THERMAL BIOLOGY AND ACTIVITY PATTERNS OF THE EASTERN BROWNSNAKE (*PSEUDONAJA TEXTILIS*): A RADIOTELEMETRIC STUDY

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Abstract: Eastern brownsnakes (*Pseudonaja textilis*) from south-eastern Australia are alert, well camouflaged, secretive, fast moving, and dangerously venomous, and they spend much of the time hidden in burrows. Thus, direct observation of this species is difficult. However, distinctive patterns in environmental thermal heterogeneity, coupled with knowledge of the thermal preferenda of the snakes, enabled us to infer their location and activity based on remotely monitored body temperatures (obtained from surgically implanted radio transmitters). We used data on 40 radio-tracked snakes to evaluate patterns of thermoregulation, activity, and habitat use.

Captive snakes actively selected body temperatures around 31 C, and free-ranging snakes displayed similar body temperature levels while active. From data on temperatures of the soil, operative models, and shaded air, we could identify activity schedules of the snakes (especially, times of emergence from and retreat into burrows). Snake activity was bimodal over the year, with the highest incidence of above-ground activity in late spring and late summer. Thermal profiles suggest that inactive snakes in burrows spent most of their time at approximately 20 cm depth, but they moved to shallower depths at some times (e.g., during summer, when they sometimes spent entire nights above ground) and deeper at other times (e.g., ≥40 cm in winter). Reproductive females remained with their eggs after oviposition in mid-summer, about 30 cm under the soil surface. Burrow temperatures were frequently high, so that the snakes did not need to emerge in order to elevate body temperature. Overall, the telemetered snakes spent an average of 56% of active-season days, 64% of all days, and 93% of all hours below ground. Hence, this species largely depends on in-ground temperature for thermal energy exchange.

Key words: Activity schedules; Microhabitat selection; Thermal preferenda; Thermoregulation; Reptile

PATTERNS of activity and habitat use are basic ecological characteristics for any individual or population, and information on these topics is an essential first step to understanding the ecological role of the organism involved. For some kinds of animals, such data are relatively easy to acquire by direct observation. For example, brightly colored, diurnally active birds in grasslands or open forests may readily be observed in the course of their daily activities (e.g., Lack, 1968; Price, 1984). Unfortunately, many other types of animals are much more elusive and more difficult to observe. Thus, for example, we know

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less about habitat use and activity patterns of most nocturnal animals than about the same topics for their diurnal relatives. The problem is exacerbated with animals that are fossorial or that inhabit densely vegetated or complex habitats where they are virtually invisible to an observer (e.g., Clutton-Brock, 1988).

Snakes offer a good example of the kinds of organisms that are difficult to observe in the field. Most species are secretive, and many are highly cryptic and only rarely active (e.g., Seigel, 1993; Webb and Shine, 1997). The venomous capability of some species also introduces problems for short-range behavioral observation. The development of miniature radio transmitters has revolutionized studies on snake ecology because it has made these animals more accessible to study. Telemetry allows routine relocation of individuals implanted with transmitters, thus overcoming observability biases in terms of the habitats occupied and the times at which activity occurs (e.g., Reinert, 1992; Weatherhead and Anderka, 1984). In addition, telemetry can potentially provide far more detailed information. With the incorporation of a temperature-sensitive resistor (thermistor) into the telemetry circuit, the transmitter facilitates remote monitoring of body temperature as well as location. In temperate-zone habitats with strong temporal and spatial heterogeneity in thermal characteristics, such information may provide clues as to the location and activity of a telemetered snake. For example, a sudden change in the profile of daily body temperature of a diurnal snake is likely to reflect emergence from shelter, followed by a period of basking (e.g., in cool months) or entry into deep shade (e.g., in the height of summer). Even for snakes within shelter-sites, the consistency of thermal profiles with soil depth means that we may be able to infer the location of a snake (i.e., distance under the soil surface of that part of the animal carrying the transmitter) from the mean and variance of its body core temperature.

We attempted to characterize activity patterns (e.g., timing and duration of activity, thermal cues used to initiate and ter-minate activity) and habitat use (e.g., times underground versus active, depth under the ground surface during inactivity) of the eastern brownsnake (*Pseudonaja textilis*), a large venomous elapid from eastern Australia. Although this species inhabits relatively open grasslands, the eastern brownsnake is difficult to observe without disturbance. The snakes are alert, fast moving, and well camouflaged. They are so highly venomous that they cause most human fatalities due to snakebite in Australia (Broad et al., 1979; Sutherland, 1992); close approach may be dangerous to the observer. Also, the snakes spend long periods underground, where routine visual observation is impossible. They are thus an ideal subject on which to apply alternative techniques for documenting activity patterns and shelter-site selection.

Information on these topics is valuable not only in its own right, but also in terms of predicting risk factors for potentially lethal snakebite. The risk posed by an individual eastern brownsnake depends upon: the activity of the snake as to whether it is above or below ground; its body temperature because thermal factors influence not only the probability of encountering a brownsnake on the ground surface, but also the snake's tolerance for disturbance (Whitaker and Shine, 1999, 2000); and the animal's location when inside a refugium because shallow snakes are more likely to be dug or ploughed from burrows. Thus, for managing potential risk, it would be useful to have information on patterns of activity, location, and choice of refugia as these change during the year. Moreover, if we could understand why these patterns occur, we might be able to generalize the findings to other areas within the snakes' range.

MATERIALS AND METHODS

Study Animal

Eastern brownsnakes (*P. textilis*) are large (≤2 m total length), slender, fast-moving, diurnal elapids (e.g., Cogger, 1992; Shine, 1977*a,b,c*, 1989). The thermal biology of captive individuals has been

studied (Heatwole and Taylor, 1986; Lillywhite, 1980; Spellerberg, 1972), but nothing is known of the thermal biology or activity patterns of free-ranging brownsnakes. Brownsnakes in our study area typically occupy burrows or soil cracks when inactive (Whitaker, 1999) or are located beneath low vegetation or ground litter when active. Hence, we specifically targeted the thermal opportunities available to the snakes while on or below the ground surface, as these locations include the overwhelming majority of situations in which *P. textilis* occurs (>98% of records, Whitaker, 1999).

Local Area and Climate

The study area comprises approximately 14 km² and is located in mid-western New South Wales (centered approximately 146° 28′ E, 34° 39′ S). The generally open flat pasture and cropland is interspaced with irrigation channels, with topographic relief mostly in the form of road verges and railway and irrigation embankments. Soils grade from sandy-loam at the ground surface to heavy clay at approximately 20–30 cm depth, with regolith generally absent to >50 cm depth in the central study area.

Long-term climatic means from 45 yr of continuous monitoring at a permanently sited climate station located 7 km west of the central study area (Watson, 1997) reveal a pattern of hot dry summers, cool moist winters, and frequent drought. Mean daily maximum and minimum air temperatures (shaded air at 1.8 m height) were 31.6 and 16.9 C in January (the hottest month) and 13.5 and 3.2 C in July (the coolest month). Mean annual rainfall was approximately 440 mm, with most occurring in October (mean 46.1 mm) and least in February (28.3 mm). Rainfall was also frequent in winter, with soil moisture content generally high due to a low evaporation rate (mean 1.5 mm per day in June and July), which resulted in increased thermal conductivity and heat capacity of the soil. During late spring through to early autumn, however, rainfall was generally inadequate for vegetation growth. Hence, vegetation cover (and thus, the amount of shade available to the snakes) was reduced over this period.

Radiotelemetry

We monitored body core temperatures (T_b) using temperature-sensitive radio transmitters (Holohil Systems, Canada; models SI-2T, PD-2T, BD-2GT) that we surgically implanted, under aseptic conditions and gaseous anesthesia, into the coelomic cavities of 40 brownsnakes (Whitaker, 1999). Radio transmitters were carried between 2 and 32 mo (mean = 12 mo; representing a total of 40 snake years) between September 1993 and May 1996. The transmitters weighed <2.5% of the body mass of the snakes carrying them (mean = 1.6%). Body temperatures (±0.1 C) were monitored every 30 min and stored on a data logger (CR10, Campbell Scientific Australia, Townsville QLD) for 4–7 d, twice each month during the active season and once each month during winter (June–August). Details of the materials and methods used to implant radio transmitters and to facilitate data reception are given in Whitaker (1999). All times are expressed as Australian Eastern Standard Time.

Monitoring Environmental Temperatures

Environmental temperatures were sampled every 30 min, concurrently with T_b, and stored on the data logger.

Soil temperature.—Temperatures below ground (T_g) were sampled in two ways: at a continuously monitored fixed site in the central study area with 45° slope and northeast aspect (to maximize solar exposure), using silicon coated thermocouples placed in direct contact with the soil at depths of 5, 10, 20, and 30 cm; and in frequently used snake burrows using thermocouples sealed inside small glass capsules that were passed through close fitting copper tubes until the thin capsule bases contacted the soil. The tubes were previously sunk to depths of 10, 20, 30, 40, and 50 cm when burrows were unoccupied (to avoid disturbing the snakes). The tubes were capped when not in use to prevent fouling. Mean 2-h T_g values for all the

depths were calculated using the combined data from three burrows and the fixed site (above).

Air temperature.—Shaded air temperature at 4 cm above the ground surface (T_a) was sampled in two ways: at the fixed central site (above) and in surrounding farmland. The first method involved a silicon coated thermocouple suspended inside a 50×100 mm open ended white plastic tube with mat black internal surface and positioned in the shade of grass tussocks over flat ground. The second method involved opportunistically sampling T_a over shaded soil at various locations where snakes were located, using an 'Asmann-type' aspirating thermometer (Casella, London). Mean 2-h T_a was calculated using the data from both sources.

Operative model temperature.—Operative snake model temperatures (Bakken and Gates, 1975; Porter et al., 1973) were monitored on the ground surface using models made of sealed copper tubes (1 mm gauge $\times$ 31 mm outer diameter $\times$ 650 mm length) with thermocouples suspended inside model midsections. We placed three models in each of the following three situations on the central study area to represent the following previously determined thermal conditions: (1) on northeast unshaded aspects with 45° slope, representing maximum operative temperature ($T_{mod\ max}$) during the morning and early afternoon; (2) on level unshaded aspects, representing $T_{mod\ max}$ approximately from mid- to late afternoon; (3) on southern shaded aspects with 45° slope, representing $T_{mod\ min}$ (minimum operative temperature) available during the day and $T_{mod\ max}$ during the night. Maximum and minimum operative temperatures were determined for each half hour of each field day.

Albedo depends on skin color and may be an important consideration for modeling operative temperature (e.g., Bakken and Gates, 1975; Gates, 1980; but see Shine and Kearney, 2001). The dorsal color of brownsnakes in our study area ranged from light straw yellow to dark chocolate brown. Unlike some other Australian elapids (Banks, 1981; Johnston, 1994; Mirtschin and Davis, 1982), our study animals did not change color seasonally, but some of them did change between years. Hence, we tested the operative temperature models after painting them in three different shades of brown, and also when coated in a thin layer of clay to represent a common condition of the snakes. For testing, we compared model temperatures against the core temperatures of fresh road killed snakes ($n = 3$, collected within 20 km of the central study area), which we implanted with temperature sensitive radio transmitters in the same manner as the live animals. During testing, the dead snakes and models were aligned parallel and 40 cm apart in similar situations. Temperatures of the dark brown earth-coated model were very similar to those of the dead snakes ($r^2 = 0.992$), so we used this type of model for all subsequent monitoring.

Interpreting Activity from Temperature

Direct observations of telemetered snakes indicated that their emergence from an overnight burrow was soon followed by a steep rise in body temperature. Likewise, retreat to a burrow was accompanied by a rapid fall in body temperature, then stabilization at a T_b approximating that of the surrounding soil. Thus, we used continuous records of body temperatures to infer the times that snakes entered and left their burrows.

This indirect method of quantifying activity undoubtedly introduces some error. For example, brief activity periods may have been missed because the data were taken at half hour intervals. Also, the method underestimates activity time since classifying all snakes in burrows as inactive may preclude hunting time. Nonetheless, hunting in burrows, until one is found to contain prey, generally involves most of the brownsnake's body remaining on the ground surface, with only the head and forebody underground (personal observations). Thus, body temperatures are unlikely to fall noticeably during this activity.

Another potential source of error involves snakes that were entirely under the ground. Our data refer to temperature of

the transmitter, which was generally close to the snake's mid-body. Because the snakes were relatively large (to 1.76 m total length) and soil temperatures changed rapidly with depth underground, mid-body temperature might differ substantially from the temperature in the head or the tail if the snake was oriented vertically inside its burrow (e.g., Gates, 1980; Webb and Heatwole, 1971). However, visual inspection of some of the snakes inside burrows (using an endoscope) indicated that most were horizontally oriented, and hence all parts of the body were at similar depths below the soil surface most of the time.

Determining Selected Body Temperature Ranges

To interpret thermal profiles of free ranging snakes, we needed to understand not only what temperatures are potentially available to them (as measured by data loggers, see above) but also the range of T_b selected by the snakes under "ideal" conditions. Hence, we used laboratory trials to quantify voluntary (VT) and target temperature (set-point, T_{set}) ranges in temperature gradients (Christian and Weavers, 1996; Hertz et al., 1993). We estimated these ranges in the mid-active season (January 1996), using eight of the telemetered animals (four adult males and four adult females).

The snakes used for this purpose were transported to the University of Sydney within 3 to 6 d following capture and allowed a 2-d settling down period before monitoring. Selected temperatures were monitored over 7 d during which time the snakes were maintained in 87 × 36 × 34 cm wooden cages, were isolated from operator movement about the room, were provided with folded paper for cover, and were illuminated with a 14:10 h photoperiod (diffuse room light between 0600 and 2000 h EST). Each cage was fitted with under the floor heating cable to provide a floor temperature gradient of 22–46 C (typical summer range, see below). We estimated VT maximum (VT_{max}) and minimum (VT_{min}) using the mean extreme T_b recorded for each animal and the T_{set}

range using the limits of 50% central tendency (25 and 75 percentiles of the overall data).

Statistical Analyses

Data were analyzed using the programs Statview 5 and SuperAnova 1.11 on a Macintosh G4 computer. For most analyses, data for different individuals were not pooled in order to avoid pseudoreplication. However, data pooling does not introduce any major problems if the among-individual variance is similar in magnitude to the within-individual variance (Leger and Didrichson, 1994). Thus, we pooled data from different individuals for a few analyses (e.g., overall means and ranges for body temperatures recorded in the field and laboratory) where this procedure greatly simplified computations.

RESULTS

Below, we first describe general attributes of the thermal environment and of the temperatures exhibited by our study animals. We then examine the degree to which body temperature records enabled us to pinpoint the location and behavior of unseen snakes. Last, we examine aspects of activity patterns as revealed by these methods.

Selected Body Temperatures in Laboratory Thermal Gradients

Overall mean selected T_b determined in the laboratory was 31.0 C (n = 2688, 1 SD = 2.9). The laboratory determined VT range was 10.9 C (25.9–36.7 C; Fig. 1), and the T_{set} range was 3.5 C (29.4–32.7 C).

Range of Available Temperatures

Data logger records show that the snakes had a wide range of temperatures potentially available to them over most of the year. Mean maximum operative model temperature typically attained >25 C (i.e., reached the approximate VT_{min} of the snakes, see below) for >14 h/d in mid-summer (January), but barely reached 20 C during the day in mid-winter (July). Similarly, mean shaded air temperature (at 4 cm height) was higher than the VT_{min} for >12 h/d in mid-summer, but barely reached 14 C in mid-winter. Soil temper-
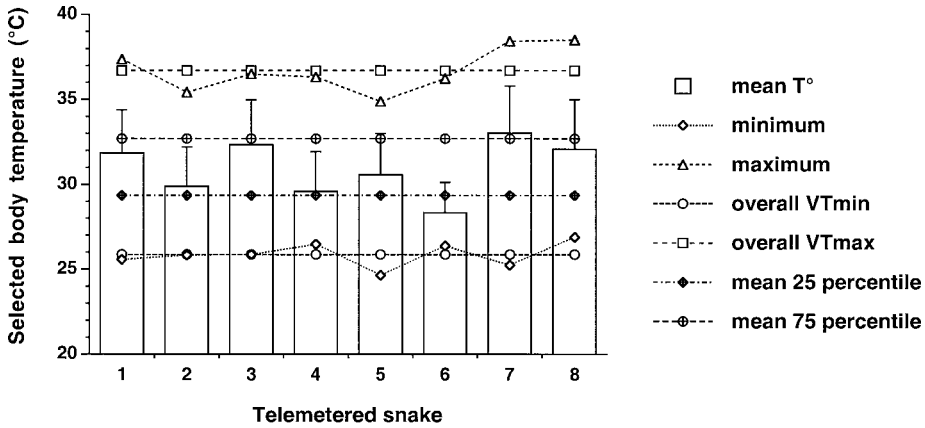
FIG. 1.—Body temperatures selected by captive specimens of the eastern brownsnake, *Pseudonaja textilis*, as monitored by radiotelemetry. The histograms show mean body temperature (Tb) and the associated standard deviation for eight adult brownsnakes. The graph also shows the minimum and maximum temperatures recorded for each snake (VTmin and VTmax), as well as the interquartile range (Tset, incorporating the central 50% of records).

atures showed very consistent patterns with respect to soil depth, being more variable closer to the soil surface (e.g., at 10 cm depth, mean range 23–29 C in mid-summer, 8–13 C in mid-winter, versus at 30 cm depth, a mean range 26–28 C in mid-summer, 9 C all day in mid-winter). Hence, mean soil temperatures were above the VT_{min} of the snakes for >12 h/d at 10 cm depth, and all day at 30 cm depth, in mid-summer. Soil temperatures did not reach VT_{min} at any depth in mid-winter, but soils deeper than 30 cm (40–50 cm) were warmer and more stable than shallow burrows at this time of year.

Body Temperatures of Active Snakes in the Field

The overall mean active T_b for free ranging snakes was 32.8 C ($n = 7316$, 1 SD = 3.1), slightly higher than determined T_{set} (above). The mean T_b range displayed by active free ranging snakes (mean lowest and highest T_b recorded during 34 field study periods when a minimum of three snakes were active) was 13.2 C (24.9–38.1 C). The maximum annual range for active snakes was 26.0 C (15.4–41.4 C), and the overall maximum range (where inactive snakes survived winter) was 33.8 C (7.6 C for an inactive snake in early August to 41.4 C for an active snake in late December). Hence, these snakes experienced a wide range of T_b through the year.

Mean active T_b varied during the year (Figs. 2–4). Body temperatures of active snakes were within T_{set} for at least part of the day during most activity months, but tended to plateau at slightly different levels as the active season progressed. Mean body temperatures gradually increased from the time of spring emergence (late August to early September) to peak in late summer (February) and then decreased again. Mean active T_b exceeded T_{set} during summer, although this was the same season in which we determined the T_{set} range (above).

By comparing temperature selection in the laboratory with that in the field, we could determine if the thermal opportunities available to free ranging snakes constrain their ability to reach T_{set}. Snakes were able to attain T_{set} on most activity days (Figs. 2–4), even if only for a few hours per day in cooler months. They did this by basking in shallow ground hollows or depressions that provided surfaces normal to the solar angle and convective shielding and by limiting their activity to the middle of the day (Figs. 2a, 4b).

Body Temperatures and Locations of Inactive Snakes in the Field

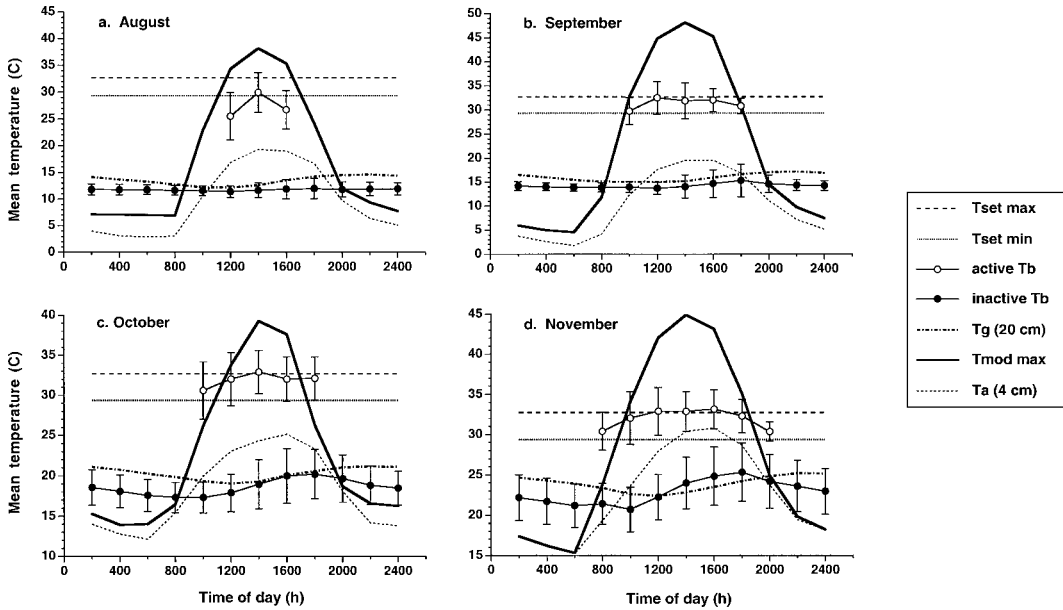The consistency of the relationship between soil temperature and soil depth al-

FIG. 2.—Body temperatures of radio-tracked free-ranging brownsnakes in relation to the snake's location ("active" = above-ground; "inactive" = below-ground), and associated environmental temperatures over the period August to November. The environmental temperatures include ground temperature 20 cm below the soil surface (Tg (20 cm)), air temperature 4 cm above the ground (Ta (4 cm)) and operative temperature inside a copper model exposed to full sun (Tmod max). The graphs also show the temperature range selected by captive snakes (Tset, incorporating the central 50% of records from captive animals).

lowed us to infer how far under the ground the telemetered snakes were sheltering (i.e., the mean depth of their midbody sections). The snakes were usually below ground when inactive and were recorded at a depth up to half a meter (based on their temperatures and confirmed by endoscopy of >30 burrows and excavation of another 30; Fig. 5). The overall mean inactive T_b for continuously monitored snakes inside burrows was 16.9 C (n = 30,182, 1 SD = 4.8). The mean monthly T_b of inactive snakes was positively correlated with soil temperatures at all the depths we measured (for all depths, r^2 > 0.76, P < 0.001), but the strongest overall correlate of snake body temperature was soil temperature at a depth of 20 cm (r^2 = 0.93, n = 144, P < 0.001).

These patterns of soil depth shifted seasonally. The mean depth of snakes in the ground was greater in winter than in summer (Fig. 5). For example, during the coolest months of the year (July and August), when T_g at 20 cm depth was <15 C

all day, the snakes occupied deeper layers. At the time that the snakes began to emerge from their winter burrows, their nocturnal body temperatures closely followed the thermal regime typical of soil at 40 cm depth, but their diurnal temperatures were at levels typical of shallower depths (Fig. 6a). This pattern suggests frequent vertical movement within burrows, with the snakes selecting shallower (warmer) depth during the day but retreating to cooler and more stable depth at night. Diurnal variances in snake temperatures were higher in summer, reflecting a shift closer to the soil surface. In late spring and early summer, many of the snakes hunted in shallow burrows made by house mice rather than in the deeper burrows of their over winter refuge area. Thus, the snakes were perforce often relatively close to the ground surface. Consequently, their inactive T_b often reached VT_{min} at some point during the day (Fig. 6b).

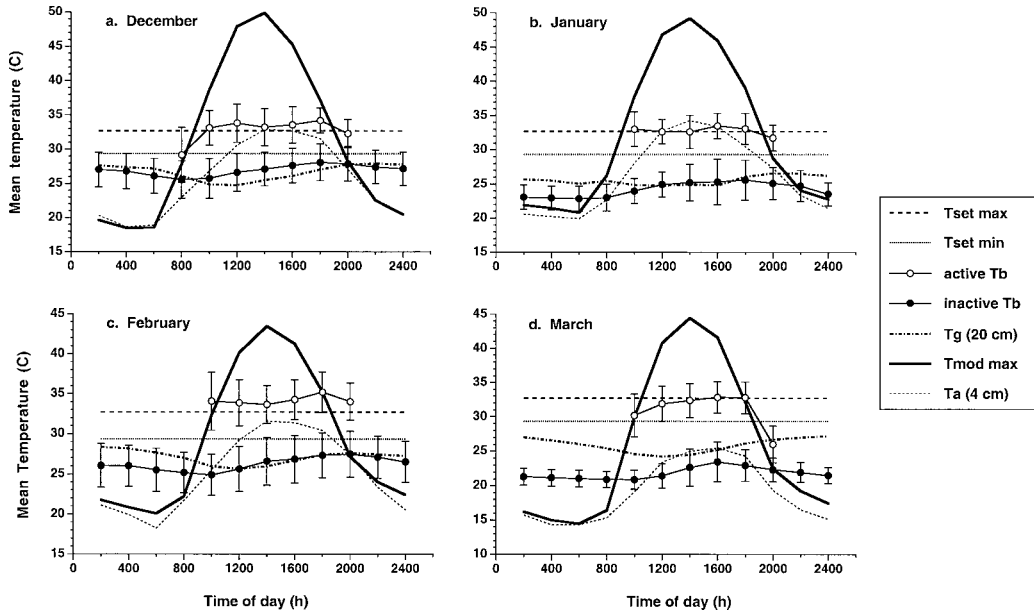Reproduction also affected seasonal patterns in the use of burrows by the snakes,

FIG. 3.—Body temperatures of radio-tracked free-ranging brownsnakes in relation to the snake's location ("active" = above-ground; "inactive" = below-ground), and associated environmental temperatures over the period December to March. The environmental temperatures include ground temperature 20 cm below the soil surface (Tg (20 cm)), air temperature 4 cm above the ground (Ta (4 cm)) and operative temperature inside a copper model exposed to full sun (Tmod max). The graphs also show the temperature range selected by captive snakes (Tset, incorporating the central 50% of records from captive animals).

and hence temperatures. By December, T_g below 30 cm became generally cooler than at shallower soil depths (Fig. 6b). Between late December and early January, the gravid females laid their eggs at a mean depth of approximately 30 cm (distance between the ground surface and the top of nesting chambers, mean = 29.4 cm, n = 10, 1 SD

= 1.17). This mean depth included separate egg masses we examined in a communal nest, where six females laid their eggs in different parts of the same large burrow system (in late 1993), and egg masses in individual burrows (nests of *Mus domesticus*) elsewhere on the refuge area (in early 1996). Mean temperature of these
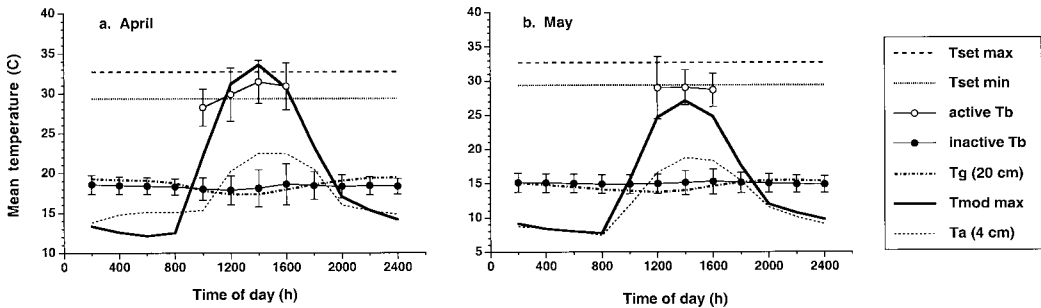

FIG. 4.—Body temperatures of radio-tracked free-ranging brownsnakes in relation to the snake's location ("active" = above-ground; "inactive" = below-ground), and associated environmental temperatures over the period April to May. The environmental temperatures include ground temperature 20 cm below the soil surface (Tg (20 cm)), air temperature 4 cm above the ground (Ta (4 cm)) and operative temperature inside a copper model exposed to full sun (Tmod max). The graphs also show the temperature range selected by captive snakes (Tset, incorporating the central 50% of records from captive animals).
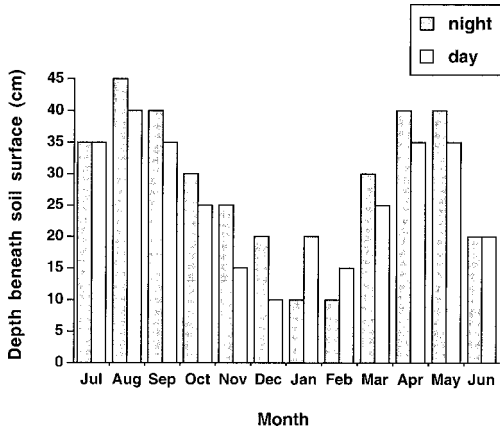
FIG. 5.—Monthly variation in the mean depth of telemetered brownsnakes under the soil surface, as inferred from temperatures of the snakes relative to soil thermal profiles measured at the same time. Data are shown separately for day and night. See text for statistical tests of these data.

burrows (where both egg masses and attending females occurred) was 29.0 C (range 27.4–31.7 C, $n = 349$, 1 SD = 0.7 C), taken over 7 d. Hence, nest temperatures tended to be warmer and more thermally stable than the mean temperature of burrows elsewhere (Fig. 6b).

Throughout most of the year, the snakes were shallower in the soil during daylight hours than they were at night. This pattern reversed in mid-summer (mid-January through February, Fig. 5) and presumably reflects high temperatures near the soil surface during daylight in mid-summer. During hot conditions late in summer, the snakes generally occupied relatively deep burrows (Figs. 5, 6c). During daylight hours in late February and March, inactive snakes tended to exploit deep burrows in relatively cool areas (e.g., crayfish burrows in ditches or burrows on southern aspects). That is, during very hot weather, either the snakes remained sequestered inside deep burrows and ceased hunting or they remained in relatively shallow burrows (*Mus*) where they could hunt but would be exposed to higher and more variable temperatures. Most snakes stayed below ground throughout winter, although unusually warm weather in early winter (June) brought the snakes closer to the soil

surface (approximately 20 cm depth: Figs. 5, 6d).

The Link between Temperature and Activity Patterns

Above, we have shown that temperature profiles in the soil varied so consistently with depth in the study area that these could be used to estimate the position (distance below the ground surface) of inactive snakes. The thermal environment above ground is far more complex and is heterogeneous over a much finer scale— in both spatial and temporal axes. Nonetheless, our data suggest that broad patterns in the activity of brownsnakes can be predicted from (and likely, are determined by) aspects of the ambient thermal environment. Below, we deal with two such aspects: the time of day that the snakes emerged from their shelter sites, and the time they returned to these sites after concluding their activities for the day.

(1) Thermal correlates of emergence.— The time that a snake emerged from its overnight shelter site was strongly associated with shallow (10 cm) soil temperature. Overall mean T_b at emergence averaged 25.6 C ($n = 626$, 1 SD = 4.6, range 13.2–36.7 C), but this was strongly dependent on the time of year (ANOVA with month as the factor, $F_{10,615} = 50.67$, $P < 0.0001$, mean monthly range = 17.3 C in August to 29.1 C in February). Emergence T_b was more highly correlated with T_g at 10 cm depth than with temperature at any other soil depth we monitored (Table 1, Fig. 7a). We also examined the relationship between T_b and T_g at shallow depths within 30 min prior to emergence. Overall mean preemergence T_b was 18.8 C ($n = 182$, 1 SD = 4.3, range 10.6–29.7 C), and again was most closely correlated with T_g 10 cm (for preemergence T_b and T_g at 10 cm: $r^2 = 0.79$, $P < 0.0001$; Fig. 7b). Therefore, both the emergence and preemergence T_b data suggest that soil temperature at 10 cm depth was strongly associated with the timing of daily emergence. Moreover, in every case where preemergence T_b was known, daily T_g profiles at other than 10 cm depth had either been increasing for some time (5 cm depth) or
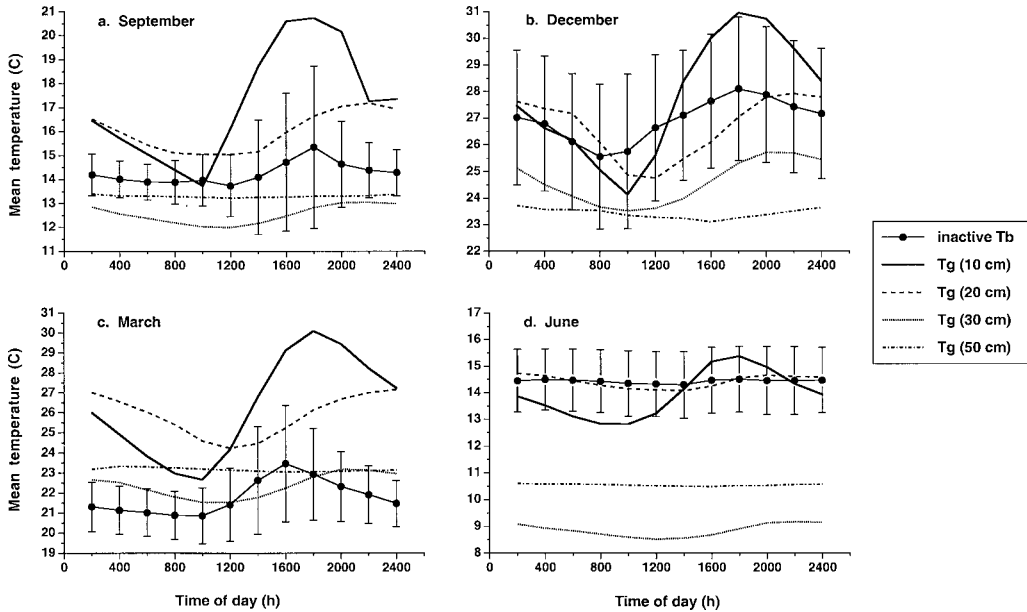
FIG. 6.—Body temperatures of inactive brownsnakes compared to simultaneously-measured soil temperatures at various depths (10, 20, 30 and 50 cm beneath the ground's surface).

had not yet begun to increase (>10 cm depth). Soil temperature at 10 cm depth, however, had either stabilized at its lowest point in the daily cycle (i.e., ceased in its daily decrease, 6% of records) or had begun to increase (within 30 min of emergence, 94% of records). This result suggests that brownsnakes in the study area use a simple rule on the days they emerge from burrows: "emerge when soil temperature at 10 cm begins to increase."

Soil temperature at 10 cm depth was also a more reliable predictor for the timing of daily emergence than any of the above

TABLE 1.—Results of linear regression analyses for the relationship between environmental temperatures and three facets of brownsnake biology (time of emergence from shelter sites, body temperature at emergence, and the duration of daily activity). Data for days where active snakes moved outside of receiver range at some point during the day have been excluded from analyses concerning the duration of activity. Definitions of abbreviations, and explanations for how they were measured, are provided in the text. T_b = body temperature; emergence T_b = body temperature at the time that the snake first emerged from its burrow. T_g = temperature in the ground at various depths; T_{mod} = internal temperature of copper models in the warmest available situation on the ground surface ($T_{mod\ max}$) or in the shade ($T_{mod\ (shade)}$), or on a NE-facing slope ($T_{mod\ (NE\ slope)}$), or on a flat surface ($T_{mod\ (flat\ surface)}$). VT_{min} = minimum selected temperature in the laboratory. T_{set} = range of 50% of central values for body temperatures of snakes in the laboratory.

| Independent variable	Dependent variable	Slope =	n	r^2
Time of day that VT_{min} equaled $T_{mod\ max}$	time of emergence	563.0 + 0.554x	218	0.104
Time of day that T_{set} equaled $T_{mod\ max}$	time of emergence	519.479 + 0.569x	217	0.106
T_g at 10 cm depth	emergence T_b	9.350 + 0.763x	208	0.461
T_g at 20 cm depth	emergence T_b	6.922 + 0.869x	176	0.447
T_a at 4 cm height	emergence T_b	13.310 + 0.496x	210	0.301
$T_{mod\ max}$	emergence T_b	13.338 + 0.307x	210	0.190
$T_{mod\ (NE\ slope)}$	emergence T_b	13.349 + 0.307x	210	0.190
$T_{mod\ (flat\ surface)}$	emergence T_b	13.930 + 0.245x	210	0.245
$T_{mod\ (shade)}$	emergence T_b	17.579 + 0.341x	191	0.332
Hours that $T_{mod\ max}$ exceeded VT_{min}	hours that snake was active	0.148 + 0.481x	126	0.202
Hours that $T_{mod\ max}$ exceeded T_{set}	hours that snake was active	0.827 + 0.472x	125	0.159
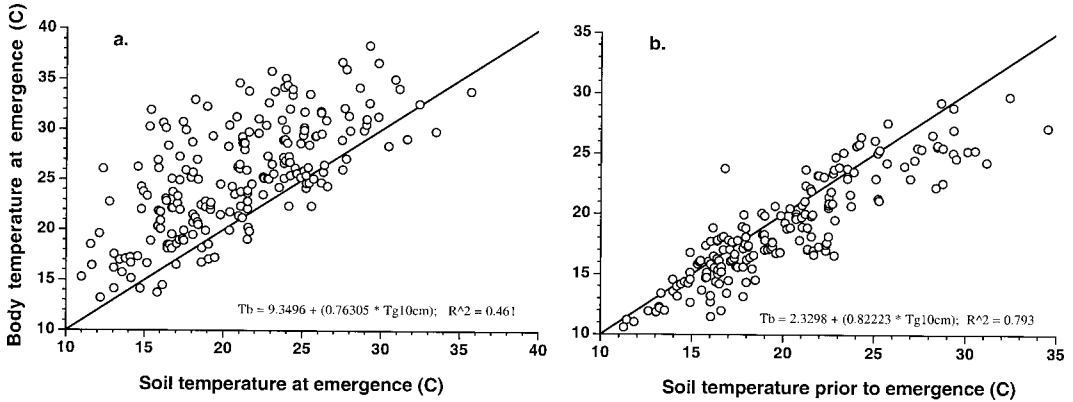
FIG. 7.—Body temperatures of radio-tracked brownsnakes at the time that they emerged from their burrows, compared to the temperatures of the surrounding soil at 10 cm depth. The left graph (a) shows data for both variables at the time of emergence, whereas the right graph (b) shows data for the period 30 min prior to emergence. The diagonal lines show a slope of 1.0, where values are identical for the two axes.

ground indices, although the shaded environmental temperatures (T_a and $T_{mod \, (shade)}$) were also highly correlated with the body temperatures of emerging snakes (Table 1). The snakes generally emerged well after $T_{mod \, max}$ reached VT_{min}, especially if this occurred early in the day (Fig. 8). When $T_{mod \, max}$ exceeded minimum T_{set}, the model was less reliable for indicating the emergence of the snakes above ground. This was
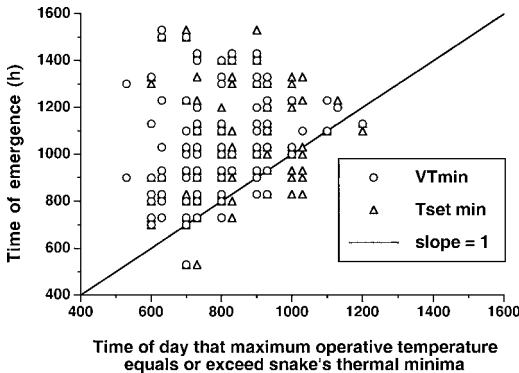

FIG. 8.—The time of day that radio-tracked brownsnakes emerged from their overnight burrows, compared to the time at which the temperature inside a copper model in full sunlight (Tmod max) equaled or exceeded the snakes' minimum voluntary temperature (VTmin) or the lower "preferred" range (Tset min) as determined in the laboratory. The snakes rarely emerged before this threshold was reached, but often delayed emergence for much longer on very hot days. The diagonal line shows a slope of 1.0, where values are identical for the two axes.

because the snakes often ventured above ground before $T_{mod \, max}$ reached T_{set} and remained there until it fell below VT_{min} in the afternoon (below). Hence, all of the above ground indices we measured were generally inferior to T_g for indicating the timing of daily emergence.

(2) *Thermal correlates of the duration of daily activity.*—Operative model temperature is the variable most likely to reflect thermal opportunity, and thus the duration of daily activity, because it tracks available radiation and attainable T_b through the day. Maximum temperatures are likely to be most important in determining daily activity, as the snakes always have access to cooler conditions (e.g., while in deep shade or in water). Consequently, $T_{mod \, max}$ can be expected to set the upper limit for available activity time in our study area. This prediction was supported by our data (Fig. 9). The numbers of hours spent active by the snakes were positively correlated with the "available activity time" as predicted from the physical models (i.e., the number of hours $T_{mod \, max} \geq VT_{min}$; see Table 1). Hence, the availability of solar radiation (as indicated by operative temperature) limited brownsnake activity time.

The intensity of solar radiation (in combination with ambient temperature), as inferred from our models, often predicted brownsnake location as well as activity

time. Unsurprisingly, the snakes tended to restrict their above ground activity to shaded areas underneath vegetation in conditions of intense solar radiation. During the warmest months, $T_{mod\ max}$ was often above T_{set} by mid-morning, and the snakes often sought cover shortly after emergence from their burrows (see the approximate length of "available activity time" in Figs. 2–4). The snakes were generally under cover or inside burrows when $T_{mod\ max} \geq 37$ C. Hence, the snakes showed a bimodal pattern of activity on hot days, being active in the mid-morning and again in the late afternoon (and see Whitaker and Shine, 1999).

It is of interest to know not only whether or not snake behavior is predictable from environmental temperatures (above), but also what overall patterns of activity result from these thermal associations. Below, we review major features of brownsnake activity in this light.

Relative Proportion of Time Spent Above Ground versus Below Ground

We obtained activity data based on relative temperature during three active and two inactive seasons (winters), including 2567 snake days during the active season and 3247 snake days overall (including winter). On average, the snakes were active (≥ 30 min each day) on 43.8% ($n = 1125$) of days during the active season and 35.8% ($n = 1162$) of all days. Overall, daily activity differed strongly among seasons and months (repeated measures ANOVA, for 11 snakes continuously monitored for 10 d each month over three active seasons, with season as the independent variable and number of activity days for each snake as the dependent variable: $F_{3,30} = 42.79$, $P < 0.0001$). Activity days showed a strongly bimodal pattern during the year (Fig. 10a), peaking in mid- to late spring (approximately mid-October through November) and again in late summer (approximately through February to mid-March). Activity was low during mid-summer (late December through January) and again during winter (late May to late August). No telemetered snake was recorded above ground in July (the coldest month).
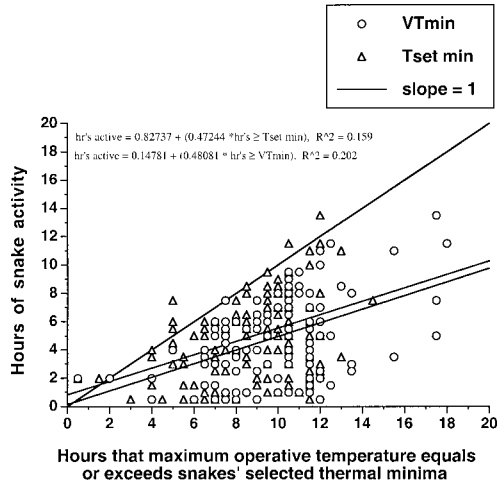

FIG. 9.—The duration of daily activity of radio-tracked brownsnakes, compared to the time period on the same day during which a copper model in full sunlight (Tmod max) equaled or exceeded the snakes' minimum voluntary temperature (VTmin) or the lower 'preferred' range (Tset min) as determined in the laboratory. The upper diagonal line shows a slope of 1.0, where values are identical for the two axes. The two lower lines are fitted to the data by least-squares regression.

The mean number of hours that the snakes spent above ground each day also varied among seasons (repeated measures ANOVA, for 12 snakes monitored in each season, with season as the independent variable and the mean number of hours each snake was active as the dependent variable: $F_{3,33} = 35.85$, $P < 0.0001$). These data also showed an annual bimodal pattern, with the time spent above ground each day corresponding to seasonal peaks in the frequency of activity (above, and see Fig. 11). Overall, the average time spent by the snakes above ground on any given day was 4.9 h (20.4% of the day, $n = 460$, 1 SD = 3.7). Hence, as the snakes were active on 35.8% of all days (above), we estimate that the telemetered snakes spent an overall annual mean of 92.7% of all hours below ground. Some snakes spent >48 consecutive hours (maximum = 65.5 h) on the ground surface underneath low vegetation during February in drought, however, and this strongly influenced the overall figures (Fig. 11). These nocturnal occurrences (where the snakes remained
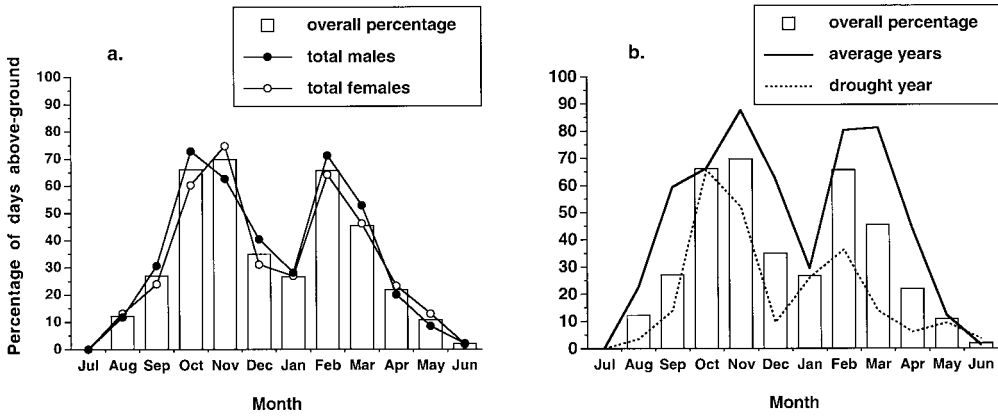
FIG. 10.—Monthly variation in the percentage of days that radio-tracked brownsnakes were recorded as "active" (i.e., emerged from their burrows). Data are shown separately for males and females (left graph) and for years with normal rainfall versus drought (right graph).

above the ground surface) were always associated with high ambient temperatures over several days (e.g., Fig. 3c, and see below).

Sex Differences in Activity Patterns

Overall, there was no significant difference in the number of days each month males versus females occurred above ground (repeated measures ANOVA with sex as the factor: $F_{1,11} = 0.20$, $P = 0.67$). However, males were significantly more
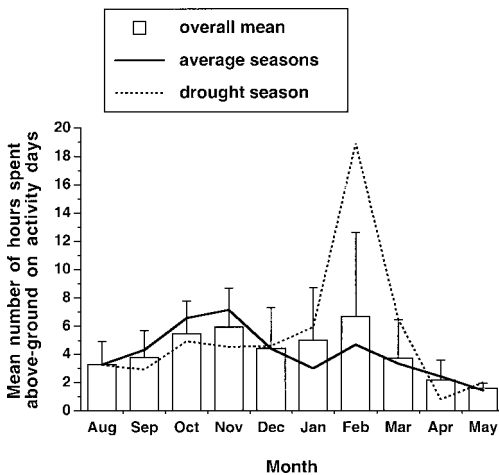

FIG. 11.—Monthly variation in the duration of activity per day (i.e., number of hours per day outside their burrows) in radio-tracked brownsnakes, in years with normal rainfall versus drought. Error bars show one standard deviation.

likely than females to occur above ground in early spring (with continuity correction applied to 2 × 2 contingency table, $\chi^2 = 4.84$, df = 1, $P < 0.05$). Overall, 100% of adult males ($n = 10$) and 54% of adult females ($n = 13$) emerged from winter inactivity between the last week of August and the first week of September (see Whitaker, 1999, for difference between the sexes in timing of winter inactivity).

Similarly, there was no significant overall difference between the two sexes in their duration of daily activity each month (repeated measures ANOVA with sex as the factor, $F_{1,11} = 1.53$, $P = 0.24$). However, females spent significantly fewer hours active than did males in December [$F_{1,46} = 23.34$, $P < 0.0001$; mean = 3.1 h ($n = 29$, 1 SD = 2.53) and 6.4 h ($n = 19$, 1 SD = 1.94), respectively]. This difference reflects reproductive behavior; reproductive females often stayed underground at this time of year and remained with their eggs following oviposition.

Effects of Drought

Drought conditions were experienced during the second year of study (for rainfall details, see Whitaker, 1999). Although the snakes were less frequently active during drought (Fig. 10b), the mean number of hours spent above ground on activity days increased significantly at this time (repeated measures ANOVA with active

season as the independent variable and mean number of hours spent above ground during summer months as the dependent variable: $F_{1,8}$ = 13.31, P < 0.01). In the two near average rainfall active seasons, the mean duration of daily activity was 4.5 h (n = 312, 1 SD = 2.6), compared to 5.7 h (n = 148, 1 SD = 5.2) during drought. During the drought summer, however, this difference became pronounced: mean hours spent active in the drought summer = 10.23 h (n = 28, 1 SD = 7.8), compared to 4.44 h (n = 112, 1 SD = 2.5) in average rainfall summers. In average years, daily activity was longest in late spring, and the time spent above ground tended to become progressively shorter as the active season progressed (Fig. 11). During drought, however, daily activity was longest in summer when the frequency of activity was decreased (above).

DISCUSSION

Our study is by no means the first to use radiotelemetry data to infer patterns of activity in snakes. We suspect that many workers have used changes in body temperature to assess when their study animals have emerged from nocturnal shelter sites and when they have retreated to those sites. However, this technique has generally been used as an adjunct to direct observation. In our case, the study animals were so elusive that we had to rely almost entirely on telemetry signals to infer patterns of activity. Importantly, we also monitored subsurface thermal profiles in enough detail to assess the locations of the snakes even when they were beneath the ground surface. This aspect proved to be important, because one of the main conclusions to emerge from our work is the fact that the snakes spend a remarkably high proportion of their time below ground. Hence, a full understanding of their biology requires knowledge of movements below as well as above the soil surface.

The study site provided several logistical advantages that facilitated our attempts to relate snake activity to ambient thermal conditions. First, the site is relatively flat and virtually treeless, reducing the spatial thermal heterogeneity that otherwise would be engendered by variations in slope and vegetation cover. Second, cover items, such as fallen logs, are scarce in this agricultural landscape, forcing the snakes to use only one main kind of retreat site (burrows in the soil). Third, the soils in the area are relatively homogeneous and do not contain large rocks (at levels occupied by the snakes) that would otherwise complicate the relationship between soil depth and temperature. In total, our site offered a relatively homogeneous thermal profile, so that most of the thermal variation was linked to temporal rather than spatial heterogeneity. This consistency made it much easier for us to detect associations between snake behavior and ambient temperatures.

One advantage of quantifying the link between environmental temperatures and snake activity (rather than simply documenting the times and places that snakes are active) is that the relationship between abiotic and biotic factors may provide insights into the causal factors that influence snake behavior. For example, our correlative data suggest that snakes use an increase in shallow (10 cm) soil temperature as the cue to emerge from their overnight retreat site. If experimental studies confirm that this is indeed the cue, then it should be relatively simple to predict emergence times (and thus, the times of elevated risk of snakebite, etc.) in other study areas. Similarly, data on burrow depths of over wintering snakes, relative to thermal profiles in the soil, could be used to predict over wintering depths of snakes in study areas with different climatic or soil characteristics.

The general picture that emerges from our data is of a species that actively selects high and relatively constant body temperatures. Snakes basked for long periods in cool weather and maintained internal temperatures within a surprisingly narrow range throughout the activity period (e.g., Figs. 2–4). In this respect, eastern brownsnakes resemble other fast moving, slender bodied, diurnal, and heliothermic snake species, such as North American "racers" (e.g., *Masticophis*, Hammerson, 1979).

Presumably, high body temperatures enhance locomotor performance (e.g., Peterson et al., 1993), permitting these snakes to exploit open habitats, where they may often encounter predators while far from escape holes.

Although the snakes may benefit from restricting their activity to times when they can maintain high stable body temperatures, this stenothermy may entail costs as well as benefits. Given the strong seasonal shifts in ambient temperatures, the restriction of activity of the snakes to periods of approximately optimal thermal conditions most of the year inevitably results in their spending long periods inactive when conditions are unsuitable. Thus, two of the main results from our study—the high and approximately constant body temperatures of active *P. textilis* and their very limited periods of activity—may be functionally related and reflect an underlying trade off between thermoregulatory precision and the overall proportion of time spent in activity. The importance of such a trade off presumably differs in relation to a number of traits of the species (e.g., a small animal may be able to heat much faster) and the environment (e.g., some environments may allow stenothermy with little overt thermoregulatory behavior, e.g., Huey et al., 1989; Shine and Madsen, 1996).

In their maintenance of high temperatures when active, brownsnakes and similar species of snakes may resemble heliothermic lizards to a greater degree than is true of most snakes. Snakes tend to maintain lower and more variable body temperatures than do many types of sympatric lizards (e.g., Avery, 1982). In turn, this difference probably reflects divergences in body size and shape between the two lineages. Snakes are typically much larger and more elongate than lizards, and both of these attributes may constrain the ability of the animal to maintain high constant body temperatures in the face of a variable thermal environment (e.g., Avery, 1982; Bartholomew, 1982). Foraging biology, as well as escape from predators (see above), may affect the costs and benefits of precise thermoregulation. Ambush predators may be under strong selection to remain im-

mobile, and hence may need to accept relatively variable body temperatures (e.g., Secor, 1994). In contrast, overt thermoregulatory behavior is not inconsistent with active foraging and, thus, may be favored so long as its advantages (e.g., enhanced speed) compensate for the time, effort and risk required for these activities. The reliance of the brownsnake on a very fast moving agile prey species (house mice) may place a special premium on the locomotor advantages likely to accrue from precise thermoregulation.

Some of the activity patterns that we observed can be interpreted in the light of other results from our telemetry study. For example, peaks in both the frequency and length of activity corresponded to periods when adult female snakes focused on hunting. This behavior occurred immediately following spring mating and after the females left their eggs in mid- to late summer. Overall, however, the sexes showed no significant difference among seasons in the frequency or length of daily activity, as activity was similarly reduced in both sexes during summer and winter. This result was surprising, as adult males move more frequently and cover greater distances between successive shelter sites than do females (Whitaker, 1999). The subjective impression that males are the more active sex (especially in spring) reflects their more overt and frequent movements rather than a sex difference in the proportion of time spent active. Activity was less frequent in adult females in early spring, however, when they tended to remain near or in their over wintering burrows, and it was also less frequent in early to mid-summer due to nesting (Whitaker, 1999).

Drought is known to strongly influence reproduction, activity, and movements of a number of taxa, including snakes (e.g., Shine, 1987; White and Kolb, 1974), and it had a strong influence on both the frequency and length of daily activity of our telemetered brownsnakes. During drought, the snakes failed to reproduce (Whitaker, 1999), the frequency of activity was greatly reduced, and the number of hours spent on the ground surface was greatly reduced during the first half of the active season.

Reduced activity in response to prey shortage has been reported in other snakes (e.g., Andrén, 1982). However, during the drought affected summer, the mean number of hours spent on the ground surface increased significantly during spells of hot weather. This was the only time during our 3-yr study when most snakes were above ground at night.

Our results have strong implications for the potential risk of snakebite from *P. textilis*. The data are encouraging in that, even in a relatively dense population of brownsnakes, few of the animals are likely to be active (i.e., above ground) at most times. The probability of encountering a snake is likely to be highest in spring and in late summer/autumn, reflecting the bimodal activity pattern of the snakes. To predict the times of day when snakes are likely to be active, knowledge of thermal profiles at 10 cm under the soil surface may be useful. Operative temperatures, as measured by simple copper models, may provide insight into the location of the snake after that time (i.e., whether the animals are likely to be in the open or under shade) and also on the time of day the animals are likely to retreat to their nocturnal shelters. The apparent seasonal and daily migration of the snakes within the soil column has obvious implications for the probability of encountering a (highly aroused) specimen in the course of agricultural activities (such as ploughing) involving the disturbance of subsurface soil.

In summary, our study suggests that the precise thermoregulatory preferences of adult brownsnakes generate consistent patterns in the ways in which ambient thermal variations correlate with (and presumably determine) the times and places at which the snakes are active. For a more eurythermic study species, or in a warmer climate where optimal temperatures are easier to attain, we would not expect to see such a strong link between microclimate and snake activity. The consistent relationships that we documented between environmental variables and emergence times suggest that we may be able to predict snake behavior from simple monitoring of thermal regimes in the environment. In this way, research into thermoregulatory biology may help to reduce the risks potentially associated with encounters between people and dangerously venomous snakes.

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