and 1093 (44%) when temperatures were constraining.

THERMOREGULATION: MACRO- *VERSUS* MICROHABITAT SELECTION

We had a substantial number of observations of snakes in all 4 macrohabitats. Comparing the thermal quality of the macrohabitat in which a snake was observed to the mean thermal quality of all macrohabitats (*i.e.*, the effectiveness of macrohabitat selection) provided little evidence that massasaugas used macrohabitat selection to thermoregulate (Table I). In contrast, snakes used thermally favourable microhabitats in all macrohabitats. Massasaugas used microhabitat selection to regulate body temperature to a greater extent in forested areas than non-forested habitats ($d = 1.6$ °C, $t_{2485} = 7.5$, $P < 0.001$; Table I). Overall, snakes maintained body temperatures above T_c in each of the macrohabitats (Table I).

THERMOREGULATION AND BASKING

We recorded snake visibility and forest cover at 2457 snake locations. Massasaugas thermoregulated more effectively as their visibility increased and forest cover decreased ($F_{3, 2453} = 97.8$, $P < 0.001$, $R^2 = 0.11$; Figure 3), with snake exposure explaining approximately 1.2 times as much variation in $d_c - d_b$ as forest cover. Basking behaviour and forest cover varied by sex and reproductive condition, season, and environmental temperature. Gravid females basked more during gestation (spring and summer) than other snakes, but only when environmental temperatures were constraining (both $d > 15.6\%$, $q_{3, 697} > 6.1$, $P < 0.001$; Figure 4). Nongravid females and males did not vary their basking in response to constraining environmental temperatures in any season (Figure 4). Gravid females used less forest cover during gestation (spring and summer) than did males and nongravid females (both $d > 9.5\%$, $q_{3, 1780} > 5.5$, $P < 0.001$; Figure 5). Males and gravid females, but not nongravid females, used more forest cover in the fall than in other seasons (Figure 5).

BODY TEMPERATURE ACCURACY (d_b)

By using sparse forest and basking more when environmental temperatures were constraining, gravid females almost always (92% of 349 observations) maintained body temperatures within the performance range while gestating. Male and nongravid female body temperatures were less often (75% of 1452 observations) within the performance range over the same time period ($\chi^2_1 = 44.9$, $P < 0.001$). Males and gravid females, but not nongravid females, thermoregulated more accurately in the spring than the fall (Figure 6). All snakes routinely experienced body temperatures outside the performance range in the fall (> 47% of observations for males, nongravid females, and gravid females; Figure 6).

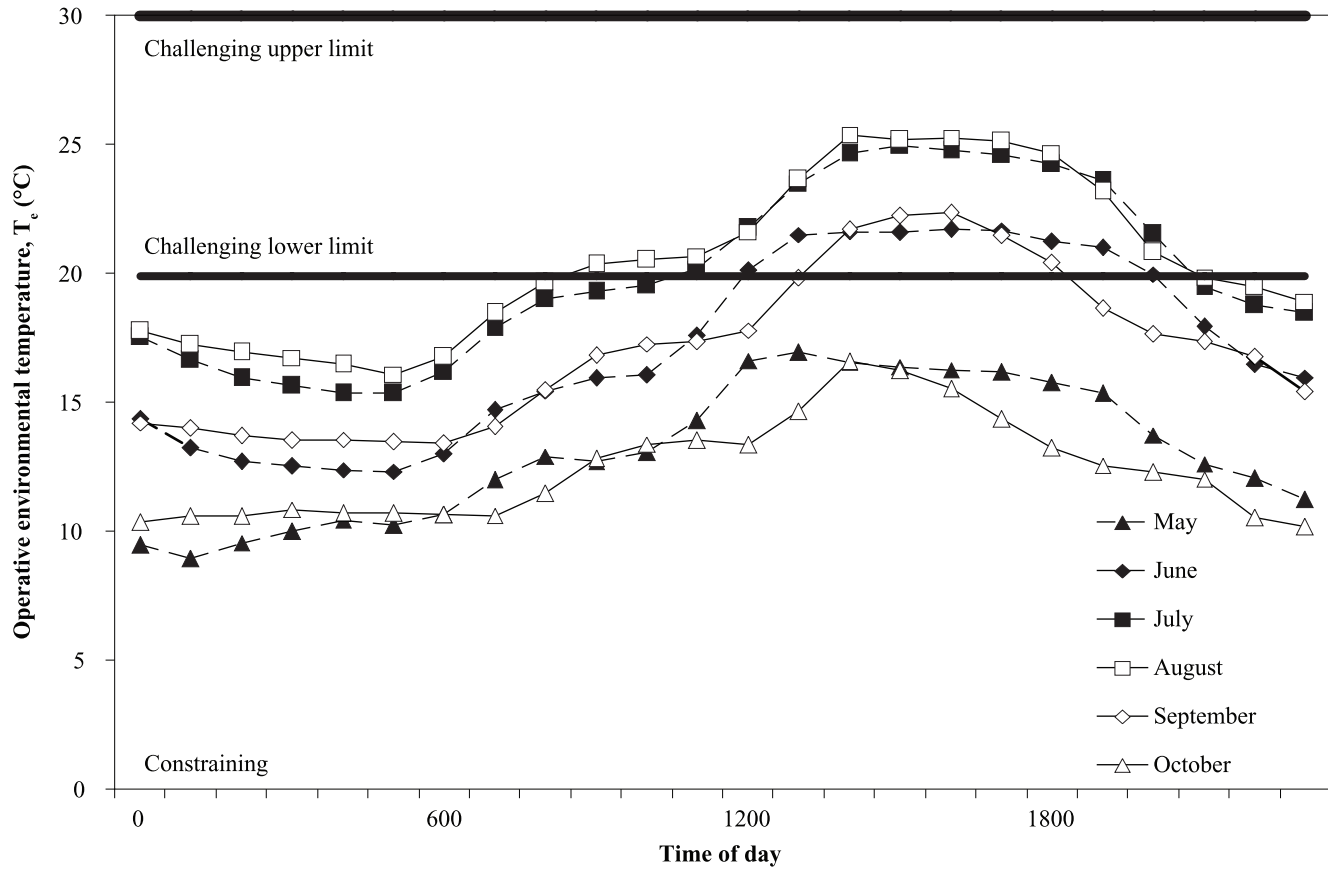


FIGURE 2. Operative environmental temperature (mean T_e , $n = 13\ 248$) for *Sistrurus catenatus* on the Upper Bruce Peninsula, Ontario, from August 2001 to July 2004 by time of day and month.

TABLE I. The relative contribution of macro- and microhabitat selection to effective thermoregulation (mean $d_e - d_b \pm SE$, °C) by massasaugas on the Upper Bruce Peninsula, Ontario.

Macrohabitat	n	Mean thermoregulatory effectiveness ($d_e - d_b$, °C)		
		Via macrohabitat	Via microhabitat	Total
Open	642	1.9 ± 0.1	2.4 ± 0.2	4.4 ± 0.2
Wetland	376	1.8 ± 0.1	1.8 ± 0.3	3.7 ± 0.2
Sparse forest	541	-1.1 ± 0.2	4.5 ± 0.2	3.4 ± 0.2
Dense forest	928	-1.0 ± 0.1	3.5 ± 0.2	2.5 ± 0.2
Overall	2487	0.2 ± 0.1	3.2 ± 0.1	3.3 ± 0.1

Discussion

Despite the wide range of body temperatures recorded from massasaugas observed above ground (from near freezing to above 40 °C), movement data indicated that the snakes functioned best when environmental temperatures (T_e) were within approximately 9 °C of T_{set} . Movement actually appeared to be curtailed when T_e was within T_{set} , which could be explained in 1 of 2 ways. Either the snakes moved less because they did not need to move to thermoregulate, or when mean T_e s were within T_{set} , movement might have been limited because some habitats were dangerously hot (Martin & Huey, 2008). Once T_e s were more than 9 °C below T_{set} , performance declined steadily with decreasing temperature. The relationship between performance and temperature that

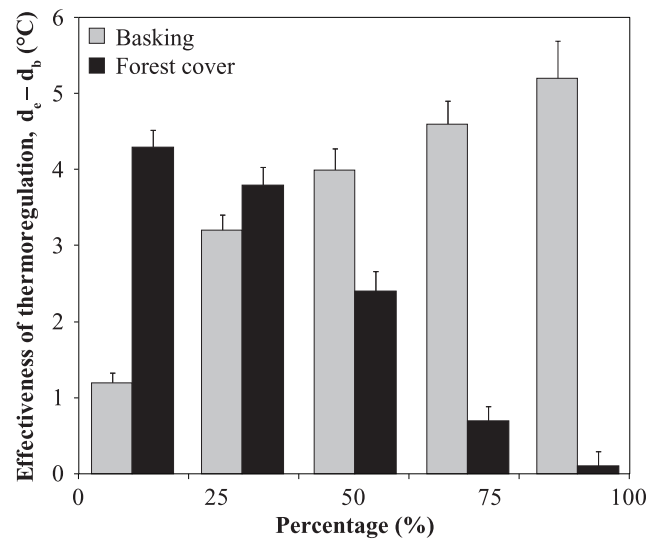


FIGURE 3. Effectiveness of thermoregulation (mean $d_e - d_b + SE$) by *Sistrurus catenatus* as a function of basking ($n = 2401$) and forest cover ($n = 2421$) on the Upper Bruce Peninsula, Ontario.

was observed for massasaugas is similar to that observed for northern populations of ratsnakes (*Elaphe obsoleta*) and watersnakes (*Nerodia sipedon*) by Blouin-Demers, Weatherhead and McCracken (2003). In snakes generally,

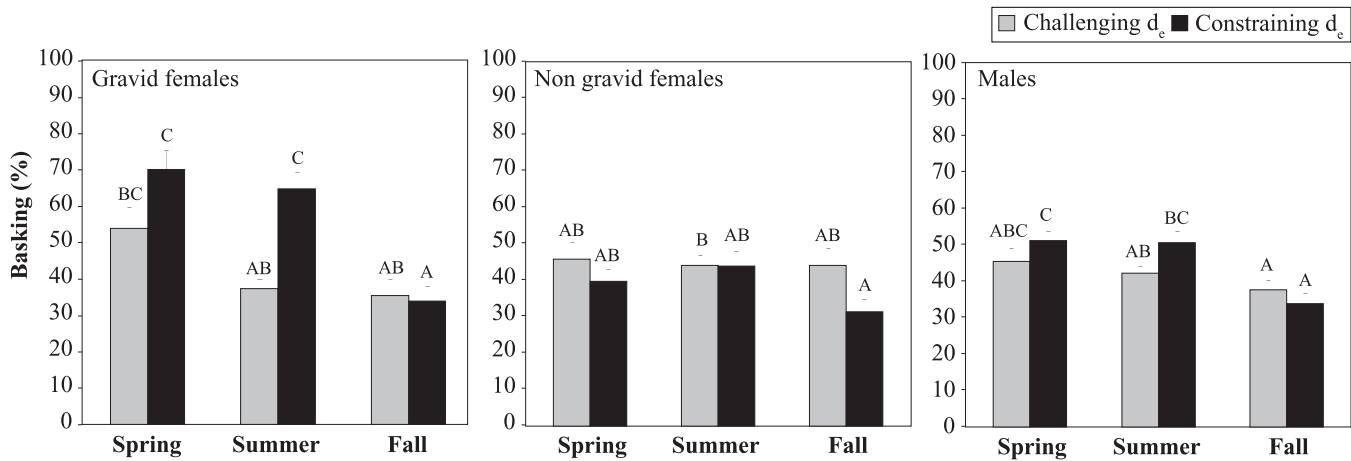


FIGURE 4. Basking (mean % exposure + SE, $n = 2401$) by *Sistrurus catenatus* on the Upper Bruce Peninsula, Ontario, by sex and reproductive condition, season, and thermal quality of the environment (challenging $d_e = 0.1-10.1$ °C, constraining $d_e > 10.1$ °C). Within sex and reproductive condition, basking was not significantly different between groups with a common letter (Tukey's test, $P > 0.05$).

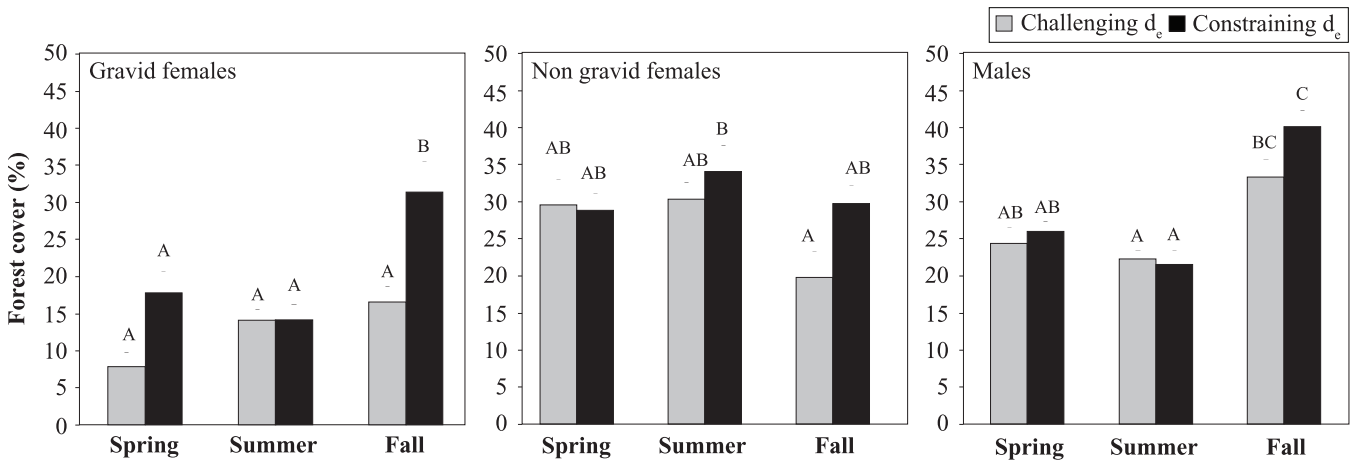


FIGURE 5. Forest cover (mean + SE, $n = 2421$) used by *Sistrurus catenatus* on the Upper Bruce Peninsula, Ontario, by sex and reproductive condition, season, and thermal quality of the environment (challenging $d_e = 0.1-10.1$ °C, constraining $d_e > 10.1$ °C). Within sex and reproductive condition, forest cover was not significantly different between groups with a common letter (Tukey's test, $P > 0.05$).

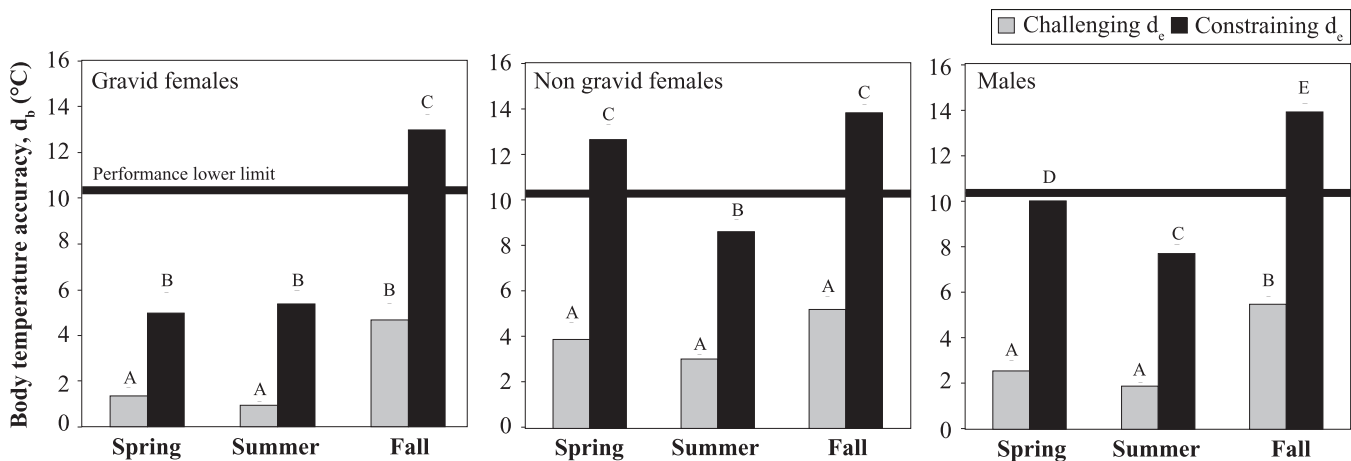


FIGURE 6. Body temperature accuracy (mean d_b + SE, $n = 2429$) of *Sistrurus catenatus* on the Upper Bruce Peninsula, Ontario, by sex and reproductive condition, season, and thermal quality of the environment (challenging $d_e = 0.1-10.1$ °C, constraining $d_e > 10.1$ °C). Within sex and reproductive condition, accuracy was not significantly different between groups with a common letter (Tukey's test, $P > 0.05$).

temperatures more than 8–10 °C below optimal substantially impair performance (Greenwald, 1974; Muth, 1980; Beuchat, 1988; Burger, 1991; Shine & Harlow, 1996; Webb & Shine, 1998).

The two-step approach we used to assess the relative importance of macro- and microhabitat selection for thermoregulation indicated that microhabitat selection was the predominant mechanism. We found little evidence that massasaugas used major habitat types on the basis of their thermal quality, whereas within habitats, the snakes were warmer than expected if use of microhabitats were random. Massasaugas used forested habitat in the months immediately pre- and post-hibernation (Harvey & Weatherhead, 2006a). Although this was in part a consequence of their hibernation sites being in forests (Harvey & Weatherhead, 2006b), open habitat was nearby and thus the snakes could have switched habitats relatively easily. Instead the snakes appeared to improve their body temperature by selecting locations with more open canopy within forests, only later moving to open habitat. The massasaugas we studied differ from northern populations of ratsnakes and milksnakes (Blouin-Demers & Weatherhead, 2001b; Row & Blouin-Demers, 2006) in their failure to use macrohabitat selection to thermoregulate.

One possible explanation for the difference among snake species is that the forests where ratsnakes and milksnakes were studied provide fewer opportunities for thermoregulation than the more open forests where we studied massasaugas, requiring ratsnakes and milksnakes to move to open habitats to thermoregulate. Alternatively, because massasaugas are ambush predators, moving to a different habitat to thermoregulate may involve a foraging cost that is greater than that experienced by active predators such as ratsnakes and milksnakes. If shuttling thermoregulation reduces foraging success by increasing conspicuousness of the snake to prey, it removes one of the primary advantages of maintaining a higher body temperature (Secor & Nagy, 1994; Ayers & Shine, 1997; Shine *et al.*, 2002; Tsairi & Bouskila, 2004). Ambush predators may instead opt to “wait it out” in current habitats until conditions become favourable for foraging. Massasaugas thermoregulated in all macrohabitats, which is again different from ratsnakes, which appear not to actively select thermally superior microhabitats when in thermally superior macrohabitats (Blouin-Demers & Weatherhead, 2002). Again, habitat differences between study locations or differences in the costs of microhabitat selection associated with differences in foraging mode could explain this difference between these species. One obvious approach to evaluating these alternatives would be to study the thermoregulatory behaviour of these snakes where all 3 species co-occur.

Selection of microhabitats with less forest cover contributed to thermoregulatory effectiveness, although somewhat less than basking. The massasaugas we studied are nearly always close to cover (Harvey & Weatherhead, 2006a), so from a thermoregulatory perspective what matters is how the snakes use that cover. Although there was some minor variation in the extent of basking with sex, season, and thermal quality of the environment, the general insight that emerged is that massasaugas spend a lot of time

basking. Based on a definition of basking as snakes being stationary and visible, Blouin-Demers and Weatherhead (2001b) estimated that ratsnakes spend approximately 20% of their time basking and Row and Blouin-Demers (2006) estimated that milksnakes basked between 35% of the time in spring to less than 10% in summer and fall. Using the same definition, the massasaugas we studied basked more than 70% of the time. This large difference between species seems unlikely to be a consequence of the massasaugas having substantially different thermal needs from the other 2 species, although the mean preferred temperature of massasaugas is approximately 2 °C higher than that of milksnakes (Row & Blouin-Demers, 2006) and 3.5 °C warmer than that of ratsnakes (Blouin-Demers & Weatherhead, 2001a). Basking clearly contributes to thermoregulation in massasaugas, but being exposed is also likely to be a requirement of being an ambush predator. The fact that basking by males and non-gravid females (*i.e.*, the snakes most likely to be feeding: Keenlyne & Beer, 1973) did not vary substantially with season or with the thermal quality of the environment is consistent with exposure being important for hunting. Better understanding of how the costs and benefits of thermoregulation vary with foraging mode in snakes is required to explain the relationships among habitat selection, basking, and thermal ecology.

Female massasaugas clearly increased thermoregulatory behaviour when gravid and by doing so maintained consistently high body temperatures during cool environmental conditions. Increased internal body temperatures in north-temperate snakes have been linked to improved offspring viability and phenotypes (Fox, Gordon & Fox, 1961; Osgood, 1978; Arnold & Peterson, 1989; Burger, 1991; Lourdais *et al.*, 2004). Gravid massasaugas achieved warmer body temperatures primarily by basking more than other snakes, a behaviour common in cool-climate reptiles (Shine, 2004). Unlike most species, however, gravid female massasaugas were able to access suitable basking locations while occupying the same macrohabitats as other massasaugas. The availability of suitable gestation sites within the snakes’ “regular” habitat presumably is advantageous because any costs (*e.g.*, predation) associated with moving to a different habitat would be avoided. Similarly, *post-partum* females do not need to change habitats to begin foraging. Whether any advantage resulting from this spatial arrangement of gestation sites is sufficient to have demographic consequences remains to be determined.

Finally, our results have implications for understanding the factors that determine the northern limit of massasauga distribution. By forgoing opportunities for behavioural thermoregulation in the spring and fall, male and nongravid female massasaugas frequently experienced body temperatures too low for movement, prey capture, digestion, and other essential functions. In effect, this reduced the length of their active season from 6 months to 4 months. A reasonable inference from this behaviour is that the benefits of a longer active season are outweighed by the costs of thermoregulation (*e.g.*, predation risk) in a low temperature environment for most massasaugas, and males and non-gravid females can afford to make this trade-off. In contrast, gravid females made the behavioural adjustments necessary

to maintain body temperatures suitable for gestation. By maintaining higher body temperatures than males or non-gravid females, gravid females decreased the length of time required for gestation by approximately 2 weeks, giving birth in late August (Harvey & Weatherhead, forthcoming), just prior to the thermal quality of the environment declining sharply. Failure to pay the costs of increased thermoregulation would give their offspring inadequate time to locate hibernation sites and accumulate enough fat reserves to survive their first winter, a hypothesis thought to apply to many temperate-zone snakes (Völkl, 1989; Burger, 1991; Martin, 1992; Bronikowski, 2000; Kissner & Weatherhead, 2005). Juvenile recruitment is often low at north latitudinal and upper altitudinal limits of reptiles and may serve as the proximate barrier to their spread (Muth, 1980; Porter & Tracy, 1983; Burger, 1991; Bobyne & Brooks, 1994; Blem & Blem, 1995; Zaiden, Kreider & Beaupre, 2003; Lourdais *et al.*, 2004; Brown, Kéry & Hines, 2007). With appropriate planning now, climate warming may soon provide herpetologists an opportunity to test these hypotheses.

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Literature cited

- Angilletta Jr., M. J., P. H. Niewiarowski & C. A. Navas, 2002. The evolution of thermal physiology in ectotherms. *Journal of Thermal Biology*, 27: 249–268.
- Arnold, S. J. & C. R. Peterson, 1989. A test for temperature effects on the ontogeny of shape in the garter snake *Thamnophis sirtalis*. *Physiological Zoology*, 62: 1316–1333.
- Ayers, D. Y. & R. Shine, 1997. Thermal influences on foraging ability: Body size, posture and cooling rate of an ambush predator, the python *Morelia spilota*. *Functional Ecology*, 11: 342–347.
- Bashey, F. & A. E. Dunham, 1997. Elevational variation in the thermal constraints on and microhabitat preferences of the greater earless lizard *Cophosaurus texanus*. *Copeia*, 1997: 725–737.
- Beaupre, S. J., 1995. Effects of geographically variable thermal environment on bioenergetics of mottled rock rattlesnakes. *Ecology*, 76: 1655–1665.
- Beck, D. D. & R. D. Jennings, 2003. Habitat use by gila monsters: The importance of shelters. *Herpetological monographs*, 17: 111–129.
- Bennett, A. F., 1980. The thermal dependence of lizard behaviour. *Animal Behaviour*, 26: 455–462.
- Beuchat, C. A., 1988. Temperature effects during gestation in a viviparous lizard. *Journal of Thermal Biology*, 13: 135–142.
- Blem, C. R. & L. B. Blem, 1995. The eastern cottonmouth (*Agkistrodon piscivorus*) at the northern edge of its range. *Journal of Herpetology*, 29: 391–398.
- Blouin-Demers, G. & P. J. Weatherhead, 2001a. Habitat use by black rat snakes (*Elaphe obsoleta obsoleta*) in fragmented forests. *Ecology*, 82: 2882–2896.
- Blouin-Demers, G. & P. J. Weatherhead, 2001b. Thermal ecology of black rat snakes (*Elaphe obsoleta*) in a thermally challenging environment. *Ecology*, 82: 3025–3043.
- Blouin-Demers, G. & P. J. Weatherhead, 2002. Habitat-specific thermoregulation by black rat snakes (*Elaphe obsoleta obsoleta*). *Oikos*, 97: 59–68.
- Blouin-Demers, G., P. J. Weatherhead & H. A. McCracken, 2003. A test of the thermal coadaptation hypothesis with black rat snakes (*Elaphe obsoleta*) and northern water snakes (*Nerodia sipedon*). *Journal of Thermal Biology*, 28: 331–340.
- Bobyne, M. L. & R. J. Brooks, 1994. Incubation conditions as potential factors limiting the northern distribution of snapping turtles, *Chelydra serpentina*. *Canadian Journal of Zoology*, 72: 28–37.
- Bronikowski, A. M., 2000. Experimental evidence for the adaptive evolution of growth rate in the garter snake *Thamnophis elegans*. *Evolution*, 54: 1760–1767.
- Brown, W. S., M. Kéry & J. E. Hines, 2007. Survival of timber rattlesnakes (*Crotalus horridus*) estimated by capture–recapture models in relation to age, sex, color morph, time, and birth-place. *Copeia*, 2007: 656–671.
- Burger, J., 1991. Effects of incubation temperature on behaviour of hatchling pine snakes: Implications for reptilian distribution. *Behavioural Ecology and Sociobiology*, 28: 297–303.
- Cowles, R. B. & C. M. Bogert, 1944. A preliminary study of the thermal requirements of desert reptiles. *Bulletin of the American Museum of Natural History*, 83: 261–296.
- Crane, A. L. & B. D. Greene, 2008. The effect of reproductive condition on thermoregulation in female *Agkistrodon piscivorus* near the northwestern range limit. *Herpetologica*, 64: 156–167.
- Diaz, J. A., 1997. Ecological correlates of the thermal quality of an ectotherm's habitat: A comparison between two temperature lizard populations. *Functional Ecology*, 11: 79–89.
- Dzialowski, E. M., 2005. Use of operative temperature and standard operative temperature models in thermal biology. *Journal of Thermal Biology*, 30: 317–334.
- Fisher, C., A. Joynt & R. J. Brooks, 2007. Reptiles and Amphibians of Canada. Lone Pine Publishing, Edmonton, Alberta.
- Fox, W., C. Gordon & M. H. Fox, 1961. Morphological effects of low temperatures during the embryonic development of the garter snake, *Thamnophis elegans*. *Zoologica*, 46: 57–71.
- Gardner-Santana, L. C. & S. J. Beaupre, 2009. Timber rattlesnakes (*Crotalus horridus*) exhibit elevated and less variable body temperatures during pregnancy. *Copeia*, 2009: 363–368.
- Grant, B. W. & A. E. Dunham, 1988. Thermally imposed time constraints on the activity of the desert lizard *Sceloporus merriami*. *Ecology*, 69: 167–176.
- Greenwald, O. E., 1974. Thermal dependence of striking and prey capture by gopher snakes. *Copeia*, 1974: 141–148.
- Hare, J. R., K. M. Holmes, J. L. Wilson & A. Cree, 2009. Modelling exposure to selected temperature during pregnancy: The limitations of squamate viviparity in a cool-climate environment. *Biological Journal of the Linnean Society*, 96: 541–552.
- Harvey, D. S. & P. J. Weatherhead, 2006a. A test of the hierarchical model of habitat selection using eastern massasauga rattlesnakes (*Sistrurus c. catenatus*). *Biological Conservation*, 130: 206–216.
- Harvey, D. S. & P. J. Weatherhead, 2006b. Hibernation site selection by eastern massasauga rattlesnakes (*Sistrurus c. catenatus*) near their northern range limit. *Journal of Herpetology*, 40: 66–73.

- Harvey, D. S. & P. J. Weatherhead, forthcoming. Thermal ecology of massasauga rattlesnakes (*Sistrurus catenatus*) near their northern range limit. *Canadian Journal of Zoology*.
- Herczeg, G., J. Saarikivi, A. Gonda, J. Perälä, A. Tuomola & J. Merilä, 2007. Suboptimal thermoregulation by male adders (*Vipera berus*) after hibernation imposed by spermiogenesis. *Biological Journal of the Linnean Society*, 92: 19–27.
- Hertz, P. E., R. B. Huey & R. D. Stevenson, 1993. Evaluating temperature regulation by field-active ectotherms: The fallacy of the inappropriate question. *American Naturalist*, 142: 796–818.
- Huey, R. B., 1982. Temperature, physiology, and the ecology of reptiles. Pages 25–91 in C. Gans & F. H. Pough (eds). *Biology of the Reptilia*, Volume 12. Academic Press, New York, New York.
- Huey, R. B., 1991. Physiological consequences of habitat selection. *American Naturalist*, 137: S91–S115.
- Huey, R. B. & A. F. Bennett, 1987. Phylogenetic studies of coadaptation: Preferred temperatures versus optimal performance temperatures of lizards. *Evolution*, 41: 1098–1115.
- Huey, R. B. & J. G. Kingsolver, 1993. Evolution of resistance to high-temperature in ectotherms. *American Naturalist*, 142: S21–S46.
- Huey, R. B., P. H. Niewiarowski, J. Kaufmann & J. C. Herron, 1989a. Thermal biology of nocturnal ectotherms: Is sprint performance of geckos maximal at low body temperatures? *Physiological Zoology*, 62: 488–504.
- Huey, R. B., C. R. Peterson, S. J. Arnold & W. Porter, 1989b. Hot rocks and not-so-hot rocks: Retreat-site selection by garter snakes and its thermal consequences. *Ecology*, 70: 931–944.
- Isaac, L. A. & P. T. Gregory, 2004. Thermoregulatory behaviour of gravid and non-gravid female grass snakes (*Natrix natrix*) in a thermally limiting high-latitude environment. *Journal of Zoology*, 264: 403–409.
- Keenlyne, K. D. & J. R. Beer, 1973. Food habits of *Sistrurus catenatus catenatus*. *Journal of Herpetology*, 7: 381–382.
- Kissner, K. J. & P. J. Weatherhead, 2005. Phenotypic effects on survival of neonatal northern watersnakes *Nerodia sipedon*. *Journal of Animal Ecology*, 74: 259–265.
- Lillywhite, H. B., 1987. Temperature, energetics, and physiological ecology. Pages 422–477 in R. A. Seigel, J. T. Collins & S. S. Novak (eds). *Snakes: Ecology and Evolutionary Biology*. McGraw-Hill, New York, New York.
- Lourdais, O., R. Shine, X. Bonnet, M. Guillon & G. Nalleau, 2004. Climate affects embryonic development in a viviparous snake, *Vipera aspis*. *Oikos*, 104: 551–560.
- Martin, W. H., 1992. Phenology of the timber rattlesnake (*Crotalus horridus*) in an unglaciated section of the Appalachian Mountains. Pages 259–278 in J. A. Campbell & E. D. Brodie Jr. (eds). *Biology of the Pitvipers*. Selva, Tyler, Texas.
- Martin, T. L. & R. B. Huey, 2008. Why “suboptimal” is optimal: Jensen’s inequality and ectotherm thermal preferences. *American Naturalist*, 171: E102–E118.
- Monasterio, C., A. Salvador, P. Iraeta & J. A. Diaz, 2009. The effects of thermal biology and refuge availability on the restricted distribution of an alpine lizard. *Journal of Biogeography*, 36: 1673–1684.
- Muth, A., 1980. Physiological ecology of desert iguana (*Dipsosaurus dorsalis*) eggs: Temperature and water relations. *Ecology*, 61: 1335–1343.
- Osgood, D. W., 1978. Effects of temperature on the development of meristic characters in *Natrix fasciata*. *Copeia*, 1978: 33–47.
- Porter, W. P. & C. R. Tracy, 1983. Biophysical analyses of energetics, time–space utilization, and distribution limits. Pages 55–83 in R. B. Huey, E. R. Pianka & T. W. Schoener (eds). *Lizard Ecology: Studies of a Model Organism*. Harvard University Press, Cambridge, Massachusetts.
- Reinert, H. K. & D. Cundall, 1982. An improved surgical implantation method for radio-tracking snakes. *Copeia*, 1982: 702–705.
- Robertson, I. C. & P. J. Weatherhead, 1992. The role of temperature in microhabitat selection by northern water snakes (*Nerodia sipedon*). *Canadian Journal of Zoology*, 70: 417–422.
- Row, J. R. & G. Blouin-Demers, 2006. Thermal quality influences effectiveness of thermoregulation, habitat use, and behaviour in milksnakes. *Oecologia*, 148: 1–11.
- Secor, S. M. & K. A. Nagy, 1994. Bioenergetic correlates of foraging mode for the snakes *Crotalus cerastes* and *Masticophis flagellum*. *Ecology*, 75: 1600–1614.
- Shine, R., 2004. Incubation regimes of cold-climate reptiles: The thermal consequences of nest-site choice, viviparity and maternal basking. *Biological Journal of the Linnean Society*, 83: 145–155.
- Shine, R. & P. Harlow, 1996. Maternal manipulation of offspring phenotypes via nest-site selection in an oviparous lizard. *Ecology*, 77: 1808–1817.
- Shine, R. & T. Madsen, 1996. Is thermoregulation unimportant for most reptiles? An example using water pythons (*Liasis fuscus*) in tropical Australia. *Physiological Zoology*, 69: 252–269.
- Shine, R., L. X. Sun, M. Kearney & M. Fitzgerald, 2002. Thermal correlates of foraging-site selection by Chinese pitvipers (*Gloydius shedaoensis*). *Journal of Thermal Biology*, 27: 405–412.
- Smolinsky, R. & L. Gvozdik, 2009. The ontogenic shift in thermoregulatory behaviour of newt larvae: Testing the ‘enemy-free temperatures’ hypothesis. *Journal of Zoology*, 279: 180–186.
- Stevenson, R. D., C. R. Peterson & J. S. Tsuji, 1985. The thermal dependence of locomotion, tongue flicking, digestion, and oxygen consumption in the wandering garter snake. *Physiological Zoology*, 46: 46–57.
- Thierry, A., M. Lettink, A. A. Besson & A. Cree, 2009. Thermal properties of artificial refuges and their implications for retreat-site selection in lizards. *Applied Herpetology*, 6: 307–326.
- Tsairi, H. & A. Bouskila, 2004. Ambush site selection of a desert snake (*Echis coloratus*) at an oasis. *Herpetologica*, 60: 13–23.
- Völk, W., 1989. Prey density and growth: Factors limiting the hibernation success in neonate adders (*Vipera berus*). *Zoologischer Anzeiger*, 222: 75–82.
- Webb, J. K. & R. Shine, 1998. Thermoregulation by a nocturnal elapid snake (*Hoplocephalus bungaroides*) in southeastern Australia. *Physiological Zoology*, 71: 680–692.
- Webb, J. K., R. M. Pringle & R. Shine, 2004. How do nocturnal snakes select diurnal retreat sites? *Copeia*, 2004: 919–925.
- Zaidan III, F., D. L. Kreider & S. J. Beaupre, 2003. Testosterone cycles and reproductive energetics: Implications for northern range limits of the cottonmouth (*Agkistrodon piscivorus leucostoma*). *Copeia*, 2003: 231–240.
- Zug, G. R., L. J. Vitt & J. P. Caldwell, 2001. *Herpetology: An Introductory Biology of Amphibians and Reptiles*. Academic Press, New York, New York.