Journal of Thermal Biology 33 (2008) 174–179

Journal of
THERMAL BIOLOGY

www.elsevier.com/locate/jtherbio

Environmental, behavioral, and habitat variables influencing body temperature in radio-tagged bullsnakes, *Pituophis catenifer sayi*

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Received 25 September 2007; accepted 16 November 2007

Abstract

Studies regarding the thermal ecology of snakes are important to understanding their life histories. Yet, little is known about the thermal ecology of the North American genus Pituophis, which includes the bullsnake (*Pituophis catenifer sayi*). In an attempt to determine which independent variables significantly affected the thermal ecology of free-ranging bullsnakes, we tracked 12–19 radio-tagged individuals weekly from 2003 to 2005 in Wisconsin (USA) with temperature-sensitive transmitters. Although snake body temperature was found to vary based on several variables treated independently, two separate three-way interactions among variables were significant. We believe our results support the notion that *P. c. sayi* thermoconforms to environmental conditions in the upper Midwest, but more research on the topic is necessary.

Keywords: Bullsnakes; Pituophis; Themal ecology; Body temperature

1. Introduction

The temperature of an organism's selected microhabitat substantially affects the flow of mass and energy between the said organism and its environment (Walsberg, 1985). As such, determining the physiological and thermal requirements of an organism in relation to its behavioral tendencies, especially with respect to habitat selection, is of importance to studying its ecology. This is especially true of squamate reptiles, for which the maintenance of body temperature (T_b) is a critically important component of their ecology and fitness (Huey and Stevenson, 1979; Lillywhite, 1987; Huey and Kingsolver, 1989; Peterson et al., 1993; Zug et al., 2001), and may be a driving force behind their patterns of habitat selection (Reinert, 1993).

While information on the thermal ecology of numerous snake species exists (e.g., Lillywhite, 1987; Peterson et al., 1993; Shine and Madsen, 1996; Brown and Weatherhead, 2000; Blouin-Demers and Weatherhead, 2002; Fitzgerald et al., 2003; Wilson and Brooks, 2006), the North American genus *Pituophis* has received less attention. This may be symptomatic of the reported decline in the number of publications involving natural history or field-based herpetological research, including those focused on thermal ecology (McCallum and McCallum, 2006). Nonetheless, despite some published research on the physiological and metabolic performance of the Sonoran Gopher snake (*Pituophis catenifer affinis*; Greenwald, 1971, 1974), and limited information involving free-ranging members of this genus (Fitch, 1956; Brattstrom, 1965; Parker and Brown, 1980; Sullivan, 1981; Himes et al., 2006), the thermal ecology of many species of *Pituophis* remains largely unknown. To the best of our knowledge, there is no published information on the thermal ecology of free-ranging bullsnakes (*Pituophis catenifer sayi*), aside from reported observations of body temperature in a handful ($n = 8$) of sampled individuals (Fitch, 1956). Given the role that ambient environmental temperatures play in the life

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0306-4565/$ - see front matter © 2008 Elsevier Ltd. All rights reserved.
doi:10.1016/j.jtherbio.2007.11.005

histories and ecology of snakes, these parameters need to be elucidated in *P. c. sayi* to better understand the biology of these reptiles, which are declining in the upper Midwest (Wisconsin Department of Natural Resources, 2005; Iowa Department of Natural Resources, 2006; Minnesota Department of Natural Resources, 2006).

The main objective of this research project was to determine the observed thermal gradients, including body and associated environmental temperatures, for free-ranging adult bullsnakes in a population from southwestern Wisconsin. To accomplish this, we compared observed differences in bullsnake body temperature based on habitat, sex, female reproductive condition, season, and behavior. Additionally, we set out to determine whether certain environmental temperatures, specifically, air, surface soil, and sub-surface soil, could accurately predict bullsnake body temperature. We hypothesized that bullsnake body temperature would be influenced by habitat, climate, season, gender/reproductive state, and behavioral variables. Comparisons with past research on this genus are made, where applicable.

2. Material and methods

The approximately 1207 ha study site was located in southwestern Wisconsin (Sauk County, USA). This property consisted of restored sand prairie, oak savanna and agriculture in the flatlands, and adjacent west- to south-facing bluff slopes with exposed limestone outcroppings cleared of over-story vegetation in some areas. For three active seasons, we recorded thermal data for 12–19 adult bullsnakes (Table 1). These data were obtained via temperature-sensitive transmitters (Holohil Systems Lmtd.; Carp, Ontario, Canada; models 9 g SI-2, 13 g SI-2, or 25 g AI-2) that were surgically implanted into the coelom of each subject using accepted methods (e.g., Reinert and Cundall, 1982); snakes were anesthetized with isoflorane and the weight of implanted transmitters did not exceed 6% of the test subject's body weight (Madsen, 1984). Snakes were split into three treatment groups: male, female, and gravid female; female gravidity was determined by palpation, and all females were gravid for a portion of each year in which they were tracked. Implanted snakes were located at least weekly with a Wildlife Materials Inc. radio receiver (Murphysboro, IL USA) and a three-pronged Yagi antenna (Table 1).

Table 1
Annual sample sizes of radio-tagged male and female bullsnakes (*Pituophis catenifer sayi*) tracked for body temperature data from 2003 to 2005 in Sauk County, Wisconsin (USA)

	2003	2004	2005
Males	10	10	7
Females	9	5	5
Total	19	15	12

When a snake was located, macrohabitat was determined by visual observation and later confirmed via analysis of aerial photos in Geographical Information Systems (ArcMap 8.2, ESRI, Redlands, CA USA). We also recorded both surface- and sub-surface soil temperature to determine which predicted body temperature, because bullsnakes are semi-fossorial, and frequently use burrows and rock crevices as refugia. We measured both parameters, centered upon snake location, within 30 s of observation. Sub-surface soil temperature was measured using a Taylor® Pocket Digital Thermometer (Oak Brook, IL, USA) inserted 15 cm below the surface. Surface soil temperature was measured by laying a glass-encased pocket thermometer (non-mercury) on soil surface until equilibration (<5 min). Because air temperature explains the variation found in body temperature data for northern water snakes (*Nerodia sipedon*; Brown and Weatherhead, 2000), we also measured air temperature by holding a Taylor® Pocket Digital Thermometer at breast height until equilibration (<5 min).

The behavior of the snake upon location was also noted. The behavioral categories were created *a priori* based on previous field observations of bullsnakes: exposed (coiled), exposed (outstretched), not seen/under cover (J.M. Kapfer, pers. obs.). In this case, "under cover" represented numerous types of cover, including woody debris, mammal burrows, or rock crevices.

To analyze our data, we conducted a multiple linear regression to determine which of the recorded environmental temperature variables (i.e., air, surface ground, or sub-surface ground) predicted snake body temperature (Zar, 1984). We also conducted a repeated measures analysis of variance with fixed effects: two between subjects factors (sex and behavior) and one within the subject factor (month) to test if (1) snake sex or gravidity, (2) associated macrohabitat, (3) season, or (4) snake behavior best predicted snake body temperature. Tests for interaction among variables was also conducted. This analysis was chosen because numerous measurements were taken per individual snake, and the number of times data were recorded per individual varied (Hurlbert, 1984; Zar, 1984). All statistical analyses were performed in Systat v. 10.0 (Point Richmond, CA), and SPSS v. 11.5 (Chicago, IL).

3. Results

We accumulated 710 readings of body and environmental temperatures from 2003 to 2005 (Table 2). Environmental temperatures varied little from month to month and among years (Table 2). The average male T_b among all 3 years (25.7 °C) was slightly greater than that of females (25.2 °C), and both of these were lower than gravid females (26.7 °C). Male, female, and gravid female body temperatures were largely consistent among the years of this study (Table 2). Of the bullsnake T_b recorded, 61% ($n = 105$) of female observations, 74% ($n = 65$) of

Table 2
Mean and standard deviations for body and environmental temperature readings (Celsius) for male and female bullsnakes (*Pituophis catenifer sayi*) by month from 2003 to 2005 in Sauk County, Wisconsin (USA)

	Body temp	Surface soil temp	Sub-surface soil temp	Air temp
Females				
April $N = 8$	15.8 (8.7)	24.8 (7.8)	11.8 (3.5)	18.6 (6.8)
May $N = 1$	15	NA	11.7 (2.6)	16.9 (2.8)
June $N = 17$	29.3 (3.8)	34.9 (4.3)	19.6 (2.9)	28.4 (3.4)
July $N = 52$	27.6 (3.8)	31.2 (6.6)	20.9 (2.9)	26.5 (3.3)
August $N = 53$	25.9 (2.8)	31.9 (6.4)	22.2 (3.3)	26.2 (4.3)
September $N = 24$	23.9 (4.0)	29.3 (7.9)	19.1 (3.5)	23.9 (4.2)
October $N = 15$	18.2 (5.3)	25.5 (7.6)	13.7 (2.9)	18.6 (7.7)
Mean (SD) $N = 170$	25.2 (5.5)	30.7 (7.1)	19.6 (4.5)	25.0 (5.3)
Gravid Females				
April $N = 7$	21.8 (11.6)	23.9 (8.3)	10.8 (2.6)	16.4 (5.5)
May $N = 37$	26.8 (5.4)	29.1 (8.3)	15.9 (4.1)	21.9 (8.7)
June $N = 44$	27.3 (3.4)	32.1 (9.6)	21.4 (3.0)	25.9 (5.7)
Mean (SD) $N = 88$	26.7 (5.2)	30.6 (9.6)	17.5 (4.8)	23.4 (7.6)
Males				
April $N = 33$	22.6 (9.4)	25.8 (7.7)	11.5 (3.7)	19.2 (5.6)
May $N = 67$	25.8 (6.6)	26.8 (6.2)	14.8 (3.2)	19.9 (4.6)
June $N = 82$	28.6 (4.6)	31.4 (6.8)	20.4 (2.9)	26.2 (4.9)
July $N = 75$	28.2 (3.4)	30.8 (6.5)	21.5 (2.9)	26.7 (4.0)
August $N = 105$	26.8 (3.3)	33.2 (6.9)	21.6 (3.1)	26.7 (3.9)
September $N = 56$	22.9 (3.7)	29.6 (8.4)	19.5 (3.1)	23.7 (5.5)
October $N = 34$	18.1 (4.2)	23.5 (7.4)	13.2 (2.9)	18 (5.9)
Mean (SD) $N = 452$	25.7 (5.7)	29.8 (7.6)	18.5 (4.9)	23.9 (5.7)

gravid female observations, and 61% ($n = 277$) of male observations were 25 °C or higher. As a further demonstration of the consistency of these temperature observations, only 46% of the female observations and 35% of the male observations of below 25 °C occurred in June, July, and August, the months that represent the warmest period of their activity.

Bullsnake body temperature differed based on several parameters. The sex and reproductive status of individual snakes ($F_{(2,\ 572)} = 4.7$; $P = 0.009$) strongly influenced body temperature, with gravid females and males having higher body temperatures than non-gravid females (Fig. 1). Also, the particular behavior witnessed during snake observations had a significant relationship with body temperature (Fig. 2). Those snakes that were "not seen" or "under cover" had lower body temperatures than those that were exposed ($F_{(4,572)} = 4.3$; $P = 0.002$). Furthermore, the season during which the observation was made had an effect on snake body temperature, with body temperatures recorded during summer being higher than those recorded during spring and fall ($F_{(2,\ 572)} = 12.7$; $P = <0.001$; Table 2).

Significant interactions among independent variables led to differences in bullsnake T_b in two instances (Table 3). In the first, the three-way interaction of sex and reproductive status, macrohabitat, and season of observation produced a significant effect. In the second, a combination of bullsnake behavior, macrohabitat, and season of observation interacted to produce a significant effect.

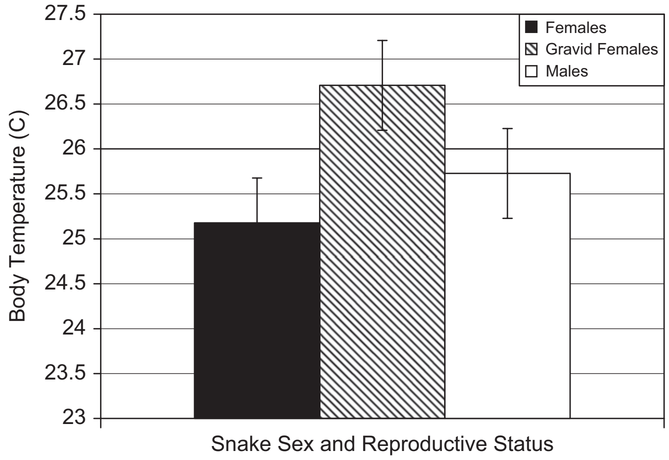

Fig. 1. Body temperatures of radio-tagged male, female, and gravid female bullsnakes (*Pituophis catenifer sayi*) recorded from 2003 to 2005 in Sauk County, Wisconsin (USA).

Air temperature, surface ground temperature, and subsurface ground temperature were all significant predictors of snake T_b ($F_{(3,\ 509)} = 79.247$; $P = <0.000$), but explained only 27.7% of the variation in the data (multiple $R^2 = 0.277$).

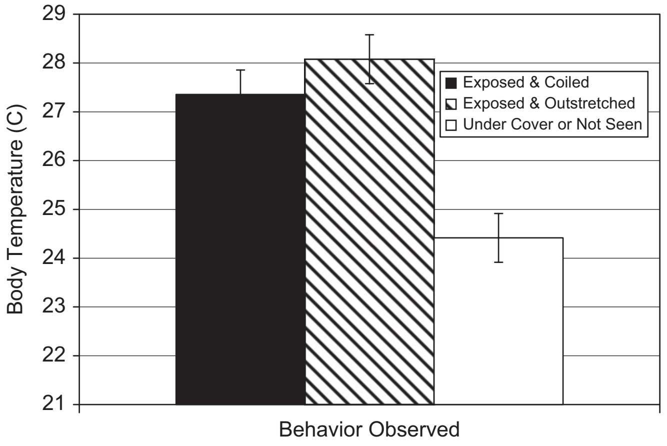

Fig. 2. Differences in body temperatures based on observed behavior of radio-tagged bullsnakes (*Pituophis catenifer sayi*) from 2003 to 2005 in Sauk County, Wisconsin (USA).

Table 3
Results of repeated measures ANOVA used to compare *Pituophis catenifer sayi* body temperatures among independent variables ($\alpha = 0.05$; significant interactions in bold font)

Independent variable(s)	Degrees of freedom	*F*-statistic	*P*-value
Sex & gravidity	**2**	**4.707**	**0.009**
Macrohabitat	5	1.727	0.126
Behavior	**4**	**4.282**	**0.002**
Season	**2**	**12.771**	**0.000**
Sex&gravid.∗macrohab.	10	1.138	0.331
Sex&gravid.∗behavior	7	1.466	0.177
Sex&gravid.∗season	3	0.645	0.586
Macrohab.∗behavior	16	1.599	**0.064**
Macrohab.∗season	**10**	**3.226**	**0.000**
Behavior∗season	7	1.520	0.158
Sex&gravid.∗macrohab. ∗Behavior	21	1.285	0.177
Sex&gravid.∗macrohab. ∗Season	**10**	**2.825**	**0.002**
Sex∗gravid.∗behavior ∗Season	7	1.817	0.081
Macrohab.∗behavior ∗Season	**23**	**2.137**	**0.002**
Sex&gravid.∗macrohab. ∗Behavior∗season	10	0.893	0.539

4. Discussion

We found that several variables had important influences on the body temperature of free-ranging *Pituophis catenifer sayi*. Not only were environmental parameters among these, but also season of observation, reproductive state, and the snake's behavior at the time of observation. Although several variables were important when considered alone, there were two significant three-way interactions involving combinations of the effects of sex and reproductive status, macrohabitat, behavior, and season that had significant predictive effects on bullsnake body temperature.

The recorded body temperatures in free-ranging *P. c. sayi* during the current study were similar to past field observations of snakes in the genus *Pituophis* (Brattstrom, 1965; Parker and Brown, 1980). These readings are also similar to the T_b of 30 °C at which Greenwald (1971) reports that a "peak in metabolic scope" is attained in *Pituophis catenifer affinis* in the lab.

We found no inter-sexual difference in body temperature, unless a female snake was gravid; this has been previously found in, for example, an unrelated snake species (*Boa constrictor occidentalis*; Chiaraviglio, 2006). Because females are only gravid during a specific season, and because gravid females typically utilize warmer macrohabitats, the significant difference in snake T_b based on a three-way interaction between snake sex/gravidity, macrohabitat, and season is reasonable. In addition, because bullsnakes encountered in certain warmer habitats (i.e., open grassland vs. forest) were more likely to be in refuges to avoid associated high temperatures based on season (i.e., summer vs. fall), the interaction between bullsnake behavior, macrohabitat, and season is also realistic.

The macrohabitat associated with bullsnake body temperature did not differ when considered independently. However, interactions among this variable, snake behavior, and season did yield significant results. Blouin-Demers and Weatherhead (2002) also found *Elaphe* (now *Pantheropsis*) *obsoleta* in Ontario to vary in T_b based on habitat; snakes were found to be warmer in barns and forest edges than forest interiors. They suggest potential scenarios to explain this phenomenon. For example, unlike what Huey and Slatkin's (1976) cost–benefit model of thermoregulation

Table 4
Comparison of average body temperatures (±standard deviation) observed for *Pituophis catenifer sayi*[a] and *Pituophis ruthveni*[b]

Month	Males (*P. ruthveni*)	Males (*P. c. sayi*)	Females (*P. ruthveni*)	Non-gravid females (*P. c. sayi*)
May	27.4 (5.8)	25.8 (6.6)	29.2 (5.6)	NA
June	28.7 (3.3)	28.6 (4.6)	26.1 (1.8)	29.3 (3.8)
August	28.8 (3.5)	26.8 (3.3)	32.2 (4.8)	25.9 (2.8)
September	26.2 (5.3)	22.9 (3.7)	31.4 (3.7)	23.9 (4.0)

[a] Current study.
[b] Himes et al. (2006).

predicts (i.e., that lizards should invest more in thermoregulation when the costs of thermoregulation are low), other factors, such as predation risk, should be considered when applying this model to snakes. Due to the structural heterogeneity of the macrohabitats preferred by *P. c. sayi* at this site (i.e., open bluffs and oak savannas; Kapfer et al., in press), a substantial range in thermoregulatory opportunities is likely present during normal daily activity. Therefore, these habitats may not be as thermally challenging for bullsnakes as the preferred habitats of *E. obsoleta*. Bullsnakes in these preferred habitats might not be required to thermoregulate as stringently, and may instead behave more like a "thermoconformer" to existing conditions. Consistent body temperatures, are often associated with actively thermoregulating species that exist in thermally challenging habitats. If it is true that bullsnakes inhabit benign thermal environments, this could explain the consistent body temperatures observed during our study. Although Sullivan (1981) reports that members of this genus sampled along roads in California exhibited higher body temperatures than the surface they were captured on, and were not thermonforming, we did not detect this type of relationship between T_b and surface soil temperature during our study. By thermoconforming, more time during the active season can be allocated for foraging or searching for potential mates. More research testing the hypothesis that *P. c. sayi* is a thermoconformer in the upper Midwest is necessary.

Himes et al. (2006) have recently completed a study on the thermal ecology of the nationally rare Louisiana Pine Snake (*Pituophis ruthveni*), a species closely related to *P. c. sayi* (Rodriguez-Robles and De Jesus-Escobar, 2000; Rudolph et al., 2006). Using a similar methodology to our own, Himes et al. (2006) found comparable patterns in the body temperatures of *P. ruthveni*, though it appears to generally exhibit higher body temperatures than *P. c. sayi* (Table 4). These differences may be attributable to the different geographic locations in which the two studies occurred (i.e., Louisiana vs. Wisconsin). Nonetheless, Himes et al. (2006) state that studies of the thermal ecology of *P. c. sayi* may be particularly important to further increase the understanding of *P. ruthveni*'s thermal ecology, and we concur. Further research on *P. c. sayi* thermal ecology, including detailed comparative studies of related taxa, is necessary. Future studies should include data collection on parameters beyond the scope of this project, such as operative environmental temperatures (T_e) and thermoregulatory effectiveness of free-ranging individuals as in other studies of snake thermal ecology (Blouin-Demers and Weatherhead, 2001a, b, 2002). The importance of analyzing interactions among independent variables potentially affecting body temperature should also not be overlooked.

Acknowledgments

We thank Peter Dunn, Linda Whittingham (UW-Milwaukee), and Erik Wild (UW-Stevens Point) for advice regarding experimental design and review of earlier versions of this manuscript, and Colin Bennell, Chad Hopper, Max Kapfer, Tom Kessenich, Tim Muehlfeld, Greig and Bjorn Stanton, Nick Schiltz, and Vannessa Torti for field assistance. We thank Steve Richter and Paul West at The Nature Conservancy (Madison, WI), and numerous private landowners for allowing us access to their property: Jean Pare, Joanne Paul-Murphy, Kurt Sladky, Chris Hanley and Anne Stewart, and their students at the UW-Madison School of Veterinary Medicine surgically implanted radio transmitters. We also thank Craig Berg and Rich Sadjak for advice on field methods.

Funding was provided by the Society for the Study of Amphibians and Reptiles Grants in Herpetology Program, the Milwaukee Zoological Society, The Wisconsin Academy of Sciences Lois Almon Foundation, The Prairie Biotic Research, Inc. Small Grants Program, the Chicago Herpetological Society, The University of Wisconsin-Milwaukee, Department of Biological Sciences Ruth Walker Memorial Fund, and The Wisconsin Department of Natural Resources-Bureau of Endangered Resources. Permission was granted from the Wisconsin Department of Natural Resources to work with a Protected Wild Animal, and research was conducted under animal care and use protocol (02–03 ♯145) issued by UW-Milwaukee.

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