Seasonal Thermal Ecology of Bog Turtles (*Glyptemys muhlenbergii*) in Southwestern Virginia

Author(s): Jeffrey B. Feaga and Carola A. Haas
Source: Journal of Herpetology, 49(2):264-275.
Published By: The Society for the Study of Amphibians and Reptiles
DOI: http://dx.doi.org/10.1670/13-147
URL: http://www.bioone.org/doi/full/10.1670/13-147

Journal of Herpetology, Vol. 49, No. 2, 264–275, 2015

Seasonal Thermal Ecology of Bog Turtles (*Glyptemys muhlenbergii*) in Southwestern Virginia

JEFFREY B. FEAGA[1,2] AND CAROLA A. HAAS[1]

[1]*Department of Fish and Wildlife Conservation, Virginia Tech, Blacksburg, Virginia, USA*

ABSTRACT.—**Aquatic and semiaquatic turtles use wetlands and thermally buffered soils to thermoregulate during the active season and to sustain body temperatures above freezing during overwintering. We deployed temperature data loggers during wintertime and summertime in wetlands occupied by Bog Turtles (*Glyptemys muhlenbergii*) in southwestern Virginia, United States, to contrast the temperatures of the wetland environment to turtle carapace temperatures over two field seasons. Temperature signatures were used to evaluate probable hibernation depth and the timing and cues of spring emergence. We measured soil temperature profiles during winter in saturated hibernacula and similar but unsaturated structures to evaluate the dependence of temperature on water-table depth. Mean daily turtle temperature ($n = 16$) during the coldest portion of two winters was 2.5°C (SE = 0.29), with one turtle experiencing 14 continuous days at temperatures between −1°C and 0°C when ambient temperatures dipped below −10°C. Water tables remained within 15 cm below the soil surface throughout both winters, preventing freezing temperatures for shallow-hibernating turtles. The date of first emergence differed by 15 d between the two study years, with both soil temperature and ambient temperature potentially serving as emergence cues. During summer activity, turtles alternated between periods of thermoregulation and thermoconformity by basking and accessing deep, thermally buffered saturated soil. The dependence of Bog Turtle body temperature on soil saturation and depth is important for understanding how hydrologic alteration in wetlands can affect Bog Turtle ecology.**

Digestion, growth, reproduction, and activity of turtles are influenced by body temperatures (Huey, 1982). Aquatic and semiaquatic turtles thermoregulate in their environments through the processes of basking and conforming to water and mud temperatures (Grayson and Dorcas, 2004; Rowe and Dalgarn, 2009; Picard et al., 2011; Millar et al., 2012). Metabolic rates in turtles are generally correlated positively to temperature (Litzgus and Hopkins, 2003); therefore, metabolic rates cannot be controlled if turtles are unable to select thermally stable areas for hibernation or if thermoregulation during the active season is not efficient and effective. Water resists rapid temperature changes because it has a relatively high specific heat compared to the surrounding air and mineral soil. During hibernation, aquatic turtles avoid freezing and desiccation by remaining dormant underwater or in saturated substrates (Ultsch, 2006). During periods of activity when conditions are warmest, water temperatures are cooler than ambient temperatures. During these conditions, turtles may be able to maintain optimal body temperatures by accessing open water (Grayson and Dorcas, 2004; Yagi and Litzgus, 2013) and may even use water in streams to provide a refuge habitat when conditions are hot and dry (Pittman and Dorcas, 2009). Turtles living in hot environments are known to avoid heat by moving into shady areas below the soil surface (Plummer, 2003).

Many species of turtles do not feed below 15°C (Ultsch, 1989), and selection of thermally unstable areas in winter could force turtles to use up lipid stores and expend metabolic energy that is vital for postemergent activities such as mating and nesting (Converse et al., 2005). Water table fluctuation has potential to affect the thermoregulation of turtles, and may be associated with winter mortality (Brooks et al., 1991; Bodie and Semlitsch, 2000; Ultsch, 2006; Yagi and Litzgus, 2013). Altered environmental temperatures can increase the energetic costs to ectotherms (e.g., Homyack et al., 2010; Sinervo et al., 2010). It follows that winter habitat use and selection of thermally and hydrologically stable hibernation sites is an important component of turtle ecology and energy use. Several authors have noted the thermal stability and selection of near-zero (°C) temperatures associated with hibernating aquatic turtles (Litzgus et al., 1999; Greaves and Litzgus, 2007; Rollinson et al., 2008; Edge et al., 2009). These observations appear particularly common for turtles living in northern climates, where turtles hibernate for up to 6 mo, ambient temperatures are consistently below freezing, and there is a layer of ice and snow. Exposure to extreme cold and ice can be damaging to turtle tissues (Costanzo et al., 1998).

The purpose of this study was to evaluate the thermal ecology of Bog Turtles (*Glyptemys muhlenbergii*) in Virginia during the periods of winter hibernation, springtime emergence, and summer activity. This study focuses on how ambient conditions result in soil and water temperature fluctuations in wetlands inhabited by Bog Turtles, affecting the possible strategies for the turtles to thermoregulate and find thermally stable microhabitats. In general, Bog Turtle habitats are noted to have abundant groundwater inflow through multiple seeps, resulting in heterogeneous areas of soil saturation (Arndt, 1977; Bury, 1979; Chase et al., 1989; Carter et al., 1999; Ernst and Lovich, 2009). Bog Turtles in the southern portion of their range live in wetlands that have a long hydroperiod and nearly constant saturation at the soil surface, allowing Bog Turtles to spend much of their lives below the soil surface (Feaga et al., 2012, 2013).

In Virginia, Bog Turtle hibernation begins in October or November (Ernst et al., 1989; Carter et al., 2000). Bog Turtles hibernate at depths of 5 to 55 cm from the soil surface in soft mud, small burrows created by small mammals or crayfish, or in hoofprints of livestock (Ernst et al., 1989; Carter et al., 2000; Bloomer, 2004; Pittman and Dorcas, 2009). Hibernation has also been observed in the root networks of wetland trees and shrubs, particularly alders (*Alnus* sp.) (S. Carter, pers. comm.; National Park Service, Center for Urban Ecology, Washington, DC). Multiple Bog Turtles using the same hibernaculum have been observed (Ernst et al., 1989; Bloomer, 2004). Bog Turtles may adjust their depth to regulate temperature while hibernating (Chase et al., 1989; Ernst et al., 1989). Although average winter temperatures in the Bog Turtle's southern range are warmer than in the northern range, extreme and rapid temperature fluctuations are still common (Natural Resources Conservation Service, 2011). In Virginia, Bog Turtle emergence generally

---

[2]Corresponding Author. E-mail: feaga05@vt.edu
DOI: 10.1670/13-147

occurs in March or April (Ernst et al., 1989; Mitchell, 1994); however, the cues for spring emergence are understood poorly. Zappalorti (1976) associated the first Bog Turtle activity of the season (approximating time of emergence) with ambient temperatures above 21°C.

In late spring to early fall, Bog Turtles move into and out of small pockets of open water or saturated soil, presumably for feeding, cover, and thermoregulation (Carter et al., 1999). A study by Ernst and Lovich (2009) found a mean cloacal temperature of 25.3°C (range 22.0°C–31.0°C) for basking turtles in the northern portion of the Bog Turtle range. A more recent study by Pittman and Dorcas (2009) in North Carolina attached temperature sensors to Bog Turtle carapaces and found mean temperatures in May to July of 23.9°C and daily maximum temperatures of 31.5°C.

Studying the temperature profiles of Bog Turtles and soils in wetlands known to support reproducing Bog Turtles is important if we desire to make thermal comparisons to profiles in hydrologically impacted wetlands or recognize temporal changes to temperature profiles. Changes to the hydrology of wetlands used by Bog Turtles are considered a major factor in the degradation of Bog Turtle habitat and one of the causes of the species' apparent decline (Bury, 1979; Mitchell, 1994; Buhlmann et al., 1997; Copeyon, 1997; United States Department of Agriculture, 2006). Hydrologic changes in wetlands result in subsequent changes to soil conditions and organic-matter content (Stolt et al., 2000; Strack et al., 2008).

Our study investigated thermal relationships in wetlands inhabited by Bog Turtles with the use of three different observational field studies. Study 1 used daily wintertime ambient, soil, and turtle temperatures to test the hypothesis that Bog Turtle temperatures would be thermally stable and remain above the freezing point, and that soil substrate temperature (responding to prolonged ambient temperature) will be an apparent cue (among other possible but untested cues) for turtle emergence. Study 2 used temperature measurements in saturated hibernation areas and similar but unsaturated substrates to evaluate the role of saturation in regulating the temperature of hibernacula. Here, we tested the hypothesis that high water tables maintain thermal stability and prevent freezing conditions. Study 3 used daily summer ambient, soil, and turtle temperatures to evaluate daily turtle temperature fluctuations and determine if thermal signatures reveal periods of basking or thermoconformity.

MATERIALS AND METHODS

Study Area.—We conducted this investigation in four wetlands in Floyd County within the southern part of the Blue Ridge physiographic province of Virginia. Data used in the analysis were collected between November 2007 and April 2009. In winter, the average temperature is 1.2°C, with average daily minimum and maximum air temperatures in December through February of −4.9°C and 7.4°C, respectively. Minimum January temperatures of −22.2°C can be expected in 2 out of every 10 yr. In summer, the average temperature is 20.2°C, with average daily minimum and maximum air temperatures in June through August of 13.5°C and 26.8°C, respectively. The average annual rainfall is 104 cm, with December being the driest month with 6.4 cm of rainfall and May being the rainiest month with 10.4 cm. Approximately 52 cm of snow falls each winter (Natural Resources Conservation Service, 2011). A drought in the summer of 2007 through early 2009 affected hydrology on all sites. Drought conditions were considered moderate to severe in 2008 according to the Palmer Hydrological Drought Index (Feaga et al., 2012).

Precise study locations and local wetland names are withheld to reduce human disturbance in wetlands used by Bog Turtles and to prevent illegal collection. We refer to study wetlands as DA, GDM, GDF, and SK. Wetlands are situated linearly along the landscape with the DA wetland approximately 3.0 km southwest of the GDM and GDF wetlands. The GDM and GDF wetlands are separated by approximately 140 m of non-wetland pasture. The SK site is approximately 8.5 km northeast of the GDM and GDF wetlands. Each of the wetlands is between 0.25 and 0.5 ha in size, irregularly shaped, and with core areas that remained saturated on the surface longer than other areas of the wetland. Cowardin et al. (1979) map-identifies two of the four study wetlands, describing them as palustrine emergent. Valley slopes where the study wetlands occurred are between 0 and 3%. All wetlands were used for livestock grazing before the study, and three of the wetlands were actively grazed throughout this study. Wetland sites contained flora typically associated with Bog Turtles (Carter et al., 1999, Ernst et al., 2009). Herbaceous vegetation covered the ground surface under all but the thickest alder areas.

Thermal Characterization.—All temperature measurements for the three field studies were made with the use of DS1921G thermochron iButton data loggers (resolution 0.5°C, reported accuracy ±1°C Dallas Semiconductor Corp, Dallas, Texas), capable of measuring and storing 2,048 temperature values over user-programmed time intervals. To reduce failure rates in wet conditions (Roznik and Alford, 2012), we prepared all thermochrons for use by coating each unit with hardening liquid plastic colored black. An 8-h test of one plastic-coated and one uncoated thermochron exposed to full sun during 95 repeated measurements revealed no interaction (determined graphically) and little difference, with the uncoated thermochron averaging 0.7°C higher (root-mean-square error = 0.96°C). Similarly, Roznik and Alford (2012) compared plastic-coated and uncoated thermochrons in varied environmental conditions and found no differences in mean temperature or in the heating pattern between the two treatments.

We captured study turtles by hand or trap and all turtles were marked with a unique number with the use of marginal scute notches in a system similar to that of Cagle (1939). We attached the 4.5-g plastic coated thermochrons to 3.8-g radio transmitters (Holohil Systems Ltd., Carp, Ontario, Canada) and then simultaneously bonded them to the posterior pleural scutes of the Bog Turtles with the use of Devcon Plastic Welder™. Radiotelemetry was used primarily for concurrent movement studies, but also served to recover the thermochrons. Total weight of equipment attached to the carapace never exceeded more than 10% of the turtle's total body mass, and typically was only 7%–8% of body mass.

Thermochrons used to measure ambient temperatures were hung in the open air on light-gauge wire, away from heat-emitting surfaces, and were exposed to sunlight. Thermochrons deployed on or in the soil were attached by wire to a nonconductive polyvinyl chloride stake to facilitate finding and recovering the units. For each study, we programmed the thermochrons to initiate temperature readings at the same time and recorded temperatures with identical time intervals. A post hoc analysis of these data was used to determine how accurately the sun-exposed ambient thermochrons estimated true air temperature, as meteorological air temperatures are recorded in the shade. The analysis revealed that the ambient thermochrons estimated average winter air temperature accurately, as measured by a dry and shaded data-recording thermometer (air temperature = 1.03 × ambient temperature, $r^2 = 0.95$). Maximum winter air temperatures were also estimated well (air temperature = 1.04 × ambient temperature, $r^2 = 0.68$). During summer, average air temperature was not estimated as accurately by ambient temperature (air temperature = 0.91 × ambient temperature, $r^2 = 0.78$). Summer maximum air temperatures were overestimated by ambient thermochron temperatures (air temperature = 0.77 × ambient temperature, $r^2 = 0.69$). Nonetheless, ambient thermochrons should reflect the potential basking (sun-exposed) temperatures available to turtles accurately.

Study 1: Wintertime Temperature Regime and Spring Emergence.—The first study used daily wintertime ambient, soil, and turtle temperatures to evaluate the thermal regime during hibernation and examine potential cues for spring emergence. This study took place in all four wetlands in the winter of 2007–2008 and in GDM, GDF, and SK wetlands in 2008–2009. The temperature record during the first winter was measured at 160-min intervals, beginning on 21 December 2007 and concluding on 4 April 2008. The temperature record during the second winter was measured at 180-min intervals, beginning on 20 October 2008 and concluding on 13 April 2009. For both winters, thermochrons were deployed on adult turtle carapaces, in ambient conditions, on the soil surface, and at 10-cm soil depth. Soil temperatures were also recorded at 25-cm soil depth during the second winter. Soil-temperature measurements were replicated (as subsamples) at three or four locations in each wetland. We selected random locations to deploy thermochrons in the soil environment with the constraint that pockets of soil surface saturation were present within 5 m of each thermochron's location. We applied this constraint because observations of Bog Turtle hibernation are limited to saturated areas (Ernst et al., 1989). In the second winter, thermochron deployments at the SK wetland were constrained to within 5 m of hibernacula known to be used the previous winter. The 32-d time period from 15 January through 15 February was selected to describe the thermal environment statistically during both 2008 and 2009, as this period was, and typically is, the coldest part of the year in the study area.

Carapace temperatures were compared to substrate and exposed temperatures from mid-February through March to look for evidence of turtle emergence (first basking). We plotted daily maximum temperature for each turtle to determine the exact day when solar heating resulted in a temperature spike that was much greater than concurrent soil substrate temperature and turtle temperatures recorded on previous days. The date of emergence was recorded as the first day a temperature spike was observed on turtle carapace-mounted thermochrons. We only recorded one emergence event for each turtle each year, although cold temperatures may have caused the turtle to move back into the hibernaculum, resulting in a second temperature spike when warm weather and basking resumed. Radiotelemetry confirmed that turtles were indeed emerging and concentrating their activity near hibernacula during the weeks when temperature spikes indicative of emergence were occurring.

We investigated whether ambient temperature, soil temperature at 10 cm, or both may have served as cues for emergence. The data source included soil temperatures from the wetland where each individual turtle resided, and ambient temperatures that were averaged across all wetlands. We recorded both the daily mean and daily maximum of soil and ambient temperatures at time of first emergence. To evaluate the hypothesis that a 1-d occurrence of a particular maximum temperature can be a cue for turtle emergence, we investigated daily maximum temperatures both before and during the date of emergence. Daily maximum temperature was the highest temperature reading (same time within a given day starting at 0000 and ending at 2400 h) found using the temperature reading averages of all the available thermochrons within a given stratum (i.e., the highest reading for an individual turtle, average of one or more readings for a soil stratum). For each turtle, we counted the number of days that occurred before the day of emergence when maximum temperature was greater than or equal to the maximum temperatures during emergence (Bernstein and Black, 2005). To be counted, days did not need to occur in consecutive order, i.e., any day prior to emergence could be counted, even if temperatures the day before emergence were much colder than those recorded at the day of emergence.

Study 2: Role of Saturation in Regulating Temperature Below Ground.—The second study attempted to identify the importance of soil saturation during hibernation by comparing the temperatures in saturated hibernacula that were used by turtles (true hibernacula) to the temperatures in unsaturated, hand-excavated, soil forms (simulated hibernacula). All hibernacula used by turtles were in saturated soils. This study took place during the winter of 2008–2009 in the SK wetland. To develop the model for simulated hibernacula, we made some basic observations and measurements of true hibernacula during the previous winter of 2007 and 2008. In this pilot study, we found that turtles at the SK wetland hibernated frequently in hollow soil forms with narrow openings that were bounded by clayey material. The soil forms may have been burrowed by muskrats, meadow voles, or other rodents (or be the remains of rotted tree root channels) and expanded by the Bog Turtles (Ernst et al., 1989). Depths of these hibernacula ranged from 10 cm to 45 cm. The upper portions of the hibernacula were approximately 15 cm in diameter, with the dimensions narrowing at the bottom. Several of the hibernacula had a mixture of soil, roots, and leaf litter that covered the upper part of the soil form, somewhat hiding the entrance. Hibernacula frequently had standing water within them, but the walls of the soil forms contained sufficient clay to maintain form and prevent sloughing of soil. We excavated four simulated hibernacula in unsaturated portions of the site to compare to the four true hibernacula similar to those described above. Simulated hibernacula were approximately 30 cm deep, 8.9 cm wide at the bottom (outside diameter of the steel mud auger), and 15 cm wide at the soil surface. Areas used for simulated hibernacula were located randomly in unsaturated areas on local microtopographical high spots bounded by saturated areas or immediately adjacent to the wetland. The furthest simulated hibernaculum was approximately 50 m from a true hibernaculum.

For each true or simulated hibernaculum, we deployed thermochrons from the soil surface to 30 cm at 10-cm depth increments, with the exception of two true hibernacula, where depth was limited to 20 cm. Temperature of the vertical soil surface inside each hibernacula was measured by tethering thermochrons at the desired depth with a light gauge wire and a galvanized nail that was pressed into the soil. We also deployed thermochrons to record ambient temperature at 180-min increments, beginning on 20 October 2008 and concluding on 13 April 2009. As we were interested in how Bog Turtles cope with the coldest winter temperatures, we limited the statistical analysis to the consistently cold 8-d period spanning between 15

January 2009 and 22 January 2009. Choosing a consistently cold period reduced the risk of observing confounding temperature inversions between the soil surface and deeper soil depths that could be caused by rapid changes in ambient temperature. We tested the statistical hypotheses that soil temperature would increase with depth in the hibernacula and that simulated hibernacula would experience colder temperatures than true hibernacula.

To support our temperature data, we measured the depth to the water table with the use of a 70-cm-deep groundwater monitoring well. This well was placed within 2 m of two of the true hibernacula. We referenced depth to the water table as the distance from the mineral soil surface to the measured water surface in the well. Depth below the soil surface was recorded as a negative value and above the soil surface as positive. Water depth was recorded with the use of a Hobo U20 Water Level Logger (Onset Computer Corporation, Bourne, Massachusetts). Water table readings were made at 120-min increments and later averaged to build a continuous record of weekly water table height from November 2007 through July 2009. Groundwater wells were not placed near simulated hibernacula, but visual observations confirmed that groundwater (the water table) was not present in the well-drained soils over the winter.

Study 3: Summertime Temperature Fluctuations.—The third study used daily summer ambient, soil, and adult turtle carapace temperatures to evaluate daily turtle temperature fluctuations. This study was completed in the summer of 2008 in all four wetlands. The 47-d temperature record was measured at 90-min intervals, beginning on 15 June 2008 and concluding on 31 July 2008. Thermochrons were deployed on turtle carapaces, in ambient conditions, on the soil surface, and at 10- and 25-cm soil depths. Soil temperature measurements were replicated at 3–4 locations in each wetland. We selected locations to deploy thermochrons in the soil environment randomly, with the constraint that abundant soil surface saturation was available within the 5-m radius around the thermochron's location. We applied this constraint because Bog Turtles use areas of wetlands that are close to small pockets of standing water (Carter et al., 1999). We calculated average temperatures measured in each stratum and on turtles from 0000 h and 2250 h based on the 90-min thermochron sampling interval.

We used the relationship between concurrently measured turtle temperatures and soil surface temperatures to gain a better understanding of the possible thermoregulatory scenarios that Bog Turtles could be using. The 90-min temperature intervals over the 47-d period provided 752 unique data pairs of soil surface and turtle temperatures for each of eight turtles. These data were plotted graphically. The possible thermoregulatory scenarios were based on whether turtle temperatures were less than or greater than soil surface temperature. Although this graphical analysis was partly exploratory, a primary emphasis was to visualize obvious basking events and to determine how turtles coped with periods of excessively high soil surface temperatures.

Sample Sizes and Statistical Analyses.—Data from 149 multi-month thermochron deployments and approximately 165,000 individual temperature records were used. Failures of thermochrons occurred during each experiment, particularly for units deployed on the turtles, in ambient conditions, and on the soil surface. Failure rate on turtles was approximately 33%. Failures were higher in thermochrons on turtles because of the increased likelihood of damage to the plastic coating around the thermochrons from friction and tampering by animals. Despite thermochron failures, thermal observations were successful for eight turtles during each study (five males and three females in the first winter; four males and four females in second winter; seven males and one female in summer. Two to four thermochron subsamples were available to estimate soil temperatures at various depths in each wetland, with the exception of the winter of 2008–2009 when estimates were made from only one successful thermochron deployment at the 25-cm soil strata in wetland GDF and at the soil surface strata at the GDM wetland. In the winter of 2007–2008, ambient temperature thermochrons were only successful at one wetland. As a result, variation among wetlands was not calculated and ambient temperatures were assumed to be equal at all study wetlands during a given period. A complete table showing the number of thermochron deployment locations and failure rates is given in Feaga (2010).

We used graphical methods and descriptive statistics to summarize thermochron temperature data. Descriptive statistics were calculated using Microsoft Excel and SAS (SAS Institute, Cary, North Carolina). For finding mean temperatures, thermochron deployments at multiple locations within a wetland were treated as subsamples to provide one average value for the entire wetland. The standard error (SE) was used to express variation around a mean calculated from independent measurements, i.e., when calculating the temperature of multiple turtles over a season or the temperature at a given soil depth from multiple wetlands. We also used the standard deviation (SD) when we desired a larger (and thus more sensitive) measure of variability, as in the case with detecting emergence of Bog Turtles in spring. Correlation coefficients and *t*-tests were calculated with the use of MINITAB Student Release Version 14.11.1 (State College, Pennsylvania). We used a linear mixed model (PROC MIXED, SAS Institute) in study 2 to test for statistical differences among depths and among groups of true hibernacula and simulated hibernacula, which consisted of four replicates in each group over the eight repeated days of temperature measurements.

RESULTS

Study 1: Wintertime Temperature Regime and Spring Emergence.—Turtles selected three different types of areas in which to hibernate: 1) Burrow hibernacula were the deepest, and consisted of hollow soil forms that appeared to be dug by rodents or were possibly the remains of rotted tree root channels. The deepest hibernaculum of this type was approximately 45 cm. These hibernacula were most likely to contain multiple Bog Turtles (up to eight were observed in one hibernaculum) and were abundant in the SK wetland. The same burrow hibernacula were used for hibernation is successive years, although hibernacula fidelity could not be established statistically. 2) Turtles in wetlands with abundant alders tended to hibernate along root systems, often in mucky (well-decomposed organic soil material) substrate formed from the inputs of alder leaves and leaves of other deciduous trees in the area. 3) Where little or no woody vegetation was present, or where burrow hibernacula were not present, Bog Turtles were found hibernating in small and shallow (approximately 15-cm diameter and 20 cm deep) depressions, most of which were created by livestock hooves. One turtle in the study (T252) hibernated in a shallow depression during two consecutive study winters.

Average turtle temperatures (±SE) between 15 January and 15 February were 2.7 ± 0.51°C in 2008 ($n = 8$, five males, three females) and 2.3 ± 0.31°C in 2009 ($n = 8$, four males, four females) (Table 1). There were no differences between average temperatures of males and females. These values were on average greater than, but far less variable than, the average ambient and soil surface temperatures. During these 32-d periods, the minimum and maximum whole-day temperatures (mean temperature from 0000 h to 2400 h) measured on a turtle carapace were 0°C and 9.5°C in 2008 and −0.7°C and 7.1°C in 2009. Turtle whole-day temperatures during both years were frequently ≤1.0°C during the coldest portion of the winter. The turtle subjected to the coldest body temperatures measured during the study, T252, never experienced freezing body temperature in 2008, yet sustained a body temperature of between −1.0°C and 0.0°C for 20 out of 32 d in 2009. Turtle 252 hibernated in a livestock hoof depression during both winter seasons and it was often visible through shallow ice cover.

Turtle carapace temperatures during the coldest part of the winter were responsive to changes in ambient and soil temperatures (Fig. 1). The variability of temperatures and the absolute value of extreme temperatures recorded on turtles were smaller than those measured in ambient conditions and on the soil surface. The most stable thermal environment was recorded at 25-cm soil depth. For all 59 days between 1 January and 28 February 2009, the root-mean-squared errors (RMSE) between the set of daily temperature values measured on the turtle's carapace versus the ambient, the soil surface, 10-cm soil depth and 25-cm soil depth were 5.2°C, 3.9°C, 0.6°C, and 1.6°C. The correlation coefficients between turtle temperatures and ambient, the soil surface, 10 cm soil depth, and 25 cm soil depth were 0.41, 0.53, 0.97, and 0.71, respectively. The tip of the approximate 15-cm radio antenna was often visibly protruding above the frozen wetland surface, providing additional evidence that turtles hibernated frequently at depths approximating 10 cm and as shallow as 5 cm.

Date of turtle emergence was variable among the turtles within the year and between years (Table 2). In 2008, emergence of all eight turtles occurred between 22 March and 4 April. In 2009, six turtles emerged between 7 March and 9 March. The last two turtles emerged on 29 March and 5 April. On average, male Bog Turtles emerged earlier than female turtles during both years; however, variation was evident within both sexes. In 2008, the average daily maximum ambient and 10-cm soil temperatures (±SE, $n = 8$) on the date of first emergence were 22.7 ± 0.7°C and 10.7 ± 0.4°C, respectively. In 2009, the average daily maximum ambient and 10-cm soil temperatures (±SE, $n = 8$) on the date of first emergence were 28.0 ± 1.3°C and 9.8 ± 1.1°C, respectively. Daily maximum ambient temperatures before the date of first emergence were frequently greater than or equal to the measured maximum ambient temperature during the day of emergence, and often occurred a week or more before the emergence date (Fig. 2). This condition occurred for seven out of eight turtles in 2008 and four out of eight turtles in 2009. High ambient temperatures a week or more before emergence occurred even in 2008, when turtles emerged approximately 2 wk later than in 2009. Ambient maximum temperatures in 2009 at time of emergence were higher than in 2008, particularly on March 7 when temperatures of 30.8°C resulted in four turtles emerging, despite daily high temperatures near freezing within the week prior to emergence. For 10-cm soil depths, daily maximum temperatures before the date of first emergence were greater than or equal to the measured maximum soil temperature for only two turtles each of the study years. When this condition occurred, it was usually during the consecutive days preceding the day of emergence.

TABLE 1. Turtle carapace and environmental temperatures during multidate periods in winters 2008 and 2009 and summer 2008. All mean temperatures calculated include error estimates (±SE) calculated from either multiple turtles ($n = 8$) or multiple wetlands in the case of soil temperatures. Daily mean is the mean of turtle temperatures over the multidate period over multiple logging events on each date. Coldest day and warmest day are entire date averages of turtle carapace temperatures calculated from the multiple logging events over one single date (not necessarily the same date for each individual turtle). Minima (min) and maxima (max) consisted of the single most extreme carapace temperature event measured over the period. Mean daily max is the mean of the highest carapace temperature recorded over each date in the period.

	Turtle carapace temperatures (°C) $n = 8$ turtles						Environmental temperatures (°C)[a]			
Period	Daily mean	Coldest entire day	Warmest entire day	Min	Max	Mean daily max	Ambient	Soil surface	Soil at 10 cm	Soil at 25 cm
Jan 15–Feb 15 Winter 2008	2.7 ± 0.51	1.2 ± 0.53	7.2 ± 0.58	1.0 ± 0.52	8.4 ± 0.56	3.2 ± 0.49	1.4	1.1 ± 0.38	2.9 ± 0.61	Not measured
Jan 15–Feb 15 Winter 2009	2.3 ± 0.31	1.0 ± 0.43	5.4 ± 0.29	0.8 ± 0.44	5.8 ± 0.42	2.7 ± 0.28	0.7	0.7 ± 0.35	2.0 ± 0.38	2.8 ± 0.20
Jun 15–Jul 31 Summer 2008	20.8 ± 0.14	16.4 ± 0.20	24.0 ± 0.24	11.8 ± 0.37	36.3 ± 0.63	29.4 ± 0.33	22.0	21.0 ± 1.21	19.2 ± 0.88	18.6 ± 0.70

[a] Average soil temperatures calculated from either three or four wetlands each period. Standard error not calculated for ambient temperature because thermochrons failed or were tampered with at all wetland locations except one during the winter of 2008.

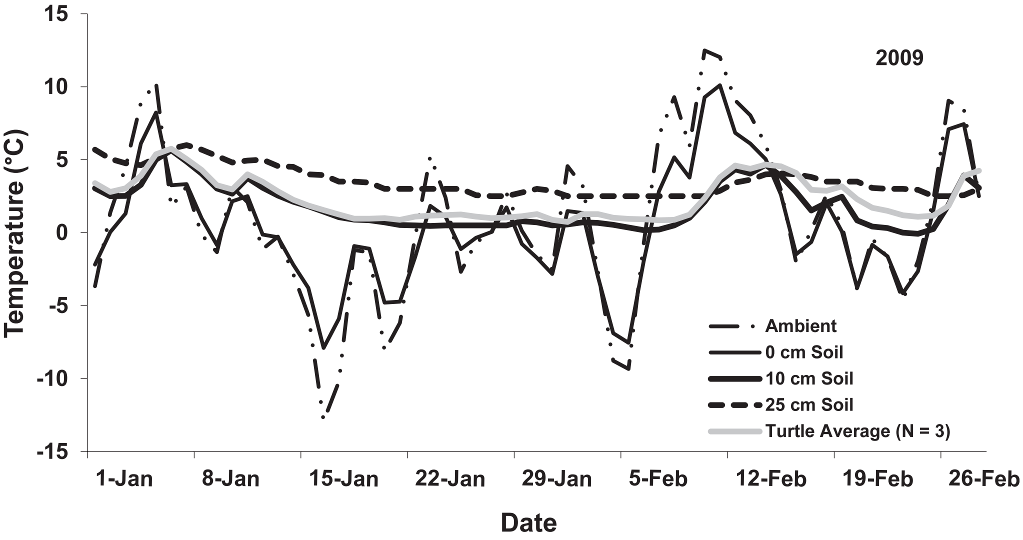

FIG. 1. Typical wintertime mean daily temperatures of ambient conditions, Bog Turtle carapaces, and surrounding soil measured at the GDF wetland in January and February, 2009.

Study 2: Role of Saturation in Regulating Temperature Below Ground.—We measured an overall average ambient temperature of −5.6°C during the 8-d period used to observe the relation between saturation, depth, and temperature. Whole-day average ambient temperature ranged from −12.5°C to −0.7°C. The least-squares mean of true and simulated hibernacula were 1.4°C and −0.02°C, respectively, with a difference in temperature of 1.4°C ($F_{1,18} = 13.99$, $P = 0.002$). Temperatures increased with depth for both hibernacula groups ($F_{3,18} = 7.64$, $P = 0.003$) (Fig. 3). Freezing temperatures were only measured on the soil surface of the true hibernacula group, whereas freezing temperatures were measured at the soil surface and down to 20-cm depth in the simulated hibernacula group. Fluctuation in ambient temperatures caused an interaction between depth and day ($F_{27,162} = 4.84$, $P < 0.001$). This interaction occurred because of relatively warm ambient temperature on January 18 and 19 that caused the soil surface to become temporarily warmer than soil at 10-cm depth.

The groundwater monitoring well installed in the vicinity of two of the true hibernacula used for comparison to simulated hibernacula provided a continuous measurement of depth to the water table from November 2007 through July 2009. Depth to water table during the two winter periods remained between the soil surface and 15 cm deep, meaning that water was consistently above the 25–30-cm-deep hibernacula (Fig. 4). Shallow hydrology conditions in winter persisted despite the

TABLE 2. Date (month/day) of emergence (first basking) and associated ambient and substrate temperatures for turtles in the spring of 2008 and 2009. Mean temperatures are from all thermochron subsamples throughout the emergence day, whereas max temperatures are the single highest temperature measured during emergence day. Soil temperatures are wetland specific, whereas ambient temperatures are the same for all wetlands.

				Temperatures on day of emergence (°C)					
Time period	Wetland	Turtle[a]	Date emerged	Ambient mean	Ambient max	10-cm soil mean	10-cm soil max	Ambient max already achieved[b]	10-cm soil max already achieved[b]
Spring 2008	GDF	54 M	3/22	12.1	19.5	7.4	9.7	Yes (2)	Yes (2)
		554 M	4/1	15.7	24.0	9.8	12.3	Yes (1)	No
	GDM	233 F	4/1	15.7	24.0	9.6	12.0	Yes (1)	No
		252 M	3/27	15.2	24.7	8.4	11.3	No	No
	SK	307 M	4/4	11.6	21.5	8.3	9.8	Yes (4)	Yes (4)
		3,000 M	3/28	15.2	19.8	9.4	10.4	Yes (4)	No
	DA	417 F	4/1	15.7	24.0	8.1	10.1	Yes (1)	No
		3213 F	4/1	15.7	24.0	8.1	10.1	Yes (1)	No
	Mean ± SE	–	3/30	14.6 ± 0.61	22.7 ± 0.74	8.6 ± 0.30	10.7 ± 0.36	–	–
Spring 2009	GDF	54 M	3/9	15.7	26.1	10.1	12.7	Yes (2)	Yes (2)
		3,216 F	4/5	14.3	25.2	9.2	14.0	Yes (3)	No
		3,227 F	3/8	17.9	28.4	9.7	12.7	Yes (1)	Yes (1)
	GDM	252 M	3/7	17.6	30.8	5.6	8.8	No	No
	SK	544 M	3/7	17.6	30.8	5.4	6.8	No	No
		546 F	3/29	11.7	21.3	8.6	9.9	Yes (10)	No
		553 F	3/7	17.6	30.8	5.4	6.8	No	No
		3,000 M	3/7	17.6	30.8	5.4	6.8	No	No
	Mean ± SE	–	3/13	16.3 ± 0.79	28.0 ± 1.25	7.4 ± 0.76	9.8 ± 1.06	–	–
Overall	Mean ± SE		3/21	15.4 ± 0.53	25.4 ± 0.98	8.0 ± 0.43	10.3 ± 0.55		

[a] M = males; F = females.

[b] Figure in parentheses is the number of days before the day of emergence when the recorded maximum temperature was greater than or equal to the measured maximum temperature during the day of emergence. Days before emergence did not need to be consecutive with the emergence day.

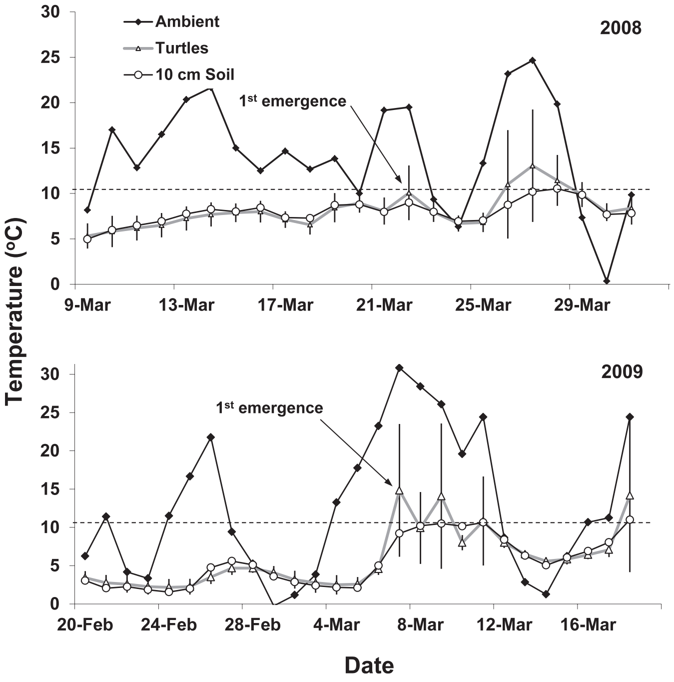

FIG. 2. Mean daily maximum temperatures of ambient conditions, soil at 10-cm depth, and carapaces of Bog Turtles ($n = 8$) before and during the time of emergence from winter hibernacula in 2008 (top) and 2009 (bottom). Error bars on average turtle temperatures show the standard deviation among the turtles. Dotted line on both graphs is at 10.3°C, the mean daily maximum temperature of soil at 10 cm at time of emergence calculated from both study winters.

severe drought of 2007 and 2008. This drought caused the water table to drop to unusually low levels throughout the study area (Feaga et al., 2012).

Study 3: Summertime Temperature Regime.—Summertime thermal fluctuations between 15 June 2008 and 31 July 2008 were characterized by daily warming and cooling cycles that showed peak temperatures for ambient, turtle, and the soil surface occurring between 1330 and 1500 h (Fig. 5). Ambient temperatures showed the earliest daily warming. Soil surface warming was a similar magnitude as ambient warming, yet was delayed by approximately 90 min. The timing of turtle heating and cooling cycles was similar to that of soil surface warming. The average daily turtle temperature range (16.0°C–26.0°C) was smaller than that of the soil surface (15.3°C–29.4°C). Deeper soil strata showed warming and cooling cycles that were delayed compared to other strata. Soil at 10 cm showed an approximate 2.3°C fluctuation, with the warmest temperatures occurring around 1930 h. Temperature fluctuation at 25 cm was negligible. Turtle, 10-cm soil, and 25-cm soil temperatures between 2100 and 730 were higher than those measured in ambient conditions and the soil surface. Turtle temperatures were greater at night than ambient or soil surface temperatures.

Data downloaded from eight turtle mounted thermochrons ($n = 8$, seven males, one female) over the 47-d period provided 6,016 data pairs of soil surface and turtle temperatures (Fig. 6). These data pairs showed that turtle temperature did not follow a linear relationship with the soil surface temperature, i.e., turtles did not always conform to soil surface temperatures, particularly when soil surface temperatures were colder or warmer than the average (21°C). When the soil surface was <12°C, turtle temperatures tended to be higher than 12°C, but when the soil surface was >30°C, turtle temperatures were lower than 30°C. Between 12°C and 30°C, turtle and soil temperatures frequently conformed, but it was also common for turtle temperatures to be greater or less than soil surface temperatures. Active basking events when turtles were apparently exposed to direct solar heating appeared frequent between soil surface temperatures of 12°C and 30°C, as indicated by turtle temperatures that exceeded soil surface temperatures by 5°C to 10°C.

DISCUSSION

Estimated average daily temperatures of Bog Turtles during the coldest parts of winters 2008 and 2009 ranged between −0.7°C and 9.5°C. The large range of wintertime temperatures measured in this study contrasts with those reported for other semiaquatic and aquatic turtle species: 0.3°C to 3.9°C for spotted *Clemmys guttata* (Litzgus et al., 1999), −1°C to 1°C for wood

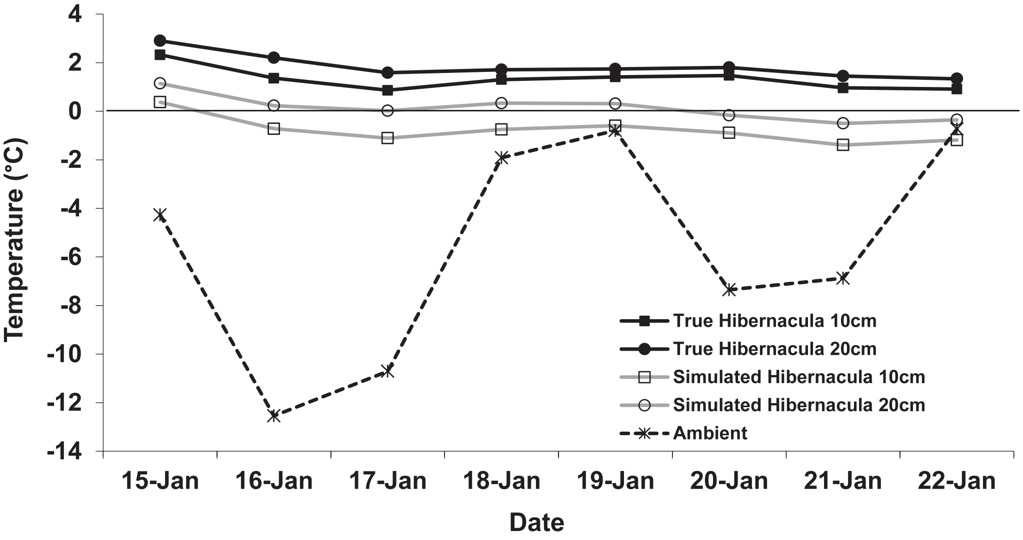

FIG. 3. Mean daily ambient and soil temperatures of true and simulated hibernacula during an 8-d consistently cold period in January 2009. Simulated hibernacula ($n = 4$) were excavated in randomly selected areas of drier soil located within an approximate 50-m distance to the true hibernacula ($n = 4$). Thermochrons were placed at the soil surface (data not shown), 10 cm, 20 cm, and 30 cm (not shown) in each replicate.

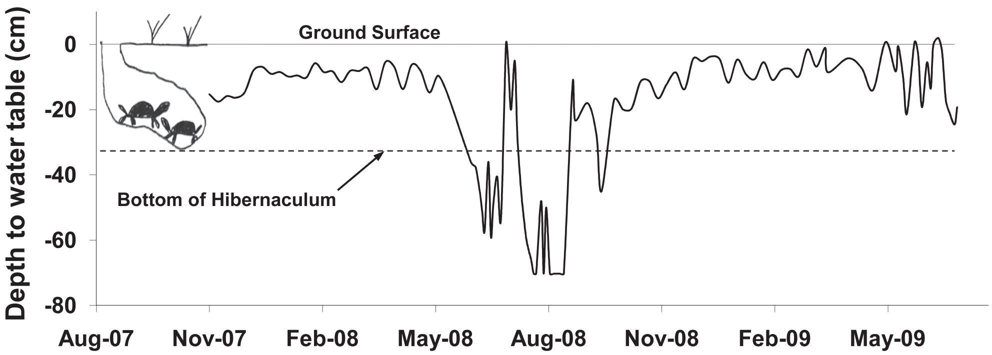

FIG. 4. Depth to the water table at the location of multiple Bog Turtle hibernacula over two winters in Southwestern Virginia. Water-table values were averaged over 7-d periods. The hibernacula were approximately 30 cm deep and the water table remained above this level during winters 2007–2008 and 2008–2009. The drawdown of the water table in the summer of 2008 resulted from a 2-yr drought (Feaga et al., 2012).

(*Glyptemys insculpta*) (Greaves and Litzgus, 2007), 0°C to 3°C for painted (*Chrysemys picta*) (Rollinson et al., 2008), 0°C–6°C for Blanding's (*Emydoidea blandingii*) (Edge et al., 2009) and 0°C–4°C for snapping turtles (*Chelydra serpentina*) (Brown and Brooks, 1994). All of these studies of other species took place in the northern portions of the species' respective ranges, and are derived from temperature readings covering 4–5 mo of dormancy. Our findings are derived only from data collected during the 32-d period from 15 January through 15 February (coldest winter period), and therefore encompass only a portion of the period between November and mid-March when Bog Turtles are inactive in Virginia. Had we used the entire period of Bog Turtle dormancy for our characterization, we would expect an even greater range of temperature (and average temperature) because of higher ambient temperatures at the beginning and end of the dormant period. Consistent with this expectation, a larger range was found by Ernst et al. (1989) when they measured wintertime cloacal temperatures of Bog Turtles between 2.6°C and 16.0°C.

Our findings suggest that Bog Turtles in the south use more thermally unstable environments than semiaquatic and aquatic turtle species living in northern climates. These conditions may be energetically costly to Bog Turtles. All of the other turtle species discussed above were found to hibernate beneath a column of standing or moving water, or covered with insulating ice and snow. As a result, minimum temperatures in these other studies were similar to, and maximum temperatures were lower than, those recorded in our study. Illustrating the capacity for snow and ice to buffer turtles thermally from extreme temperatures, Litzgus et al. (1999) observed ambient air temperatures at an Ontario swamp to fluctuate between −35°C and 2°C over a 5-d period, whereas the carapace temperature of a spotted turtle remained between 1°C and 2°C. Thermal buffering by snow and ice, at least for periods longer than a week or two, would not be expected to be the normal condition for this study in Floyd County, Virginia.

We found that approximately half of the radioed Bog Turtles were visible hibernating between 5 and 15 cm below the water surface or a layer (approximately 5 cm thick) of frozen mud and ice, similar to the observations of Chase et al. (1989) in Maryland. We observed Bog Turtles at the SK wetland hibernating deeper (down to 45 cm) than turtles in the other three wetlands, explaining the narrower range of extreme temperatures experienced by the SK turtles. Deeper hibernation was possible because the burrow-type hibernacula were mostly filled with water rather than soil, enabling turtles to move to the

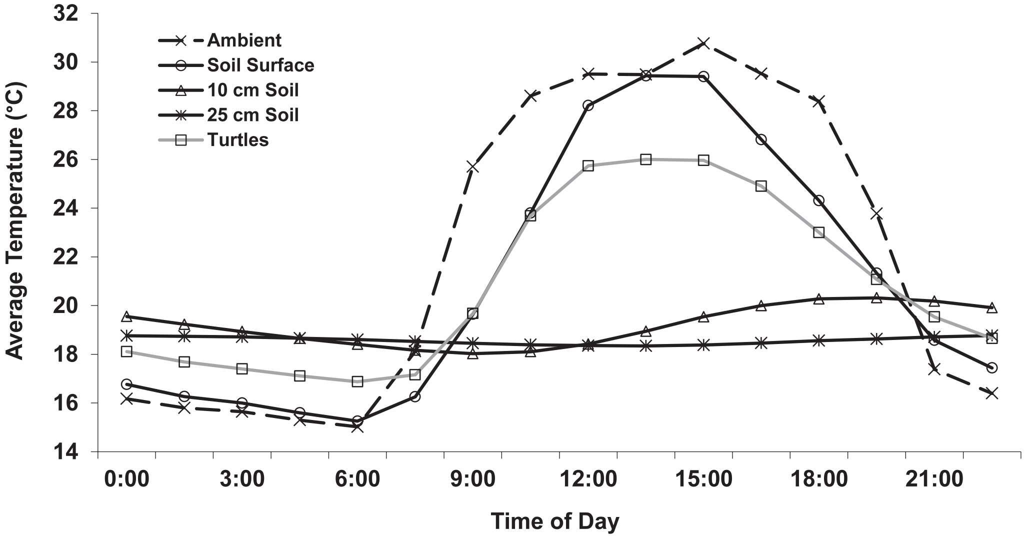

FIG. 5. Mean daily temperatures between 15 June 2008 and 31 July 2008 at four wetlands in southwestern Virginia for ambient conditions, soil at several depths, and Bog Turtle carapaces ($n = 8$). Soil at 10- and 25-cm depths were cooler than ambient conditions during the day and warmer than ambient conditions at night, providing a thermal buffer available to moderate turtle temperature.

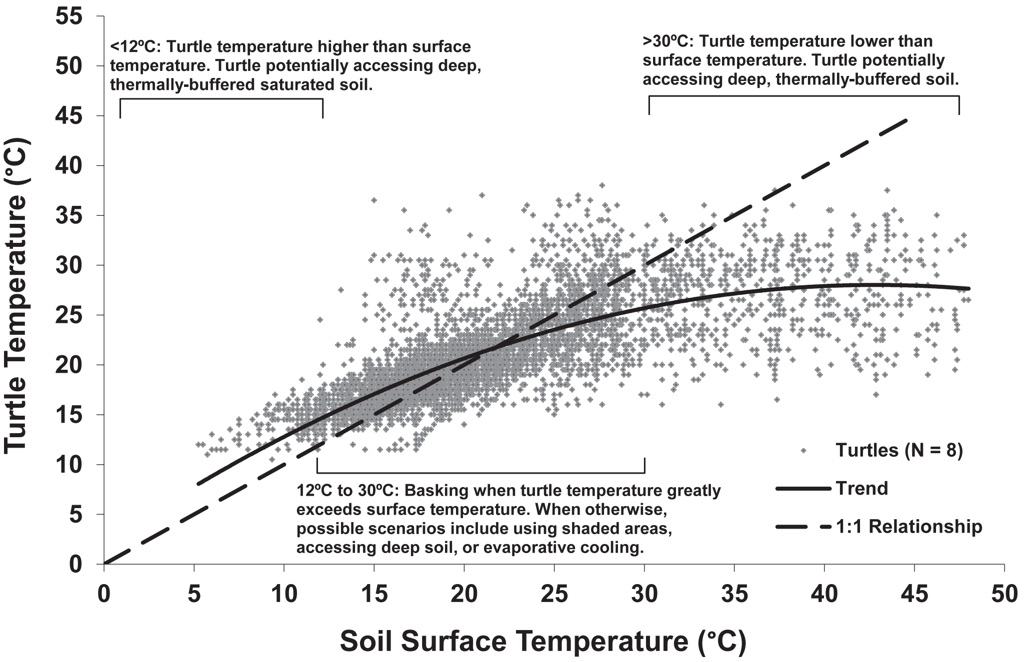

FIG. 6. Relationship between Bog Turtle carapace temperatures and soil surface temperatures from 15 June to 30 July 2008 at four wetlands in southwestern Virginia. Points represent each unique temperature pair measured at each 90-min interval.

bottom easily, without resistance. In contrast, the carapace temperatures of one turtle (T252) using a shallow soil depression (hoof print) remained between −1°C and 0°C for 20 d during January to February 2008 when ambient temperatures were consistently below freezing and at times were less than −10°C. Numerous nonlethal freezing events (greater than or equal to −1.4°C) of maximum durations of 4 h were also recorded for one Bog Turtle in North Carolina that was hibernating in a shallow soil depression (Pittman and Dorcas, 2009). Our findings indicate that Virginia Bog Turtles generally hibernate in substrates deep enough to avoid lethal freezing temperatures, but do not always access depths that prevent direct influence from the wide range of ambient temperatures inherent to Virginia winters.

The wetland habitats characterized in this study are considered high quality because they show consistent adult recaptures and successful recruitment of juvenile turtles. Further, similar patterns of Bog Turtle hibernation have been personally observed in other Virginia wetlands. As a majority of known wetlands inhabited by Bog Turtles are currently or historically grazed by cattle, pristine reference wetlands not impacted by humans or cattle are difficult to identify. Thus, we assume that the hibernation habitat selection observed in this study is not a function of extensive reduction in availability. Shallow hibernation may be the only option for Bog Turtles living in wetlands with shallow soils underlain by bedrock or gravel alluvium, or in soils lacking the large-rooted woody vegetation or burrowing rodents that can create the soil structure and voids opportunistically used by Bog Turtles. Shallow hibernation may increase exposure to predators at a time when cold conditions diminish the mobility needed to avoid predation (Ultch, 2006; Greaves and Litzgus, 2007). A potential benefit to shallow hibernation is that it would facilitate aerobic respiration (Litzgus et al., 1999; Edge et al., 2009; Newton and Herman, 2009). Whether Bog Turtles more frequently use aerobic or anaerobic metabolism during hibernation is unclear, although the association of Bog Turtles with mud burial and hibernation periodically under ice suggests that the species is anoxia-tolerant (Ultsch, 2006).

Based on thermal measurements in true and simulated hibernacula, depth was a factor and presence of saturation was likely a factor controlling temperature. The presence of consistent saturation was confirmed by the groundwater monitoring well installed in the vicinity of the SK hibernacula. Average depth to water table remained at approximately 15 cm during both winters of the study and was frequently at the soil surface. During cold ambient temperatures, the average temperature difference was 2°C higher at 10-cm depth in saturated true hibernacula compared to simulated hibernacula where the water table was not present. Freezing temperatures were consistently recorded in the simulated hibernacula.

Should Bog Turtles be forced to choose unsaturated areas with conditions similar to those measured in the simulated hibernacula, they may be more susceptible to freezing and desiccation. Not only would Bog Turtles lack the thermal buffering capacity of the water, but drier soil, coarser soil, or soil with less organic matter could result in innoculative freezing (Costanzo et al., 1998). Innoculative freezing occurs when the formation of tissue-damaging crystallized ice is facilitated by contact with other ice or particulate impurities. Costanzo et al. (1998) showed that innoculative freezing occurred more readily in sandy soils with little organic matter. It follows that the risk of damaging Bog Turtle tissues during cold conditions could be more severe if turtles are forced to hibernate in wetland soils that have become coarser or have lost organic matter, a condition that may occur following ditching or restoration activities that disturb or grade wetland soils (Paz-Gonzalez et al., 2000; Stolt et al., 2000; Bruland and Richardson, 2005; Strack et al., 2008).

The emergence of Blanding's and Spotted Turtles, both species that can live at northern latitudes, have been associated with the physical breakup of ice (Litzgus et al., 1999; Newton and Herman, 2009). In more southern climates where continuous ice cover is uncommon, turtle emergence is not physically limited and other cues must be involved, such as air temperature, substrate temperature, or dissolved oxygen level. Our results do not suggest that there is a singular cue for emergence, but that daily maximum soil temperatures measured at 10-cm depth and ambient temperature were both cues for emergence. Soil temperatures at 10-cm depth approximating 10.3°C may cue emergence following moderately high ambient temperatures that steadily warm the soil. This cue may occur because of net metabolic energy costs associated with remaining buried at relatively warm and stable temperatures. Grobman (1990) found an emergence response of terrestrial *T. ornata* to temperatures of 7°C that lasted 5 d at 10–20-cm depth. However, the existence of a specific temperature cuing emergence is not strongly supported in our data because turtles emerged when mean temperatures at 10-cm soil depth ranged between 5.4°C and 9.8°C. Our results appear more similar to those of Bernstein and Black (2005), who found that *T. ornata* emerged when soil temperatures were around 8.8°C, but ranged between 6.4°C and 13.1°C. Those authors also measured many days prior to emergence with temperatures greater than those recorded at time of emergence.

Bog Turtles may be stimulated to emerge during extremely high ambient temperatures, even in the absence of warm soil temperatures. For this to occur, Bog Turtles must be able to detect the high ambient temperatures or a temperature gradient that changes from warmer temperatures being deeper in the soil to warmer temperatures closer to the surface when solar heating occurs (Ultsch, 2006). This is plausible, particularly at SK, where Bog Turtles hibernated in the burrow-type hibernacula that contained open water and air-filled channels leading directly to the soil surface. Within these hibernacula, warm surface temperatures could be detected, particularly if Bog Turtles move toward the soil surface in expectation of spring emergence, as observed in *T. ornata* and *T. carolina* (Grobman, 1990; Bernstein and Black, 2005). In 2009, turtles at SK emerged when daily max soil temperatures at 10 cm were only 6.2°C (lower than average), yet ambient temperatures were 30.8°C. Several researchers have observed Bog Turtles moving out of hibernacula during warm spells in winter, indicating that high ambient air temperature can stimulate early or temporary emergence (Chase et al., 1989; Lovich et al., 1992; S. Carter, pers. comm.).

Average turtle carapace temperatures over the course of a typical summer day were cyclic and followed a similar pattern observed on active *C. picta* in Michigan (Rowe and Dalgarn, 2009). These authors recognized a warming phase between 0800 and 1200 h, a peak between 1200 and 1800 h, and a gradual cooling phase from 1800 h until thermal warming resumed the following day. Bog Turtles in our study experienced the highest mean carapace temperatures during the midday period, with turtle temperatures around 25°C for approximately 4.5–6 h each day. A controlled laboratory study of the targeted temperature range (T_{set}) preferred by Bog Turtles has not been published; however, our field results indicate that the T_{set} for Bog Turtles may be similar to the laboratory derived 20°C–26°C range found for spotted turtles (Yagi and Litzgus, 2013). Mean daily maximum carapace temperatures in this study were 29.4 ± 0.3°C (±SE, $n = 8$) (Table 1). This compares to daily maximum temperatures of 31.5°C measured by Pittman and Dorcas (2009) in a North Carolina Bog Turtle study. Ernst and Lovich (2009) found mean cloacal temperature of 25.3°C (range 22.0°C–31.0°C) for basking Bog Turtles. Previous summer activity studies with the use of carapace-attached thermochrons have shown a strong correlation of turtle shell temperature to turtle cloacal temperature (Grayson and Dorcas, 2004). However, the potential exists for maximum turtle shell temperatures to exceed internal body temperatures, particularly when turtles are basking (Edwards and Blouin-Demers, 2007). This could explain the higher maximum daily temperature measured in this study and the study by Pittman and Dorcas (2009).

Differences in bog turtle carapace temperatures when compared with the usually closely correlated ambient and soil surface temperatures, suggested that Bog Turtles were thermoregulating by basking, making vertical movements and burying themselves in the soil, or possibly moving to shade in order to moderate their temperature throughout the daily temperature cycle. When the soil surface was <12°C (occurring between 2100 and 0730 h), Bog Turtle carapace temperatures were higher, suggesting that Bog Turtles were accessing deeper and warmer soils or moving to ideal locations. Turtle carapace temperatures often exceeded soil temperatures by up to 15°C–20°C when soil temperatures were between 12°C and 30°C, suggesting that turtles frequently basked at this temperature range. In addition to basking, turtles frequently conformed to surface soil temperatures in the range of 12°C–30°C, indicating that these turtles were likely maximizing their efficiency of thermoregulation because they did not need to search actively for warmer or cooler sites (Yagi and Litzgus, 2013). When the soil surface was between 30°C and 48°C (occurring between 1200 and 1630 h), turtle temperatures frequently remained between 20°C and 30°C. These findings suggest that turtles avoided high soil surface temperatures either by accessing deeper soil depths or well-shaded areas. Available soil temperatures at 10 cm and deeper were in this range (Figs. 5 and 6). Heat avoidance by turtles during periods of warm weather may be a normal thermoregulation strategy (Plummer, 2003). In our study, regular changes in location of radioed turtles suggest that most turtles were not aestivating (unpublished data). Previous telemetry work on these or nearby study sites also showed frequent above-ground activity through the summer (Carter et al., 2000).

Pittman and Dorcas (2009) found a strong correlation between turtle carapace temperatures and soil at 5 cm depth, suggesting that Bog Turtles were frequently in a partially buried or submerged position. Temperatures at 5-cm soil depth were often >25°C, which is higher than the average daily bog turtle temperatures measured in this study. Considering the findings from Pittman and Dorcas (2009) and this study, it appears that that Bog Turtles could achieve optimal body temperatures through passive association (thermoconformity) with soil substrate rather than active basking out of water. Thermoconforming Bog Turtles may explain the findings of Pittman and Dorcas (2009) when they observed fewer daily basking events in August relative to June and July. Millar et al. (2012) found a similar pattern of basking in semiaquatic Blanding's Turtles in midsummer, with turtles reaching relatively high temperatures without the need for active basking. It is unknown whether mid- and late-summer basking out of mud and water is important to Bog Turtles for other physiological processes besides thermoregulation.

Conclusions

Bog Turtle and soil temperatures were dependent on ambient temperature, soil depth, and degree of soil saturation. In winter, Bog Turtles hibernated at relatively shallow depths. Despite this, Bog Turtle temperatures generally remained above freezing, with thermal stability provided by consistent saturation in the hibernacula. Although Bog Turtles can regulate their body temperature through use of their wetland habitats, they may also be passive subjects to wetland temperatures, particularly when they are inactive during the winter or when dry conditions prevent turtles from accessing deep soil or shade (grazed or water-starved vegetation can be too sparse to provide shade). As temperature characteristics in Bog Turtle habitats are spatially dependent on saturation and temporally dependent on daily, seasonally, and climactic temperature cycles, it follows that Bog Turtle conservation and management relies on understanding the cause-and-effect relationship of wetland alteration to wetland temperatures. Conditions at these sites with reproducing turtles are important to study, as they provide a baseline for comparison to future habitat changes or degraded sites. Alteration of wetlands inhabited by Bog Turtles could be caused by natural processes, such as the succession of herbaceous to scrub shrub and forested vegetation. Wetland alterations could also be anthropogenic such as changes to hydrology caused by ponding, increased storm-water flow, ditching, incision of stream channels, or reductions in recharge areas by creating impervious surfaces. The specific ways that Bog Turtles used their habitats in this study suggest that wetland habitats that rapidly become hotter, colder, or more thermally variable as a result of wetland alterations or climactic changes may become uninhabitable by Bog Turtles.

Acknowledgments.—Funding for this research was provided by the United States Fish and Wildlife Service through a State Wildlife Grant administered by the Virginia Department of Game and Inland Fisheries. We thank M. Pinder for his grant management and biological expertise. We thank the National Park Service, particularly T. Davis, and Virginia Polytechnic Institute and State University for their logistical support. We thank E. Matusevich, G. Laing, E. Owens, J. Stills, J. Goodhart, J. Marshall, C. Walker, and J. West for field assistance and T. Gorman for reviewing this manuscript. This research was conducted under National Park Service Permit BLRI-2006-SCI-0029, Virginia Department of Game and Inland Fisheries Permits 31313, 33376, and 36243, and Virginia Tech Institutional Animal Care and Use Committee Protocol 07-057-FIW.

Literature Cited

Arndt, R. G. 1977. Natural-history of the bog turtle, *Clemmys muhlenbergii* (Schoepff), in Delaware. Chesapeake Science 18:67–76.

Bernstein, N. P., and R. W. Black. 2005. Thermal environment of overwintering ornate box turtles, *Terrapene ornata ornata*, in Iowa. American Midland Naturalist 153:370–377.

Bloomer, T. J. 2004. *Clemmys muhlenbergii*: A Natural History. 4th rev. ed. Longwing Press, Gainesville, Florida, USA.

Bodie, J. R., and R. D. Semlitsch. 2000. Size-specific mortality and natural selection in freshwater turtles. Copeia 2000:732–739.

Brooks, R. J., G. P. Brown, and D. A. Galbraith. 1991. Effects of a sudden increase in natural mortality of adults on a population of the common snapping turtle (*Chelydra-serpentina*). Canadian Journal of Zoology–Revue Canadienne de Zoologie 69:1314–1320.

Brown, G. P., and R. J. Brooks. 1994. Characteristics of and fidelity to hibernacula in a northern population of snapping turtles, *Chelydra serpentina*. Copeia 1994:222–226.

Bruland, G. L., and C. J. Richardson. 2005. Spatial variability of soil properties in created, restored, and paired natural wetlands. Soil Science Society of America Journal 69:273–284.

Buhlmann, K. A., J. C. Mitchell, and M. G. Rollins. 1997. New approaches for the conservation of bog turtles, *Clemmys muhlenbergii*, in Virginia. Pp. 359–363 in J. VanAbbema (ed.), Proceedings: Conservation, Restoration, and Management of Tortoises and Turtles: An International Conference. New York Turtle and Tortoise Society, New York, New York, USA.

Bury, R. B. 1979. Review of the ecology and conservation of the bog turtle *Clemmys muhlenbergii*. U.S. Fish and Wildlife Service, Special Scientific Report, Wildlife 219:1–9.

Cagle, F. R. 1939. A system of marking turtles for future identification. Copeia 1939:170–173.

Carter, S. L., C. A. Haas, and J. C. Mitchell. 1999. Home range and habitat selection of bog turtles in southwestern Virginia. Journal of Wildlife Management 63:853–860.

———. 2000. Movements and activity of bog turtles (*Clemmys muhlenbergii*) in southwestern Virginia. Journal of Herpetology 34: 75–80.

Chase, J. D., K. R. Dixon, J. E. Gates, D. Jacobs, and G. J. Taylor. 1989. Habitat characteristics, population-size, and home range of the bog turtle, *Clemmys muhlenbergii*, in Maryland. Journal of Herpetology 23: 356–362.

Converse, S. J., J. B. Iverson, and J. A. Savidge. 2005. Demographics of an ornate box turtle population experiencing minimal human-induced disturbances. Ecological Applications 15(6):2171–2179.

Copeyon, C. K. 1997. Endangered and threatened wildlife and plants: final rule to list the northern population of the bog turtle as threatened and the southern population as threatened due to similarity of appearance. Federal Register 62:59605–59623.

Costanzo, J. P., J. D. Litzgus, J. B. Iverson, and R. E. Lee. 1998. Soil hydric characteristics and environmental ice nuclei influence supercooling capacity of hatchling painted turtles *Chrysemys picta*. Journal of Experimental Biology 201:3105–3112.

Cowardin, L. M., V. Carter, F. C. Goelt, and E. T. LaRoe. 1979. Classifications of wetlands and deepwater habitats of the United States. U.S. Fish and Wildlife Service, Washington, DC, USA.

Edge, C. B., B. D. Steinberg, R. J. Brooks, and J. D. Litzgus. 2009. Temperature and site selection by Blanding's Turtles (*Emydoidea blandingii*) during hibernation near the species' northern range limit. Canadian Journal of Zoology–Revue Canadienne de Zoologie 87: 825–834.

Edwards, A. L., and G. Blouin-Demers. 2007. Thermoregulation as a function of thermal quality in a northern population of painted turtles, *Chrysemys picta*. Canadian Journal of Zoology 85:526–535.

Ernst, C. H., and J. E. Lovich. 2009. Turtles of the United States and Canada. 2nd edition. The Johns Hopkins University Press, Baltimore, MD, USA.

Ernst, C. H., R. T. Zappalorti, and J. E. Lovich. 1989. Overwintering sites and thermal relations of hibernating bog turtles, *Clemmys muhlenbergii*. Copeia 1989:761–764.

Feaga, J. B. 2010. Wetland Hydrology and Soils as Components of Virginia Bog Turtle (*Glyptemys muhlenbergii*) Habitat. Unpubl. Ph.D. diss., Virginia Polytechnic Institute and State University, Blacksburg, Virginia, USA.

Feaga, J. B., C. A. Haas, and J. A. Burger. 2012. Water table depth, surface saturation, and drought response in Bog Turtle (*Glyptemys muhlenbergii*) wetlands. Wetlands 32:1011–1021.

———. 2013. Bog turtle (*Glyptemys muhlenbergii*) wetland habitat; an emphasis on soil properties. Natural Areas Journal 33:404–412.

Grayson, K. L., and M. E. Dorcas. 2004. Seasonal temperature variation in the painted turtle (*Chrysemys picta*). Herpetologica 60:325–336.

Greaves, W. F., and J. D. Litzgus. 2007. Overwintering ecology of wood turtles (*Glyptemys insculpta*) at the species' northern range limit. Journal of Herpetology 41:32–40.

Grobman, A. B. 1990. The effect of soil temperatures on emergence from hibernation of *Terrapene-carolina* and *T-ornata*. American Midland Naturalist 124:366–371.

Homyack, J. A., C. A. Haas, and W. A. Hopkins. 2010. Influence of temperature and body mass on standard metabolic rate of eastern red-backed salamanders (*Plethodon cinereus*). Journal of Thermal Biology 35:143–146.

Huey, R. B. 1982. Temperature, physiology, and the ecology of reptiles. Pp. 25–91 in C. C. Gans, and F. H. Pough (eds.), Biology of the Reptilia. Vol. 12, Physiology. Academic Press, New York, New York, USA.

Litzgus, J. D., J. P. Costanzo, R. J. Brooks, and R. E. Lee. 1999. Phenology and ecology of hibernation in spotted turtles (*Clemmys guttata*) near the northern limit of their range. Canadian Journal of Zoology 77: 1348–1357.

Litzgus, J. D., and W. A. Hopkins. 2003. Effect of temperature on metabolic rate of the mud turtle (*Kinosternon subrubrum*). Journal of Thermal Biology 28:595–600.

Lovich, J. E., D. W. Herman, and K. M. Fahey. 1992. Seasonal activity and movements of bog turtles (*Clemmys muhlenbergii*) in North Carolina. Copeia 1992:1107–1111.

Millar, C. S., J. P. Graham, and G. Blouin-Demers. 2012. The effects of sex and on patterns of thermoregulation in Blanding's turtles (*Emydoidea blandingii*) in Ontario, Canada. Chelonian Conservation and Biology 11:24–32.

Mitchell, J. C. 1994. The Reptiles of Virginia. Smithsonian Institution Press, Washington, DC, USA.

Natural Resources Conservation Service. 2011. United States Department of Agriculture. National Water and Climate Center. Available from: http://www.wcc.nrcs.usda.gov/. Accessed 16 December 2011.

Newton, E. J., and T. B. Herman. 2009. Habitat, movements, and behaviour of overwintering Blanding's turtles (*Emydoidea blandingii*) in Nova Scotia. Canadian Journal of Zoology 87:299–309.

Paz-Gonzalez, A., S. R. Vieira, and M. T. T. Castro. 2000. The effect of cultivation on the spatial variability of selected properties of an umbric horizon. Geoderma 97:273–292.

Picard, G., M. Carriere, and G. Blouin-Demers. 2011. Common musk turtles (*Sternotherus odoratus*) select habitats of high thermal quality at the northern extreme of their range. Amphibia-Reptilia 32:83–92.

Pittman, S. E., and M. E. Dorcas. 2009. Movements, habitat use, and thermal ecology of an isolated population of bog turtles (*Glyptemys muhlenbergii*). Copeia 2009:781–790.

Plummer, M. V. 2003. Activity and thermal ecology of the box turtles, *Terrapene ornata*, at its southwestern range limit in Arizona. Chelonian Conservation and Biology 4:569–777.

Rollinson, N., G. J. Tattersall, and R. J. Brooks. 2008. Overwintering habitats of a northern population of painted turtles (*Chrysemys picta*): Winter temperature selection and dissolved oxygen concentrations. Journal of Herpetology 42:312–321.

Rowe, J. W., and S. F. Dalgarn. 2009. Effects of sex and microhabitat use on diel body temperature variation in midland painted turtles (*Chrysemys picta marginata*). Copeia 2009:85–92.

Roznik, E. A., and R. A. Alford. 2012. Does waterproofing Thermochron iButton dataloggers influence temperature readings? Journal of Thermal Biology 37:260–264.

Sinervo, B., F. Mendez-de-la-Cruz, D. B. Miles, B. Heulin, E. Bastiaans, M. V. S. Cruz, R. Lara-Resendiz, N. Martinez-Mendez, M. L. Calderon-Espinosa, R. N. Meza-Lazaro, et al. 2010. Erosion of lizard diversity by climate change and altered thermal niches. Science 328: 894–899.

Stolt, M. H., M. H. Genthner, W. L. Daniels, V. A. Groover, S. Nagle, and K. C. Haering. 2000. Comparison of soil and other environmental conditions in constructed and adjacent palustrine reference wetlands. Wetlands 20:671–683.

Strack, M., J. M. Waddington, R. A. Bourbonniere, E. L. Buckton, K. Shaw, P. Whittington, and J. S. Price. 2008. Effect of water table drawdown on peatland dissolved organic carbon export and dynamics. Hydrological Processes 22:3373–3385.

United States Department of Agriculture. 2006. Fish and wildlife habitat management leaflet. Bog turtle (*Clemmys muhlenbergii*). Number 44. United States Department of Agriculture, USA.

Ultsch, G. R. 1989. Ecology and physiology of hibernation and overwintering among fresh-water fishes, turtles, and snakes. Biological Reviews of the Cambridge Philosophical Society 64:435–516.

———. 2006. The ecology of overwintering among turtles: where turtles overwinter and its consequences. Biological Reviews 81:339–367.

Yagi, K. T., and J. D. Litzgus. 2013. Thermoregulation of spotted turtles (*Clemmys guttata*) in a beaver-flooded bog in southern Ontario, Canada. Journal of Thermal Biology 38:205–213.

Zappalorti, R. T. 1976. The Amateur Zoologist's Guide to Turtles and Crocodilians. Stackpole Books, Harrisburg, Pennsylvania, USA.

Accepted: 10 July 2014.