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BODY TEMPERATURE VARIATIONS OF THE LOUISIANA PINE SNAKE (*PITUOPHIS RUTHVENI*) IN A LONGLEAF PINE ECOSYSTEM

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Abstract. The thermal ecology of the Louisiana pine snake, *Pituophis ruthveni*, was studied from 1993–97 in Louisiana and Texas. All snakes were implanted with temperature-sensitive radiotransmitters. Temperatures were recorded from snakes located above ground and underground and were compared between size and sex classes (juveniles, adult males, adult females). Associated air and substrate temperatures were also recorded. Collectively, body temperatures of snakes were lowest during winter (11.4°C), increased during spring (22.3°C), peaked during summer (27.7°C), and decreased during autumn (22.7°C). Seasonal body temperatures were most similar between juveniles and adult males, primarily because adult females had higher body temperatures during summer. During spring and autumn, snake, air, and substrate temperatures were generally 3–4°C higher above-ground than underground. Temperatures of snakes of all size and sex classes increased from morning through evening and most closely approximated the air and substrate temperatures at 1800 h and 1900 h, when snakes were located predominantly underground. Temperatures of juveniles and adult males showed no consistent relationship to air or substrate temperatures from 0700–1700 h. However, temperatures of adult females were significantly lower than air temperature from 1000–1600 h. Temperatures of juveniles and adult males were significantly higher above ground than underground from 1100–1400 h and 1100–1700 h, respectively, with no consistent relationship between hourly above-ground and underground temperatures of adult females. Overall, temperature patterns of *P. ruthveni* and *P. catenifer deserticola* appear to be similar, except that *P. c. deserticola* maintains higher temperatures in the spring than does *P. ruthveni*.

Key Words. Body temperature; Longleaf pine; Louisiana pine snake; *Pituophis ruthveni*; Thermal ecology.

The body temperature of snakes has a profound effect on most, if not all, facets of their ecology. Snakes are nearly exclusively ectothermic, deriving their body heat primarily from external (environmental) sources. Thus, body temperature in snakes (and thus the level and type of activity in which snakes are physiologically capable of engaging) is limited by the range of thermal conditions available in the environment (Peterson et al. 1993). The thermal environment itself is subject to daily and seasonal fluctuations and thus body temperature in snakes may be expected to fluctuate accordingly. However, most snakes are very adept at behavioral thermoregulation in an effort to offset (at least partially) the potentially debilitating effects of suboptimal thermal conditions, resulting in a corresponding change in the types of activities in which snakes may engage (Heatwole and Taylor 1987). Consequently, the timing of basic and essential

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activities, such as those associated with foraging and reproduction, is proximately determined by body temperature and ultimately determined by the thermal environment (Lillywhite 1987).

Peterson et al. (1993) posed five fundamental questions about thermal ecology and associated body temperature variation. These questions aim to assess (1) the range of possible body temperatures under natural conditions; (2) the proximate factors that determine which body temperatures a snake selects from that range of possibilities; (3) the variation of body temperatures of individual snakes under natural conditions over extended periods of time; (4) the functional effects (i.e., developmental, physiological, behavioral) of body-temperature variation; and (5) the ecological consequences of body-temperature variation. Ideally, studies on the thermal ecology of snakes should cover each of these five areas.

Our main objective was to assemble data to cover these five areas of Peterson et al. (1993) for the Louisiana pine snake, *Pituophis ruthveni*. This species is a highly threatened endemic of the relictual longleaf pine forests of western Louisiana and adjacent Texas (Jennings and Fritts 1983; Reichling 1988; Rudolph and Burgdorf 1997). The few remaining natural populations of *P. ruthveni* are highly disjunct and occur at extremely low densities. Until the 1990s, when *P. ruthveni* was known in the wild from only 100 specimens (Rudolph, unpubl. data) and the U.S. Forest Service initiated an intensive ecological project on this species, no quantitative studies had been conducted on the natural history of *P. ruthveni*. In fact, what little information is available on *P. ruthveni* (e.g., morphological variation, reproductive biology) was collected from snakes maintained in captivity (e.g., Reichling 1989), and nothing, to our knowledge, has been reported on the thermal ecology of *P. ruthveni*.

Pituophis ruthveni occurs in a unique habitat that is distinctive from that of other species of *Pituophis*. In addition, clutch sizes of *P. ruthveni* (*n* = 4 eggs; no deviation from mean) are smaller than those of all other species of *Pituophis*, and its eggs (mean length = 11.94 ± 0.88 [95% CI] cm, 10.00–13.00 cm, *n* = 8; mean width = 3.56 ± 0.33 cm, range 3.00–4.00 cm, *n* = 8) and hatchlings (mean total length = 54.4 ± 2.5 cm, range 52.0–55.5 cm, *n* = 4; mean mass = 106.7 ± 5.7 g, range 104.0–108.0 g, *n* = 3) are the largest of all snakes in the United States (Reichling 1989, 1990). Thus, the energetics of growing the exceedingly large eggs would suggest that gravid females spend more time basking, thus gaining heat energy needed for the physiological demands of vitellogenesis. On the other hand, this species is highly fossorial (Himes et al. 2005), which would seem to contradict the higher thermal needs of egg development. Therefore, understanding more about the thermal relationship of the Louisiana pine snake to its environment might contribute to a better understanding of the thermal ecology of species with extreme reproductive characteristics.

Mean cloacal temperatures of other taxa of *Pituophis* include 25.5°C in *P. c. catenifer* (Cunningham 1966), 28.0°C in *P. c. sayi* (Fitch 1956), and 28.6°C in *P. c. deserticola* (Diller and Wallace 1996). In all three studies, temperatures were recorded from snakes only once and thus daily and seasonal fluctuations in body temperature could not be determined. Daily fluctuations in body temperature of single individuals of *P. c. sayi* (Dill 1972) and *P. c. deserticola* (Parker and Brown 1980) varied from 26–32°C and 19–35°C, respectively. However, snakes were monitored over a one- to two-day period and thus seasonal fluctuations in body temperature could not be determined.

Parker and Brown (1980) recorded 155 cloacal temperatures from *P. c. deserticola* that emerged from or retreated into a communal hibernaculum during spring (*n* = 44) and autumn (*n* = 38), respectively. Cloacal temperatures were significantly higher in spring (mean = 27.88°C) than in autumn (mean = 24.43°C). However, no temperatures were recorded from snakes during winter and temperature differences by size and sex class were not noted.

Parker and Brown (1980) also recorded 416 body temperatures from nine *P. c. deserticola* implanted with temperature-sensitive radiotransmitters. The mean body temperature of surface-active snakes from spring through autumn averaged 27.9°C. Mean inactive body temperatures of snakes underground and under rocks varied from 19.68°C (autumn) to 27.01°C (summer) and approximately 12°C (autumn) to 24°C (summer), respectively. Body temperatures of snakes underground were below air and insolated substrate temperatures, similar to shaded substrate temperatures, and significantly higher in summer compared to autumn. When snakes were under rocks, body temperatures were similar to air and shaded substrate temperatures, consistently below insolated substrate temperatures, and significantly higher during cloudy days in summer compared to spring. Again, no temperatures were recorded from snakes during winter and temperature differences by size and sex class were not noted.

Greenwald (1971) determined that the aerobic energy available for activity (metabolic scope) of *P. catenifer affinis* was maximum at a body temperature of 30°C. In 1974, Greenwald determined that strike velocity and frequency of prey capture were maximum at body temperatures of 27°C and 33°C, respectively. This was a rather surprising finding because it indicated that snakes captured prey less frequently at a lower temperature (27°C), when strike velocity was greatest. Thus, from these data, it is difficult to determine the preferred range of active body temperature in *P. c. affinis*. However, it is clear from these findings that there is a complicated relationship among body temperature, behavior, and the metabolic scope in *Pituophis*.

All *Pituophis* for which body temperature data are available occur in open habitats with few trees (e.g., grasslands, brushlands, deserts) of the midwestern and western United States. In contrast, *P. ruthveni* occurs predominantly in pine forests (Dundee and Rossman 1989; Rudolph and Burgdorf 1997). These habitats have different thermal qualities that may result in different thermal relationships between the snakes and their environment. For example, solar radiation and conduction should be less intense on the forest floor than in a desert. In fact, thigmothermy is an important heat exchange mechanism used by many ectotherms, including *Pituophis* living in deserts (Sullivan 1981).

As part of a range-wide natural history study on *P. ruthveni*, eight juveniles, 17 adult males and 13 adult females were implanted with temperature-sensitive radiotransmitters and individually studied for up to 43 mo in Louisiana and Texas from 1993–97. Temperatures were recorded of all 38 snakes, during all seasons and hours of the day (over the course of the five-year period), and when snakes were located above-ground (on the surface and generally amid thick herbaceous vegetation) and underground (generally in self-made burrows or in burrows excavated by pocket gophers [*Geomys breviceps*] or moles [*Scalopus aquaticus*]). Comparisons of body, substrate, and air temperatures helped us determine the thermoregulatory capability of *P. ruthveni*. In addition, we determined the effects that size and sex class of snakes and the time of year and day have on the thermal ecology of *P. ruthveni*.

MATERIALS AND METHODS

Study Areas

This study was conducted within the historic longleaf pine (*Pinus palustris*) region of Bienville, Sabine, and Vernon Parishes in Louisiana, and in Angelina, Jasper, Newton, and Sabine Counties in Texas. Sandhills that are dissected by intermittent and small perennial streams characterize all sites. Pine forest consisting of longleaf pine, shortleaf pine (*P. echinata*), loblolly pine (*P. taeda*), and the introduced slash pine (*P. elliottii*), with occasional hardwoods, dominates the uplands. By contrast, several species of hardwoods (*Carya* spp., *Fagus grandifolia*, *Liquidambar styraciflua*, *Nyssa sylvatica*, *Quercus* spp., etc.) dominate the lowland areas. At most sites, silvicultural practices have resulted in the formation of clearcuts and pine plantations, as well as in the suppression of fire, leading to hardwood encroachment and consequential suppression of herbaceous vegetation.

Survey Methods and Study Subjects

Snakes were trapped and hand-captured from 1993–97. Traps were constructed of a plywood frame, top, and bottom, and hardware cloth walls (6-mm mesh), forming 1.3 x 1.3 x 0.3 m boxes with a funnel entrance on each side to permit entry of snakes. Drift fences, also of 6-mm hardware cloth (height = 0.5 m), extended for 16 m from each funnel entrance. Traps were operated on a variable schedule at 10–15 sites during the months of March–October.

Wild-caught snakes were obtained at (n = 26 snakes) or near (n = 4) one of the study sites. In addition, eight captive-bred snakes obtained from the Memphis Zoo and Aquarium (MZA) were used in this study. These latter snakes were the offspring of snakes from Bienville Parish that were used to establish a captive breeding program (S. Reichling, pers. comm. 1995). Prior to shipping from Memphis, these snakes were inspected by an accredited veterinarian from the American Association of Zoo Veterinarians and were determined to show no signs of disease. Specific identification numbers were assigned to each snake, and sex, length, and mass were recorded of all snakes immediately before and after the study (see Table 1 in Himes et al. 2002).

Surgical Procedures and Transmitter Implantation

Snakes were implanted either subcutaneously (Sabine Parish, Vernon Parish, and Texas snakes) or intraperitoneally (Bienville Parish and MZA snakes) with SI-2T transmitters (44 x 10 mm, 12 g; Holohil Systems LTD, Carp, Ontario, Canada), each of which was equipped with a 20 cm whip antenna (see Reinert and Cundall [1982] and Weatherhead and Anderka [1984]). The transmitter mass exceeded 5% of the body mass of one snake (a juvenile); this individual survived and showed no ill effects throughout the study. Anesthesia was achieved by intramuscular injection (80 mg/(kg • snake) of Ketamine (Mallinckrodt Veterinary, Inc., Mundelein, Illinois, USA; Sabine Parish, Vernon Parish, and Texas snakes) or inhalation of Halothane (Ayerst Labs, Inc., New York, USA; Bienville Parish and MZA snakes). All transmitters had an approximate battery life of 18 mo and were replaced as necessary.

Each snake was only handled during surgery (once every 14–15 mo). Thus, reproductive status could not be determined and gravid and non-gravid females were not distinguished. Sexual maturity, although not known for *P. ruthveni* in the wild, is attained at 3–4 yr of age in other species of *Pituophis* (Fitch 1970). Therefore, we considered our captive snakes, which were 1-yr-olds (and did not exceed 101 cm in total length) at the time of their release, to be juveniles. One wild-caught snake, which had a comparable initial total length and snout–vent length, but lower initial mass than all captive juveniles, was also considered to be a juvenile. All other wild-caught snakes exceeded 120 cm in total length at the time of their release and thus were considered to be adults.

When not in surgery, one to two snakes were maintained in fiberglass and plastic cages (56 x 30 x 23 cm) at 20–25°C, with an approximate 12 h:12 h light:dark photoperiod. Additional heat was supplied by lamps and heating pads. Fresh water was provided *ad libitum* and one freshly killed mouse was offered as food once a day to each snake. The interior of each cage was washed with soap and rinsed clean every other day and the exterior was covered with newspaper to minimize disturbance to snakes.

Release and Radiotracking Protocols

Snakes were allowed 2–14 d for recovery in the lab prior to release. Twenty-six of 30 wild-caught snakes were released at their point of capture. The remaining four wild-caught snakes were captured by local residents in nearby areas of Bienville Parish that were not accessible for telemetry studies and were at risk because of adjacent highways. These snakes were released at safe distances (5-40 km from their point of capture) and where other snakes were under observation. The risks to the four repatriated snakes and their receiving populations were considered to be less than the imminent danger posed by a busy highway and much human activity; the extreme rarity of this species justified the repatriation of snakes to a safer habitat. MZA snakes were individually released at habitat edges (to give the snakes a choice of habitat) at the Bienville Parish study site; each snake was released at least 100 m from all other snakes under study. Following their release into the field, all snakes were relocated 1–7 times per week.

Upon locating a transmitter-bearing snake, date, time, and location were recorded. The snake's position was recorded as above-ground or underground. For each location, transmitter pulse rate was recorded for three consecutive 10-sec periods and then averaged and converted to a per minute pulse rate. Shaded air and substrate temperatures were recorded with an alcohol thermometer within 5 min of locating a snake and generally within 2 m of the snake (unless the snake was on the surface, when temperatures were recorded 2–5 m from the snake to prevent disturbance). Substrate temperatures were recorded at a depth of 10–15 cm, corresponding to the approximate depth at which snake and mammal burrows were located (and in which snakes were located when underground). Radiotracking seasons were defined as winter (December–February), spring (March–May), summer (June–August), and autumn (September–November).

A temperature calibration equation for each transmitter was plotted (x-axis = pulse rate in ms; y-axis = transmitter temperature in °C), allowing determination of snake body temperature (because pulse rates were recorded when transmitters were located within the snake, transmitter and body temperatures were assumed to be equal). Snake body temperatures were then plotted with the associated air and substrate temperatures by month and hour. Temperatures are listed below, giving the mean ± 95% CI, as well as the temperature range. To prevent biased statistical analyses due to unequal or low sample sizes, a minimum of ten body temperatures each of juveniles, adult males, and adult females was used to analyze size and sex class temperature differences by month and hour. An ANOVA ($P \leq 0.05$)

was used to test for temperature differences between all size and sex classes within the same season, month, or hour. A *t*-test ($P \leq 0.05$) was used to test for temperature differences between two size/sex classes within the same season, month, or hour.

RESULTS

Mean snake temperatures were lower during winter (11.4 ± 1.97°C, 5.0–18.0, $n = 78$), increased during spring (22.3 ± 1.28°C, 8.5–36.5, $n = 372$), peaked during summer (27.7 ± 0.71°C, 20.0–38.5, $n = 563$), and decreased during autumn (22.7 ± 0.36°C, 10.0–38.5, $n = 824$; Fig. 1A–C). Snake temperatures ranged from a mean of 10.0 ± 2.25°C (5.0–16.0, $n = 12$) in adult males located underground during January (Fig. 1B) to a mean of 32.2 ± 3.72°C (24.5–38.5, $n = 16$) in adult females located above ground during August (Fig. 1C). Air and substrate temperatures showed similar seasonal trends. During spring and autumn, snake, air, and substrate temperatures were generally 3–4°C higher above ground than underground (Fig. 1A–C). However, during summer, temperatures between juveniles and adult males were not significantly different above ground ($t = 0.78$, $P > 0.05$; Fig. 1A, B) or underground ($t = 0.03$, $P > 0.05$; Fig. 1A, B), whereas temperatures of adult females were significantly higher above ground than underground ($t = 2.93$, $P \leq 0.05$; Fig. 1C).

During summer, temperatures were significantly higher in adult females than in juveniles ($t = 2.25$, $P \leq 0.05$; Fig. 1A, 1C) and adult males ($t = 3.69$, $P \leq 0.05$; Fig. 1B, C). Moreover, during summer, temperatures of adult females were significantly higher above ground than underground ($t = 2.86$, $P \leq 0.05$; Fig. 1C), whereas above-ground and underground temperatures were not significantly different in juveniles ($t = 1.72$, $P > 0.05$; Fig. 1A) or adult males ($t = 1.18$, $P > 0.05$; Fig. 1B).

Few monthly temperatures were significantly different between size and sex classes. Above-ground temperatures during March were significantly higher in adult males than in juveniles (Table 1) and during May were significantly higher in adult females than in juveniles (Table 1). Above-ground temperatures were also significantly higher in adult females than in adult males during August and September (Table 1). Underground temperatures during June were significantly higher in adult males than in juveniles and adult females (Table 1).

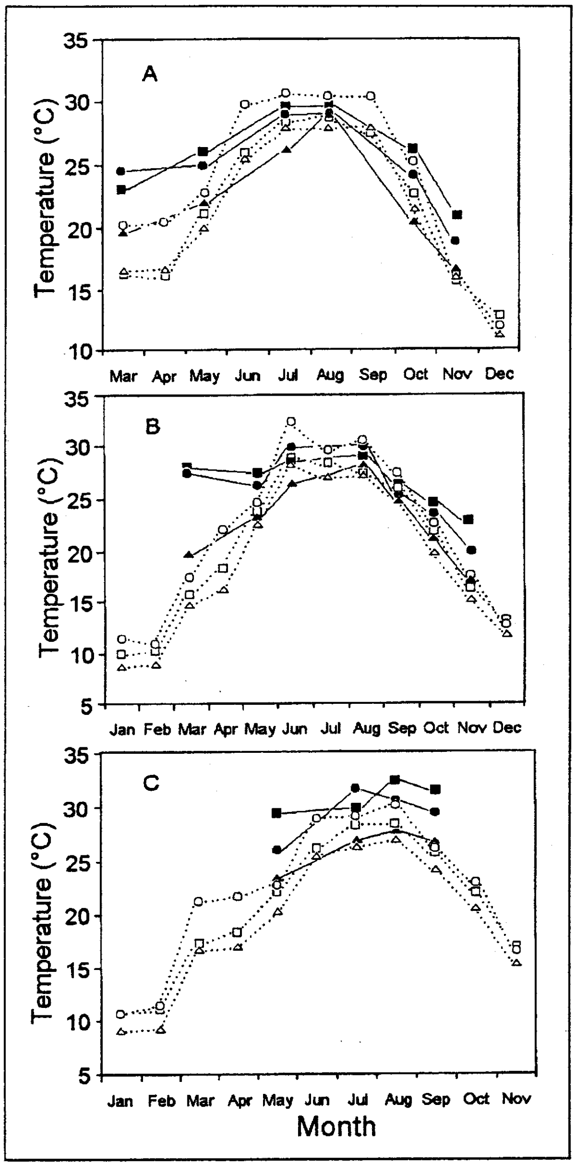

Figure 1. Monthly mean body temperatures (°C; squares) of juveniles (A), adult males (B), and adult females (C) of *Pituophis ruthveni* located above ground (solid lines; black symbols) and underground (dashed lines; open symbols), with means for associated air (circles) and substrate (triangles) temperatures. Each temperature plotted on the graph represents the mean of ≥ 10 recordings; temperatures are not plotted for months with < 10 recordings. See Table 1 for statistics on significant differences.

Some general trends are apparent in daily variations in temperatures. Mean above-ground snake temperatures increased from 19.6°C in juveniles (9th hour) and 21.5°C in adult males (10th hour) to a respective 28.7°C (11th hour) and 29.8°C (13th hour; Fig. 2A, B). Mean underground snake tem-

TABLE 1. Monthly mean (±1 SD) body temperatures (°C) recorded from juvenile, adult male, and adult female *Pituophis ruthveni* located above ground (T_{ab}) and underground (T_{be}); ranges and samples sizes in parentheses. Months during which (1) neither T_{ab}s or T_{be}s differed significantly between at least two size/sex classes, or (2) < 10 recordings of T_{ab}s and T_{be}s were taken for each size/sex class, have been omitted. An ANOVA tested for temperature differences between all size and sex classes within the same month. A *t*-test ($P \leq 0.05$) tested for temperature differences between two size/sex classes within the same month; *t*-tests between pairs that are not identified in the *t*-test column were not significant.

Month	Class			ANOVA	*t*-test
	Juveniles	Males	Females		
March (T_{ab})	23.0 ± 5.4 (16.0–30.5, *n* = 10)	27.9 ± 4.4 (18.5–34.5, *n* = 10)	–	–	$t = 2.23$
May (T_{ab})	26.0 ± 4.9 (19.0–36.0, *n* = 53)	27.4 ± 5.8 (15.0–35.0, *n* = 28)	29.2 ± 5.6 (19.0–36.5, *n* = 18)	*	$t = 2.29$ (Juveniles, Females)
June (T_{be})	25.9 ± 2.8 (20.5–34.5, *n* = 38)	28.7 ± 3.3 (25.0–38.0, *n* = 20)	26.1 ± 1.8 (22.5–30.5, *n* = 27)	*	$t = 2.64$ (Juveniles, Males) $t = 3.78$ (Males, Females)
August (T_{ab})	29.7 ± 1.9 (26.5–33.5, *n* = 11)	28.8 ± 3.5 (22.5–33.5, *n* = 14)	32.2 ± 4.8 (24.5–38.5, *n* = 16)	*	$t = 2.22$ (Males, Females)
September (T_{ab})	-	26.2 ± 5.3 (14.0-35.5, n = 36)	31.4 ± 3.7 (23.0-38.5, n = 17)	-	$t = 3.45$

*$P \geq 0.05$

peratures increased from 20.1°C in juveniles (8th hour), 20.4°C in adult males (10th hour), and 21.5°C in adult females (8th hour) to 27.0°C (18th hour), 27.5°C (18th hour), and 26.5°C (19th hour), respectively (Fig. 2A–C).

Snake temperatures most closely approximated the air and substrate temperatures during the 18th and 19th hours, when snakes were located predominantly underground (Fig. 2A–C). The temperatures of juveniles and adult males showed no consistent relationship to the associated air and substrate temperatures from the 7th to the 17th hours (Fig. 2A, B). However, air temperatures were significantly higher than the associated temperatures of adult females from the 10th to the 16th hours ($t = 2.49$; $P \leq 0.05$; Fig. 2C), whereas these latter temperatures were not significantly different from the associated substrate temperatures ($t = 1.08$, $P > 0.05$; Fig. 2C).

There was no consistent relationship between the hourly temperatures of snakes located above ground versus underground, particularly for adult females, which were infrequently located above ground. However, juvenile temperatures were significantly higher above ground than underground from the 11th through the 14th hours ($t = 2.76$, $P \leq 0.05$; Fig. 2A), and adult male temperatures were significantly higher above ground than underground from the 11th through the 17th hours ($t = 7.88$, $P \leq 0.05$; Fig. 2B).

The only significant difference in hourly temperatures between size classes occurred during the fifteenth hour, when above-ground temperatures were significantly higher in adult males than juveniles ($t = 2.09$, $P \leq 0.05$; Fig. 2A, B), whereas there were no significant differences in hourly temperatures between sex classes.

DISCUSSION

Because the magnitude of most pathways of heat exchange between an animal and its environment is dependent in part on the size of the animal (Pough et al. 1998), similarly sized individuals of the same species (that are exposed to the same environmental conditions) should exhibit similar temperature patterns. In particular, the smaller size and correspondingly higher body surface to volume ratio of juveniles may enable them to more efficiently thermoregualate than the adults since juveniles increase locomotor speed more than adults (Heckrotte 1967), probably due to ontogenetic increases in both aerobic and anaerobic capacity (Pough 1978), and since net energy gains are maximized at environmental temperatures very close to their preferred body temperature of about 29°C (Stephenson et al. 1985 for *Thamnophis elegans*). In turn, this should result in different temperature patterns between size classes because the juveniles can exchange heat with external sources more readily than can the adults. For example, juveniles may be able to access more underground microhabitats (e.g., small mammal tunnels) while attempting to locate a site that offers thermally optimal conditions. Moreover, juveniles are probably less conspicuous to potential predators while thermoregulating above ground due to their small size (J. Himes, pers. obs. 1996) and tend to move less frequently and over shorter distances compared to adults (Himes et al., unpubl. data).

In spite of this predicted relationship between animal size and temperature, the seasonal and hourly temperature patterns of juveniles and adult males were more similar to each other than either was to the temperature patterns of adult females. Assuming adult females and males have similar physiological capacities, the former may exhibit different behavioral and activity patterns (particularly when they are gravid) that result in a different thermal regime for adult females than for juveniles and adult males. While all snakes tended to avoid direct exposure to sunlight (each snake was found in sunlight in < 10% of the total observations on each individual), particularly during summer (< 5%), the most notable difference was the higher summer temperatures in adult females than in juveniles and adult males. No information is available on the reproductive biology of natural populations of *P. ruthveni*. However, adult females that were emaciated and thought to have recently oviposited have been found above ground in July and August (T. Vandeventer, pers. comm. 1995). Therefore, adult females may maintain higher temperatures during late spring-early summer to enhance the development of their eggs.

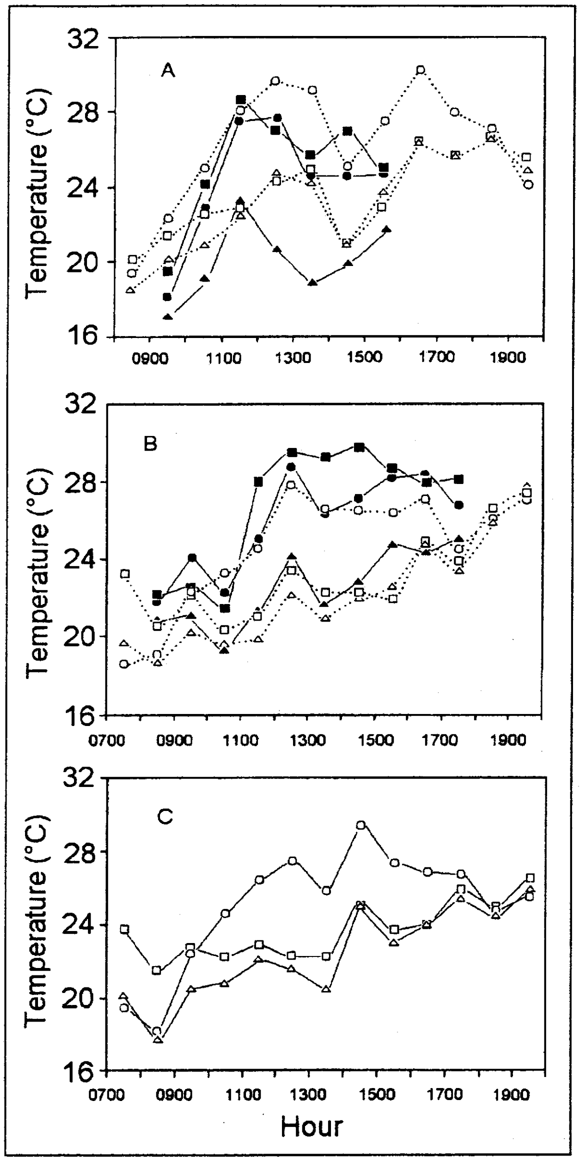

Figure 2. Hourly mean body temperatures (°C; squares) of juveniles (A), adult males (B), and adult females (C) of *Pituophis ruthveni* located above ground (solid lines; black symbols) and underground (dashed lines; open symbols), with means for associated air (circles) and substrate (triangles) temperatures. Each temperature plotted on the graph represents the mean of ≥ 10 recordings; temperatures are not plotted for hours with < 10 recordings (including all hourly above-ground temperatures of adult females). Temperatures are pooled across months. See text for statistics on significant differences.

Conversely, adult males move more frequently and over longer distances than do adult females (Himes et al., unpubl. data), probably in part because males are searching for mates and gravid females tend to be sedentary. However, juveniles move even less frequently and over shorter distances than do adult females. Thus, the disparate temperature patterns between size and sex classes are probably attributable to the behavioral and activity patterns exhibited by the adults and juveniles. However, because all but one of the juvenile snakes was captive-bred, the disparate temperature patterns between size classes may also be due in part to captive-bred snakes exhibiting different thermal behavior than wild-caught snakes.

Adult females were located above ground less frequently than were juveniles and adult males. Yet, it was during three of the four months in which an adequate number of temperatures (≥ 10) was recorded (for statistical analysis) of adult females above ground (May, August, September) when there was a significant difference in temperatures between size and sex classes. Therefore, it appears that adult females spend less time above ground than do juveniles and adult males, but maintain a higher body temperature when they are above ground.

In contrast to *P. c. deserticola* in northern Utah (Parker and Brown 1980), *P. ruthveni* did not have significantly higher temperatures in spring than in autumn. In fact, the mean temperatures of *P. ruthveni* were higher in autumn (22.7°C) than in spring (22.3°C); these temperatures were lower than those of *P. c. deserticola* in autumn (24.43°C) and spring (27.88°C). *Pituophis c. deserticola* may have attained higher temperatures than did *P. ruthveni* during the spring because the former taxon frequently basked on the surface shortly after emerging from hibernation. By contrast, *P. ruthveni* was located above ground only about 20% of the time, when it was usually secluded amid the shade of thick herbaceous vegetation.

Because individuals of *P. c. deserticola* emerged in the spring after spending 210–229 d in hibernation (Parker and Brown 1980), they probably needed to maintain elevated body temperatures during the first several weeks of activity to be physiologically capable of engaging in sustained types of activity (e.g., foraging and mate seeking). In contrast, *P. ruthveni*, which inhabit an area with a far milder winter and spring compared to the foothills of northern Utah inhabited by individuals of *P. c. deserticola*, spent only approximately 150 d in hibernation, during which they occasionally moved up to 200 m (J. Himes, pers. obs. 1996, 1997). Thus, unlike *P. c. deserticola*, individuals of *P. ruthveni* that have recently emerged from hibernation in the spring may already be physiologically capable of sustained activity without further elevation of their body temperatures.

Despite these temperature differences between *P. ruthveni* and *P. c. deserticola*, the mean temperatures of snakes located above ground from spring through autumn were similar (26.6°C [*P. ruthveni*] versus 27.9°C [*P. c. deserticola*]; Parker and Brown 1980). Moreover, the mean temperatures of snakes located underground were actually higher in *P. ruthveni* than in *P. c. deserticola* during autumn (22.5°C [*P. ruthveni*] versus 19.68°C [*P. c. deserticola*]) and summer (27.9°C [*P. ruthveni*] versus 27.01°C [*P. c. deserticola*]). Therefore, *P. c. deserticola* maintained higher temperatures than did *P. ruthveni* only at the beginning of its active season (spring), before temperatures of both taxa became more similar in the summer.

The relationship between snake, air, and substrate temperatures is very similar between *P. ruthveni* and *P. c. deserticola*. In both taxa, underground body temperatures were below air temperatures and were similar to shaded substrate temperatures (Parker and Brown 1980). Thus, snakes may have been thermoregulating at similar capacities. However, unlike *P. ruthveni*, *P. c. deserticola* occurred in an area containing numerous surface boulders and rock piles, under which it frequently sheltered. When *P. c. deserticola* was sheltering under this additional microhabitat, its body temperature was similar to the associated air and shaded substrate temperatures (no significant difference between temperatures).

In addition to *P. ruthveni*, three other taxa of *Pituophis* inhabit similar sandy-soiled pine forests in the southeastern United States: *Pituophis m. melanoleucus*, *P. m. lodingi*, and *P. m. mugitus* (Tennant and Bartlett 2000). Therefore, studies on the thermal ecology of these latter *Pituophis* would help determine whether the seasonal and diel temperature patterns of *P. ruthveni* are typical of southeastern *Pituophis* or are unique to *P. ruthveni*. However, *P. ruthveni* is most closely related to *P. c. sayi* (Reichling 1995; Rodríguez-Robles and De Jesús-Escobar 2000), which inhabits the open plains of the midwestern United States and northeastern Mexico (Tennant and Bartlett 2000). Therefore, studies on the thermal ecology of *P. c. sayi* could provide valuable insight into the origin of temperature patterns of *P. ruthveni*. In fact, the temperature patterns of *P. ruthveni* may be more similar to *P. c. sayi* than to the other southeastern *Pituophis*, depending on the relative importance of historical versus present-day factors in shaping the natural histories and associated temperature patterns of snakes.

In answer to the questions posed by Peterson et al. (1993), as they apply to *P. ruthveni*, (1) the range of possible body temperatures (°C) under natural conditions is 5.0–18.0 (winter), 8.5–36.5 (spring), 20.0–38.5 (summer), and 10.0–38.5 (autumn), (2) the proximate factors that determine which body temperatures a snake selects from that range of possibilities include its size and sex class, reproductive status, and location relative to the surface (above ground versus underground), and the time of year and day, (3) the variation of body temperatures of individual snakes under natural conditions over extended periods of time is 5.0 (winter) to 38.5°C (summer and autumn), (4) the functional effects of body-temperature variation include enhanced rates of growth in juveniles and perhaps adult males, and enhanced rates of egg development in adult females, and (5) the ecological consequences of body-temperature variation include relatively limited time spent on the surface and no surface activity from December-February.

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