Body Temperatures and Winter Activity in Overwintering Timber Rattlesnakes (*Crotalus horridus*) in Tennessee, USA

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Abstract.—At high latitudes and elevations, snakes spend considerable time in overwintering refugia. Although brumation is generally associated with periods of inactivity, some evidence supports the occurrence of limited above and below ground activity during winter. Observations of such events are rare due to the inaccessibility of the typical subterranean refugia of snakes. Our study examined occurrences of both surface and subterranean activity during winter in the Timber Rattlesnake, *Crotalus horridus*. We monitored hourly body temperatures (T_bs) and small-scale above and below ground movement bouts throughout the overwintering period in Tennessee, USA. High frequency monitoring of body temperatures and movement patterns allowed us to identify mid-winter activity as well as shuttling behavior during ingress and egress. We recorded environmental temperatures and snake operative temperatures to estimate periods when snakes were surface active. Snake ingress into brumation occurred on 10 October ± 12 d, and egress occurred on 7 April ± 17 d. We recorded 53,041 T_bs (mean snake T_b = 11.0 ± 3.6° C; range 1.1–33.7° C) collected over two overwintering periods (2011–2012 and 2012–2013). Snakes made on average 6.1 ± 1.2 movement bouts throughout winter, accumulating a total distance of 146.4 ± 35.5 m. All individuals made small (< 10 m) movements throughout winter. We speculate that milder winters and the increased prevalence of suitable surface temperatures will promote additional winter activity.

Key Words.—basking; brumation; hibernation; movement; thermal biology; snake

Introduction

Reptiles in temperate climates commonly exhibit reduced periods of activity or brumation as an essential behavioral mechanism to escape unfavorable temperatures (Gregory 1982). Local conditions contribute to the length and intensity of such inactive periods; unsuitable surface conditions may last a few weeks (Hein and Guyer 2009; Waldron et al. 2013) or up to as long as eight months (Prestt 1971; Bauwens 1981; Weatherhead 1989; Cobb and Peterson 2008). In cool-climate regions where brumation is lengthy, lethal surface temperatures often exist for extended periods, making the selection of appropriate overwintering refugia necessary for survival. Additionally, low environmental temperatures suppress metabolic activity and locomotor performance, which limits many activities including prey capture, predator avoidance, and digestion (Naulleau 1983; Stevenson et al. 1985; Lillywhite 1987; Peterson et al. 1993).

In ectotherms, brumation is generally considered a period of inactivity, although a few studies have suggested that brumation may be more of a period of reduced activity (Cobb and Peterson 2008; Nordberg and Cobb 2016). Cobb and Peterson (2008) show evidence of subterranean movement and shuttling during the early part of brumation in a population of Western Rattlesnakes (*Crotalus oreganus*) in Idaho, USA. Although surface activity was not documented, telemetered snakes made movement bouts near the entrance of the den site and then moved deeper into the den (away from the entrance) as environmental temperatures dropped during mid-winter. This behavior is hypothesized to be a response to changes in underground thermal gradients as an attempt to maintain desired body temperatures (Viitanen 1967; Sexton and Hunt 1980; Brown 1982). A majority of the literature on snake brumation does not document significant movement or activity during this time, which may simply be attributed to inaccessibility of overwintering refugia for visual observations or infrequent sampling due to presumed inactivity.

Overwintering sites vary geographically and by habitat, but the primary function of such refugia is to allow snakes to maintain body temperatures above freezing environmental temperatures (Prior and Weatherhead 1996; Shine and Mason 2004; Gienger and Beck 2011). Most brumation studies focus on northern populations where snakes overwinter communally and in large aggregations (Brown et al. 1974; Macartney et al. 1989; Cobb and Peterson 2008). More southerly populations of snakes (whether brumation is communal or individual) tend to have shorter periods of winter inactivity compared to northern populations (Mushinsky et al. 1980; Hein and Guyer 2009; Sperry

and Weatherhead 2009), and mild environmental temperatures may be suitable for limited surface activity (Sperry and Weatherhead 2012).

A good model to study environmental effects on brumation in snakes is the Timber Rattlesnake (*Crotalus horridus*), which is a large pitviper with a historical range across most of the eastern United States (Conant and Collins 1998). Like many other temperate snake species, *C. horridus* seeks refuge underground in communal or individual refugia during winter (Klauber 1972; Martin 2002). Communal brumation is more common in *C. horridus* across northern populations, while snakes in southern populations tend to overwinter individually (Sexton et al. 1992). In spring, *C. horridus* emerge from brumation and disperse to forage and search for mates (Martin 1992; Ernst and Ernst 2011).

We chose to use *Crotalus horridus* as our model species because (1) it has a large latitudinal geographic range; (2) previous studies on brumation in *C. horridus* were available for comparison; and (3) this species was locally abundant and exhibits communal brumation at our study site. The objectives of our study were to describe (1) characteristics of overwintering den sites and their use; (2) body temperature variation among individuals and among months; and (3) behavioral activity and movement in overwintering snakes in a geographic region that represents an intermediate overwintering climate. Middle Tennessee exhibits a climate that promotes the brumation of snakes for approximately five months, usually with several short-term warming events throughout winter (Nordberg and Cobb 2016). We suspected such warming events may stimulate activity during brumation and create more variation in body temperatures during the ingress and egress periods.

Materials and Methods

Study area.—We studied *C. horridus* from September to May in 2011/2012 (year 1) and 2012/2013 (year 2) on a state natural area in central Tennessee, USA. Available habitat included mixed hardwood forests, Redcedar (*Juniperus virginiana*) forests, old growth fields, and cedar glades. The nature preserve was surrounded by agricultural lands and rural housing, which buffer it from the edge of a nearby city (population about 110,000).

Environmental measurements.—We monitored environmental temperatures (T_es) hourly using single-channel data loggers (LT-2 LOGiT®, Sealed Unit Parts Company, New Jersey, USA) and thermocouple wire. We measured 2 m shaded air temperature, 5 cm and 20 cm soil profiles, and subterranean den cavities at depths of 1–2 m.

Operative snake models.—We used operative snake models constructed of sealed hollow copper pipe painted to match the reflectance of *C. horridus* skin to measure available surface temperatures near the den site (see Peterson et al. 1993; Wills and Beaupre 2000 for model construction). Detailed description of the operative models are given in Nordberg and Cobb (2016). We used operative snake models to define the maximum (T_{eMax}) and minimum (T_{eMin}) environmental temperatures available to snakes on the surface. To record hourly temperatures throughout winter, we placed a miniature data logger (1922L iButton®, Maxim Integrated Products, California, USA) inside each operative snake model. We selectively placed 27 snake models around the den site; 15 models in direct sunlight to measure the warmest available surface temperatures during the day, and 12 models in full shade to capture the coolest available surface temperatures not exposed to solar radiation. We calibrated our operative snake models against an adult *C. horridus* carcass by recording the temperatures of both simultaneously. We placed an operative snake model and the carcass in direct sunlight and recorded temperatures every minute for 5.5 h. We placed an iButton® inside the snake model and the snake carcass (mid-body). The operative snake models heated and cooled faster than the snake carcass, as expected due to the snake carcass having greater thermal inertia, but when temperatures stabilized, both the snake operative model and snake carcass temperatures were similar (Spearman's correlation test; $rho = 0.937$, $P < 0.001$). Snake operative models and snake carcass temperatures during equilibrium were within $0.92 \pm 0.13°$ C (mean ± SE) of each other.

Snake capture and radio transmitters.—We captured all snakes along drift fences with funnel traps, during opportunistic encounters, or as part of systematic searches during ingress and egress periods. We anesthetized each snake with isoflurane vapor delivered through a clear acrylic tube prior to surgery. We implanted transmitters (SB-2 or SI-2, Holohil Systems, Inc., Ottawa, Ontario) into snake body cavities through a 2-cm lateral incision made between the first and second dorsal scale rows approximately two thirds the distance from the head to the cloaca following methods similar to Reinert and Cundall (1982). We adhered an iButton® to each radio transmitter for recording snake core T_b. Implanted transmitter package coating consisted of a thin layer of 50:50 mixture of beeswax and paraffin to seal the transmitter and data logger before surgery. The implanted package did not exceed 5% of snake body mass ($2.0 \pm 1.3\%$). We collected snout-vent length (SVL), tail length, body mass, and sex immediately following surgery. We maintained post-operative snakes

at temperatures of 27–30° C for 2–3 d to initiate healing and to allow full recovery from anesthesia before snakes were released at their capture sites.

Radio telemetry and snake movements.—We located snakes 3–4 times per week using a three-element Yagi antenna (Wildlife Materials International, Inc., Murphysboro, Illinois, USA) and a handheld receiver (R-1000, Communications Specialists, Inc., Orange, California, USA). During ingress and egress when larger movement bouts occurred, we obtained snake locations using a handheld GPS unit (GPSMAP 76CSx, Garmin International, Inc., Olathe, Kansas, USA; accuracy ≤ 5 m). As snakes approached the den site and smaller movement bouts became more prominent, we marked new snake locations with colored flags and documented distance and directionality of winter movements using a measuring tape and compass.

Data analyses.—We calculated brumation duration for each snake as the difference between ingress date (first day of brumation) and egress dates (last day of brumation). We defined ingress date as when an individual remained underground in the same location for a minimum of 10 consecutive days in late fall. We defined egress date as when an individual emerged from the den site in the spring and was captured in a drift fence trap surrounding the denning area, or moved > 50 m away from the denning area. We used two-sample Student's t-tests to test for sex and yearly differences in the number of movement bouts, distance traveled, ingress dates, egress dates, and brumation duration. We used an adjusted alpha level of 0.025 (0.05/number of tests = 2; test 1 = sex differences, and test 2 = year differences) to maintain experiment-wise error at 0.05. We used a paired t-test to test for changes in mass before and after brumation for each sex. We identified basking events by visual observations of individuals on the surface or by analyzing T_b profiles from iButtons®. We identified non-observed basking events when snake T_b increased ≥ 5° C during a heating event. We used Spearman's correlation analyses to determine the relationship between snake T_b profiles and subterranean environmental temperatures (5-cm soil profile, 20-cm soil profile, and a 2-m denning cavity). We also used Spearman's correlation analyses to test the relationship between snake size (SVL) and distance traveled, and the relationship between SVL and number of movement bouts. We performed a Kruskal-Wallis test followed by pairwise Wilcoxon comparisons if differences were significant to test for differences in distance traveled among months. We set all nominal α-levels at 0.05 except when we required Bonferroni adjustments (P-value 0.05/8 = 0.006 in post-hoc Wilcoxon comparisons). We conducted all analyses using the program SigmaStat 3.1 (Systat Software Inc.,

San Jose, California, USA) and the program R (R Core Team 2016).

RESULTS

Brumation and denning.—Timber Rattlesnakes in this population historically overwinter in a rocky ridge near the north-central boundary of the nature preserve to which all but two individuals (#8 and #10) returned. Snakes that returned to the ridge chose southerly exposed limestone outcrops and tree root systems that led to underground cavities and denning areas. Many individuals possess high den site fidelity and return to the exact locations yearly (Vincent Cobb, pers. obs.); often within 1 m. Snake #8 was thought to have overwintered individually under rocks at the base of a large tree approximately 200 m from the communal ridge den. This individual had been captured initially at the communal den site during egress in spring 2012, so it appears that some snakes may periodically overwinter in alternate localities. Snake #10 overwintered down a subtle vertical crevasse shared with un-telemetered snakes (Timber Rattlesnakes, *Crotalus horridus*; Black Racers, *Coluber constrictor*; and Common Garter Snakes, *Thamnophis sirtalis*). Snake #10 was not initially captured at the communal den, and did not overwinter near the communal ridge den, but rather in a mixed hardwood forest (1.3 km from the communal den). We do not know if this individual ever overwinters at the communal ridge den site, despite sharing summer foraging areas with the communal den snakes.

Snakes returned to the winter denning areas in late September and throughout October. The date of ingress (mean ± SD; ingress year 1: 24 October 2011 ± 9.4 d, ingress year 2: 7 October 2012 ± 10.4 d; t = 3.34, df = 4, P = 0.021) and brumation duration (year 1: 146 ± 14.0 d, year 2: 185 ± 20.3 d; t = -3.80, df = 5, P = 0.014) varied between years, whereas the date of egress (year 1: 23 March 2011 ± 19.4 d, year 2: 12 April 2012 ± 13.8 d; t = -1.64, df = 3, P = 0.214) did not (Table 1). Ingress date (t = 0.147, df = 7, P = 0.887), egress date (t = 0.413, df = 6, P = 0.694), and brumation duration (t = 0.011, df = 7, P = 0.992) did not differ between male and female snakes. *Crotalus horridus* in this study lost 3.6 ± 4.4 % of their ingress body mass over the course of brumation and did not differ significantly between sexes (t = 0.630, df = 6, P = 0.551).

Winter activity and movements.—The frequent monitoring of snake body temperatures and individual locations via radio telemetry (year 1: 215 relocations of four individuals; year 2: 731 relocations of 13 individuals) allowed for close monitoring of small scale movement bouts throughout the brumation period. We observed that snakes moved both above and
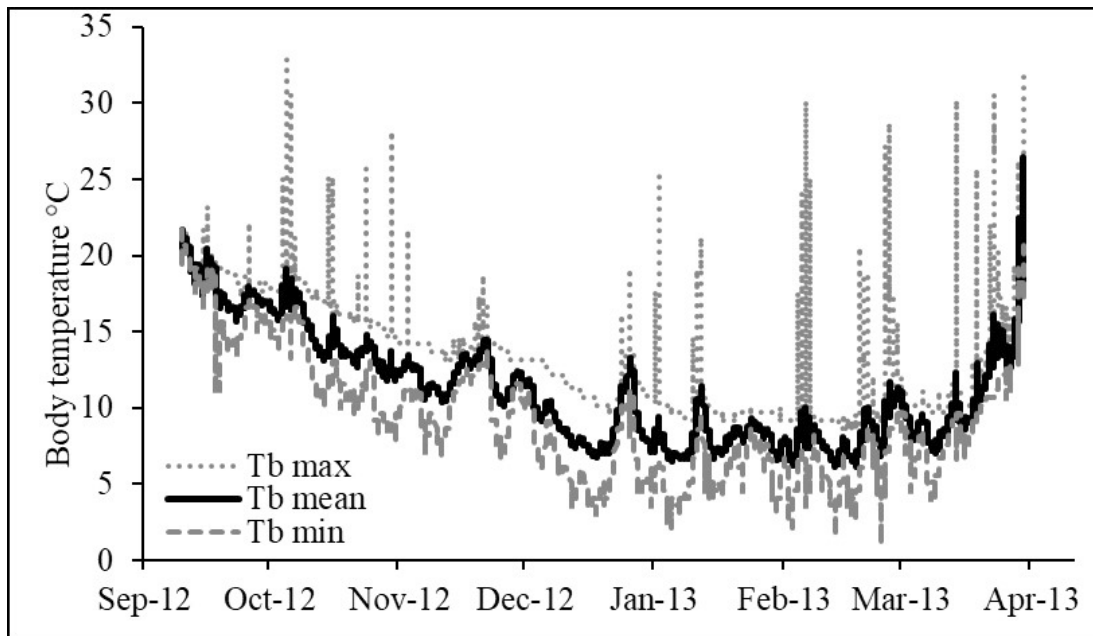
FIGURE 1. Mean, minimum, and maximum body temperature profiles of overwintering Timber Rattlesnakes (*Crotalus horridus*) in a state natural area in central Tennessee, USA. Major spikes in temperature throughout winter represent surface-active snakes and elevated body temperatures.

below ground throughout the brumation period, with the greatest frequency of movement bouts distributed around ingress and egress (Table 2). Large proportions of snake movement bouts associated with surface exposure (58%) and elevated T_bs, both corroborated from recovered implanted iButtons® or inferred from visual observations of surface active snakes. We found snake SVL did not correlate to the total number of movement bouts (*rho* = -0.261, *P* = 0.310) throughout brumation, nor did SVL correlate to the total distance traveled during winter (*rho* = 0.402, *P* = 0.109). The number of movement bouts (*t* = 0.268, df = 5, *P* = 0.799) and the distance traveled (*t* = 0.778, df = 13, *P* = 0.451) did not differ between sexes. Individuals moved an average of 6.1 ± 1.2 times accumulating a total distance of 146.4 ± 35.5 m. Winter movement bouts were not solely subterranean as approximately 80% of snakes made one or more movement bouts to the surface

throughout winter (Fig. 1). Individuals that traveled the farthest throughout the overwintering period did not necessarily move the greatest number of times. The mean distance traveled by snakes between years was not significantly different (*t* = -0.252, df = 4, *P* = 0.814), yet differences among months (*H* = 37.22, df = 6, P < 0.001) did exist (Table 2).

Snake body temperatures.—We recorded 53,041 body temperatures from 14 *C. horridus* throughout brumation (Table 2; Fig. 2). Mean snake body temperatures between year 1 (11.9 ± 1.5° C) and year 2 (11.0 ± 1.2° C) were not significantly different (*t* = 0.703, df = 12, *P* = 0.495). Snake T_bs significantly correlated (*rho* = 0.959, *P* < 0.001) with den cavity temperatures (about 2 m) suggesting overwintering snakes experienced temperatures similar to the deeper cavities we measured (Fig. 3). While underground,

TABLE 1. Sex (M = male, F = female), age class (SA = sub-adult), sample size for year 1 (n1) and year 2 (n2), snout-vent length (SVL), ingress date (ID by Julian date), egress date (ED by Julian date), brumation duration (BD in days), the number of movement bouts (MB), the distance traveled (DT in meters), the number of basking events (BE), and the change in body mass (CBM) for overwintering Timber Rattlesnakes (*Crotalus horridus*) in a state natural area in central Tennessee, USA. Values represent means ± SD (range).

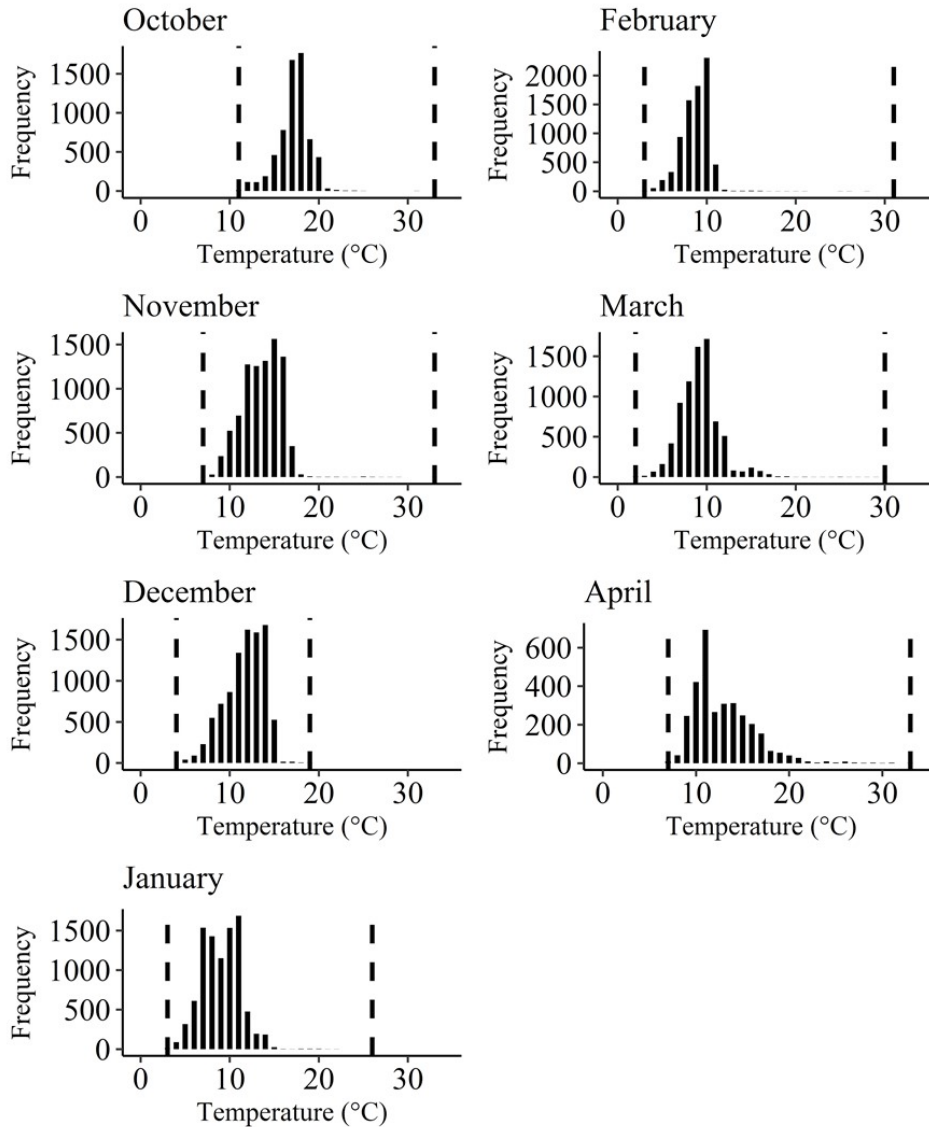| Sex	Age Class	n1	n2	SVL (cm)	ID	ED	BD (d)	MB	DT (m)	BE	CBM (%)
M	Adult	2	3	103.3 ± 18.2	283 ± 13	95 ± 16	177 ± 22	7 ± 8	143 ± 125	5 ± 4	1.1 ± 3.8
				(85.0–123.5)	(262–296)	(73–106)	(147–197)	(1–20)	(1.7–139.5)	(1–10)	(-2.3–5.3)
F	Adult	2	7	103.9 ± 7.3	284 ± 13	103 ± 17	182 ± 26	5 ± 2	169 ± 178	3 ± 2	-4.4 ± 3.1
				(98.0–114)	(271– 309)	(70–134)	(132–217)	(2–8)	(2.2–426)	(0–6)	(-7.6--0.5)
F	SA	—	3	68.1 ± 2.1	286 ± 5	85 ± 15	156 ± 25	9 ± 6	85 ± 74	7 ± 5	-8.5 ± 1.6
				(66.8–69.8)	(282–291)	(75–96)	(138–173)	(3–15)	(28.7–75.4)	(2–10)	(-9.7--7.4)

FIGURE 2. Body temperature distributions of Timber Rattlesnakes (*Crotalus horridus*) during brumation in a state natural area in central Tennessee, USA. Dotted lines represent the limits (minimum - maximum) for the distributions.

snake T_bs remained relatively stable, but periodically individuals emerged to the surface, presumably to bask (Fig. 1). Snakes achieved maximum T_bs (year 1 = 32.2° C; year 2 = 33.7° C) by emerging from the den site and basking on the surface. The minimum T_bs experienced by any individual (year 1 = 5.9° C; year 2 = 1.1° C) remained above freezing regardless of air temperatures periodically dropping below 0° C. Snake T_bs varied over winter by gradually declining through early brumation, stabilizing during mid-winter, and increasing again in late brumation before egress. Body temperatures from one individual in year 1, and three individuals in year 2 could not be retrieved due to premature radio transmitter failure (n = 3) or suspected predation (n = 1) and we excluded these individuals from analyses.

DISCUSSION

Brumation and denning.—The large geographic distribution of *C. horridus* likely contributes to variation in brumation characteristics (e.g., ingress date, egress date, and brumation duration). *Crotalus horridus* in this study exhibited a brumation period of approximately five months. During ingress to the den site, it was common for snakes to shuttle above and below ground prior to brumation as cooler winter temperatures became more prevalent. Annual variation observed in ingress dates and egress dates likely associated with both environmental temperatures and relatively low
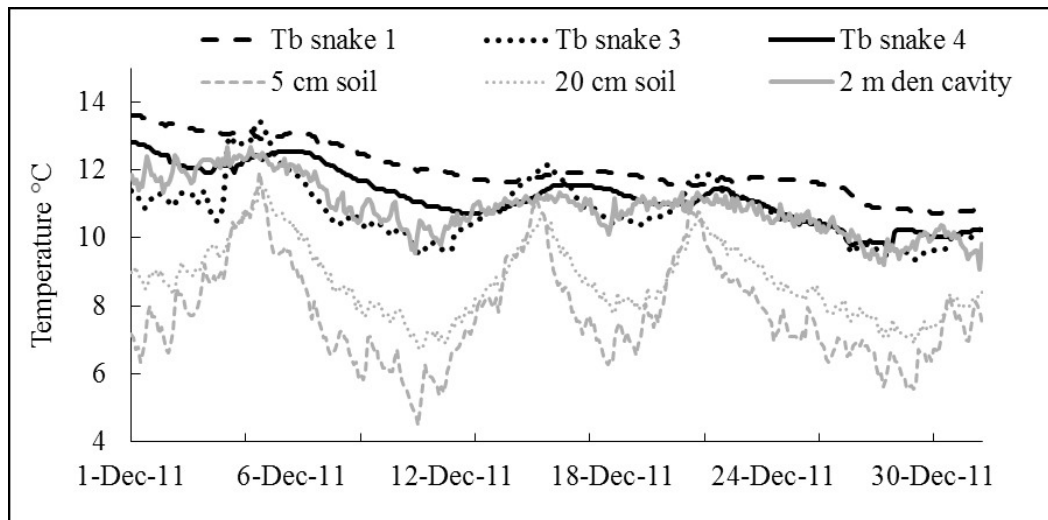
FIGURE 3. Body temperature variation among three communally brumating (± 1 m from each other) Timber Rattlesnakes (*Crotalus horridus*) from a state natural area in central Tennessee, USA, and subterranean environmental temperatures during 2012–2013.

sample sizes. Delayed egress in spring 2013 may have been due to cooler environmental temperatures in late March. When snakes returned to the general area of their overwintering refugia, snakes often spent multiple days underground and then relocated to new rocky crevices. Similarly, when snakes emerged in spring, it was difficult to determine if a snake was on the surface basking or if it had emerged from its overwintering refugia for the active season. Furthermore, when we discovered a snake in a funnel trap it was difficult to determine if the snake was leaving the denning area or simply making localized movements. Overall, we believe our estimates for dates of ingress and egress are conservative.

Most snakes (100% in year 1 and 62% in year 2) overwintered at communal den sites with high den site fidelity, as is common in northern populations (Brown et al. 1982; Clark et al. 2008). Although we identified some snakes as overwintering individually, we cannot be certain snakes without radio-transmitters were not present, just that these individuals chose different refugia than most other radio-equipped snakes. Timber Rattlesnake populations in Tennessee likely represent an intermediate zone between communal and individual overwintering strategies. While winter environmental temperatures in Tennessee are mild compared to the northeastern United States, air temperatures in Tennessee commonly drop below 0° C in January and February.

Winter activity and movements.—As snakes retreat underground to brumate, researchers often reduce the frequency of telemetry relocations to once every week (Brown 1982; Cobb and Peterson 2008) or even once per month (Waldron et al. 2006). In this study, snakes

were monitored 3–4 times per week, which allowed for a more detailed examination of snake movement patterns and activity throughout brumation. As noted in prior studies, subterranean movement is greatest during the beginning of brumation (Sexton and Hunt 1980; Macartney et al. 1989; Cobb and Peterson 2008). In our study, snakes often made small movement bouts (< 10 m) around the den site during ingress and egress, but also throughout mid-winter. We suspect most movement bouts were due to changes in subterranean thermal gradients (Viitanen 1967; Sexton and Hunt 1980; Graves and Duvall 1990), which may have allowed for behavioral thermoregulation even while remaining underground.

While winter movement may be uncommon or at least undocumented in *C. horridus*, we found winter movement and surface activity to be common in this population (Nordberg and Cobb 2016). Most large-scale movement bouts (> 100 m) were bimodally distributed near ingress and egress as snakes transitioned between the active season and the overwintering period. Cobb and Peterson (2008) similarly found underground movement bouts of *C. oreganus* in Idaho were common in the first two months of brumation as snakes shuttled further away from the den site entrance. During mid-winter in this study, most movement bouts ranged between 1–10 m and often associated with surface basking events. Some individuals made lengthy movements early in the brumation period that increased their overall distance traveled, but remained relatively sedentary through the winter, while others made small but frequent movement bouts throughout winter.

Snake body temperatures.—Few studies have documented the body temperatures of rattlesnakes

TABLE 2. Mean monthly body temperatures, number of movement bouts, and distance traveled (m) for overwintering Timber Rattlesnakes (*Crotalus horridus*) in a state natural area in central Tennessee, USA. Body temperatures (T_bs; ° C) represent mean values and monthly minimum and maximum in parentheses; movement bouts represent the total number of underground movements followed by surface active movement bouts in parentheses; and distance traveled represents the mean monthly distance traveled followed by the standard error of the mean in parentheses. Data for three snakes (one from 2011–2012, and two from 2012–2013) could not be retrieved due to suspected predation or transmitter battery failure.

Month Snakes monitored	2011–2012 T_bs (° C) n = 3	Movement Bouts (#)	Distance Traveled (m)	2012–2013 T_bs (° C) n = 11	Movement Bouts (#)	Distance Traveled (m)
September	—	—	—	19.4 (15.7–21.7)	1	17.5
October	17.1 (13.9–22.7)	—	—	16.6 (10.6–32.9)	22 (9)	28.5 (8)
November	14.8 (11.4–32.2)	6 (4)	59.8 (31.2)	12.8 (6.7–28.2)	24 (15)	32.5 (8.4)
December	11.3 (9.4 - 13.6)	0	0	11.1 (3.6–18.7)	14 (4)	4.1 (2.2)
January	9.9 (8.2–11.0)	0	0	8.4 (2.1–25.2)	14 (6)	4.9 (2.4)
February	9.8 (7.5–27.7)	3 (1)	1.7 (0.2)	7.9 (2.1–30.1)	8 (5)	2 (0.9)
March	12.6 (6.0–29.6)	2 (5)	31 (1)	8.3 (1.1–28.7)	5 (8)	19.9 (6.4)
April	15.3 (12.7–26.1)	1 (1)	77	12.1 (6.6–32.2)	13 (11)	49.9 (13.9)
May	—	—	—	15.8 (12.7–33.7)	3 (1)	70.5 (15.2)

throughout brumation, especially at high enough sampling rates to detect subtle changes in temperature. The body temperatures of *C. horridus* in this population (mean T_b = 11.0° C) closely resembled those of other rattlesnake species previously studied (*C. horridus* in New York, mean T_b = 10.5° C, Brown 1982; Prairie Rattlesnakes, *C. viridis*, in New Mexico, mean T_b = 10.0° C, Jacob and Painter 1980; *C. oreganus* in Idaho, mean T_b = 4–10° C, Cobb and Peterson 2008). Although it is difficult to estimate the depth of overwintering snakes, it appears even communally denning snakes can experience different body temperatures. The structural design of the den site (e.g., multiple cracks, holes, or entrances) may allow airflow or drafts of cold air to penetrate overwintering chambers. Overwintering refugia likely play a significant role in how thermally stable environmental temperatures are within the den, leading to variations in T_bs of communally overwintering snakes. Small microclimates within the den site may have allowed some snakes to maintain relatively stable T_bs (snake #1) while others exhibited higher variation in T_bs (snake #3).

Surface activity in overwintering snakes is rarely documented except for anecdotal observations. Such behavioral events and corresponding changes in body temperatures can be overlooked without monitoring at a high frequency. Combining multiple tools (radio telemetry and high capacity data loggers) allows for a better understanding of complex behaviors, such as surface basking, between telemetry relocations. Monitoring body temperatures frequently (e.g., hourly) captures heating events in the absence of visual observations.

Our study provides documentation of the activity and thermoregulatory behavior of a small population of overwintering *C. horridus*. Frequent mid-winter movement bouts and basking events are not well documented in snakes and likely do not occur in northern populations (Brown 1982). However, the climate of southern temperate regions provides surface temperatures potentially supporting limited mid-winter activity (Sperry and Weatherhead 2012; Nordberg and Cobb 2016). We can only speculate regarding the significance of surface activity and elevated T_bs throughout brumation. Surface exposure (e.g., basking or traveling) is a risky behavior because low snake T_bs result in reduced locomotor function, rendering snakes vulnerable to predation (Sperry and Weatherhead

2012). Given surface activity was common in our study, we suspect there must be some benefit (i.e., food acquisition, bolstering the immune system, or to initiate gamete production) to this seemingly counterproductive behavior (see Nordberg and Cobb 2016 for further discussion). Two snakes tested positive for Snake Fungal Disease (SFD; *Ophidiomyces ophiodiicola*). Initially we suspected that infection may be the cause of increased surface activity and body temperatures, but although our sample size was small, we saw no trends in body temperature or surface activity between infected and non-infected snakes. One infected snake emerged often (10 times) while the other did not (two times). Larger samples sizes of infected and non-infected snakes from the same population would increase the likelihood of identifying if winter surface activity is a direct result to battle SFD. Future studies can benefit from exploring mid-winter activity in *C. horridus* and other reptiles across latitudinal gradients implementing rapid sampling of body temperatures and telemetry relocations to identify detailed movement patterns during winter. Further studies addressing latitudinal and interspecific differences are going to be essential for identifying trends in winter thermoregulation and potentially identifying the mechanisms for this seemingly adaptive behavior.

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