HOT ROCKS AND NOT-SO-HOT ROCKS: RETREAT-SITE SELECTION BY GARTER SNAKES AND ITS THERMAL CONSEQUENCES[1]

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Abstract. Studies of behavioral thermoregulation of ectotherms have typically focused only on active animals. However, most temperate-zone ectotherms actually spend more time sequestered in retreats (e.g., under rocks) than active above ground. We documented retreat-site selection during summer by gravid garter snakes (*Thamnophis elegans*) at Eagle Lake in northeastern California, USA. To explore the thermal consequences of retreat-site selection, we measured potential body temperatures in retreats and combined these with data on thermal tolerances, thermal preferences, and thermal dependence of metabolism and digestion.

Garter snakes at Eagle Lake usually retreated under rocks of intermediate thickness (20–30 cm) even though both thinner and thicker rocks were available. Empirical and biophysical analyses of temperatures under rocks of various sizes and shapes demonstrated that rock thickness had the dominant effect on potential T_b available to snakes and in turn on thermal physiology. Snakes selecting thin rocks (<20 cm thick) or very shallow burrows would die of heat stress in midafternoon and would have strongly impaired physiological capacity from cold at night. Snakes selecting very thick rocks (>40 cm thick) or remaining at the bottom of deep burrows would not experience such extreme T_b, but neither would they warm to T_b in their preferred range. However, snakes selecting intermediate-thickness rocks would never overheat but would achieve preferred T_b for long periods—far longer than if they remained on the ground surface or moved up and down within a burrow. Interestingly, snakes selecting burrows or intermediate-thickness rocks may be able to have either the highest energy gain or the lowest overall metabolic rate, depending on the particular T_b they select. Medium-thickness rocks, the size rocks normally selected by the snakes, offer them a variety of suitable thermoregulatory opportunities.

Key words: body temperature; garter snake; habitat selection; operative temperature; telemetry; Thamnophis elegans; thermoregulation.

INTRODUCTION

Many terrestrial ectotherms behaviorally regulate body temperature (T_b) during periods of aboveground activity by exploiting spatial and temporal variation in microclimates (Cowles and Bogert 1944, Porter et al. 1973, Casey 1981, Willmer 1982, Lillywhite 1987). Careful thermoregulation reduces the possibility that ectotherms will be exposed to extreme, potentially lethal T_b; and it also increases the time that they spend at physiologically favorable T_b (Avery 1982, Avery et al. 1982, Huey 1982, Stevenson et al. 1985, Grant and Dunham 1988, Hailey and Davies 1988).

The apparent careful thermoregulation of exposed,

active ectotherms may, however, present an incomplete and potentially misleading portrait of their thermal biology over the entire 24-h day (Dawson 1975, Humphreys 1978, Huey 1982, Christian et al. 1984, Peterson 1987). For example, many temperate-zone reptiles actually spend only a few hours each day above ground and thus spend most of the day sequestered under rocks or in other retreats (Avery 1976, Huey 1982). Depending on the thermal properties of their retreat site, sequestered ectotherms may have different opportunities for thermoregulation and thus may experience T_b very different from those associated with aboveground activity (Sergeyev 1939, Bustard 1967, McGinnis and Dickson 1967, Regal 1967, Stebbins and Barwick 1968, DeWitt 1963, Ruben 1976, Dial 1978, Humphreys 1978, Henderson et al. 1980, Christian et al. 1984, Peterson 1987). Consequently, the retreat sites selected by ectotherms may have a pro-

found impact not only on energy budgets and growth (Bennett and Nagy 1977, Stevenson et al. 1985, Arnold and Peterson 1989) but also on the evolution of the thermal sensitivity of physiological performance and development (Dawson 1975, Huey and Slatkin 1976, Huey 1982, Lynch and Gabriel 1987). Despite these considerations, thermoregulatory and physiological consequences of retreat-site selection have rarely been studied either in ectotherms (McNab and Auffenberg 1976, Ruben 1976, Bennett and Nagy 1977, Huey 1982, Christian et al. 1984) or in endotherms (Kenagy 1973, Buttemer 1985, Walsberg 1985, 1986).

Garter snakes (*Thamnophis elegans*) are excellent subjects for a study of retreat-site selection and its physiological consequences. They regularly spend long periods in retreats (e.g., under rocks), are abundant in many areas, and are large enough for implanting temperature-sensitive transmitters. Moreover, their thermoregulatory behavior (Carpenter 1956, Ruben 1976, Gibson and Falls 1979, Scott et al. 1982, Peterson 1987) and thermal physiology (Aleksiuk 1976, Stevenson et al. 1985, Arnold and Peterson 1989) are well studied.

We address several questions: (1) Do snakes select retreat rocks that are of particular sizes? (2) What are the body temperatures of snakes in self-selected retreats? (3) What are the potential body temperatures of snakes sequestered under rocks of different sizes, at various depths in burrows, or on the ground surface? (4) Are some sites too hot or too cold for snakes to tolerate or to survive? (5) Are certain retreat sites seemingly optimal for physiological activities? Specifically, do certain rock sizes (or depths in burrows) maximize the total time that snakes can maintain T_b within their preferred range, maximize their energy gain, or minimize their metabolic costs? (6) Do the retreat sites selected by free-ranging snakes possess thermal properties that are physiologically favorable for the snakes?

To study retreat-site selection by garter snakes, we implanted temperature-sensitive radiotransmitters in several snakes and then monitored both the use by these snakes of retreats and the body temperatures of many of the snakes themselves. To characterize the potential thermoregulatory opportunities available to snakes sequestered in particular retreats, we placed thermocouples in a variety of available retreat sites and monitored for 24 h the associated operative temperatures (T_e; the steady-state T_b of a snake, see Materials and Methods; Bakken 1976, Roughgarden et al. 1981, Tracy 1982, Grant and Dunham 1988). Thus we consider retreat sites as potential thermal resources to snakes (Magnusson et al. 1979, Tracy and Christian 1986). Following Huey (1983) we then estimated the physiological performance of snakes in various retreat sites by combining data on available T_e (above) with that on the known physiological effects of particular T_b (Stevenson et al. 1985).

Although our data are insufficient to provide defin-

itive answers to the specific questions outlined above, we believe that our data, as well as those of Christian et al. (1984), Buttemer (1985), and Walsberg (1985, 1986), clearly demonstrate the importance of understanding the relationship between retreat-site selection and physiological performance. We hope that the patterns emerging from these studies encourage additional work in this general area.

MATERIALS AND METHODS

Study site

Our study site was located at Pikes Point, Eagle Lake, Lassen County, California (40°33'24" N, 120°47'5" W, altitude 1555 m), a semiarid region in the Transition Life Zone. The vegetation is largely sagebrush and pine forest (Kephart 1982). Pikes Point consists of a series of basaltic ridges that extend into the lake and interdigitate with small meadows (Kephart and Arnold 1982). Basalt rocks are abundant and are used as retreat sites by garter snakes that live along the lake shore. These rocks range in size from small pebbles and flakes to boulders >2 m in diameter, have a density of 2.6 g/cm³, and have visible (400–700 nm) and overall (290–2600 nm) reflectances of 10 and 16%, respectively, measured as described by Porter (1967). Our studies were conducted on clear days in the summers of 1983–1987.

Telemetry and retreat-site selection

To discover the retreat sites selected by snakes and to monitor snake body temperatures, we surgically implanted Model T, temperature-sensitive radiotransmitters (pulse-interval modulated, Mini-Mitter Company, Sunriver, Oregon) in the body cavities of several adult, gravid snakes in the summers of 1983–1986. Calibration, implantation, and monitoring procedures followed Peterson (1987) except that we used Brevital Sodium (dosage = 10 mg/kg) instead of cold anesthesia. In 1985, we used transmitters (equipped with mercury switches) that doubled or halved their pulse rate whenever snakes moved. Snakes were released near the original capture site within 2 d after surgery and monitored for periods of up to 2 wk.

We also obtained (courtesy of Donald G. Kephart) body temperature and microhabitat data for a garter snake on 28–30 July 1979. A gravid female was force fed a custom-made, 1 g, AM radiotransmitter and monitored at varying intervals for the next 3 d.

To determine whether snakes used only a subset of the available size range of rocks, we compared the size distribution of selected vs. available rocks. By following telemetered snakes, we found and measured 13 rocks on Pikes Point that snakes regularly used as nighttime retreat sites. We then estimated the size distribution of available rocks by measuring the maximum linear dimensions of rocks encountered along four transects (each 20 m long and 2 m wide) extending

east, west, north, and south from each of the selected rocks. We excluded some rocks on the basis of several a priori criteria: (1) rocks under which snakes could not crawl, (2) rocks that were too small (i.e., <20 cm long or 10 cm wide) to cover a coiled, adult snake, (3) rocks that were shaded for much of the day, (4) rocks that were in the water or wet underneath, and (5) rocks that were on top of other rocks. No more than 10 rocks were sampled along any transect. To determine if the snakes nonrandomly selected rocks for nighttime retreat sites, we compared the frequency of selected vs. available rocks in three size classes (<20, 20–40, and >40 cm; see Discussion for justification) using a chi-square analysis.

Environmental temperature measurements

To determine how size and shape of rocks affected their thermal properties, we selected basalt rocks in three size categories (≈10, 30, and 80 kg) and in three shape categories (flat, domed, and spherical), each with one replicate (thus $N = 18$). To standardize conditions of exposure, we positioned these rocks on a modified Latin-square grid (hereafter called Snakehenge) on the open, south-facing slope of Pikes Point, ≈20 m from the water's edge. This slope, the remains of an ancient pebble beach, is gentle (≈5°). Except near local sunrise, nearby pines did not cast shadows on the plot. Local sunrise in midsummer is 0640–0700, and local sunset is ≈2000.

In an attempt to bound the range of potential T_b of snakes under rocks, we attached two copper-constantan thermocouples to the bottom of each rock (one at the thickest point, and one near the south-facing margin). Thermocouple temperatures on the undersurface of a 30-cm thick rock (Point D rock, see below) agreed closely with those of a snake model (see below) placed under the rock ($r^2 = 0.96$; mean and maximum differences were 1.0° and 2.2°C, respectively; $N = 10$). However, this correspondence may not hold for rocks that are partially separated from the underlying soil by a large air pocket (see Dial 1978), especially if the soil is moist (not the case during our studies).

On 27–28 July 1983 we monitored temperatures (at hourly intervals during the day and at bihourly intervals at night) beneath the rocks, in the soil (at depths of 15 and 30 cm), and of a model snake on the ground surface. The snake model was constructed of copper tubing painted flat-gray to match the reflectivity of *Thamnophis elegans*. The temperature of the model (operative environmental temperature or T_e, Bakken 1976, Tracy 1982) should closely approximate the steady-state T_b of a snake in the same location (see Peterson 1987). The model was placed on the ground along a north-south axis in the open (in direct sun during daylight hours).

On 28 June 1985, we added five new rocks (ranging in size from 6 to 714 kg) to Snakehenge and used a Campbell CR-5 datalogger to monitor temperatures at 15-min intervals of the rocks (south edge and thickest point), of the soil (surface and depths of 2.5, 5, 10, 15, 20, 30, 40, and 50 cm), and of snake models both in open sun and in shade. Measurements in both years were made on clear days. We pooled the samples from these 2 yr because the model and soil temperatures (15 and 30 cm) for June 1985 were similar to those in the July 1983 study (15-cm soil temperatures [°C], lowest = 20.4° [June] vs. 22.4° [July], highest = 24.6° [June] vs. 26.2° [July]; open snake models, lowest temperatures = 6.3° [June] vs. 2.6° [July], highest temperatures = 55.6° [June] vs. 52.3° [July]).

On 11–12 July 1987 we made measurements on another large, flat rock (Point D rock) because our telemetry data indicated that snakes that had selected this rock were able to stay warmer at night than we had predicted based on our results from the Snakehenge site. This rock measured 185 cm long by 107 cm wide by 30 cm thick, had a density of 2.6 g/cm³, and weighed ≈1260 kg (estimated using Archimedes's principle). We estimated its specific heat at 764.7 $J \cdot kg^{-1} \cdot kJ^{-1}$ using lava rock data in Porter and Tracy (1983). This rock should have a time constant (Porter et al. 1973, Porter and James 1979) of 10 h: peak midrock temperatures should occur about midnight if peak daytime surface temperatures occur between 1300 and 1400. We used this rock to compare (see above) under-rock temperatures with those of a snake model. We also measured two edge temperatures (east and south) rather than a single edge as for the other rocks. Because this rock differed from the rocks at Snakehenge in exposure to radiation and wind, we did not include it in the statistical analyses of the effects of rock size and shape on rock temperature. However, we did include it in the simulations (see below).

Physiological data and simulations

To explore the physiological consequences of retreat-site selection, we ran simulations that integrate data on the thermal sensitivity of physiology with the data on T_e in various retreats (see also Huey 1983, Christian et al. 1984, Hailey and Davies 1988). Physiological data on critical thermal limits (temperatures at which the righting response is lost; minimum = $CT_{min} = 2°$, maximum = $CT_{max} = 43°$), voluntary thermal maximum (36°), and preferred T_b range (28°–32°, values of laboratory body temperature [T_p] selected by gravid females) for *Thamnophis elegans* are taken from Scott et al. (1982), Stevenson et al. (1985), and C. R. Peterson (1987, *personal observation*). Using the temperature data for each retreat site and for the models, we calculated by linear interpolation the cumulative times during a 24-h day at which snake temperatures in each microhabitat would be: (1) below the critical thermal minimum, (2) above the critical thermal maximum, (3) above the voluntary thermal maximum, and (4) within the thermal preference range. We made the following assumptions: (1) snakes under rocks could

achieve any temperature between the edge and center temperatures; (2) snakes at the surface could choose any temperature between the exposed and shaded model temperatures; (3) snakes in burrows could choose any temperature between those at 2.5 cm and the maximum depth of the burrow; and (4) if a choice was available, snakes would select temperatures in the preferred range and avoid extreme T_b.

To simulate the effect of retreat-site selection on energy balance for snakes digesting food, we adopted equations for the thermal dependence of digestion and of resting metabolic rate from Stevenson et al. (1985). We adjusted for specific dynamic action (SDA) by decreasing the energy obtained from the digestion of prey by 25% (Bennett and Dawson 1976). (We decided to adjust for SDA in this way [rather than by increasing metabolic rate] because data on the thermal sensitivity of SDA are not available for snakes.) "Net energy available," defined as the difference between the energy obtained from digestion and the energy lost from metabolism (Waldschmidt et al. 1987), is maximal for these garter snakes at 29° if they have enough food in their guts (Stevenson et al. 1985). Net energy available is negative for garter snakes at temperatures <12° because digestion ceases at this temperature. Combining data on the thermal dependence of net energy available for snakes (Stevenson et al. 1985) and the thermal data for rocks, we then simulated net energy available over 24 h for a 100-g snake under each rock and at each soil depth.

We also simulated the effects of different thermal environments on the metabolic rates of fasting snakes, which might be attempting to reduce energy expenditures (Regal 1966, Brett 1971, Huey 1982). Resting metabolic rates (Stevenson et al. 1985) over 24 h were calculated for snakes under rocks, snakes on the surface in the shade, and snakes in burrows (allowed to move between 2.5 and 50 cm depth). When a range of T_e was available in a given retreat, we assumed that the snake always chose the coldest available temperature.

RESULTS

General patterns of activity and of body temperatures

Based on our experiences capturing ≈2000 garter snakes over the past 15 yr at Pikes Point, we can make several general statements regarding retreat-site selection and activity patterns of garter snakes: (1) Snakes usually use rocks (occasionally burrows) as retreat sites at night and on cold days. They seldom retreat under exposed small rocks (<15 cm thick). (2) During midmorning hours, they typically bask on sunlit ground near rocks or shrubs. Later in the day, they may forage along the lake shore (often in the water) or in nearby meadows, but often they return to retreat sites. (3) However, some snakes (especially those that are gravid, shedding, or digesting food) apparently never emerge from retreats even on clear days.

Focal animal studies, using radiotelemetered snakes, confirm these general observations. The gravid female observed by Donald G. Kephart on 29–30 July 1979 (snake 1, Fig. 1a) spent the night under a 30 cm thick rock and emerged the following morning between 0900 and 0933. She basked with her body fully exposed to the sun until ≈1100, when she moved most of her body under the rock, leaving only a loop of her body in direct sun. By 1400 she retreated completely under the rock and remained there for the rest of the day. Her body temperature pattern showed the triphasic, plateau pattern that is typical of T. elegans (Peterson 1987): a rapid heating phase in the morning, an extended plateau phase during the day, and a long cooling phase during the night. During the 14-h plateau phase, she controlled her T_b precisely (range = 27.6°–31.6°C; mean ± SD = 30.3 ± 1.12°; N = 22). Moreover, her T_b never declined <23.6° over the entire 24 h.

Snakes occasionally spend entire days sequestered, even on clear days. For example, a gravid female (snake 2, Fig. 1b) remained under a 30 cm thick rock for all of 11 July 1985, a sunny day. She was able to maintain warm body temperatures throughout the entire day (range = 25.2°–30.9°; mean ± SD = 28.2 ± 1.90°; N = 48), and she maintained her T_b within the preferred range for 13 h.

Retreat-site selection

A comparison of rocks selected vs. rocks available by telemetered snakes for nighttime retreats suggests that snakes almost always avoided thin rocks (<20 cm thick) and differentially utilized rocks of intermediate thickness (20–40 cm; Table 1).

The few snakes that selected either thin (<20 cm) or thick (>40 cm) rocks or a burrow had minimum daily body temperatures 1°–7° lower than snakes that selected rocks of intermediate thickness. The snake that spent the night under the 15-cm rock (the thinnest rock utilized) emerged at 0835 and did not remain under the rock during the day.

Daily cycles of operative temperatures

Operative temperatures underneath given rocks showed a clear daily cycle (Fig. 2a, b). Depending on rock size and thermocouple position, temperatures were lowest from 0600 to 1300, rose to a maximum from 1400 to 2400, and then declined through the night.

Temperatures under the edge of rocks typically varied more and changed more quickly than did temperatures under the center (Fig. 2a, b). Edge and central temperatures of a given rock were often very different (up to 24°). (Moreover, different edges of the same rock can also differ substantially in temperature. For example, the mean and maximum differences between the east- and south-edge temperature of the Point D rock [Fig. 2b] were 3.5° and 9.3°, respectively.) Thus, snakes often have thermal gradients available to them even under a single rock.
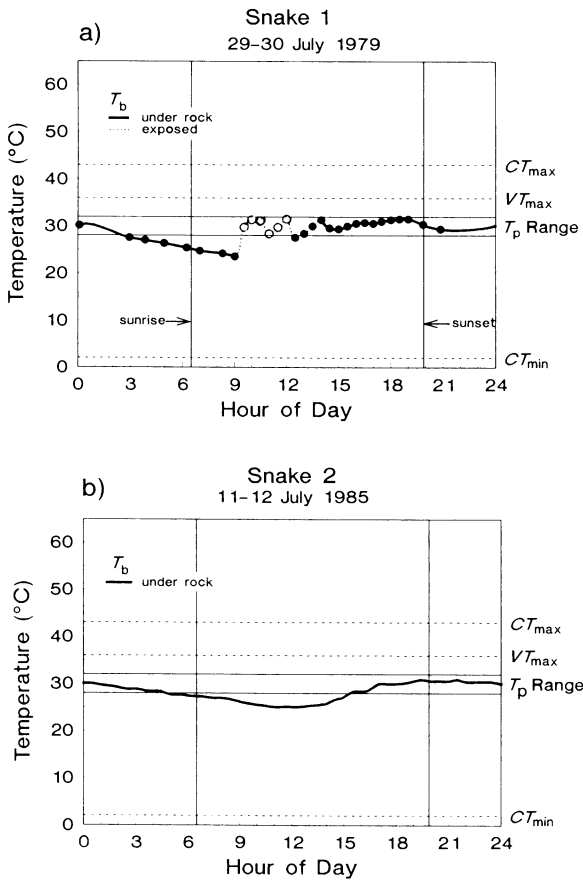
FIG. 1. (a) Body temperatures of snake 1, a gravid female *T. elegans* that was monitored by telemetry at Eagle Lake, California. $\bigcirc$ T_b when snake was exposed on the ground surface, $\bullet$ T_b when snake was under a rock. Solid and dotted lines connecting $\bullet$ and $\bigcirc$, respectively, were generated by a splining function of a graphics program (Mirage). Horizontal lines (—— or – – –) indicate temperature levels of CT_{max} (critical thermal maximum), VT_{max} (voluntary maximum T_b), T_p (preferred temperature) range, and CT_{min} (see Materials and Methods: Physiological Data and Simulations). Approximate times of local sunrise and sunset are indicated by vertical lines. (b) T_b of snake 2, which remained under a rock for the entire 24-h period. Note that both snakes were able to maintain temperatures within or near the T_p range for much of the day, even when sequestered in retreats.

atures for the centers of the rocks (T_{min} and T_{max}, respectively), and the times of minimum and maximum temperatures. Rock shape (flat, domed, or spherical) was treated as a classification variable with rock thickness and mass as covariates. Rock thickness was the only variable that had a significant effect (P < .01 for all dependent variables; Type III sums of squares). In light of these results, we focused only on the effects of rock thickness in the following analyses.

Maximum temperatures (range for all rocks = 25.1° to 60.5°) were highest under thin rocks ($r^2 = 0.81$, $N = 23$, Fig. 3). Maximum temperatures also occurred earlier in the day (range = 1500–2400) under thin rocks ($r^2 = 0.82$, $N = 23$).

Minimum temperatures (4.6°–19.4°) of rocks (Fig. 3) and the times of T_{min} (0530–1150) were both positively related to thickness ($r^2 = 0.79$ and 0.83, respectively; $N = 23$). No rock cooled below the critical thermal minimum (2°) at any time, but small rocks got much colder than large rocks (Fig. 3).

Temperatures in the soil also cycled during the day, and fluctuations were greatest at the surface (Figs. 2c, 3). For example, near-surface temperatures varied over 24 h by 47.5°, whereas the temperatures at a depth of 10 cm varied by only 6.8°. The general patterns are similar to those for rocks, except that the soil cycle at any depth was less pronounced and cooler than the temperature cycle under a rock of equivalent thickness (Fig. 3). At or below a depth of 15 cm, soil temperatures never exceeded 26.5°. Deep soil (50 cm) temperatures were cool and stable (19.8°–20.5°).

Temperatures of snake models at the surface (Fig. 2d) showed large daily cycles that were more pronounced in the open (daily range of T_e = 48.2°) than in the shade (daily range = 21.1°). A snake positioned in the sun would be exposed to above-lethal temperatures during most daylight hours, but a snake in the shade would never reach temperatures above the voluntary maximum (36°). Snakes remaining on the surface at night would get cold enough (<10°; Figs. 2d, 3) to have greatly depressed locomotor capacity (Stevenson et al. 1985).

Temperatures under individual rocks were highly repeatable at the same times of day for comparable weather conditions. For example, the correlation between temperatures (at the thickest points of Snakehenge rocks) on 28 vs. 29 June 1985 was 0.99 at 0600 and 0.97 at 1200 ($N = 5$ rocks). These high correlations prevailed even though rock temperature averaged 2° higher on the 2nd d.

The daily thermal cycles under rocks were primarily affected by rock thickness, not by rock shape or mass. We performed an analysis of covariance of rock thermal characteristics using the General Linear Model Procedure in PC-SAS (SAS Institute 1985). Dependent variables included minimum and maximum temper-

TABLE 1. Rock selection by garter snakes for nocturnal retreats at Eagle Lake, California. Rocks are divided into three (physiologically relevant) size categories.*

|	N†	Rock thickness (cm)		
		<20	20–40	>40
		Proportion of rocks		
Selected by snakes	13	7.7	61.5	30.8
Available to snakes	182	32.4	34.6	33.0

* Snakes selected rocks of intermediate thickness and avoided thin rocks (P < .05, chi-square test with the two extreme sizes combined because of small expected values).

† Twelve different rocks were selected by the snakes. However, we use $N = 13$ in our calculations because one of the rocks was selected by two different snakes.
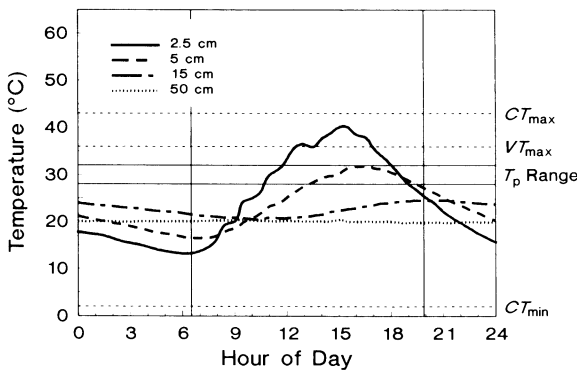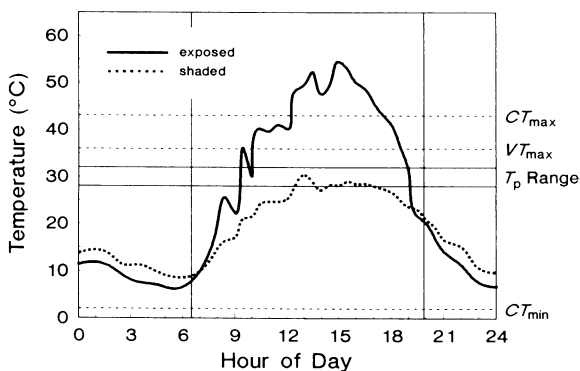
a) Thin and Thick Rock Temperatures
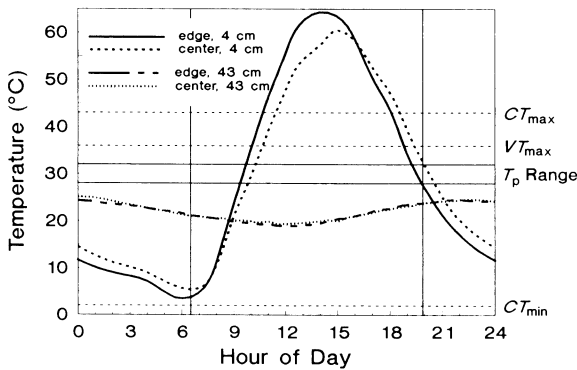
b) Medium Thickness Rock Temperatures
11 July 1987
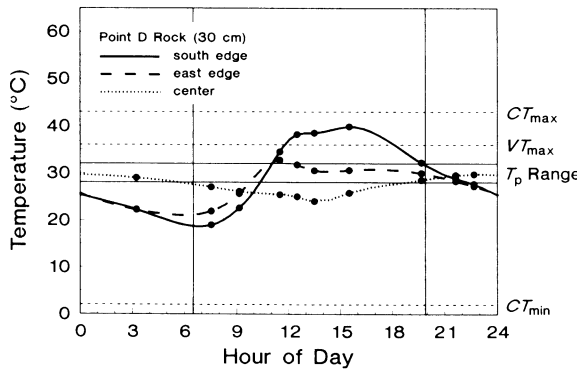
c)   Soil Temperatures

d) Surface Operative Temperatures

DISCUSSION

With a few notable exceptions (e.g., Stebbins and Barwick 1968, McNab and Auffenberg 1976, Pearson and Bradford 1976, Ruben 1976, Bennett and Nagy 1977, Boersma 1982, Huey 1982, Christian et al. 1984, Peterson 1987), most studies of behavioral thermoregulation of reptiles have focused only on behavior during aboveground activity. Such temporally and spatially restricted studies have therefore yielded only a partial portrait of the thermal opportunities and experiences of ectotherms during the entire 24-h day. Our studies suggest that thermoregulatory opportunities in retreats (i.e., burrows and under rocks) are often equivalent and sometimes superior to those available on the ground surface (Huey 1982, Christian et al. 1984) and that snakes appear to take advantage of those opportunities. Here we first summarize the opportunities for thermoregulation available to snakes in various microhabitats and describe the biophysical bases for those patterns. Then, by combining field data on available T_e in these microhabitats with laboratory data on the physiological significance of particular T_b, we simulate the physiological consequences of microhabitat selection (Huey 1983, Tracy and Christian 1986). This enables us to determine if physiologically optimal retreat sites exist. Finally, we integrate data from telemetry and field observations to determine if snakes appear to select retreat sites based on their thermal properties.

Microhabitats and thermoregulatory opportunities

Snakes spending 24 h under rocks could exploit a broad range of possible body temperatures, but the physiological suitability of rocks depends strikingly on rock thickness. Snakes under thin rocks would overheat by day and become very cold at night (Figs. 2a, 3). Snakes under intermediate-thickness rocks would spend the longest amount of time in their preferred T_b range (Fig. 2b, see below). Snakes under very thick boulders (>43 cm) would never reach T_b in their preferred range (Fig. 2a, see Discussion: Maximizing Time in the Preferred Temperature Range).

Garter snakes staying only on the ground surface for

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FIG. 2. (a) Daily cycle of temperatures under a thick (43 cm) and a thin (4 cm) rock, the rocks with the least and the most variable (respectively) temperatures. Various symbols as per Fig. 1. Both edge and center temperatures are indicated, and these delimit the thermal gradient available to snakes under each rock. Rock temperatures were taken at 30-min intervals, and spline functions are plotted. (b) Daily cycle of temperature underneath the Point D rock (intermediate thickness). Note differences between temperatures available on the south and east edges. Note also the long time that temperatures within the T_p range were available to a snake under this rock. (c) Temperature cycles at four representative depths in the soil at Snakehenge. Measurements were taken at 30-min intervals. (d) Operative temperatures from model snakes (shaded, exposed) on the ground surface at Snakehenge. Measurements were taken at 30-min intervals.
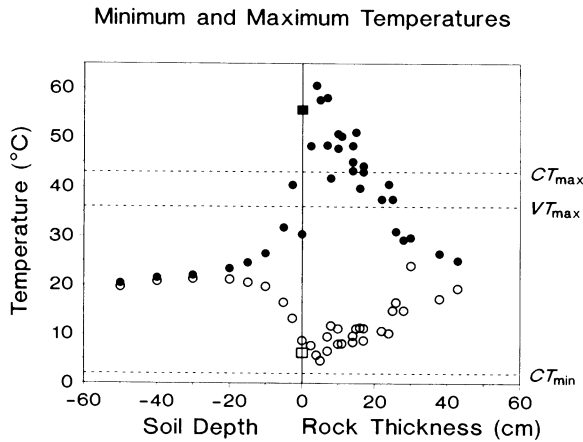
Minimum and Maximum Temperatures

FIG. 3. Maximum (solid symbols) and minimum (open symbols) temperatures over 24 h under rocks (center T_e) and in the soil as a function of rock thickness or soil depth. Symbols on the (vertical) 0-cm line represent a snake model in sun by day (■) and by night (□) and a snake model in shade by day (●) and by night (○). Other symbols as per Fig. 1.

24 h at Eagle Lake can potentially exploit a diverse thermal mosaic (e.g., sun vs. shade) and thereby should be able to control body temperature within narrow and preferred limits, but only during daylight hours (Fig.

2d). Even so, such a snake would have to limit time in sunny spots during most of the day and would have severely reduced locomotor capacity from cold at night (Figs. 2d, 3).

The range of temperatures available to snakes spending 24 h in burrows depends on the depth of the burrow, similar to the effect of thickness in rocks (Figs. 2c, 3). Snakes at 2.5 cm would heat above their voluntary maximum temperature during the day and become relatively cool at night (Fig. 2c). Burrows deeper than 5 cm allow snakes to avoid temperatures above their voluntary maximum. Over the depth of soil temperatures that we measured (2.5–50 cm), the snakes do not appear to gain any thermal options by selecting burrows deeper than 30 cm (Fig. 3). However, a snake moving among depths would be able to maintain high temperatures for long periods.

Biophysical considerations

Heat-flux patterns in and under rocks can be complex. However, if a rock is the same color and composition as the substrate and is in close contact with the soil, then the isotherms are bent upwards (Figs. 4, 5) as though the overlying rock were continuous with the substrate (Kreith 1965).
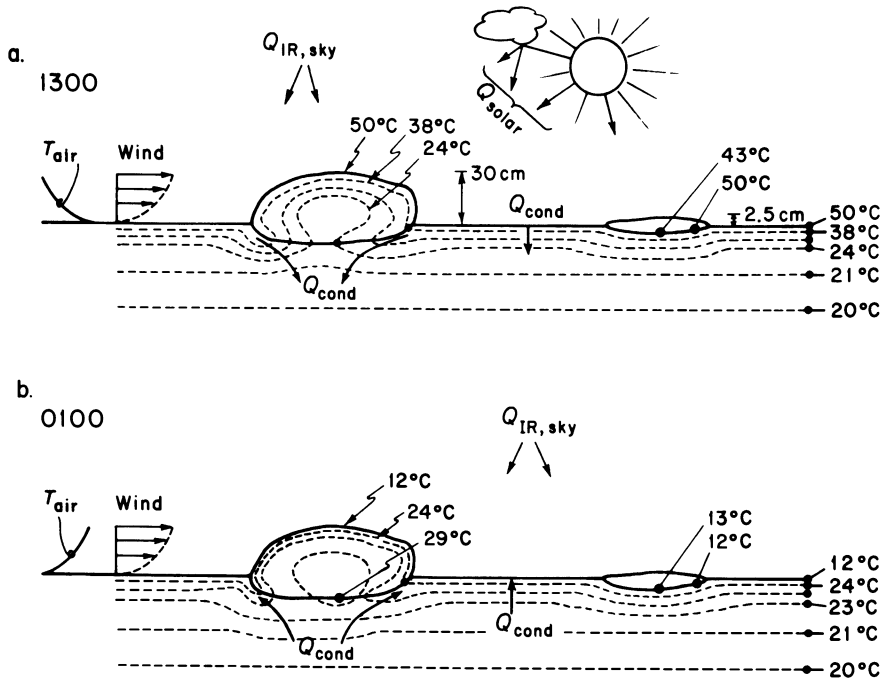

FIG. 4. (a) Temperature gradients within thick (30 cm) and thin (2.5 cm) rocks and within soil at 1300 on a clear summer day. We have assumed that the rocks and soil are in direct contact and have similar thermal properties (reflectance, thermal conductivity, and specific heat capacity). Isotherms are extrapolated from actual temperature measurements (indicated by ●). Note that (i) the center temperatures underneath the rocks are lower than the edge temperatures; and (ii) the temperatures under the thin rock are much higher than under the thick rock. Symbols: Q_{solar} = heat flux due to solar radiation; $Q_{IR,sky}$ = heat flux due to longwave radiation; Q_{cond} = heat flux due to conduction. Air temperature (T_{air}) and wind profiles are shown at the left. (b) Temperature gradients within thick (30 cm) and thin (2.5 cm) rocks and within soil at 0100 on a clear summer night. The isotherms are extrapolated as in Fig. 4a. Note that (i) the center temperatures underneath rocks are now warmer than the edge temperatures, (ii) that the temperatures under the thick rock are much warmer than either those under the thin rock or those in a burrow.
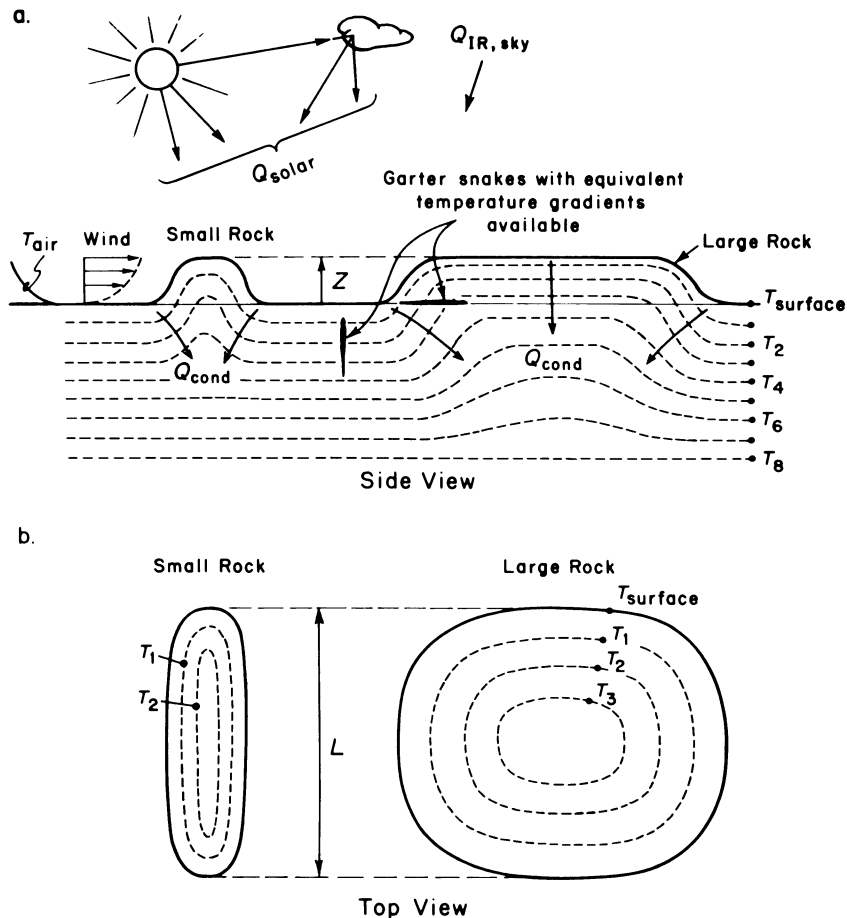
FIG. 5. (a) A simplified view of the thermal gradients available to snakes under rocks and in burrows during the day. Predicted isotherms (T_1-T_8) project up from the soil into the rocks, providing vertical thermal gradients in the soil and horizontal gradients under rocks. The arbitrary temperature contours illustrated could be increasing or decreasing with distance from the surface, depending on whether heating or cooling is occurring. The rocks depicted here could also represent other topographic features such as mounds of soil or stream banks. Symbols as in Fig. 4, with Z = rock thickness. (b) Isotherms within horizontal sections through the small and large rocks pictured in Fig. 5a. Note that the greater width of the large rock will usually result in a broader thermal gradient within or underneath it.

The actual isotherms are determined by the rock's time constant, which is in turn a function of several variables (linear dimensions, wind exposure, emissivity, density, specific heat, thermal conductivity, radiant temperature of the environment, etc.) as discussed in Porter et al. (1973). The top of the rock will heat and cool faster than the bottom (Fig. 4) because the top gets hotter due to absorbed sunlight and because the top experiences greater temperature gradients between the rock surface and the air, sky, and ground temperatures resulting in greater exchange by radiation and convection during both day and night.

Heat flux of a rock is dominated by the length of the rock's minimum axis (usually its thickness). Most heat flux occurs between a rock's top and bottom because the temperature gradient per unit length is large. In contrast, less heat flux occurs along the larger axes (rock's length and width), which act like thermal insulators.

If a rock is very thin, heat transfer between top and bottom is fast; and temperatures under the rock closely track those of the soil surface at any time of day (Fig. 4a, b). If the rock is of intermediate thickness, reduced rates of heat transfer cause the rock bottom to stay cool by day (Fig. 4a) and warm by night (Fig. 4b), relative to soil surface temperatures (Fig. 4a, b). If the rock is very thick, rates of heat transfer between the top and the bottom are small; and the rock's bottom is always relatively cool (except at the edges) and has temperatures (and time phase) equivalent to a burrow (Fig. 5a).

The relative lengths of the two other axes have secondary influences on heat flux and thus on bottom temperatures of a rock (Fig. 5a, b). (Note that the top views [5b] of the small and large rock in this figure show that the "length" in side view [5a] is "width" in top view.) Given equal thicknesses as well as equal lengths in one horizontal dimension (width), the critical dimension now is length. An object (rock or snake)

that is much longer than wide (small rock in Fig. 5b) will tend to behave thermally like a rock that is small in all dimensions.

Temperatures in burrows are dominated by depth (Gates 1980). Surface temperatures cycle dramatically over 24 h, whereas those at depth are stable (Fig. 4a, b).

Rocks offer snakes thermal options unavailable in burrows. At night, for example, warmer temperatures exist under certain rocks than anywhere in the soil (Figs. 3, 4b). Moreoever, if the horizontal dimension of a rock is relatively large (i.e., several times longer than thick), a snake moving laterally under a rock achieves the same thermal result as descending to a burrow depth equivalent to the rock's thickness (see right-hand rock in Fig. 5a). A similar thermal result should hold for snakes moving in horizontal burrows in sandy mounds under desert vegetation or in banks of a stream bed.

An implicit assumption in Figs. 4 and 5 is that the rock and substrate are the same color. A rock that is darker than the substrate will also get hotter than the substrate; and high temperature isotherms could wrap around the rock, potentially creating three-dimensional spherical or ellipsoidal isotherms (depending on rock geometry) within the rock, although the isotherms would be off center, because most absorbed sunlight is only on one side.

Partial burial of a rock will also influence temperatures under the rock (Fig. 4). A basin under the rock can collect moisture from rains or from nighttime condensation from the air, because ground surface temperatures are colder than the air above or the soil below (compare air temperature profiles at 1300 vs. 0100, Fig. 4a, b). Moreover, cycles of condensation and evaporation in the air gaps between soil particles can enhance thermal conductivity in soil by more than an order of magnitude (van Wijk 1963) and could play an important role in the heat balance. The effect of liquid water and water vapor under rocks on heat transfer and on soil moisture is a potentially important, but unexplored subject.

Some rocks have a shelf that covers or projects over the ground and thereby creates a shady mini-cave that animals can use. Such cavities will tend to have operative temperatures similar to local shaded air temperatures at the height of the downward-facing rock surface (W. P. Porter, *personal observation*). This happens because the cavities are sheltered from the sun during the day and from the cold sky at night and because the rock surfaces lining the cavities will exchange heat primarily by convection and infrared radiation from other shaded surfaces that are all at very similar temperatures (Porter and Gates 1969).

The biophysics of heat exchange under rocks is obviously complex, and many factors (e.g., shading) could contribute to and alter the temperature profiles we observed at Snakehenge. A sensitivity analysis of the rel-

ative significance of these various factors remains to be done.

Physiologically optimal microhabitats

Because of the marked differences in potential body temperatures available to snakes in various microhabitats (above), we wished to evaluate whether certain sites might be physiologically better for the snakes. The answer depends on the animal's thermoregulatory needs (or currency used in optimization, see Schoener 1971) and on the time period (here assumed to be 24 h on clear days in summer). We analyze retreat-site selection with respect to four potential thermoregulatory needs. These needs include most of the possible ones of snakes, but other options are possible. (Note: Huey [1983] and Tracy and Christian [1986] used maximization of sprint speed as a thermoregulatory need, but this need would usually be inappropriate for snakes in retreats [but see Larsen 1987].) We evaluate the relative benefits of various microhabitats to snakes by integrating field data on potential body temperatures in the various microhabitats with laboratory data on the physiological consequences of particular body temperatures (see Materials and Methods: Physiological Data and Simulations). Snakes were constrained to stay in one retreat.

Avoiding lower critical temperatures. — A snake with a body temperature below its critical thermal minimum (2°C) would be incapable of coordinated locomotion and thus probably incapable of defending itself. However, snakes at Eagle Lake would never have experienced body temperatures at or below the critical thermal minimum in any of the microhabitats (Fig. 3). By this criterion, therefore, all retreat sites should be acceptable, at least in midsummer.

Avoiding upper critical temperatures. — A snake with a body temperature greater than its critical thermal maximum (43°) would soon die from heat stress (Cowles and Bogert 1944). During the afternoon at Eagle Lake, T_e under thin sunlit rocks (<17 cm, Fig. 6a) exceed lethal levels, sometimes for long periods. In the extreme case of a rock only ≈4 cm thick, T_e would exceed the voluntary maximum temperature (36°) for >8 h/d and the CT_{max} for >6 h/d (Fig. 6a, b)! Therefore, simply to survive under an exposed rock during the afternoon, snakes would generally have to retreat under rocks thicker than ≈20 cm. To avoid temperatures above the voluntary maximum (36°), snakes would have to select rocks at least 22 cm thick (Fig. 6b).

Not surprisingly, snakes positioned on the ground surface in full sun during the afternoon would get very hot ($T_e > 50°$) and could not survive (solid square in Fig. 6a). However, snakes on the surface in the shade or down burrows at depths >2.5 cm could survive during the afternoon (Fig. 6a, b). Moreover, at burrow depths of ≥5 cm, snakes would not be exposed to temperatures above their voluntary maximum (Fig. 6b). If one excludes sites that had temperatures greater than the voluntary maximum during any part of the
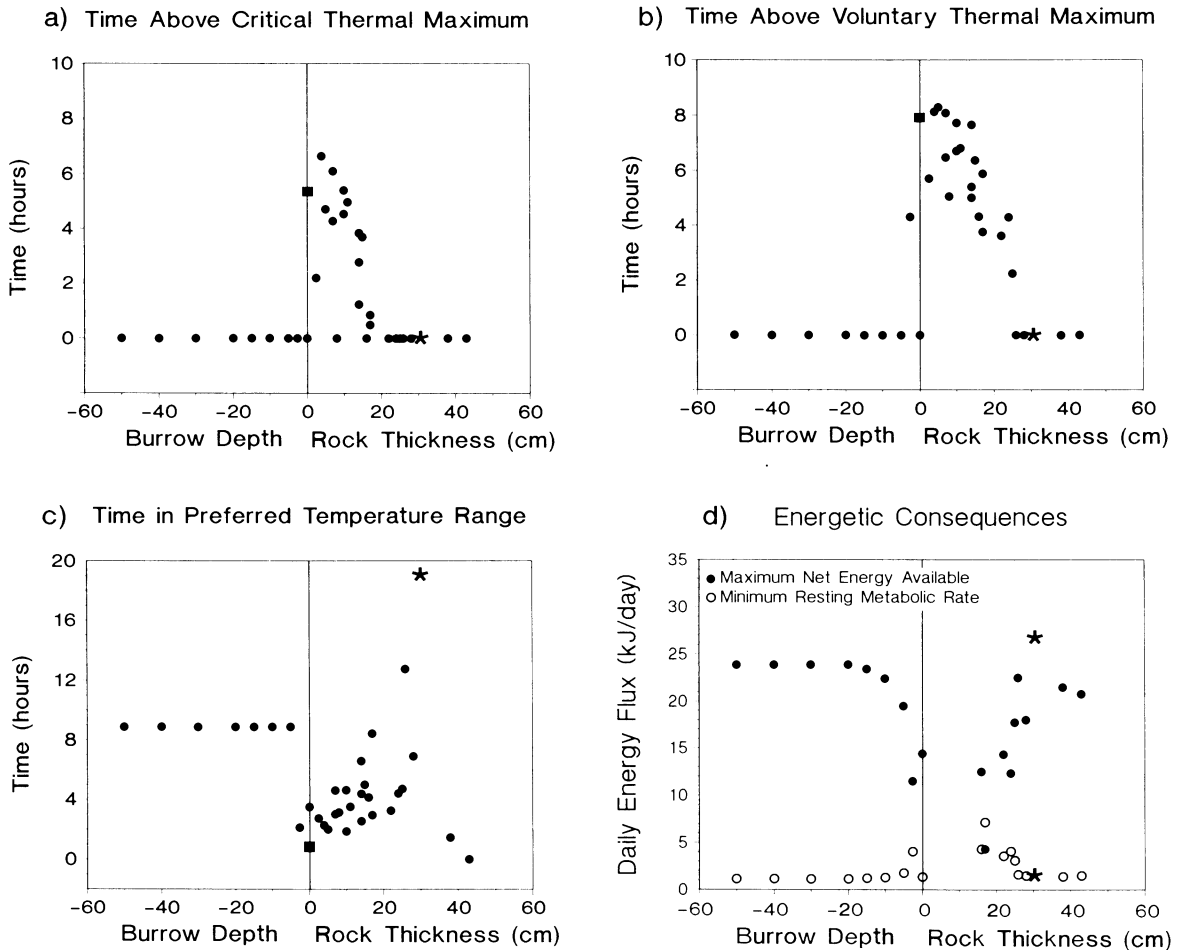
FIG. 6. (a) Cumulative time (over 24 h) during which temperatures under rocks of different heights or in burrows at different depths exceeded the CT_{max} (43°C) of *T. elegans.* (Note: in Fig. 6a–d, the various values for snakes in burrows assume the snake could move between the listed burrow depth and 2.5 cm from the ground surface.) * represents the value for the Point D rock (see Fig. 2b), ■ is the snake model in the open, and ● at 0 rock thickness is the snake model in the shade. (b) Cumulative time when the thermal gradient under a rock (or in a burrow) exceeded the voluntary maximum temperature (36°) for snakes. (c) Cumulative time when at least part of the thermal gradient under a rock was within the preferred temperature range (28°–32°). (d) Estimated energy consequences of retreat site selection.

Open symbols represent the minimum daily resting metabolic flux (in kilojoules per day) for a 100-g snake as a function of retreat site. Solid symbols represent the maximum net energy available for growth, reproduction, or activity (calculated by subtracting the metabolic rate from the energy gained through digestion, see Materials and Methods: Physiological Data and Simulations). Both the minimum resting metabolic rate and the net energy available for a snake under the Point D rock are indicated by asterisks. Excluded are retreats (0–15 cm thick rocks) that exceeded the CT_{max} of the snake at some time during the day.

24 h, then suitable retreat sites are restricted to include rocks thicker than ≈ 25 cm, burrows at least 5 cm deep, or the ground surface in shade.

Maximizing time in the preferred temperature range.—The preferred temperature of *Thamnophis* and of other reptiles is often correlated with the temperature at which many physiological processes are maximized (Dawson 1975, Bennett 1980, Stevenson et al. 1985, Hailey and Davies 1988; see Huey 1982 for review). In fact, growth rate in neonate *Thamnophis sirtalis* in the laboratory increases with the length of time available for thermoregulation (Arnold and Peterson 1989). The amount of time that snakes in different

microhabitats could achieve temperatures in their preferred range (28°–32°) varied dramatically, from 0 h/d to as much as 19.4 h/d (Figs. 6c, 7). The specific amount of time depended, for example, on rock thickness (Fig. 6c). Snakes could maximize the time (up to 19.4 h) within the T_p range by moving under rocks ≈15–30 cm thick. Snakes selecting rocks smaller than this would have heated and cooled quickly through the T_p range (Figs. 2a, 7). (Recall, however, that snakes would not remain continuously under rocks <25 cm thick because they would experience temperatures exceeding their voluntary maximum during the afternoon [Fig. 6b]. Thus the size range that maximizes time in the T_p

range is 25–30 cm thick.) A snake selecting the largest rock (43 cm height) that we monitored would have never heated into the T_p range (Figs. 2a, 7).

A snake that stayed entirely underground but that moved among depths could stay within the T_p range for 8.9 h (Figs. 6c, 7). The depth that provided temperatures at or closest to 30° was ≈15 cm at midnight, dropped gradually to 30 cm at 0900, then shifted abruptly to the surface, and remained at 5 cm from 1200 to 2000. A snake constrained to a single depth would maximize its time in the T_p range (6.3 h) by selecting a depth of 5 cm (Fig. 2c).

Snakes choosing to remain on the surface could maintain T_p only for 0.8 h if positioned exclusively in the sun, but for 3.5 h if exclusively in the shade (Figs. 6c, 7). However, by varying the amount of their bodies exposed to the sun or by moving between sun and shade, snakes exposed on the ground surface could maintain T_p for 10 h/d (Figs. 2d, 7).

A "Panglossy" snake, one that always selected the best available microhabitats, would have been able to maintain T_b within the preferred temperature range for >15.5 h/d at the Snakehenge site. If the Point D rock had been incorporated in these estimates, a Panglossy snake could have stayed within the T_p range for 20.3 h. To achieve this (see Fig. 7), the snake would need to spend the night under an intermediate-thickness rock and then bask early in the morning. During the late morning and afternoon, the snake could stay within the T_p range in several locations (shaded surface, down burrows, or under intermediate-thickness rocks) but by 2100 it would need to crawl back under an intermediate-thickness rock.

Real snakes did achieve preferred body temperatures for long periods of time (Fig. 1a, b). For example, snakes 1 and 2 were able to maintain T_b within the preferred range for 14 and 13 h, respectively (Fig. 1a, b), even though they rarely (or not at all) left the cover of their rock (see Results). However, temperature readings made in 1987 of the Point D rock (Fig. 2b) suggest that snake 2 should have been able to achieve T_p for as long as 19 h, but the reasons for this discrepancy are unclear.

Maximizing net energy availability.—Snakes digesting food would maximize net energy availability over 24 h (up to 27 kJ/d) by selecting T_b near 29° (Stevenson et al. 1985, see also Materials and Methods). To achieve temperatures near 29°, snakes should retreat under rocks ≈25–30 cm (Fig. 6d; retreats exceeding the critical thermal maximum are excluded). Net energy availabilities for snakes under the largest rocks, which remained relatively cool for the entire day (Fig. 2a), would be slightly less. A snake moving up and down within a burrow at least 15 cm deep could also have a high net energy availability (Fig. 6d, 23.9 kJ/d). However, snakes using surface sites and rocks <25 cm thick were either too hot or too cold (or both) for significant periods.

Minimizing energy expenditures.—Snakes without

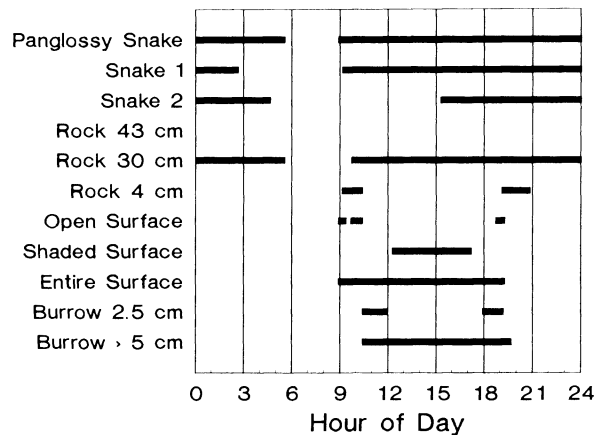## Time in Preferred Temperature Range

FIG. 7. Times during the day that a snake could achieve T_b within its preferred range (28°–32°C) if it stayed within a given microhabitat (e.g., under a 43-cm thick rock), or if it always selected the best available microhabitat (Panglossy snake). Note that the best single site is a rock ≈30 cm thick, similar to the Point D rock. Note that a slightly thicker rock (43 cm) never warms to the T_p range.

food in their digestive systems might attempt to minimize energy expenditures and thus, unlike the above snakes, should choose retreats with low T_e (Regal 1966, Brett 1971, Huey 1982). Such fasting snakes could minimize energy expenditures (to <1.5 kJ/d) either by retreating under rocks >26 cm thick or by moving within a burrow at least 10 cm deep (Fig. 6d). Snakes under rocks <20 cm thick would get very cool at night but recall would be too hot during afternoon for snake to survive (see above). Snakes under rocks between 20 to 25 cm would have slightly higher energy expenditures than would snakes under thicker rocks (Fig. 6d).

Retreat-site selection and thermoregulation

The marked thermal differences among rocks, burrows, and surface sites present snakes with varied opportunities for thermoregulation. Did garter snakes actually use those opportunities at Eagle Lake? Several kinds of evidence suggest that they did.

Rocks, especially ones of intermediate thickness, clearly provide snakes with better opportunities for staying warm at night than do surface sites or burrows (Figs. 2a, b, 4, 7). Indeed, all eight of the telemetered snakes chose rocks as nighttime retreat sites, and more snakes selected rocks of intermediate thickness than would be expected by chance (Table 1).

The telemetry and Snakehenge data also demonstrate that snakes under rocks do maintain body temperatures within the preferred range for much longer times than should be possible on the ground surface or down a burrow (Fig. 7). A snake that selected retreats randomly with respect to temperature would be unlikely to achieve such thermoregulatory precision.

Several snakes, however, did not select the warmest

nighttime retreat sites. As a result these snakes (three that chose thick rocks and one that chose a thin rock) experienced relatively low nighttime temperatures. Interestingly, three of these snakes chose medium-thickness rocks on other nights. Why these snakes sometimes selected cooler rocks is unknown (perhaps they were fasting, had other needs, or even made inappropriate choices).

CONCLUSIONS

Our observations (and those of Christian et al. 1984) lead to some interesting conclusions and implications for the importance of retreat-site selection to ectotherms:

1) Ectotherms can sometimes thermoregulate more effectively in retreats than in the open (Fig. 7). However, the overall advantages of being exposed vs. being in a retreat are complex and are not predictable from thermoregulatory considerations alone (Porter et al. 1973, Huey 1982, Christian et al. 1984). For example, although ectotherms in retreats may be able to thermoregulate carefully and may also be well protected from predators (especially while under large rocks, but see Larsen 1987), they may also be removed from sources of food and from social interactions (Simon and Middendorf 1976, Rose 1981, Huey 1982).

2) The type of retreat selected should be sensitive to the thermoregulatory needs of the snake (i.e., fasting snakes may choose different retreats from digesting ones). Nevertheless, a nonintuitive result of our simulations is that snakes attempting to maximize the time in the T_p range, to maximize energy available for growth and reproduction, or to minimize their resting metabolic rates, can retreat either under intermediate-sized rocks or down burrows (Figs. 6, 7). However, their position or depth within these retreats should vary with their thermoregulatory need.

3) Our telemetry data (mercury switches) suggest that snakes within retreats (day or night) may not be inert but may move around. Surprisingly, snakes occasionally move between retreat sites at night. Whether such movements reflect thermoregulatory adjustments (Dial 1978) or escape from predators is currently unknown.

4) Body temperatures experienced in retreats may play an important role in the evolution of thermal sensitivity of performance and development (Dawson 1975, van Berkum 1986, Huey and Bennett 1987, Hailey and Davies 1988), especially given that many reptiles have short activity periods (Avery 1976, Huey 1982, Hailey and Davies 1988). Even by exploiting the best available microhabitats (Fig. 7), ectotherms may not be able to maintain temperatures near preferred levels for 24 h/d, especially at night during cool seasons (Peterson 1982) or at high altitude or latitude (Avery 1976, Pearson and Bradford 1976). Some reptiles select low temperatures at night even when higher temperatures are available (Regal 1966, 1967, Christian et al. 1984, herein). Accordingly, the evolution of the ther-

mal sensitivity of physiology might reflect a balance between body temperatures experienced during retreat as well as during surface activity (Dawson 1975, Huey 1982, Lynch and Gabriel 1987, Hailey and Davies 1988). Studies that examine correlations only between thermal preferences of surface-active ectotherms and optimal temperatures of physiological performance or development may thus be incomplete.

Suggestions for future research

1) Our measurements and analyses of rocks at Snakehenge (an open, unshaded, south-facing slope) obviously oversimplify the cycles of T_e under rocks and in the soil. As noted above (Discussion: Biophysical Considerations), many factors beside rock size and shape could affect rock temperatures; and snakes, of course, probably exploit these factors. For example, snakes at Eagle Lake sometimes are positioned in cracks in rocks, where they are simultaneously warmed by the rock, exposed to direct solar radiation, sheltered from the wind, and yet protected from predators. Development of a mechanistic heat-transfer model for rocks would help us evaluate the importance of these complicating factors and would enable us to make more accurate predictions of the thermoregulatory opportunities provided by rocks.

2) Empirical and biophysical analyses of the effects of latitude, altitude, season, and weather fronts on the thermal consequences of microhabitat selection would be of considerable interest. Our data were collected only on clear days in midsummer, and our specific results are almost certainly applicable only to those conditions. Snakes at Eagle Lake are intermittently active in late spring and early fall. At these times solar heat loads will be lower, and maximum rock and soil temperatures will necessarily be lower as well. During these seasons snakes may be able to achieve temperatures in the preferred range only by basking in the open or under flat rocks, and snakes under 25–30 cm thick rocks (optimal in summer) are probably too cool. Consequently retreat-site selection may change dynamically with weather or season, as shown in other ectotherms (Humphreys 1978, Christian et al. 1984). Ideally future studies should monitor simultaneously both available T_e in diverse microhabitats as well as actual T_b of free-ranging snakes.

3) We restricted our telemetry studies to gravid snakes, which are thought to be more precise thermoregulators than are nongravid females or males (Gibson and Falls 1979, Beuchat and Ellner 1987, Lillywhite 1987, Peterson 1987). To obtain a more complete picture of retreat-site selection, future studies should include nongravid females, males, and juveniles.

4) A study of the behavioral aspects of retreat-site selection would be very worthwhile. In a controlled laboratory setting (or field enclosure), snakes could be offered a choice of retreats differing in thermal prop-

erties. (Observations of Larsen [1987] suggest that gar-
ter snakes may in fact be very selective in choosing
retreat sites.) Such studies would permit direct tests of
predictions derived from our observations and simu-
lations, namely, that garter snakes can learn to dis-
criminate among sites based on their thermal prop-
erties and that the physiological state of a snake
influences its retreat-site selection.

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