

# Thermal ecology of Massasauga Rattlesnakes (*Sistrurus catenatus*) near their northern range limit

Daniel S. Harvey and Patrick J. Weatherhead

**Abstract:** Using populations at their northern range limits, we compared the thermoregulatory behaviour of Massasauga Rattlesnakes (*Sistrurus catenatus* (Rafinesque, 1818)) to published results for Ratsnakes (*Elaphe obsoleta* (Say in James, 1823)) and Northern Watersnakes (*Nerodia sipedon* (L., 1758)) to test the hypothesis that given similar benefits of thermoregulation, costs associated with foraging ecology should shape thermoregulatory behaviour. More than 32 000 body temperature measurements from 34 individual snakes over 4 years were used to quantify thermoregulation by Massasauga Rattlesnakes using standard indices and a new index (%MaxE) that describes how much of the thermoregulatory potential available to a snake is realized. On average, Massasaugas were much cooler ( $d_b = 6.9$  °C) than their preferred body temperature range (30–33.6 °C) but warmer ( $d_e - d_b = 3.3$  °C) than were they not thermoregulating. Massasaugas realized more than half of their environmental potential for effective thermoregulation (%MaxE = 64%). Consistent with there being less conflict between foraging and thermoregulation for ambush predators than active foragers, Massasaugas were more effective thermoregulators than Ratsnakes or Watersnakes during the day. All three species were effective thermoregulators at night, supporting the assumption that species in a cool environment will thermoregulate when there are few competing interests.

**Résumé :** En utilisant des populations à la limite nord de leur aire de répartition, nous comparons le comportement thermorégulateur du crotale massasauga (*Sistrurus catenatus* (Rafinesque, 1818)) aux données publiées pour les couleuvres obscures (*Elaphe obsoleta* (Say in James, 1823)) et les couleuvres d'eau du Nord (*Nerodia sipedon* (L., 1758)) afin de tester l'hypothèse selon laquelle, lorsque les bénéfices de la thermorégulation sont semblables, les coûts associés à l'écologie alimentaire devraient contrôler le comportement thermorégulateur. Plus de 32 000 mesures de la température corporelle chez 34 individus sur une période de 4 ans nous ont servi à déterminer la thermorégulation chez les crotales massasaugas à l'aide d'indices standards et d'un nouvel indice (%MaxE) qui décrit la proportion du potentiel thermorégulateur disponible au serpent qui est en fait réalisée. En moyenne, les massasaugas se retrouvent à une température beaucoup plus fraîche ( $d_b = 6,9$  °C) que leur gamme de température préférée (30–33,6 °C), mais à une température supérieure ( $d_e - d_b = 3,3$  °C) à celle qu'ils auraient sans thermorégulation. Les massasaugas réalisent plus de la moitié de leur potentiel environnemental de thermorégulation effective (%MaxE = 64 %). En accord avec le fait qu'il existe moins de conflit entre l'alimentation et la thermorégulation chez les prédateurs qui chassent à l'affût que chez ceux qui recherchent activement leurs proies, les massasaugas font une thermorégulation plus efficace durant le jour que les couleuvres obscures et les couleuvres d'eau. Les trois espèces font une thermorégulation efficace la nuit, ce qui appuie la proposition que les espèces placées dans un environnement frais vont faire de la thermorégulation s'il y a peu d'autres intérêts en compétition.

[Traduit par la Rédaction]

## Introduction

The thermal dependence of physiological processes makes body temperature ( $T_b$ ) regulation a fundamental aspect of ectotherm ecology (Huey 1982; Heatwole and Taylor 1987; Peterson et al. 1993). In addition to contributing to our general knowledge of ectotherm ecology, understanding the thermoregulatory behaviour of ectotherms is also important

to anticipating how ectotherm populations are likely to be affected by climate warming (Deutsch et al. 2008; Kearney et al. 2009). Although for some time we have had both a general theory (Huey and Slatkin 1976) and the analytical tools for quantifying thermoregulation (Hertz et al. 1993; Christian and Weavers 1996; Brown and Weatherhead 2000; Blouin-Demers and Weatherhead 2001a), comprehensive empirical studies of the thermal ecology of free-living reptiles remain scant. Two general research approaches for identifying the ecological factors that shape thermoregulatory strategies are to document how the thermal ecology of the same species varies across environmental gradients, or to compare how species that differ ecologically deal with similar thermal challenges (Blouin-Demers and Weatherhead 2001a). Our general goal here was to follow the latter approach and compare the thermal ecology of three species of snakes near their northern range limits. We do so by documenting daily, seasonal, and sex-specific patterns of

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thermoregulation by Massasauga Rattlesnakes (*Sistrurus catenatus* (Rafinesque, 1818)) and compare those patterns to data previously reported for Northern Watersnakes (*Nerodia sipedon* (L., 1758); Brown and Weatherhead 2000) and Ratsnakes (*Elaphe obsoleta* (Say in James, 1823); Blouin-Demers and Weatherhead 2001a).

Thermoregulation is assumed to provide the benefit of improved physiological performance, which should ultimately increase fitness, at the cost of time spent locating thermally favourable sites, which could entail energetic costs, predation risk, and reduced time available for other activities (Huey and Slatkin 1976). If latitudinal range limits of ectotherms are imposed by thermal constraints (e.g., Kiester 1971; Pianka 1977; Gregory 1982; Porter and Tracy 1983), then the benefits of thermoregulation should be high for all snakes near their northern range limits. One could argue that because locomotory ability increases with  $T_b$  (Huey 1982; Stevenson et al. 1985; Blouin-Demers et al. 2003), the benefit from maintaining high  $T_b$ s could be greater for species that are active foragers (e.g., Watersnakes and Ratsnakes) than for species that are stationary foragers (Massasaugas). Because the speed of normal movement and striking speed both increase with  $T_b$  (Blouin-Demers et al. 2003), however, we assume that all three species we consider here realize similar locomotory benefits from thermoregulation. Other benefits of higher  $T_b$  such as faster digestion also seem unlikely to vary much between these species.

Unlike the benefits, the costs of thermoregulation seem likely to differ between the snake species considered here. Specifically, the cost resulting from the trade-off between thermoregulation and foraging should differ between species based on their foraging mode. If a species forages in a way that is compatible with thermoregulation (i.e., both can be done simultaneously), that species should thermoregulate more than one for which thermoregulation conflicts with foraging. Specifically, an ambush predator may be able to combine hunting and thermoregulation more effectively than an active hunter and thus should thermoregulate more. Watersnakes actively hunt for fish and frogs in water, which is often a thermally inferior habitat (Robertson and Weatherhead 1992; Brown and Weatherhead 2000). Similarly, Ratsnakes actively hunt for small mammals and bird nests, and thus spend considerable time in habitat other than that preferred for thermoregulation (Blouin-Demers and Weatherhead 2001b). In contrast, Massasaugas hunt by ambushing small mammals. Massasaugas are well camouflaged and often are at most partially concealed when hunting (D.S. Harvey, personal observation), suggesting that by selecting hunting locations in thermally favourable microhabitats, Massasaugas should be able to thermoregulate while hunting.

The general prediction we test is that Massasaugas should thermoregulate more than Watersnakes and Ratsnakes. This means that they should take greater advantage of opportunities for thermoregulation and more often realize  $T_b$ s closer to their preferred temperature range. Because all three species are diurnally active, however, the predicted thermoregulation advantage for Massasaugas should occur only during the day. At night, when there are few competing demands, we expect these snakes to thermoregulate effectively, as already documented for Watersnakes and Ratsnakes (Brown

and Weatherhead 2000; Blouin-Demers and Weatherhead 2001a). Because we are comparing our results for Massasaugas to published results for Watersnakes and Ratsnakes, this paper is largely devoted to the analysis of Massasauga thermal ecology, with predictions regarding differences among species addressed in the Discussion.

Within Massasaugas, we expect differences in thermoregulation based on sex and reproductive status. Overall, males should thermoregulate less than females, given that mate searching is likely to conflict with thermoregulation. We assume that males engage in mate searching more than females (Shine et al. 2000), although there is evidence that female snakes do search for mates (Blouin-Demers et al. 2005). A comparison of reproductive and nonreproductive females allows us to test our central assumption that foraging and thermoregulation are compatible activities. Thermoregulation is a priority for gravid females (e.g., Charland and Gregory 1990; Dorcas and Peterson 1998), whereas foraging should be a priority for nongravid females; so if the assumption is correct, then there should be little difference between these two classes of females.

## Materials and methods

### Study site and radio telemetry

The study was conducted on the Upper Bruce Peninsula (45°10'N, 81°29'W), Ontario, Canada, approximately 50 km from the northern distribution limit of Massasaugas. The study location is west of the Ontario study site used for both the Watersnake and the Ratsnake studies, but the study locations are less than 1° of latitude apart. Two study areas 12.5 km apart were used, collectively containing a mix of the principal local habitats, details of which are provided by Harvey and Weatherhead (2006).

To the extent possible the field and analytical methods used by Brown and Weatherhead (2000) and Blouin-Demers and Weatherhead (2001a) were followed.  $T_b$ s were recorded from snakes implanted with temperature-sensitive radio transmitters (model SI-2T; Holohil Systems Ltd., Carp, Ontario, Canada). Surgical procedures generally followed Reinert and Cundall (1982), with transmitters implanted in snakes' body cavities. Propofol (10 mg/kg) was injected caudally prior to surgery to partially immobilize the snake. Anaesthetic procedures followed Blouin-Demers et al. (2000), using isoflourane as the anaesthetic. After the surgery, snakes were held for 3 days and then released at their point of capture.

Snakes were initially captured opportunistically, with most subsequent captures resulting from finding snakes temporarily associated with those being tracking. Snakes were sexed using cloacal probes and the reproductive condition of females was based on whether or not they gave birth that season. From 2001 to 2003, we implanted transmitters in 19 males, 9 gravid females, and 6 nongravid females. Five females were gravid in 1 year and nongravid the next year, and one female went from nongravid to gravid between years. The mass of implanted snakes was  $287 \pm 113$  g (mean  $\pm$  SD).

Snakes were located, on average, every 2 days until they entered hibernation and again when they re-emerged the following spring. The pulse rate of the transmitter was used to

estimate the temperature of the transmitter (thus, the snake's  $T_b$ ) using calibration equations calculated for each transmitter using polynomial regression (including all terms up to degree four) with eight calibration points ( $R^2 > 0.99$  for all equations). In addition to collecting  $T_b$  values when snakes were located, two automated data loggers (SRX 400; Lotek Wireless Inc., Newmarket, Ontario, Canada) were used to record  $T_b$ s remotely. Data loggers were moved between two locations in both study areas throughout the 2002 and 2003 active seasons to try and maximize the number of snakes within range of the data loggers. Because snakes often moved into and out of the data loggers' range, however, there are no snakes for which continuous thermal data were collected.

### Preferred temperature range ( $T_{set}$ )

A thermal gradient chamber was used to determine the snakes' preferred temperature range ( $T_{set}$ ). The chamber was a 183 cm  $\times$  61 cm  $\times$  61 cm plywood box with a plexiglass top. A fluorescent light provided homogenous illumination from 0600 to 1800; at night the chamber was dark. A heating lamp was placed under one end of the chamber and an open cooler of ice was placed under the other end, separated from the chamber by sheet metal to prevent condensation on the chamber. This produced a relatively smooth gradient from  $\sim 18$  to 45 °C. The hot and cool ends of the chamber were switched for each trial to ensure snakes were not orienting to some cue other than temperature. Because snakes were put in the chamber randomly with regard to when they had eaten (i.e., we were unaware of their foraging history), the data collected should accurately represent the temperature preferences of the population.

Temperature preference trials were conducted with three gravid females, four nongravid females, and seven males; all of which had transmitters implanted at least 8 weeks prior to testing. Each trial was run for 24 h. Following Hertz et al. (1993), the central 50% of temperatures selected by a snake were used to define the lower and upper values of its  $T_{set}$ .

### Operative environmental temperature ( $T_e$ )

Operative environmental temperature ( $T_e$ ) represents the temperature an animal would experience if it behaved neutrally with regard to the thermal environment and is estimated using physical models with the same thermal properties as the animal of interest (Dzialowski 2005). We constructed models using copper tubing painted to mimic Massasaugas and similar in length and diameter (59 cm  $\times$  3 cm) to the snakes implanted with transmitters. Radio transmitters were placed inside models before filling the models with water and sealing them at both ends. Previous studies have shown that under most conditions, copper models constructed in a similar manner accurately represent the thermal properties of the snakes that they imitate (Peterson et al. 1993; Brown and Weatherhead 2000; Wills and Beaupre 2000; Blouin-Demers and Weatherhead 2001a). Because Massasaugas are relatively small and sedentary, no adjustment of  $T_e$ s for thermal inertia was required (Seebacher and Shine 2004).

We quantified the thermal environment in the study area by rotating four models through 5–15 locations within each

of the four major habitats (open canopy, wetland, sparse forest, dense forest; Harvey and Weatherhead 2006) for up to 3 weeks per location. Locations were chosen to reflect the variation in available microhabitats. Backward stepwise multiple regression was used to select the combination of weather variables (solar radiation, air temperature, relative humidity, air speed) recorded at a nearby weather station that best predicted (maximized  $R^2$ ) model temperatures in each habitat. Because water-filled models heat and cool slowly, weather variables recorded an hour previous to model temperatures were also included in the stepwise regression procedure. Many terms from the previous hour were retained in the final regression equations, improving their predictive power. Using these regression equations and weather data,  $T_e$  was estimated in all habitats throughout the study. To determine the mean  $T_e$  available to a given snake at a given time,  $T_e$  was weighted by the relative availability of each habitat to the snake (*sensu* Herczeg et al. 2003).

### Thermoregulation indices

The accuracy of thermoregulation ( $d_b$ ) measures how close  $T_b$ s were, on average, to  $T_{set}$  and is calculated as the absolute value of the difference between  $T_b$  and  $T_{set}$  (Hertz et al. 1993). The value of  $d_b = 0$  when  $T_b$ s are within  $T_{set}$  and increases as  $T_b$ s deviate farther from the lower or upper bounds of  $T_{set}$ . Similarly, the thermal quality of the environment ( $d_e$ ) estimates the deviation of  $T_e$  from  $T_{set}$  and is calculated as the absolute value of the difference between  $T_e$  and  $T_{set}$ .

Following Blouin-Demers and Weatherhead's (2001a) modification of the original index, we calculate the effectiveness of thermoregulation as  $d_e - d_b$ . High values of  $d_e - d_b$  represent effective thermoregulation, low values represent thermoconformity, and negative values represent avoidance of thermally preferable sites. We also introduce a further modification of this index that better captures the thermoregulatory performance relative to the environmental potential for thermoregulation. The value of  $d_e - d_b$  is potentially constrained by the range of  $d_e$ . For example, if  $d_e$  varies little between habitats, then a snake that consistently chooses the best thermal habitat available (i.e., thermoregulating maximally) would realize  $d_b$ s only slightly above mean  $d_e$ s. The resulting low value of  $d_e - d_b$  would incorrectly suggest little thermoregulatory effort. Our new index quantifies how much of the available thermoregulatory potential is used. We first determined the maximum value of  $d_e - d_b$  that a snake could achieve during each observation. Numerically, this is  $d_e$  averaged over all habitats minus  $d_e$  in the most thermally favourable habitat (i.e., minimum  $d_e$ ). Next, each observed  $d_e - d_b$  is expressed as a percentage of the maximum possible  $d_e - d_b$  at that time, i.e.,  $[(d_e - d_b)/(d_e - \text{minimum } d_e)] \times 100$ . Any values  $>100$  are rounded to 100% (snakes were thermoregulating as effectively as possible) and values  $<0$  are rounded to 0% (snakes were not thermoregulating). This index is undefined when mean  $d_e = 0$ , because there is no opportunity to thermoregulate. Hereafter we refer to this index as "percent maximum effectiveness" (%MaxE). The new index is similar in essence to the thermal exploitation index developed by Christian and Weavers (1996) ( $E_x$ ) but is applicable at all times rather than only when ideal  $T_e$ s are available.

## Data analyses

$T_b$ s and  $T_e$ s were recorded in 10 min intervals and averaged for each hour. For inferential statistics hourly means were further condensed into daily means to increase the independence of observations, with observations during the day and night considered separately because Massasauga behaviour differs during the day and night. Sample sizes were inadequate to consider the effects of time of day, month, sex, and reproductive condition on thermoregulation simultaneously. The effect of time of day (i.e., day vs. night) on thermoregulation was analyzed using ANOVA, with individual snakes considered a random effect. The effects of reproductive class (i.e., males, gravid females, nongravid females) and month on thermoregulation were also analysed using ANOVA, with individual snakes considered a nested effect within reproductive class. JMP version 4.0.0 and Systat standard version 11 were used to perform statistical analyses. Values are presented as mean  $\pm$  1 SE unless otherwise noted.

## Results

From June 2001 to July 2004, we recorded 32 044  $T_b$ s from 34 individual snakes, which produced 9 215 hourly values (hereafter “observations”). The number of  $T_b$  observations from a single snake varied from 26 to 1115. No data were collected when snakes were hibernating (November–April).

Snakes in the thermal gradient chamber selected temperatures between  $30.0 \pm 0.5$  °C (25% quartile) and  $33.6 \pm 0.3$  °C (75% quartile) with a mean of  $31.7 \pm 0.3$  °C. Neither the 25% nor the 75% quartile temperatures differed among snakes of different sex and reproductive condition (both  $F_{[2,22]} < 0.3$ , both  $P > 0.5$ ). During the day, snakes selected temperatures between  $28.4 \pm 0.5$  and  $33.3 \pm 0.4$  °C; during the night, snakes selected temperatures between  $31.6 \pm 0.6$  and  $33.9 \pm 0.4$  °C. We used the daily (i.e., 24 h) preferred temperature range (30–33.6 °C) in analyses to remain consistent with the methods used to quantify thermoregulation in Watersnakes (Brown and Weatherhead 2000) and Rattlesnakes (Blouin-Demers and Weatherhead 2001a).

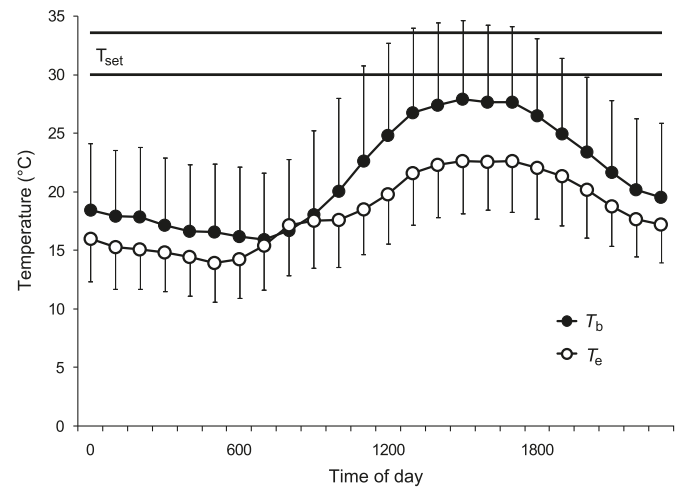
Multiple regression equations explained substantial variation in model temperatures in each habitat based on combinations of weather variables ( $R^2 = 0.51 - 0.65$ , all  $P < 0.001$ ). Mean  $T_e$  was below  $T_{set}$  for 99% (9142 of 9215) of  $T_b$  observations. The mean deviation of  $T_e$  from  $T_{set}$  was  $10.7 \pm 0.1$  °C.

The lowest recorded  $T_b$  was 1.1 °C and the highest was 44.0 °C, an activity range of 42.9 °C. The general daily pattern was for snakes to warm up in the morning, maintain  $T_b$ s near preferred levels in the early afternoon, and then gradually cool until the following morning (Figs. 1, 2). On average,  $T_b$  was above  $T_e$  but below  $T_{set}$  (Fig. 1).

## Thermoregulation

To assess thermoregulatory behaviour, the 9215 hourly  $T_b$  observations were condensed into 3062 daily  $T_b$  observations. Mean accuracy of thermoregulation ( $d_b$ ) was  $6.9 \pm 0.1$  °C (day:  $6.3 \pm 0.1$  °C; night:  $9.6 \pm 0.2$  °C). The mean effectiveness of thermoregulation ( $d_e - d_b$ ) was  $3.3 \pm 0.1$  °C (day:  $3.4 \pm 0.1$  °C; night:  $2.7 \pm 0.2$  °C). The mean value of

**Fig. 1.** Daily variation (hourly means) in body temperature ( $T_b$  + SD) and operative environmental temperature ( $T_e$  – SD) for Massasauga Rattlesnakes (*Sistrurus catenatus*) on the Upper Bruce Peninsula, Ontario, from 2001 to 2004. The preferred temperature range ( $T_{set}$ ) is shown for reference.



%MaxE was  $63.9 \pm 0.8\%$  (day:  $65.5 \pm 0.9\%$ ; night:  $57.1 \pm 1.8\%$ ), indicating that snakes realized 64% of their potential for thermoregulation overall. Massasaugas were more accurate ( $d_b$ ) thermoregulators during the day than at night ( $F_{[1,3021]} = 113.8$ ,  $P < 0.001$ ), but were equally effective ( $d_e - d_b$ ) thermoregulators during the day and night ( $F_{[1,3021]} = 3.5$ ,  $P = 0.062$ ). Massasaugas realized more of their potential for effective thermoregulation during the day than at night ( $F_{[1,3013]} = 14.4$ ,  $P < 0.001$ ).

All indices indicated an interactive effect between reproductive class and month on thermoregulation (Table 1). The general pattern among males and gravid females was for thermoregulation to remain relatively steady or decrease from June through August and then sharply decrease in the fall (Fig. 3). Nongravid females followed the same general trend but thermoregulated less in the spring than in the early summer (Fig. 3). We had predicted that reproductive status should not affect thermoregulation by females if foraging and thermoregulating were compatible activities. In general, however, nongravid females not only thermoregulated less than gravid females, they also thermoregulated less than males (Fig. 3).

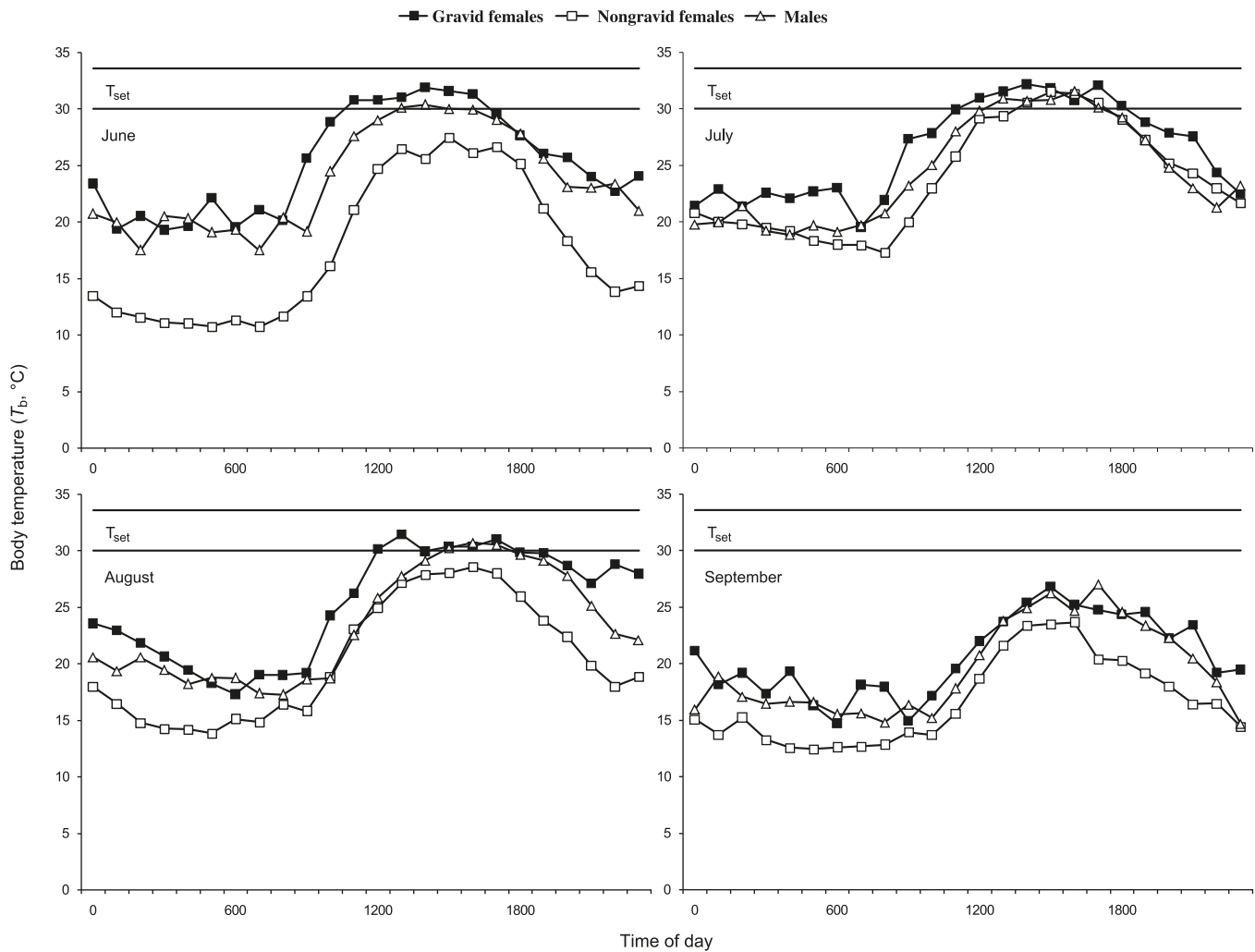
## Discussion

In the thermally challenging environment in which we studied them, Massasaugas realized preferred  $T_b$ s infrequently, but also performed much better than were they not thermoregulating. We first discuss results obtained for Massasaugas and then address the broader objective of comparing thermoregulation among the three species studied extensively at their northern range limits.

### Massasauga thermal ecology

We assumed that ambush predators such as Massasaugas should be able to select thermally superior hunting locations so that thermoregulation by gravid females (for promoting embryo development) and nongravid females (for foraging and digestion) would be similar. Although both groups of

**Fig. 2.** Monthly variation (hourly means) in body temperature ( $T_b$ ) for Massasauga Rattlesnakes (*Sistrurus catenatus*) on the Upper Bruce Peninsula, Ontario, from 2001 to 2004. The preferred temperature range ( $T_{set}$ ) is shown for reference.



females (and males) did not differ in the temperatures preferred in the thermal gradient chamber, gravid females thermoregulated more extensively than nongravid females in the field. Massasaugas prey primarily on small mammals (Weatherhead et al. 2009), which may be encountered more frequently in the structurally complex microhabitats preferred by males and nongravid females than the open, rocky microhabitats preferred by gravid females (Harvey and Weatherhead 2006). Thus, nongravid females may choose thermally superior locations in the habitats in which they forage, but those locations are not as good as those available to gravid females.

Females of numerous snake species both feed less (e.g., Keenlyne and Beer 1973; Reinert et al. 1984; Macartney and Gregory 1988; Wallace and Diller 1990) and thermoregulate more (e.g., Graves and Duvall 1993; Prival et al. 2002; Pearson et al. 2003; Crane and Greene 2008; Gardner-Santana and Beaupre 2009) while gravid. The length of the gestation period, offspring viability, and offspring phenotypes have all been related to maternal temperatures during embryogenesis in squamates (Fox et al. 1961; Osgood 1978; Arnold and Peterson 1989; Burger 1991; Shine and Harlow 1996; Lourdaïs et al. 2004, Ji et al. 2007). At distribution

limits, extensive thermoregulation may be essential for successful reproduction, regardless of the costs (Martin 1993; Brown and Weatherhead 2000; Gregory 2009). Gravid females maintained  $T_b$ s 4.5 °C closer to  $T_{set}$ , on average, than had they reacted passively to their thermal environment. Timber Rattlesnakes (*Crotalus horridus* L., 1758) reduced the length of gestation by 6.9–10 days/°C that  $T_b$ s were maintained closer to  $T_{set}$  (Martin 1992). Assuming a similar relationship for Massasaugas, females gave birth more than a month earlier than if they were thermoconformers, and about 2 weeks sooner than if they maintained  $T_b$ s similar to males and nongravid females. Reduced gestation times allow postpartum females and neonates more foraging time prior to hibernation (Charland and Gregory 1990; Burger 1991; Martin 1993; Weatherhead et al. 1999), which should improve overwinter survival (Brown and Weatherhead 1997; Bronikowski 2000; Kissner and Weatherhead 2005).

Males generally thermoregulated more than nongravid females. Males may prefer higher  $T_b$ s to assist with spermatogenesis (Viitanen 1967; Patterson and Davies 1978; Saint Girons 1982; Herczeg et al. 2007). Consistent with this interpretation, males thermoregulated more in the months prior to and during the mating season (June–August;

**Table 1.** ANOVA results for the effect of sex and reproductive condition (“class”) and month on thermoregulatory accuracy ( $d_b$ ), effectiveness ( $d_e - d_b$ ), and percent maximum effectiveness (%MaxE) by Massasauga Rattlesnakes (*Sistrurus catenatus*) on the Upper Bruce Peninsula, Ontario, from 2001 to 2004.

Group	df	Mean square	F	P
<b><math>d_b</math></b>				
$d_e$ (covariate)	1	26 115.6	1 752.5	<0.001
Snake	37	62.0	4.2	<0.001
Class	2	476.0	31.9	<0.001
Month	3	999.8	67.1	<0.001
Class × month	6	50.0	3.4	0.003
Error	2580	14.9		
<b><math>d_e - d_b</math></b>				
Snake	37	64.6	4.2	<0.001
Class	2	425.1	27.9	<0.001
Month	3	824.4	54.2	<0.001
Class × month	6	45.7	3.0	0.006
Error	2578	15.2		
<b>%MaxE</b>				
Snake	37	6 193.5	4.3	<0.001
Class	2	44 081.6	30.3	<0.001
Month	3	79 911.8	54.9	<0.001
Class × month	6	5 782.1	4.0	0.001
Error	2570	1 454.7		

**Note:** The effect of individual snakes (“snake”) was nested within reproductive classes.

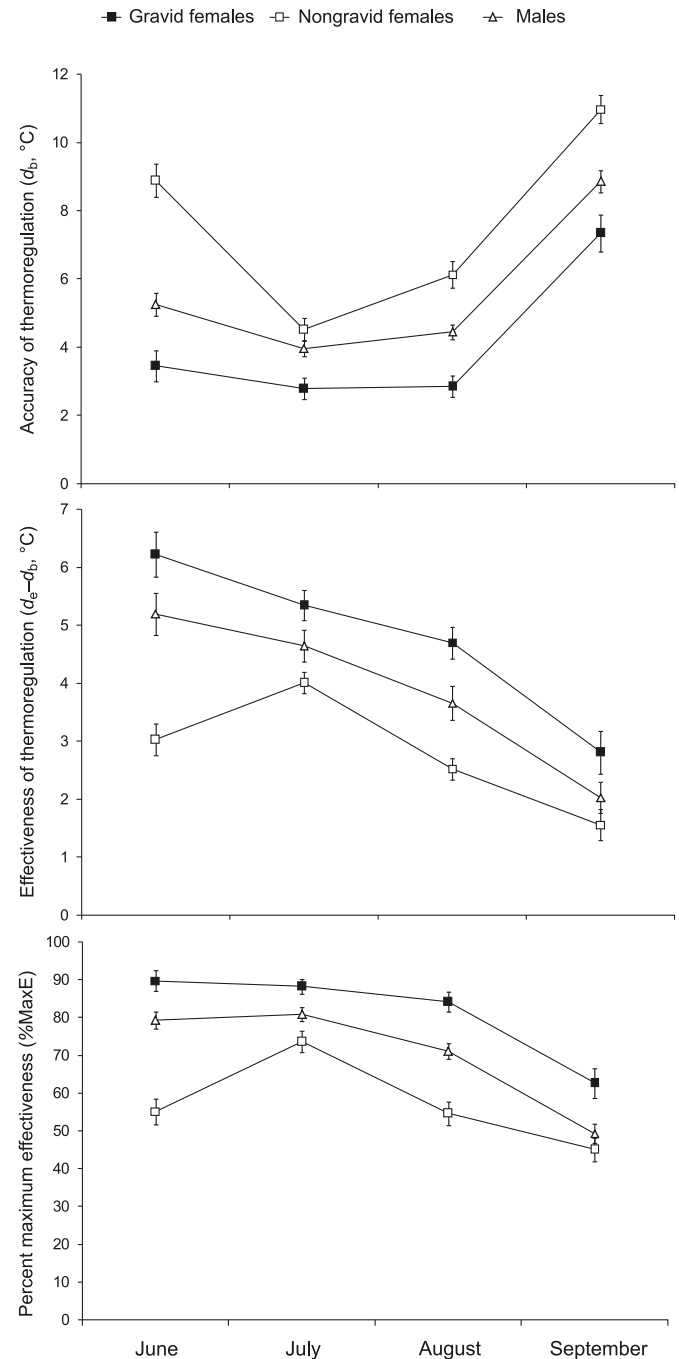
Fig. 3). Differences in thermoregulation could also have been due to differences in habitat use. Although both males and nongravid females used habitats with variable canopy cover, we sampled more nongravid females from the more heavily forested portion of our study sites (Harvey and Weatherhead 2006). Within forested habitats it may have been more difficult to access thermally favourable sites, resulting in less thermoregulation by nongravid females.

Thermoregulatory effort decreased in the fall, particularly during the day. Most aspects of the Massasauga annual life cycle (e.g., gestation, mating, shedding) are completed by September at our study site, perhaps lessening the importance of maintaining physiologically optimal temperatures. With few potential benefits, snakes may adopt a “survival” strategy in the fall by minimizing the costs of thermoregulation (Christian and Bedford 1995; Brown and Weatherhead 2000). Interestingly, gravid females continued to thermoregulate more than other snakes in the fall, despite giving birth in late summer. Females are often emaciated following parturition and must forage to replenish energy reserves before hibernating. Males and nongravid females may be less reliant on fall foraging, and therefore less reliant on maintaining favourable temperatures for hunting and digestion (Herczeg et al. 2008).

**Comparison of thermoregulation among species**

We predicted that Massasaugas would thermoregulate more than either Ratsnakes or Watersnakes based on our assumption that Massasaugas would be able to hunt and thermoregulate simultaneously. The fact that gravid female Massasaugas thermoregulated much more than nongravid fe-

**Fig. 3.** Thermoregulatory (mean ± SE) accuracy ( $d_b$ ), effectiveness ( $d_e - d_b$ ), and percent maximum effectiveness (%MaxE) by Massasauga Rattlesnakes (*Sistrurus catenatus*) on the Upper Bruce Peninsula, Ontario, from 2001 to 2004.



males challenged that assumption, although it is still possible that within the constraints of the habitat in which they forage, nongravid females still select thermally superior hunting locations. A second assumption was that the thermal environments for the three species should be similarly challenging because the study populations were all near their species’ respective range limits and all at similar latitude. However, overall mean  $d_e$  was higher for Massasaugas (10.2 °C) than for Ratsnakes (8.1 °C), and much higher than for Watersnakes (4.0 °C), indicating that the thermal

environment was more challenging for the terrestrial species than for the aquatic species. Part of that difference results from Massasaugas preferring warmer temperatures (mean = 31.7 °C) than either Watersnakes (27.1 °C) or Ratsnakes (28.1 °C). Therefore, in interpreting species differences in thermoregulation, it should be kept in mind that Massasaugas were operating in the most thermally challenging environment. Mean-based indices of thermoregulation (e.g.,  $d_e - d_b$ ) generally allow more reliable comparisons of thermoregulation between species than range-based indices (i.e.,  $E_x$ , %MaxE) because they are less sensitive to the warmest and coldest environmental temperatures considered available. Thus, we use  $d_e - d_b$  to compare thermoregulation between species.

During the day, Massasaugas were effective thermoregulators (3.4 °C), whereas both Watersnakes and Ratsnakes were thermally passive (<1.0 °C; Brown and Weatherhead 2000; Blouin-Demers and Weatherhead 2001a). This result supports the hypothesis that given similar benefits from thermoregulation, the amount a species thermoregulates should vary with the costs. An even stricter test of this hypothesis could be achieved by excluding gravid females from analyses. Gravid females may forage little if at all during gestation, so predictions based on foraging behaviour are more applicable to males and nongravid females. Also, the distribution of thermally favourable sites should affect thermoregulation by gravid females less because they spend long periods of time at relatively few sites, and therefore make fewer habitat selection decisions. Removing gravid females slightly lowered our estimate of daytime  $d_e - d_b$  for Massasaugas (from 3.4 to 3.1 °C). In contrast, gravid Watersnakes and Ratsnakes thermoregulated significantly more than males and nongravid females during the day (Brown and Weatherhead 2000; Blouin-Demers and Weatherhead 2001a). Therefore, differences in thermoregulation between Massasaugas and the other two species would be greater than previously stated if gravid females were excluded from comparison.

All three species thermoregulated effectively at night ( $d_e - d_b > 2$  °C), consistent with our assumption that species in a cool environment will thermoregulate when there are few competing interests. Thermoregulation during inactivity can be achieved by selecting thermally favourable retreat sites (Huey et al. 1989; Kearney and Predavec 2000). Because snakes at climatic extremes spend more time inactive than active, thermoregulation during inactivity will have important consequences for life-history characteristics through the effects of temperature on growth and reproduction (Autumn and De Nardo 1995; Beaupre 1996; Niewiarowski 2001; Rock et al. 2002; Sears 2005).

Although our results support the general hypothesis that thermoregulatory strategies result from the trade-off of costs and benefits of thermoregulation (Huey and Slatkin 1976), our knowledge of the specific ecological factors that constrain or promote thermoregulation remains limited. At least two research approaches will help increase that knowledge. First, we need to document the thermal ecology of a more ecologically diverse array of snake species, ideally studied under similar environmental conditions as we did here. Second, we need more detailed behavioural information to complement the thermal data. Although data loggers such as

those we used here provide highly detailed records of snake temperatures, for nearly all of those data we do not know the exact location of the snake or what it was doing at the time the temperature was recorded. Automated telemetry should help address the issue of location, but acquiring the behavioural data is likely to remain a challenge.

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