

Daily Variation in the Body Temperatures of Free-Ranging Garter Snakes Author(s): Charles R. Peterson Source: *Ecology*, Vol. 68, No. 1 (Feb., 1987), pp. 160–169 Published by: <u>Ecological Society of America</u> Stable URL: <u>http://www.jstor.org/stable/1938816</u> Accessed: 28/08/2013 18:05

Your use of the JSTOR archive indicates your acceptance of the Terms & Conditions of Use, available at http://www.jstor.org/page/info/about/policies/terms.jsp

JSTOR is a not-for-profit service that helps scholars, researchers, and students discover, use, and build upon a wide range of content in a trusted digital archive. We use information technology and tools to increase productivity and facilitate new forms of scholarship. For more information about JSTOR, please contact support@jstor.org.



Ecological Society of America is collaborating with JSTOR to digitize, preserve and extend access to Ecology.

http://www.jstor.org

DAILY VARIATION IN THE BODY TEMPERATURES OF FREE-RANGING GARTER SNAKES¹

CHARLES R. PETERSON²

Department of Zoology, Washington State University, Pullman, Washington 99164 USA

Abstract. This study describes how the body temperatures $(T_{\rm b})$ of individual garter snakes varied on a daily basis under field conditions. Temperature-sensitive radio transmitters were surgically implanted into 10 Thamnophis elegans vagrans in eastern Washington. The snakes were released and monitored at 15-min intervals for periods of up to several days from June 1979 to May 1980. Operative environmental temperatures were estimated with painted metal models and were used to indicate possible T_{b} 's. The combination of telemetered body temperatures with operative temperature data permitted detailed description of $T_{\rm b}$ variation and evaluation of the relative importance of the physical environment and behavior in determining that variation. The physical environment usually prevented the snakes from attaining preferred (selected) $T_{\rm b}$'s and thus limited when and where they could be active and potentially reduced their physiological performance. On cool days or at night, when operative temperatures (T_e) were <15°C, the snakes remained underground and body temperatures changed gradually. On moderate days (15° $< T_e <$ 30°), the snakes usually emerged but were unable to maintain preferred body temperatures, and $T_{\rm b}$ variation was marked. On warm days ($T_{\rm e} > 30^{\circ}$), the snakes selected $T_{\rm b}$'s within their preferred temperature range, and variation in $T_{\rm b}$ was small (e.g., range = 28.0°-32.5°, $\bar{X} = 29.9^{\circ}$, sp = 1.32°). The snakes stayed within their preferred temperature range >90% of the time when $T_{\rm e} > 30^{\circ}$. Their high thermoregulatory precision and thermal utilization presumably maintained high levels of physiological performance on warm days. Delays in emergence accounted for most instances in which the snakes did not utilize available thermal opportunities.

Key words: body temperature; garter snake; operative environmental temperature; radiotelemetry; reptiles; snakes; Thamnophis elegans vagrans; thermal ecology; thermal preference; thermoregulation; Washington.

INTRODUCTION

The body temperatures of reptiles depend on both the magnitude of temperature variation present in the environment and the ability of these animals to regulate heat exchange with the environment. Most studies to date have emphasized the success of reptiles at maintaining relatively constant, often high, body temperatures (T_b) and the consequences of this stenothermy for organismal performance (Avery 1982, Huey 1982; but see Huey and Webster 1976). This emphasis may be misplaced, however, for several reasons, including: (1) phylogenetic and ecological biases in the species studied; (2) inadequate descriptions of thermal environments; and (3) incomplete data on temporal variation in the T_b 's of individual animals (especially when inactive).

The vast majority of studies of T_b variation have focused on diurnal lizards in open habitats (Avery 1982, Huey 1982). Studies of reptiles with less access to heat (e.g., nocturnal, fossorial, aquatic, or forest forms) suggest that such animals usually exhibit lower and/or

¹ Manuscript received 21 June 1985; revised 30 April 1986; accepted 7 May 1986.

² Present address: Department of Anatomy, 1025 East 57th Street, University of Chicago, Chicago, Illinois 60637 USA. more variable body temperatures when active (Huey and Slatkin 1976, Avery 1982). Consequently, studies of a wider variety of species (both phylogenetically and ecologically) are needed to obtain a general view of body temperature variation in reptiles (Avery 1982, Huey 1982).

Descriptions of thermal environments that indicate the range of T_b 's available to an ectotherm are needed to determine the extent to which body temperatures (and thus physiology and behavior) are constrained by physical factors. Without such descriptions, it is often difficult or impossible to determine whether environmental factors or the physiology and behavior of the animal are responsible for particular T_b patterns (Heath 1965). Few studies of reptilian body temperatures have accurately described the potential range of T_b 's so that the distinction between environmental and organismal determinants of T_b could be made; notable exceptions include Christian et al. (1983), Porter and Tracy (1983), Waldschmidt and Tracy (1983), and Crawford et al. (1983).

The usual procedure for measuring the body temperatures of reptiles may also bias results. Most field $T_{\rm b}$ data are based upon nonrepetitive temperature measurements of different animals. Such data will mask individual differences in temperature selection. FurFebruary 1987

thermore, because most of these $T_{\rm b}$ measurements are from active animals, relatively little is known about body temperature variation during periods of inactivity (e.g., during sleep, aestivation, or hibernation) even though these periods account for the majority of time spent by most reptiles (Huey 1982).

The concepts and techniques needed to address these problems have been developed during the past two decades. Mathematical models of heat transfer or physical animal models can be used to measure the potential range of an ectotherm's body temperatures for a given environment (Porter et al. 1973, Bakken and Gates 1975, Campbell 1977, Tracy 1982). Radio transmitters can be used to measure repeatedly the body temperatures of individual animals (e.g., Mackay 1964, Stebbins and Barwick 1968, Osgood 1970, Lang 1979). Continuous T_{b} and environmental measurements make it possible to determine the extent to which reptiles utilize the thermal opportunities available to them, in addition to providing more accurate field measurements of body temperature selection. These techniques have seldom been integrated in a single study, however (e.g., Christian et al. 1983).

The study reported here investigated: (1) how the body temperatures of individual garter snakes (Thamnophis elegans vagrans) from eastern Washington varied in the field and (2) the importance of the environment and behavior in determining that variation. The approach consisted of (1) using physical models of the snakes to characterize their thermal environments and (2) using surgically implanted, temperature-sensitive radio transmitters to monitor the body temperatures of free-ranging snakes for entire days during different seasons. The body temperatures preferred (selected) by garter snakes in laboratory thermal gradients were used to indicate when environmental conditions may have constrained body temperatures. This approach revealed that the snakes were unable to attain preferred body temperatures during much or all of each day throughout the year but that, with several interesting exceptions, they thermoregulated precisely when environmental conditions permitted.

MATERIALS AND METHODS

Study site

The study was conducted at the Turnbull Pine Research Natural Area, a 81-ha tract located within the Turnbull National Wildlife Refuge (Spokane County, Washington; R 43 E, T 21 N, Section 25). The elevation ranges from 685 to 715 m. Monitoring of the snakes was concentrated around three small (<6 ha), shallow (<3 m), eutrophic lakes surrounded by 3–8 m basalt cliffs and slopes. The vegetation of the natural area includes: (1) colonies of cattails (*Typha latifolia*) and tule (*Scirpus*); (2) moist meadows dominated by *Phalaris arundinacea* and *Deschampsia caespitosa*; (3) stands of quaking aspen (*Populus tremuloides*); (4) grassland dominated by bluebunch wheatgrass (Agropyron spicatum), Idaho fescue (Festuca idahoensis), and Bromus spp.; and (5) two types of Ponderosa pine forest communities, Pinus ponderosa/Festuca idahoensis and Pinus ponderosa/Symphoricarpos albus/Calamagrostis rubescens (Franklin et al. 1972).

Implantation of transmitters

Six female and four male garter snakes (snout-vent length 482–703 mm, mass 50–209 g) were collected and brought to the laboratory. Individuals were identified by clipping ventral scales (Brown and Parker 1976).

Each snake was placed in crushed ice for 3–4 h (to ensure immobilization) before implantation of the transmitter. The site of the incision ($\approx 65\%$ of the way down the body, just posterior to the spleen and pancreas) was swabbed with a povidone-iodine solution (Betadine) followed by 70% ethyl alcohol. The presterilized transmitter was implanted subcutaneously through the incision in the lateral portion of 5–6 ventral scutes and forced posteriorly. Although the transmitters were implanted superficial to the peritoneum, they usually were surrounded by it upon removal (which occurred ≈ 30 d after implantation). The incision was sutured shut and then sprayed with furazolidone (Topozone).

The snakes rapidly recovered and were released at the site of capture within 24 h after the operation and no more than 5 d after capture. Subsequent behavior (movements, feeding, gestation, etc.) appeared normal. The snakes were followed for 7 to 122 d (mean = 43 d). After ≈ 1 mo, surgical procedures were repeated on five of the snakes to replace transmitter batteries.

To determine if the head, body, and tail regions differed in temperature, I compared telemetered body temperatures with esophageal and cloacal temperatures (measured with a Schultheis thermometer) from snakes captured in the field. The means and the variances of 21 pairs of body and cloacal temperature measurements were not significantly different (paired t test of means, P > .3; F test of variances, P > .1). The means of 17 pairs of esophageal and cloacal temperature measurements (some from snakes without transmitters) were not different (P > .2), but the esophageal temperatures were significantly less variable than the cloacal temperatures (P < .025) (Peterson 1982).

Radiotelemetry system

Model T temperature-sensitive radio transmitters (Mini Mitter Company, Sunriver, Oregon) and two 1.5-V silver oxide batteries were contained in a plastic capsule coated with a paraffin/silicone mixture (approximately 12×30 mm and 4 to 5 g). These transmitters resolve temperature differences of 0.5°C, transmit under field conditions for ≈ 30 d, and have a range of ≈ 5 -100 m depending upon orientation and the de-



FIG. 1. Representative comparison of body temperatures (--) of an anesthetized *Thamnophis elegans vagrans* with snake model temperatures (--). The experiment began at 0820 (Local Solar Time) on 7 October 1979.

gree of obstruction. To minimize calibration drift, the transmitters were allowed to run for 1 mo before they were implanted (after a change of batteries). The transmitters were calibrated against a Schultheis quick-reading thermometer both before and (if recovered) after use in the snakes, but no significant calibration shifts occurred.

Lafayette HA 420 "walkie talkies," modified with beat frequency oscillators, were used as receivers. The built-in telescoping antenna or a 15 to 30 m length of insulated 1-mm (18-gauge) copper wire was used as an antenna. A cassette tape recorder, powered by a 6-V battery and controlled by a custom-built timer, recorded the signals from the receiver for \approx 40 s at intervals of 15 min.

Physical model

Operative temperatures (T_e ; Bakken and Gates 1975) were estimated by using a physical model of a garter snake. The model consisted of a straight, 700 mm long piece of hollow copper tubing, 16 mm in diameter, 1 mm wall thickness, that weighed 170 g, and was painted gray. The spectral reflectances of the dorsal surfaces of a light and a dark *T. e. vagrans* and of a copper plate (spray-painted with Western Auto gray auto primer) were measured with a Beckman DK-2a spectroreflectometer at wavelengths between 290 and 2600 nm (Porter 1967). The average reflectance (18.1%) of the paint fell between the reflectance values for the light and dark snakes (18.4 and 15.7%, respectively).

To test the accuracy of the model for predicting T_{b} 's for a particular microclimate, I compared the temperatures of the model snakes (T_{m}) with temperatures of anesthetized snakes under field conditions. Model and anesthetized snake temperatures generally agreed well (correlation coefficient = 0.96, N = 45) even though the model changed temperature more rapidly than did the snake. A representative comparison is shown in Fig. 1.

From 14 June to 19 August 1979, the model was

placed on the ground, in the open, within several metres of the snake being monitored at the time. However, because of shading by trees and other objects, the model was later moved onto an open ridge on the northwest corner of Middle Findley Lake, ≈ 20 m from the site of most subsequent monitoring. All model readings after 19 August 1979 were from this location. The model was placed in the open at the surface to determine the maximum T_{e} 's during the day (relatively low $T_{\rm e}$'s were always available underground). A Tempscribe $(-34^{\circ} \text{ to } +49^{\circ}\text{C})$ recording thermometer, calibrated to within 1°, was used to measure and record model temperatures. The 7-d temperature charts could be read to within 30 min. The probe from this thermometer was placed in the middle of the snake model, the ends of which were then closed with foam rubber or rubber stoppers.

A Tempscribe $(-5^{\circ} \text{ to } + 15^{\circ})$ recording thermometer was used to measure 20 cm deep soil temperatures and rock temperatures 20 cm deep in the talus of the Middle Findley Lake denning site in the spring of 1980.

Sampling procedure

Body temperatures of snakes were monitored each week (irrespective of weather conditions) from 14 June to 23 October 1979 and from 29 March to 19 May 1980. Seven snakes were monitored in 1979 and three snakes were monitored in 1980. Body temperature recordings of individual snakes were made at 15-min intervals for periods of up to 67 h. Although measured continuously, model temperatures are reported at 30min intervals because of resolution limitations of the recording thermometer.

The snakes usually were recaptured each week and the condition of each was noted: mass, digestive state (via palpation), reproductive condition (via palpation and cloacal smears), shedding state, and general health. In addition, direct observations of their behavior (basking, hunting, mating, etc.) occasionally were made. The snakes were very sensitive to the presence of people. Although considerable care was taken to avoid frightening the snakes, inadvertent disturbances occurred on $\approx 10\%$ of the monitoring days. Data from disturbed snakes were discarded. Further details on all of the materials and methods employed in this study can be found in Peterson (1982).

RESULTS AND DISCUSSION

Temperature selection in the laboratory

The body temperatures selected by garter snakes in laboratory thermal gradients were used to indicate when environmental conditions may have constrained body temperatures. The preferred (=selected) body temperature range is the range of temperatures maintained by an ectotherm in a laboratory temperature gradient (Pough and Gans 1982). The mean preferred body temperatures of garter snakes (*Thamnophis* spp.) average



FIG. 2. Daily body temperature patterns. (A) Plateau pattern. (B) Oscillating pattern. (C) Smooth pattern. Telemetered body temperatures (T_b) from individual free-ranging *Thamnophis elegans vagrans*, snake model temperatures (T_m) at the surface, and 20 cm deep ground temperatures (T_g) are plotted vs. time of day (Local Solar Time). Sunrise (1) and sunset (1) are indicated on time axis. Note that during the heating phase on 5 August the snake was able to find a microhabitat that was warmer than that where the model was placed.

≈28°C, ranging from 24.5° to 30.7° depending on the season of the year, ingestive status, reproductive condition, etc. (Stewart 1965, Scott 1978, Scott and Pettus 1979, Lysenko and Gillis 1980). The mean preferred T_b for nine *T. e. vagrans* from eastern Washington that were exposed to substrate thermal gradients in the laboratory was 29.6° (SE = 0.25°, N = 45) (B. P. Kinney and C. R. Peterson, *personal observation*). In this study, I considered the physical environment to be a potential constraint on snake temperatures if the surface model temperature was <30°.

Daily body temperature patterns

Daily body temperature (T_b) records were of three types: plateau, oscillating, or smooth (Fig. 2). The first

type, termed the plateau pattern (Fig. 2A), consisted of three phases: heating, plateau, and cooling. This was the most common pattern and was observed only on warm days ($T_m > 30^\circ$; Table 1). During the morning heating phase, the snakes usually warmed quickly (mean rate = $0.22^\circ/\text{min}$) from the minimum daily T_b and soon reached the preferred temperature level. The initial sharp rise in T_b presumably corresponded to the snake's emergence and exposure to the sun. During the plateau phase, body temperatures were relatively stable (see Thermoregulatory Precision). The duration of the plateau phase ranged from 4 to 12 h. The snakes often were active during this phase and selected a variety of microhabitats (above or below ground; on rocks, dirt, under bushes, in the grass, or in the water; and in open



FIG. 3. Body temperature frequency distribution for a plateau pattern T_b record. The relative frequencies are based on 97 T_b readings taken from a free-ranging, gravid *Thamnophis* elegans vagrans over a 24-h period on 22–23 June 1979. Temperature readings from the \blacksquare cooling, \square heating, and \blacksquare plateau phases are distinguished.

sun, shade, or a sun/shade mosaic). The cooling phase began in the afternoon and ended the following morning. Cooling rates were relatively low ($<0.03^{\circ}$ /min). During the cooling phase, the snakes were underground (in a burrow or talus) or under cover (e.g., under a log or a large rock). Body temperature frequency distributions for plateau patterns were bimodal (Fig. 3); the low and high portions of the distributions corresponded to the cooling and plateau phases, respectively.

The second type, the oscillating pattern (Fig. 2B), was characterized by a period of variable rather than stable T_b 's during the day (i.e., an oscillating rather than a plateau phase). This pattern usually occurred on moderate days, when daytime model temperatures ranged between 15° and 30° (Table 1). Snake T_b 's often exceeded the model temperatures by several degrees during these oscillating periods, presumably because the snakes could select warmer microhabitats and make behavioral adjustments such as coiling. Initial rates of cooling were often relatively high (up to 0.56°/min). Observations of other garter snakes at the study site indicated that they moved less extensively and spent more time in the open under oscillating phase conditions than during plateau phases.

The third type, the smooth pattern (Fig. 2C), was characterized by gradual or no change in T_b throughout an entire 24-h period. This pattern usually occurred on cool days ($T_m < 15^\circ$; Table 1) and, with one exception, the snakes did not reach the preferred temperature level. Snakes displaying smooth patterns were underground or under surface objects for the entire day.

These pattern types were strongly correlated with the daily weather conditions (Table 1). Plateau patterns occurred on 20 of 23 (87%) of the warm days ($T_m > 30^\circ$ during the day); oscillating patterns on 10 of 11 (91%) of the moderate days ($15^\circ < T_m < 30^\circ$); and smooth patterns on 5 of 5 (100%) of the cool days ($T_m < 15^\circ$) ($\chi^2 = 53.36$; P < .005).

Both the thermal environment and the behavior of the snakes determined the daily patterns of body temperature variation. The importance of behavior in determining $T_{\rm b}$ patterns generally increased as the range of operative temperatures increased, and was most evident during the plateau phases, when $T_{\rm b}$'s showed a low correlation with model temperatures (e.g., Fig. 2). In contrast, no behavior could maintain $T_{\rm b}$'s within the preferred range on cold days (when there was a relatively narrow range of possible $T_{\rm b}$'s), and the rcsulting smooth $T_{\rm b}$ patterns were primarily determined by the environment. Although physiological factors (such as metabolic heat production or cardiovascular adjustments) were not studied, they probably played a minor role in determining $T_{\rm b}$ patterns because of the snakes' small size, elongate shape, and absence of limbs (Bartholomew 1982, Turner, in press).

Most published accounts of daily T_b variation in reptiles describe triphasic patterns similar to the plateau pattern found in garter snakes (Stebbins and Barwick 1968, Osgood 1970, Smith 1975, Hammerson 1979, King 1980, Sanders and Jacob 1981, Christian et al. 1983). Few studies describe oscillating-type patterns (King 1980, Sanders and Jacob 1981) and none previously has reported smooth-type T_b patterns. Although this distribution of described patterns certainly is related to the species studied, it also reflects the emphasis that researchers have placed on the study of T_b regulation during warm periods, when most activity occurs. Body temperature variation during cool or inactive periods should receive more attention if we are to achieve a complete view of T_b variation in reptiles.

Environmental constraints

Body temperatures. — The physical environment usually prevented the snakes from attaining body temperatures within their preferred T_b range. Body tem-

TABLE 1. Classification of daily model and body temperature patterns. T_m patterns are based on daytime model temperatures. N = the number of days on which a particular pattern occurred.

Snake model			Live snake		
$T_{\rm m}$ pattern	N	% days	$T_{\rm b}$ pattern	N	% days
Warm $T_{\rm m} > 30^{\circ}{\rm C}$	23	59.0	Plateau Oscillat- ing Smooth	20 2	51.3 5.1
$\frac{\text{Moderate}}{15 < T_{\text{m}} < 30^{\circ}\text{C}}$	11	28.2	Plateau Oscillat- ing	0 10	0.0 25.6
Cool $T_{\rm m} < 15^{\circ}{\rm C}$	5	12.8	Smooth Plateau Oscillat- ing	1 0 0	2.6 0.0 0.0
Total	39	100.0	Smooth	5 39	12.8 100.0

peratures were constrained in this way to some extent on all days when T_b 's were monitored. The duration of this constraint ranged from entire days during cold periods in the spring and fall to ≈ 7 h during the night on warm summer days.

On some days, the snakes never were able to achieve preferred body temperatures. Model temperatures did not exceed 15° (the T_e threshold for surface activity) on 5 of 39 days (13%), and the snakes remained underground or under cover for the entire day at less than preferred T_b 's (e.g., Fig. 2C).

On some other days, snakes were unable to achieve preferred temperatures consistently because of varying environmental conditions. Daytime T_m 's ranged between 15° and 30° on 11 days (28%). All of the snakes except one emerged on these days, but none was able to maintain preferred temperatures. Body temperatures usually oscillated with the varying operative temperatures (e.g., Fig. 2B). Consequently, body temperatures from the oscillating phases (when $T_{\rm b}$'s were often constrained) were lower and more variable than in the plateau phases (when preferred T_{b} 's were consistently attainable). The mean $T_{\rm b}$'s for individual oscillating and plateau phase records were 26.2° and 29.9°, respectively; mean $T_{\rm b}$ ranges were 9.0° and 4.6°, respectively; and median standard deviations were 2.81° and 1.32°, respectively.

Even on the 23 days (59%) when model temperatures were $> 30^{\circ}$ (e.g., Fig. 2A), the plateau phase times were of limited duration (<12 h). The potential and actual durations of the plateau phases varied seasonally as the warmth of the environment and the likelihood of inclement weather changed throughout the year (Peterson 1982).

On all days, environmental heat sources diminished as the sun set, and the snakes were unable to maintain their T_b 's within the preferred T_b range throughout the night (e.g., Fig. 2). During the cooling phases, which ranged from 10.75 h to 19.47 h, body temperatures dropped below the preferred range 42 to 100% of the time.

Activity times. – Potentially lethal temperatures at the surface often limited the amount of time that was available for activity above ground. The critical thermal minimum for *T. e. vagrans* from the Turnbull site is $\approx 2^{\circ}$ (Stevenson et al. 1985). The critical thermal maximum for *T. e. vagrans* from Colorado is $\approx 43^{\circ}$ (Scott et al. 1982). Either or both of these critical temperatures occurred at the surface on most days during the present study. Potentially lethal temperatures, calculated from energy budget equations, also occurred often in the environments of *T. e. vagrans* in Colorado (Scott et al. 1982).

Potential activity times were further limited because the snakes usually did not emerge unless operative temperatures at the surface were greater than underground temperatures (or 15°) and the snakes usually retreated when surface temperatures became cooler than underground temperatures (e.g., in the late afternoon). High environmental temperatures were less constraining than low T_e 's because the snakes could avoid overheating by shuttling between hot and cool microhabitats (e.g., in the shade, in water, or under rocks) or by exposing only part of the body to the sun. Even on days when open surface T_e 's exceeded 49°, some snakes were active.

Temperature selection in the field

The garter snakes selected a relatively narrow range of body temperatures around 30° during the plateau phases. Overall, plateau phase T_b 's ranged from 25.4° to 36.0° and averaged 30.1° (N = 490). The average plateau phase T_b range was 28.0° to 32.5°. The means of individual plateau phase T_b records varied seasonally, decreasing from 32.2° in the spring to 26.9° in the fall, and averaged 29.9° (N = 20).

Body temperatures during the plateau phases were similar to temperatures selected by garter snakes in the laboratory. The overall mean plateau phase T_b of 30.1° (se = 0.06°, N = 490) was close to the mean preferred T_b (29.6°, se = 0.25°, N = 45) for nine garter snakes from eastern Washington (B. P. Kinney and C. R. Peterson, *personal observation*). Garter snakes in the field and laboratory also show similar seasonal patterns of decrease in selected T_b 's from spring to summer to fall (Scott 1978, Scott and Pettus 1979, Peterson 1982).

The temperatures selected by reptiles in the field are sometimes different from those selected in laboratory thermal gradients (DeWitt 1967, Pough 1974, Huey 1982). The results from this study indicate that continuous $T_{\rm e}$ and $T_{\rm h}$ data can help determine the causes of such differences. Several studies have reported mean cloacal T_b 's from active garter snakes in the field that are several degrees lower than the plateau phase $T_{\rm b}$'s found in this study or body temperatures selected in the laboratory. Activity T_{b} 's (measured cloacally with a Schultheis rapid-reading thermometer) for T. e. vagrans from the Turnbull site ranged from 17.7° to 34.0° and averaged 26.7° (se = 0.49° , N = 70) (C. R. Peterson, personal observation). Scott (1978) reported field $T_{\rm b}$'s ranging from 13° to 35° and averaging 27.8° (se = 0.18°, N = 313). Activity $T_{\rm b}$'s for T. e. vagrans on Vancouver Island averaged 25.7° (N = 107) (Gregory and Mc-Intosh 1980). These cloacal measurements are lower than telemetered plateau phase $T_{\rm b}$'s largely because of the inclusion of records taken when T_e 's were lower than preferred temperatures and records taken from animals still in their heating phases. For example, the mean field activity temperature decreased from 28.7° to 27.0° if records for $T_{\rm b}$'s in the water or on cold days were included (Scott 1978). In this study, the addition of 151 oscillating phase $T_{\rm b}$ measurements to the plateau phase readings decreased the overall mean by 0.9° and the inclusion of 83 heating phase $T_{\rm b}$ measurements further reduced the overall mean $T_{\rm b}$ by 0.6° to 28.6°.

The cloacal T_{b} measurements for T. e. vagrans from

eastern Washington aré generally similar to field temperatures reported for other members of this genus (Carpenter 1956, Fitch 1965, Gibson and Falls 1979, Gregory and McIntosh 1980, Stewart 1965, and others) and for many other species of snakes (Avery 1982). These results are in agreement with the generalization that snake temperatures are usually lower than the body temperatures of diurnal lizards from open habitats (Brattstrom 1965, Avery 1982).

Although many factors influence temperature selection in reptiles (Huey 1982), the sex or physiological condition of the snakes did not appear to affect temperature selection. The plateau phase T_b 's of three snakes before ecdysis (eyes clouded) and of four snakes that had recently fed were not obviously different from those of other snakes. Three records for a gravid female showed typical plateau phase T_b 's except that the standard deviations were quite low (0.93°, 0.78°, and 0.72°). The standard deviations for two plateau phase records following parturition were considerably higher (1.63° and 1.54°) and perhaps were related to increased activity.

Thermoregulatory precision

There are various ways of defining and measuring thermoregulatory precision, none of which estimates all aspects of the extent of temperature regulation (Huey 1982). In this study, thermoregulatory precision is defined as the maintenance of body temperature near the mean temperature selected in a thermal gradient. In accordance with the distinction between temperature regulation and temperature control (Bartholomew 1982), I have considered only those times when the environment allowed the snakes to thermoregulate at preferred T_b levels (i.e., $T_m > 30^\circ$). The ranges and standard deviations of the plateau phase T_b 's can reasonably be used as indices of thermoregulatory precision because of the close correspondence between preferred T_b 's and plateau phase T_b 's.

Body temperature variation during the individual plateau phases was relatively low. The difference between the minimum and maximum plateau phase T_b 's for any given day varied from 1.7° to 6.3° and averaged 4.5° (N = 20 days). The standard deviations of the plateau phase T_b 's ranged from 0.63° to 1.97° (median = 1.32°, N = 20 days). The T_b frequency distributions for plateau phases were unimodal with a narrow T_b range (Fig. 3). Three of seven plateau phase T_b distributions analyzed were normally distributed; three were positively skewed; and one was negatively skewed.

Continuous T_b data are important because differences in the set points of individuals may lead to underestimates of thermoregulatory precision if T_b measurements from a number of animals are pooled. For example, the average range and the standard deviation for the individual plateau phase records (4.5° and 1.22°, respectively) are lower than the range and standard deviation for the same readings that are pooled (10.2° and 1.69°). Operative temperature data are also important because they make it possible to distinguish between the effects of the physical environment and behavior on thermoregulatory precision (e.g., compare Fig. 2A and Fig. 2B).

The occurrence of relatively precise thermoregulation (mean plateau phase $T_{\rm b}$ range = 4.5° and mean $s_D = 1.22^\circ$) in garter snakes contradicts Avery's (1982) generalization that snakes are less precise thermoregulators than lizards. The few comparable data sets for other reptiles indicate that thermoregulatory precision in diurnal colubrids is similar to that of diurnal lizards. The standard deviations of telemetered $T_{\rm b}$'s for active striped racers (Masticophis lateralis) in outdoor enclosures ranged from 1.6° to 2.3° (Hammerson 1979). The standard deviation of midday (0900–1800) $T_{\rm b}$'s for four male Cyclura nubila was 1.4° (Christian et al. 1986). The average standard deviations of body temperatures for individuals of 11 African lizard species in outdoor enclosures ranged from 0.71° to 1.58° (Bowker 1984). The average ranges and standard deviations of body temperatures for individuals of three species of Cnemidophorus exposed to laboratory thermal gradients ranged from 4.6° to 5.6° and from 0.94° to 1.26°, respectively (Bowker and Johnson 1980, R. Bowker, personal communication). In Dipsosaurus dorsalis, a desert lizard often considered to exemplify precise thermoregulation in reptiles, DeWitt (1967) found that 68% of the body temperatures in laboratory thermal gradients ranged between 36.1° and 40.1°. In light of these comparisons, the more variable activity $T_{\rm b}$'s of snakes as a group (Avery 1982) may be due to other factors (such as lesser access to heat sources) rather than to limited thermoregulatory ability.

As a result of precise thermoregulation within the preferred temperature range, snakes are able to maintain high rates of physiological processes such as metabolism, digestion, and locomotion (Stevenson et al. 1985). The maintenance of high performance levels presumably benefits snakes by decreasing the risk of predation and enhancing growth and reproduction, but this awaits documentation. Precise thermoregulation during warm periods may be especially important because snake T_b 's are constrained by the environment most of the time.

Thermoregulation involves costs (in time and energy) and risks (e.g., exposure to predation during the heating phase) as well as benefits (Huey and Slatkin 1976, Huey 1982). In the present study, the costs associated with precise thermoregulation during high T_e conditions appear to have been low, especially for snakes that were relatively sedentary (e.g., gravid females or individuals that had recently fed upon a large prey item). Limited observations indicate that a garter snake can thermoregulate precisely during much of the day without extensive activity (or energy cost) simply by varying its exposure to the sun or its position within thermal gradients under surface objects (such as large

February 1987

rocks) or within burrows (C. R. Peterson, *personal observation*; D. G. Kephart, *personal communication*). Because the snakes are not exposed or moving during much of this time, the risk of predation may also be reduced. In contrast, the snakes controlled their temperatures less carefully than was possible during periods of low or medium T_e 's, when costs and risks may have been higher (see Utilization of the Thermal Environment). These observations are consistent with the generalization that precise thermoregulation is associated with low costs (Huey and Slatkin 1976).

Utilization of the thermal environment

Another important aspect of temperature selection in reptiles is the extent to which they utilize their thermal environment. The concept of thermal utilization is related to but different from those of thermal constraint, preference, and regulatory precision. It can be defined as the extent to which an animal chooses temperatures within or close to its preferred T_b range. The measurement of thermal utilization requires an assumption about the animal's thermal preference (based on laboratory studies) and a comparison between the temperatures the animal actually selected and the temperatures it could have selected. Possible shifts in thermal preference during the period of study (e.g., due to the time of day or to changes in the animal's physiological condition) also need to be considered.

Even though the thermal environment limited the absolute amount of time in which snakes could achieve preferred body temperatures, the snakes were remarkably effective at thermoregulating during those periods when high operative temperatures were available. The percentage of the potential plateau phase time during which the snakes were at preferred temperatures was used as an index of thermal utilization. On 11 warm days, such as the one depicted in Fig. 2A, the snakes maintained their body temperatures within their preferred $T_{\rm b}$ range for $\approx 93\%$ of the time that model temperatures equalled or exceeded 30° (Fig. 4). Similarly, Galapagos land iguanas (*Conolophus pallidus*) regulate their temperatures within a narrow range nearly all of the time, when possible (Christian et al. 1983).

High utilization has several important implications. First, body temperatures at which many physiological processes are maximal (for crawling, swimming, tongue-flicking, and digestion; Stevenson et al. 1985) were usually selected in the field when the snakes could do so. Also, possible constraints upon thermoregulation (such as predation risk, competition, or energetic costs of thermoregulatory adjustments) seldom prevented the snakes from obtaining preferred temperature levels when they were not constrained by the thermal environment. This result is important to predictions of activity periods based upon thermoregulatory behavior and T_e data. A critical assumption underlying such predictions is that the animals consistently attempt to thermoregulate within their preferred range (e.g., Por-



FIG. 4. Thermal utilization. The amount of time per day that snake body temperatures (T_b) were within the preferred temperature range (PBTR = 25°-35°C) when the temperature of the model snake (T_m) exceeded 30°, plotted vs. the amount of time per day that the model temperatures exceeded 30°. The 100% utilization line is broken and the regression line is unbroken. N = 11, $r^2 = 0.92$, slope = 1.06, and intercept = -60.3.

ter et al. 1973). A high thermal utilization value validates that assumption.

Thermal utilization appeared to decrease at operative temperatures $<30^{\circ}$. On eight days when daytime model temperatures ranged between 15° and 30° (e.g., Fig. 2B), snake T_{b} 's were within or close to the preferred range only 65% of the time. In other words, for $\approx 35\%$ of this time the snakes were not selecting the available temperatures that were closest to their preferred body temperatures. Delayed emergence or early retreat accounted for most of the time that the snakes failed to utilize available temperatures. Perhaps this is an indication of increased costs or risks associated with precise thermoregulation or activity under marginal thermal conditions.

Although T_b data were available for nights and cold days, the question of utilization could not be quantitatively addressed because (1) the range of temperatures underground (where maximum T_e 's would occur at these times) was unknown; and (2) there is insufficient laboratory data on nocturnal thermal preferences of garter snakes. During the night or on cold days, body temperatures were higher than model temperatures at the surface because the snakes were underground (Fig. 2). In the spring, snake T_b 's were usually higher than ground or talus temperatures at a depth of 20 cm (e.g., Fig. 2B), indicating that the snakes were even deeper underground. However, it was impossible to determine if the snakes had selected the warmest temperatures available, because of the lack of underground data.

The characterization of thermal utilization when operative temperatures are less than preferred temperatures is important because most of the snakes' time is spent under such conditions. Consequently, behavioral control of $T_{\rm b}$ (e.g., nocturnal microhabitat selection and possible subterranean movements) during these periods could have profound physiological and ecological consequences. Despite its potential significance, however, the thermal biology of inactive (but nonhibernating) reptiles remains virtually unknown (Huey 1982).

In several situations, the snakes did not select available temperatures that were within (or closer to) their preferred temperature range. (1) The snakes often delayed emergence even though the model temperature was greater than body temperature (e.g., Fig. 2B). The intervals between the time when model temperatures exceeded $T_{\rm b}$ and the time when snakes emerged averaged 90 min and ranged from 0 to 4 h 45 min (N =29). Model temperatures at emergence ranged from 10.6° to 38.6° (mean = 24.0° , sp = 7.58°). Snakes failed to emerge on only 2 of 45 days (4.4%) on which $T_{\rm m}$'s were greater than T_{b} 's. (2) Snakes retreated underground (as indicated by a sharp drop in T_{b}) early on 4 of 30 days (13%). (3) Snakes occasionally selected nocturnal habitats that were not the warmest available. Four snakes spent some nights under surface objects near the lake or in the fields (cf. in talus or under large rocks) and consequently experienced unusually low $T_{\rm b}$'s.

Although cases in which the snakes did not choose temperatures within the normal preferred range were rare in this study, they nonetheless may be important in several ways. Delays in emergence times may have resulted from time lags in some cue that indicated when warmer temperatures were available at the surface, or they may represent an adaptation to avoid predation by minimizing the time that the snakes would be exposed when their body temperatures are low and their ability to escape from predators is limited. The low nocturnal $T_{\rm b}$'s of some snakes may represent temporary shifts in preferred temperatures. Voluntary nocturnal hypothermia has been reported for several reptiles (e.g., Regal 1967, Spellerberg 1974), including garter snakes (Scott 1978; but see Lysenko and Gillis 1980) and may function to minimize energy expenditure or may be due to other factors not directly related to temperature (e.g., predation risk). Further fieldwork may reveal other situations in which thermal utilization or thermoregulatory precision is lowered (e.g., to gain access to prey) or in which there are shifts in preferred body temperatures (e.g., during extended periods of low food availability, such as droughts).

Conclusions

The results from this study support some generalizations concerning the thermal biology of reptiles, yet disagree with others. In contrast to the prevailing emphasis on the ability of reptiles to thermoregulate, the most striking result was that most of the time the physical environment prevented the garter snakes from attaining preferred temperatures. Nevertheless, the existence of a range of operative temperatures even at night or on cool days suggests that temperature control by snakes at these times is potentially very important and deserves further study. In warm conditions, the snakes thermoregulated precisely but (like other snakes) selected temperatures lower than those chosen by many lizards. The combination of data on the thermal environment with telemetered body temperatures revealed that the snakes utilized their thermal environment to stay within their preferred temperature range most of the time that it was possible to do so. Similar behavior has been assumed for many other reptiles but has seldom been verified. Those time periods in which the snakes did not appear to utilize their thermal environments (e.g., emergence delays) provide good opportunities for studying the costs associated with behavioral thermoregulation.

ACKNOWLEDGMENTS

I would like to thank the following persons for their assistance. Donald White, manager of the Turnbull National Wildlife Refuge, kindly granted permission to conduct this study at the Turnbull Pine Research Natural Area. Raymond A. Soltero (former director of the Turnbull Laboratory for Ecological Studies, Eastern Washington University) arranged for the use of facilities and equipment at the laboratory. David Osgood (Mini Mitter Co.) supplied, repaired, and provided information on the radiotelemetry equipment. Gaylon S. Campbell and Cornelius Calissendorf designed and constructed several instruments. Warren Porter provided the reflectance analyses of the snakes and paint samples. Robin S. Simons and Sherwood S. Smith assisted with the fieldwork. Brian E. Smith and Chai Ching Louie helped to process the data. Stevan J. Arnold, Gaylon S. Campbell, Martin E. Feder, G. A. Griffith, Raymond B. Huey, Victor H. Hutchison, James R. King, John H. Larsen, Jr., Harvey B. Lillywhite, Jon M. Mallatt, F. Harvey Pough, Robert D. Stevenson, Suzanne Kammel, Steven Waldschmidt, and B. Mike Walton commented on various stages of the manuscript. Financial support was provided by the Gaige Fund (American Society of Ichthyologists and Herpetologists), the Theodore Roosevelt Memorial Fund (American Museum of Natural History), the Society of Sigma Xi, the Washington State University Graduate School and Department of Zoology. Additional financial support for preparation of the manuscript was provided by NSF Grant BSR 83-07089 to M. E. Feder and NIH Grant GM 35492-01 to S. J. Arnold.

LITERATURE CITED

- Avery, R. A. 1982. Field studies of body temperatures and thermoregulation. Pages 93–116 in C. Gans and F. H. Pough, editors. Biology of the reptilia. Volume 12. Academic Press, London, England.
- Bakken, G. S., and D. M. Gates. 1975. Heat transfer analysis of animals: some implications for field ecology, physiology, and evolution. Pages 255–290 *in* D. M. Gates and R. B. Schmerl, editors. Perspectives in biophysical ecology. Springer–Verlag, New York, New York, USA.
- Bartholomew, G. A. 1982. Physiological control of body temperature. Pages 167–274 in C. Gans and F. H. Pough, editors. Biology of the reptilia. Volume 12. Academic Press, London, England.
- Bowker, R. G. 1984. Precision of thermoregulation in some African lizards. Physiological Zoology **54**:401–412.
- Bowker, R. G., and O. W. Johnson. 1980. Thermoregulatory precision in three species of whiptail lizards (Lacertilia: Teiidae). Physiological Zoology 53:176–185.
- Brattstrom, B. H. 1965. Body temperatures of reptiles. American Midland Naturalist 73:376-422.

- Brown, W. S., and W. S. Parker. 1976. A ventral scale clipping system for permanently marking snakes (Reptilia, Serpentes). Journal of Herpetology 10:247–249.
- Campbell, G. S. 1977. An introduction to environmental physics. Springer-Verlag, New York, New York, USA.
- Carpenter, C. C. 1956. Body temperatures in three species of *Thamnophis*. Ecology 37:732–735.
- Christian, K. A., I. E. Clavijo, N. Cordero-Lopez, E. E. Elias-Maldonado, M. A. Franco, M. V. Lugo-Ramirez, and M. Marengo. 1986. Thermoregulation and energetics of a population of Cuban iguanas (*Cyclura nubila*) on Isla Magueyes, Puerto Rico. Copeia 1986:65–69.
- Christian, K., C. R. Tracy, and W. P. Porter. 1983. Seasonal shifts in body temperature and use of microhabitats by Galapagos land iguanas (*Conolophus pallidus*). Ecology 64: 463-468.
- Crawford, K. M., J. R. Spotila, and E. A. Standora. 1983. Operative environmental temperatures and basking behavior of the turtle *Pseudemys scripta*. Ecology **64**:989–999.
- DeWitt, C. B. 1967. Precision of thermoregulation and its relation to environmental factors in the desert iguana, *Dip-sosaurus dorsalis*. Physiological Zoology **40**:49–66.
- Fitch, H. S. 1965. An ecological study of the garter snake *Thamnophis sirtalis*. University of Kansas Publications of the Museum of Natural History **15**:493–564.
- Franklin, J. F., F. C. Hall, C. T. Dyrness, and C. Maser. 1972. Federal Research Natural Areas in Oregon and Washington: a guidebook for scientists and educators. United States Forest Service Pacific Northwest Forest and Range Experiment Station, Portland, Oregon, USA.
- Gibson, A. R., and J. B. Falls. 1979. Thermal biology of the common garter snake *Thamnophis sirtalis*. I. Temporal variation, environmental effects and sex differences. Oecologia (Berlin) 43:79–97.
- Gregory, P. T., and A. G. D. McIntosh. 1980. Thermal niche overlap in garter snakes (*Thamnophis*) on Vancouver Island, Canada. Canadian Journal of Zoology 58:351–355.
- Hammerson, G. A. 1979. Thermal ecology of the striped racer, *Masticophis lateralis*. Herpetologica 35:267–273.
- Heath, J. E. 1965. Temperature regulation and diurnal activity in horned lizards. University of California Publications in Zoology 64:97–136.
- Huey, R. B. 1982. Temperature, physiology, and the ecology of reptiles. Pages 25–91 in C. Gans and F. H. Pough, editors. Biology of the reptilia. Volume 12. Academic Press, London, England.
- Huey, R. B., and M. Slatkin. 1976. Costs and benefits of lizard thermoregulation. Quarterly Review of Biology 51: 363–384.
- Huey, R. B., and T. P. Webster. 1976. Thermal biology of *Anolis* lizards in a complex fauna: the *Cristatellus* group on Puerto Rico. Ecology **57**:984–994.
- King, D. 1980. The thermal biology of free-living sand goannas (Varanus gouldii) in southern Australia. Copeia 1980: 755–767.
- Lang, J. W. 1979. Crocodilian thermal behaviors: alligators vs. crocodiles. American Zoologist 19:975.
- Lysenko, S., and J. E. Gillis. 1980. The effect of ingestive status on the thermoregulatory behavior of *Thamnophis sirtalis sirtalis* and *Thamnophis sirtalis parietalis*. Journal of Herpetology **14**:155–159.
- Mackay, R. S. 1964. Galapagos tortoise and marine iguana deep body temperatures measured by radiotelemetry. Nature 204:355–358.

- Osgood, D. W. 1970. Thermoregulation in water snakes studied by telemetry. Copeia 1970:568–571.
- Peterson, C. R. 1982. Body temperature variation in freeliving garter snakes (*Thamnophis elegans vagrans*). Dissertation. Washington State University, Pullman, Washington, USA.
- Porter, W. P. 1967. Solar radiation through the living body walls of vertebrates with emphasis on desert reptiles. Ecological Monographs **39**:245–270.
- Porter, W. P., J. W. Mitchell, W. A. Beckman, and C. B. DeWitt. 1973. Behavioral implications of mechanistic ecology. Oecologia (Berlin) 13:1–54.
- Pough, F. H. 1974. Preface to facsimile reprint of "A preliminary study of the thermal requirements of desert reptiles" by R. B. Cowles and C. M. Bogert. Miscellaneous Publications, Society for the Study of Amphibians and Reptiles, Milwaukee, Wisconsin, USA.
- Pough, H., and C. Gans. 1982. The vocabulary of reptilian thermoregulation. Pages 17–23 *in* C. Gans and F. H. Pough, editors. Biology of the reptilia. Volume 12. Academic Press, London, England.
- Regal, P. J. 1967. Voluntary hypothermia in reptiles. Science 155:1551-1553.
- Sanders, J. S., and J. S. Jacob. 1981. Thermal ecology of the copperhead (*Agkistrodon contortrix*). Herpetologica 37: 264–270.
- Scott, J. R. 1978. Thermal biology of the wandering garter snake. Dissertation. Colorado State University, Fort Collins, Colorado, USA.
- Scott, J. R., and D. Pettus. 1979. Effects of seasonal acclimation on the preferred body temperature of *Thamnophis elegans vagrans*. Journal of Thermal Biology **4**:307–309.
- Scott, J. R., C. R. Tracy, and D. Pettus. 1982. A biophysical analysis of daily and seasonal utilization of climate space by a montane snake. Ecology 63:482–493.
- Smith, E. N. 1975. Thermoregulation of the American alligator, *Alligator mississippiensis*. Physiological Zoology 48: 117-194.
- Spellerberg, I. F. 1974. Influence of photoperiod and light intensity on lizard voluntary temperatures. British Journal of Herpetology **5**:412–420.
- Stebbins, R. C., and R. E. Barwick. 1968. Radiotelemetric study of thermoregulation in a lace monitor. Copeia 1968: 541–547.
- Stevenson, R. D., C. R. Peterson, and J. S. Tsuji. 1985. The thermal dependence of locomotion, tongue flicking, digestion, and oxygen consumption in the wandering garter snake. Physiological Zoology 58:46–57.
- Stewart, G. R. 1965. Thermal ecology of the garter snakes Thamnophis sirtalis concinnus (Hallowell) and Thamnophis ordinoides (Baird and Girard). Herpetologica 21:81– 101.
- Tracy, C. R. 1982. Biophysical modeling in reptilian physiology and ecology. Pages 275–321 in C. Gans and F. H. Pough, editors. Biology of the reptilia. Volume 12. Academic Press, London, England.
- Turner, J. S. *In press.* Cardiovascular control of heat exchange: interactions with body shape and size. American Zoologist.
- Waldschmidt, S., and C. R. Tracy. 1983. Interactions between a lizard and its thermal environment: implications for sprint performance and space utilization in the lizard *Uta stansburiana*. Ecology **64**:476–484.