

Temperature Patterns of Rattlesnakes at Natural Bridges National Monument, Utah

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Abstract. We implanted 12 western rattlesnakes (*Crotalus viridis*) with temperature-sensitive radios; 4 each in 1989 and 1990 and 7 in 1991 (3 snakes were tracked for 2 years). Individual snakes were tracked for 1 to 2 years and were located daily while active. Average body temperature for this population was $22.5^{\circ}\text{C} \pm 6.98^{\circ}$ (range $18.4\text{--}26.7^{\circ}\text{C}$). Body temperatures were low relative to body temperatures reported for *C. viridis* and other species of rattlesnakes. Substrate temperature best predicted body temperature, but air temperature played a role in determining body temperature for many snakes. In 1990, an incubating female maintained a higher and more constant body temperature than any other snake in the study during the 3 years, including her own temperature in 1989. Except during gestation, western rattlesnakes at Natural Bridges apparently will accept lower body temperatures to meet other physiological needs.

Key words: Body temperature, *Crotalus*, radiotelemetry, reproductive ecology, thermoregulation.

Body temperature (T_b) plays a critical role in snake ecology, regulating behavioral and physiological responses to the environment. As ectotherms, snakes must rely on external heat to raise body temperatures above the activity threshold and thus are tightly coupled to their physical environment. Body temperature results from interactions between physiological, behavioral, and

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physical factors in ectotherms. Behavior determines the particular physical microenvironment of the snake and is the most important (Lillywhite 1987).

Metabolic processes are temperature dependent with maximum rates occurring at specific temperatures (Huey 1982). This pattern has generated predictions that ectotherms have an optimum T_b for metabolic activity, and that they thermoregulate to keep T_b 's as near optimum as possible (Huey and Stevenson 1979; Pough 1980; Huey 1982). It is often assumed that the mean of a range of observed activity T_b 's represents this optimum T_b for the species (Huey and Slatkin 1976; Huey et al. 1977; Magnuson and Beitingner 1978; Greenwald and Kanter 1979; Huey 1982; Pough and Gans 1982). An alternative hypothesis is that each metabolic process (e.g., digestion, locomotion, gestation, etc.) has its optimum temperature (Bustard 1967; Pough 1974, 1980; Lang 1979; Gier et al. 1989). Observed T_b 's represent either a compromise among various needs optimized at different temperatures or optimization of one process at the expense of other activities (Gibson et al. 1989; Huey et al. 1989; Peterson et al. 1993).

Whereas research into thermoregulation by reptiles has increased over the past 20 years, more work has been done with lizards than with snakes (Lillywhite 1987). Body temperatures have been reported for over 100 species of snakes, but there are few studies where T_b has been collected systematically along with ecological and physiological characteristics (Avery 1982; Lillywhite 1987). Thermal relations of rattlesnakes (*Crotalus* spp.) are poorly known (Cowles and Bogert 1944; Brattstrom 1965; Cunningham 1966; Hirth and King 1969; Moore 1978; Brown et al. 1982; Beck 1991), and studies of free-ranging rattlesnakes are rare (Brown et al. 1982; Beck 1991).

Western rattlesnakes (*Crotalus viridis*) are frequently seen at Natural Bridges National Monument (NABR), especially near the residence area (including the visitor center). Safety concerns for employees and visitors resulted in funding for a study of rattlesnakes in the residence area. We designed the study to learn more about the ecology of western rattlesnakes at NABR and to determine what attracts snakes to the residence area. We considered their thermal relations important. Two objectives were to correlate snake T_b with ambient conditions (e.g., air and substrate temperatures at snake locations and microhabitat characteristics of snake locations) and physiological events (e.g., feeding, shedding, gestation). We report on some aspects of the thermal ecology of *C. viridis* at NABR.

Methods

Natural Bridges is about 2,000 m in elevation on the lower slopes of the Abajo Mountains in southeastern Utah. The habitats occupied by snakes were predominantly piñon-juniper woodland, and ledgy, rocky slopes along upper canyon edges.

Temperature-sensing radios were surgically implanted in snakes (4 each in 1989 and 1990 and 7 in 1991—3 were tracked for 2 years for a total of 12 individual snakes). Snakes were released where captured and located once daily in 1989 and 1991 and twice daily in 1990. At each location, T_b was determined from radio pulse frequency (Beck 1991). Air temperature (T_a) was measured in the shade at a height of 1 m within 2 m of the snake. Substrate temperature (T_s) was measured with the thermometer tip barely below the soil or litter surface, in the same thermal environment as the snake (e.g., full sun, vegetation-filtered sun, under rock, etc.), and as near the snake as possible (usually within 0.1–0.5 m). Taylor digital thermometers and Schultheis thermometers were used for T_a and T_s . Minimum (T_{min}) and maximum (T_{max}) daily temperatures were recorded near the visitor center at the NOAA weather station.

Analyses of variance were performed on the data to compare mean temperatures of individual snakes. Tukey's multiple means comparisons were used to test for significant differences between pairs of means (Sokal and Rohlf 1981; Minitab, Inc. 1991). Stepwise multiple regressions (Minitab, Inc. 1991) were run using T_s , T_a , date, and time of observation to learn which environmental factors regulate T_b . One female (12) tagged in 1989 and 1990 was gravid in 1990 and incubated her young 24 May to 10 August. Snake T_b 's were compared during this period using analysis of variance and Tukey's tests.

Results

Snake 32 was killed 9 days after release—its T_b data were excluded from these analyses. Mean T_b for all snakes in the study was $22.5^\circ\text{C} \pm 6.98^\circ$. Snakes in 1989 and 1990 (except 12 in 1990) had lower T_b 's than any snake in 1991 (Fig. 1). Figure 2 shows T_b 's for each snake in 1989 plotted with T_{min} and T_{max} (at visitor center) and T_s for each snake location. Figure 3 has similar plots for snakes in 1990, and the T_b 's for snakes in 1991 are plotted with environmental temperatures in Fig. 4. Results of stepwise multiple regression for individual snakes are shown in

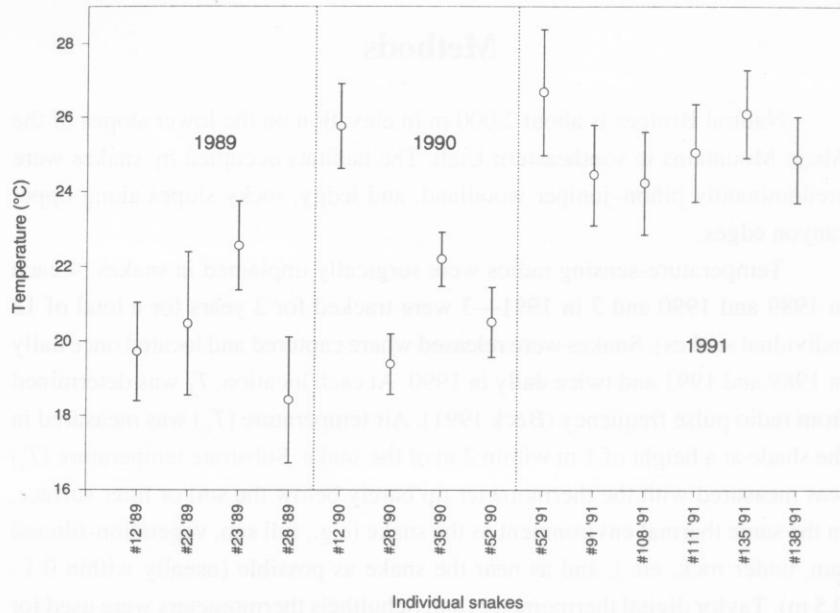


Fig. 1. Body temperature ($\bar{x} \pm 95\%$ CI) of 11 snakes measured during each individual's entire observation period in 1989, 1990, or 1991. Three snakes were each monitored in 2 consecutive years. Mean snake T_b 's (body temperatures) in 1991 were significantly warmer than all snakes in 1989 or 1990 except snake 12 in 1990; mean T_b 's of snakes in 1989 and 1990 did not differ except for snake 12 in 1990.

the Table. Substrate temperature accounted for most of the variation in T_b in 11 snakes, T_a was most important in 2 snakes, and the T_b of 1 snake correlated best with date.

Average T_{min} and T_{max} measured at the visitor center were warmer in 1989 than 1991, but temperatures in 1990 did not differ from either 1989 or 1991. Results of Tukey's multiple means comparison tests for T_a and T_s from all snakes over all their observation periods for each year showed that average T_s for 28 in 1989 differed from all 1990 snakes and from snakes 91, 108, and 111 in 1991. Mean T_a comparisons found that snake 35 in 1990 differed from snake 28 in 1989 and snake 52 in 1991.

During incubation in 1990, snake 12's T_b was significantly higher than all other snakes in the study (Fig. 5). Variation in T_b was significantly smaller for snake 12 than any other snake as well. The coefficient of variation (CV) of snake 12's T_b was 6.33%—CVs ranged from 11.4 to 39.8% for the other snakes.

Comparing snake 12's T_b in 1989 and 1990 emphasizes the difference in T_b between nongravid and gravid snakes. Snake 12's average T_b 's in 1989 and 1990 for the entire observation period (15 June to 6 October 1989, 16 April to 17 August 1990) were different (Fig. 1), but variation about the means was similar in both years ($CV_{1989} = 30\%$, $CV_{1990} = 33\%$). During the time snake 12 was incubating (24 May to 10 August 1990), average temperatures were again different between years (Fig. 5), but T_b in 1990 was more constant ($CV_{1989} = 27\%$, $CV_{1990} = 6\%$).

No differences in T_{min} or T_{max} existed during the incubation period for the 3 years. Average T_s at locations for snake 28 in 1989 differed from all four snakes in 1990, and from snakes 91 and 108 in 1991. Snake 28 in 1990 had T_s 's that differed from all snakes in 1989 and from snake 138 in 1991. Means for both T_a and T_s for snake 12 in 1990 differed from snake 28 in 1989, and from snakes 108, 135, and 138 in 1991. Average T_s 's for both snakes 35 and 52 in 1990 were different from snakes 23 and 28 in 1989, and from snakes 135 and 138 in 1991. Mean T_a differed between snake 28 in 1989 and all snakes in 1990. Both snakes 35 and 52 in 1990 T_a 's differed from snakes 135 and 138 in 1991; snake 108 T_a 's were also different from those of snake 35.

Discussion

Mean T_b 's for active *C. viridis* reported in the literature range from 25.4 to 31.7° C (Cowles and Bogert 1944; Brattstrom 1965; Cunningham 1966; Hirth and King 1969; Moore 1978; Brown et al. 1982; Charland and Gregory 1990; Beck 1991). At NABR, individual mean T_b 's ranged from 18.4 to 26.7° C; the average T_b was 22.5° C \pm 6.98°. The low mean T_b 's in this study could result from including cool days in spring and fall, but Hirth and King (1969) reported warmer spring (25.5° C) and fall (29° C) T_b 's for *C. v. lutosus* in northeastern Utah. Snakes at NABR tracked only during summer (e.g., 22, Fig. 2B; and 111, Fig. 4D) also had low mean T_b 's. Whereas these data represent only daily snapshots of snake activities, we believe the large number of observations for each snake provides a realistic range of T_b 's. Most published T_b 's are single measurements of one or more individual snakes, not extended series of daily measurements of the same snakes, and thus may not be directly comparable to results of this study.

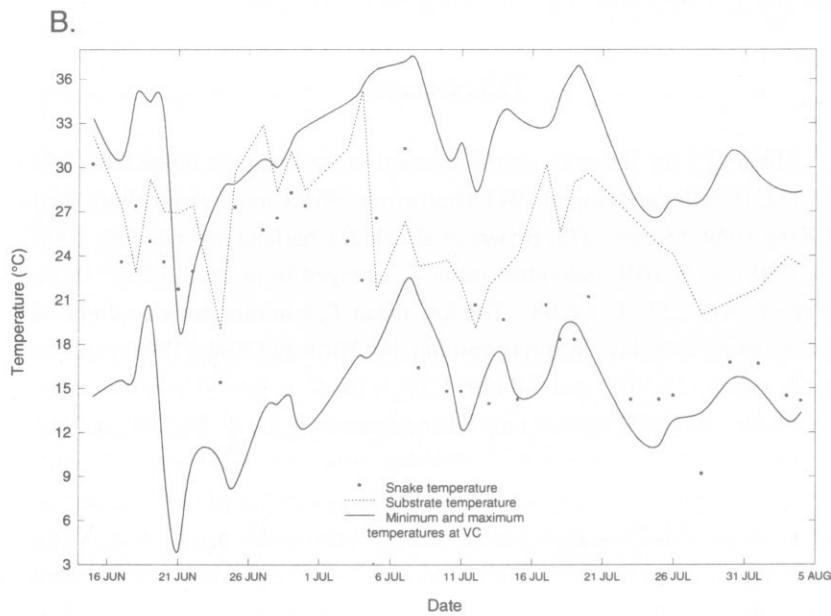
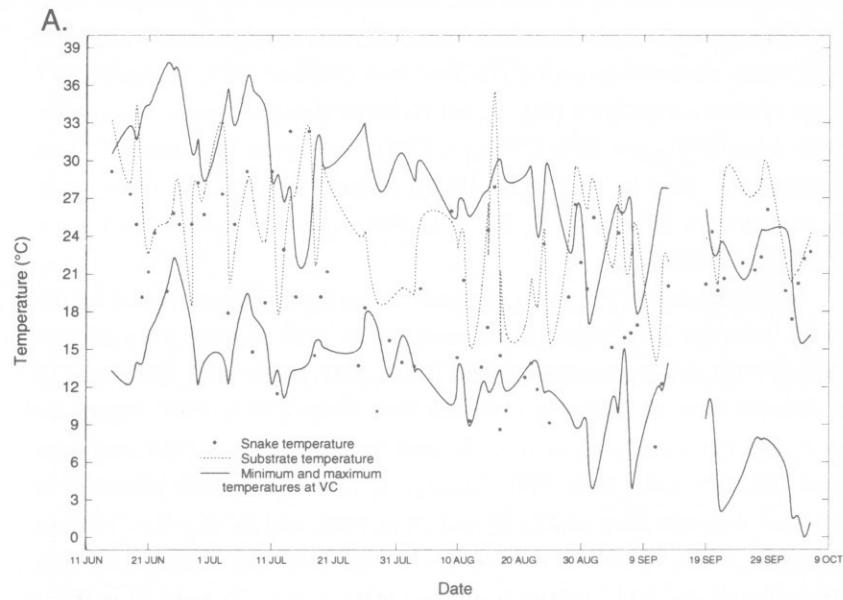


Fig. 2. Daily body temperatures of four snakes monitored in 1989, plotted with T_{min} and T_{max} (minimum and maximum daily temperatures) at the visitor center, and T_s (substrate temperature). Breaks in the data are due to surgeries to implant new radiis. A. snake 12, B. snake 22, C. snake 23, and D. snake 28.

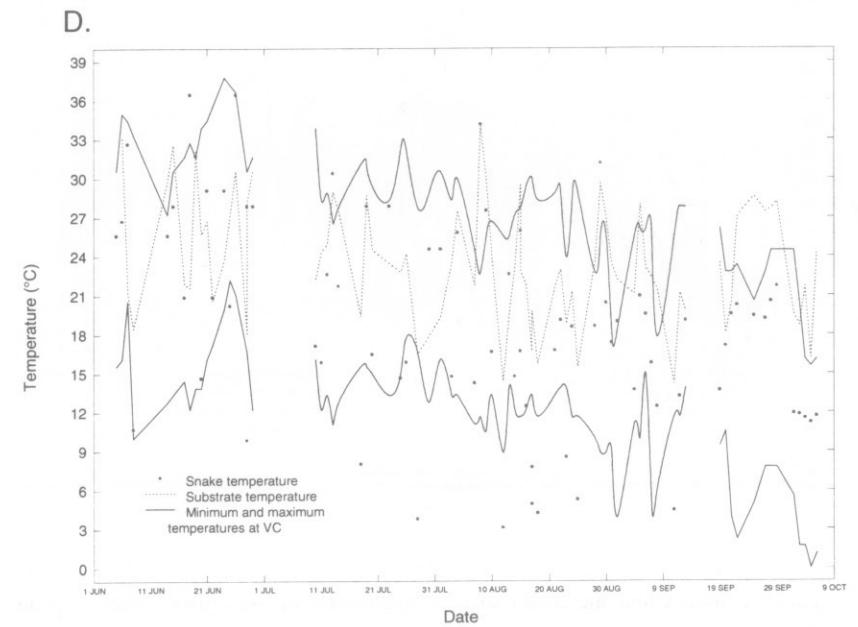
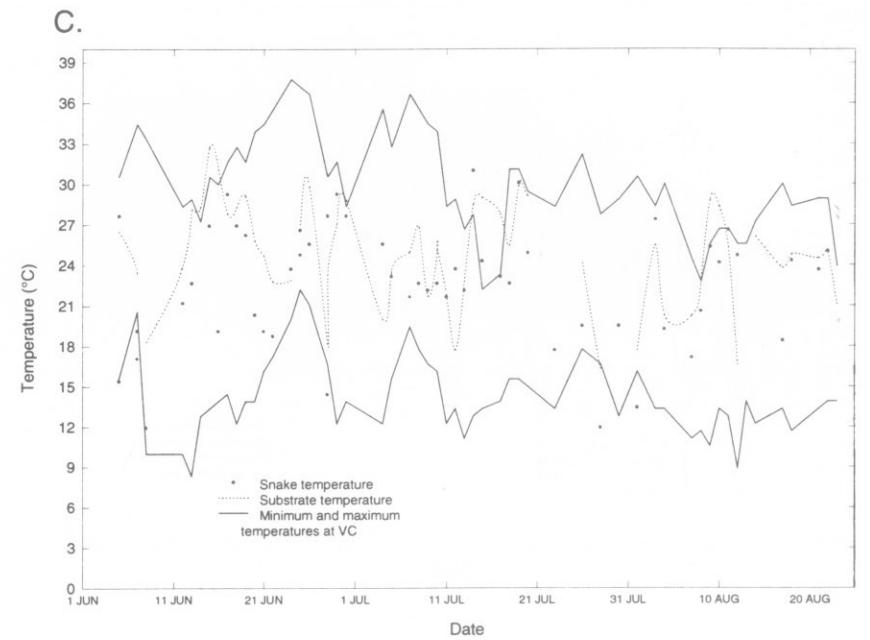


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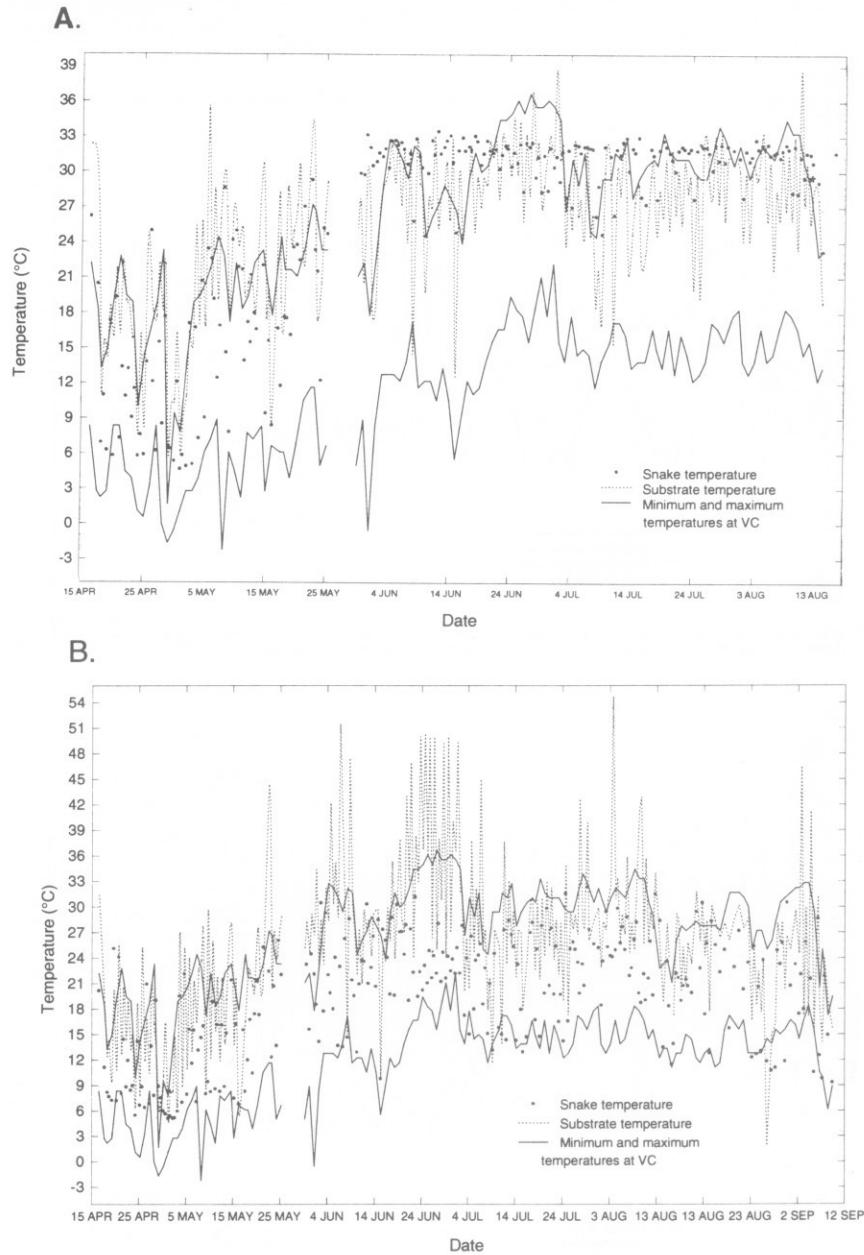


Fig. 3. Daily body temperatures of four snakes monitored in 1990, plotted with T_{min} and T_{max} (minimum and maximum daily temperatures) at the visitor center, and T_s (substrate temperature). Breaks in the data are due to surgeries to implant new radios. A. snake 12, B. snake 28, C. snake 35, and D. snake 52.

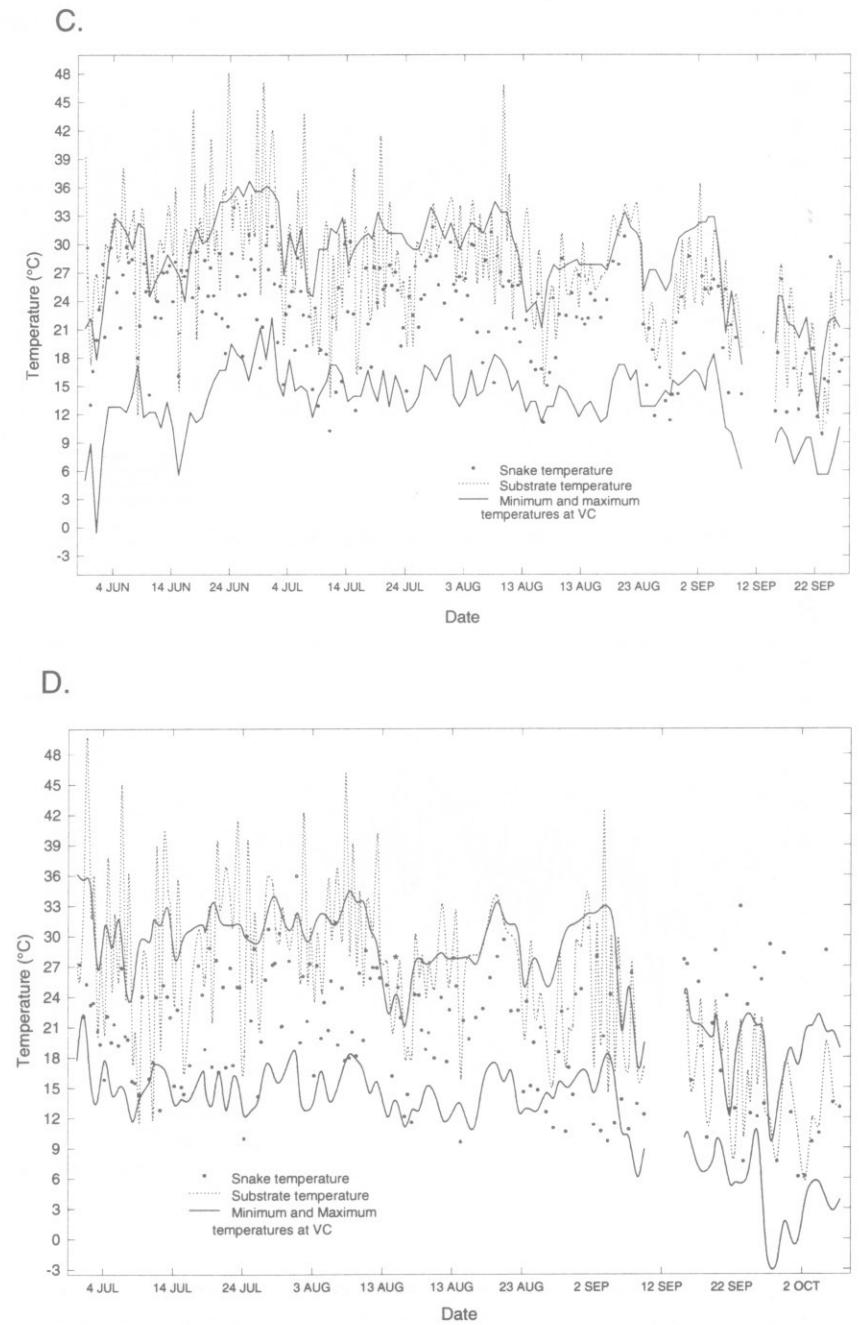


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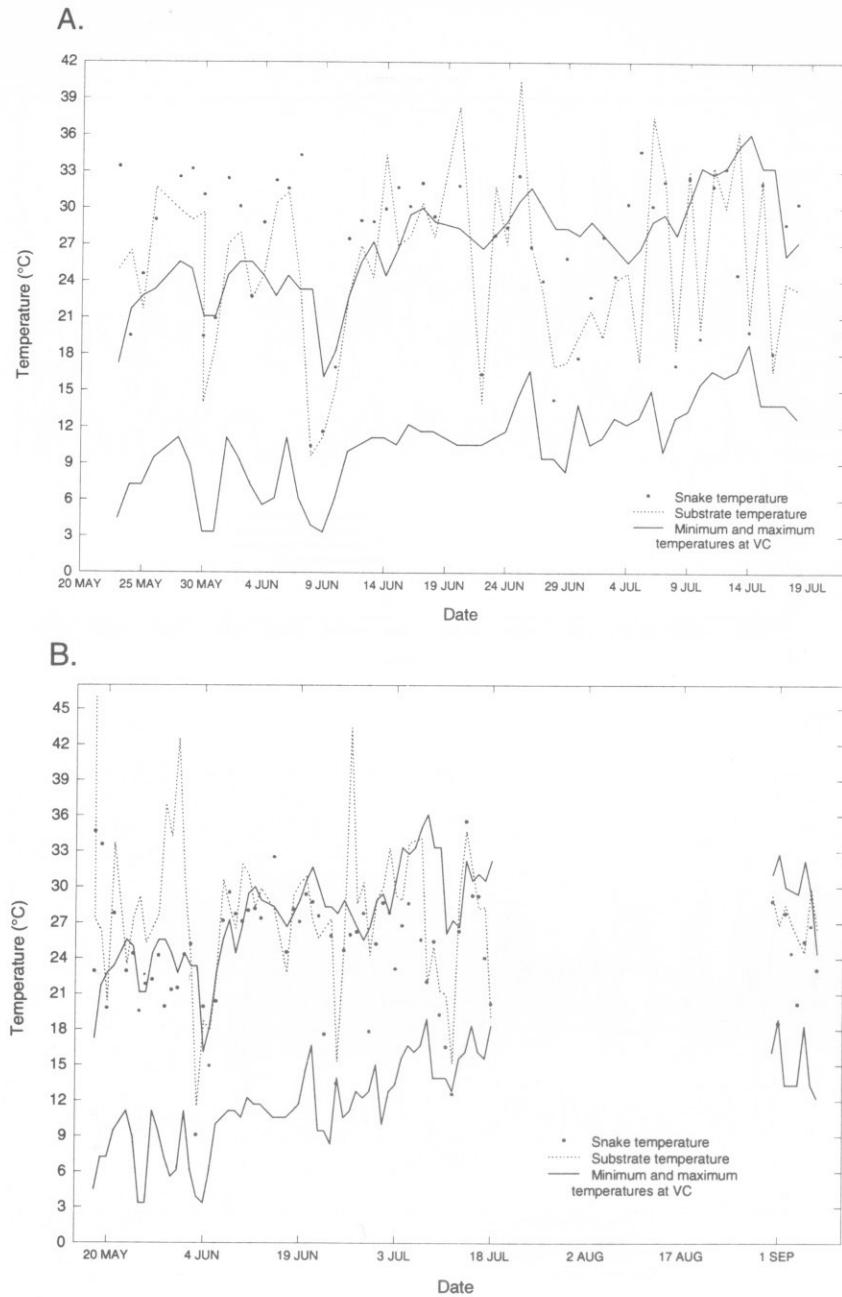


Fig. 4. Daily body temperatures of six snakes monitored in 1991, plotted with T_{min} and T_{max} (minimum and maximum daily temperature) at the visitor center, and T_s (substrate temperature). Breaks in the data are due to surgeries to implant new radios, or equipment failure. A. snake 52, B. snake 91, C. snake 108, D. snake 111, E. snake 135, and F. snake 138.

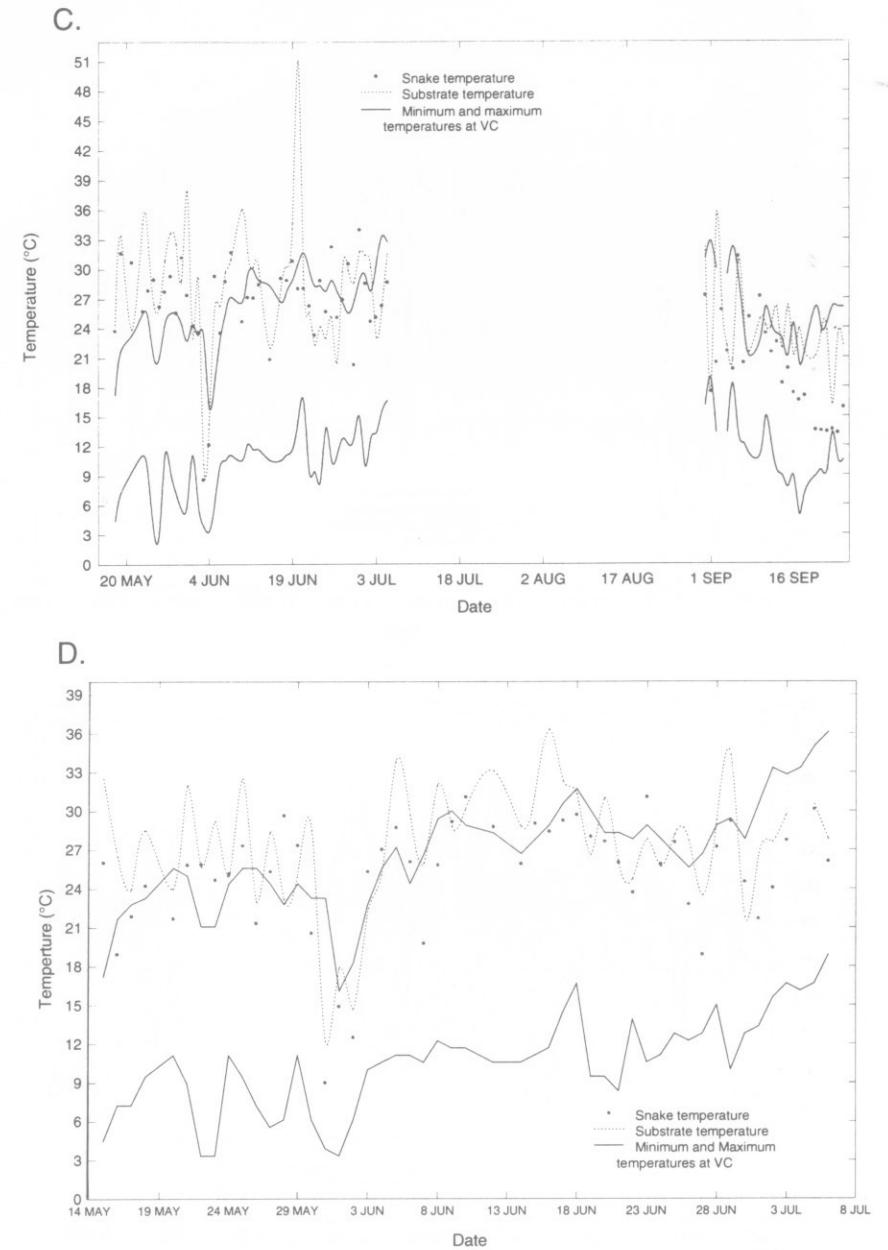


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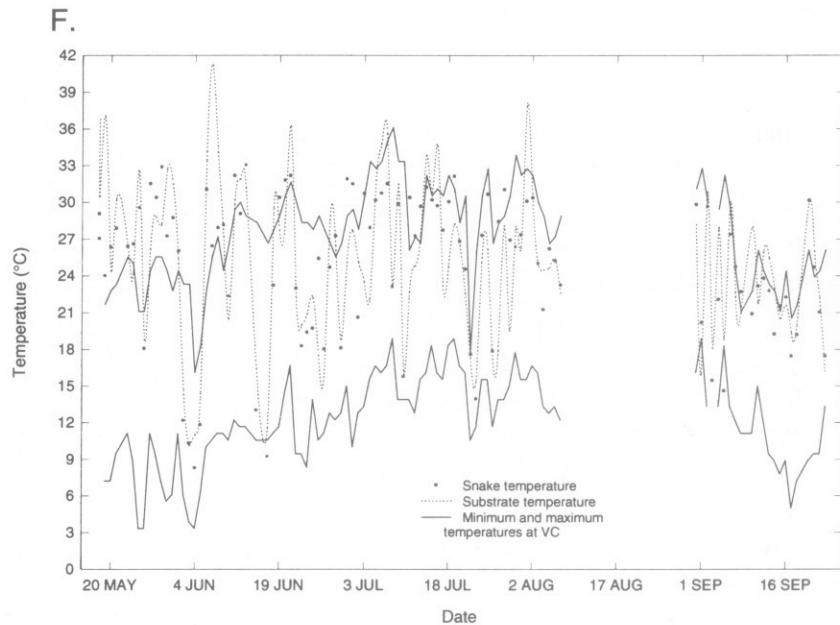
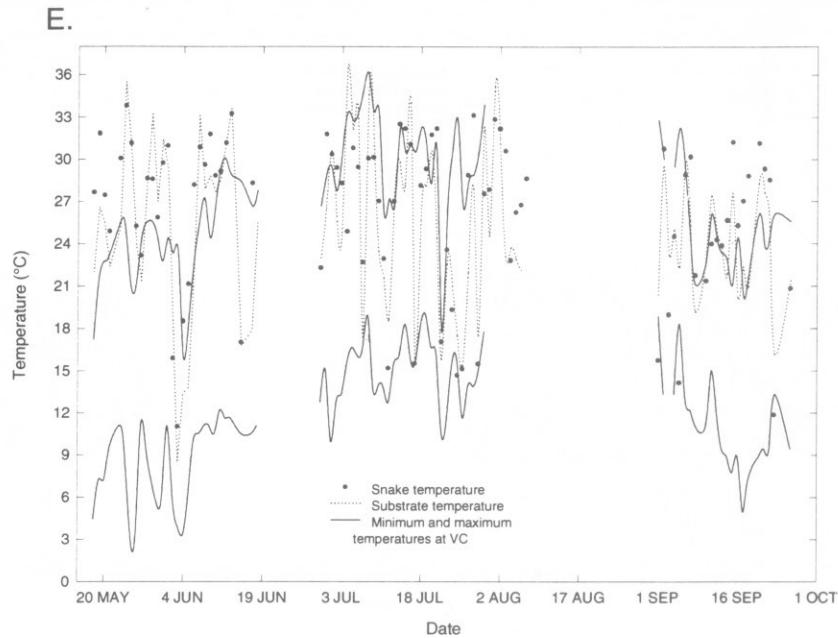


Fig. 4. Continued.

Table. Regression coefficients for stepwise multiple regression analysis of western rattlesnake body temperature (T_b) on substrate temperature (T_s), air temperature (T_a), date,^a and time^b of observation for 14 snake observation periods. Only significant regression coefficients ($P < 0.05$) are shown.

Snake	Year	T_s	T_a	Date	Time	Total
12	1989	69.11			2.80	73.02
22	1989		19.59	52.63		77.81
23	1989	40.02				47.57
28	1989	21.67	14.91	4.58		41.91
12	1990	61.98		16.79		79.93
28	1990	1.41	60.49	1.48	2.22	68.24
35	1990	1.62	50.68	1.54		55.37
52	1990	41.62			4.99	49.15
52	1991	50.02				50.73
91	1991	39.53	10.51		4.92	56.76
108	1991	40.32	6.01	13.50		66.44
111	1991	60.22	6.67			67.67
135	1991	60.76			5.89	70.17
138	1991	61.82	9.16	2.71		74.43

^aDate = stepwise multiple regression of the date of observation.

^bTime = stepwise multiple regression of the time of observation.

Intraspecific variation in temperature preferences does occur in reptiles (Dawson 1975; Huey 1982). Western rattlesnakes at NABR could have lower preferred temperatures than other populations, and they may have cooler T_b 's than many other rattlesnake populations because they live in a cooler thermal environment. Keeping T_b 's above ambient temperature at NABR may require so much active thermoregulation that other needs can't be met. As a result, snakes operate at lower T_b 's. Data from a population in Wyoming support this hypothesis. Graves and Duvall (1993) found gravid females had higher T_b 's than nongravid females in this population but that gravid females engaged in active thermoregulation at the expense of almost all other activities, whereas nongravid females spent their time in long-distance foraging moves during summer.

Body temperatures were similar between snakes within years but differed between years, even for the same snakes. This suggests that snake T_b 's were determined by some component(s) of the physical environment that differed between years, or that thermoregulatory signals differed consistently between years, or that different snakes had different preferred T_b 's. Examination of Figs. 2–4 reveal that in 1989 and 1990, T_b 's were between the daily maximum

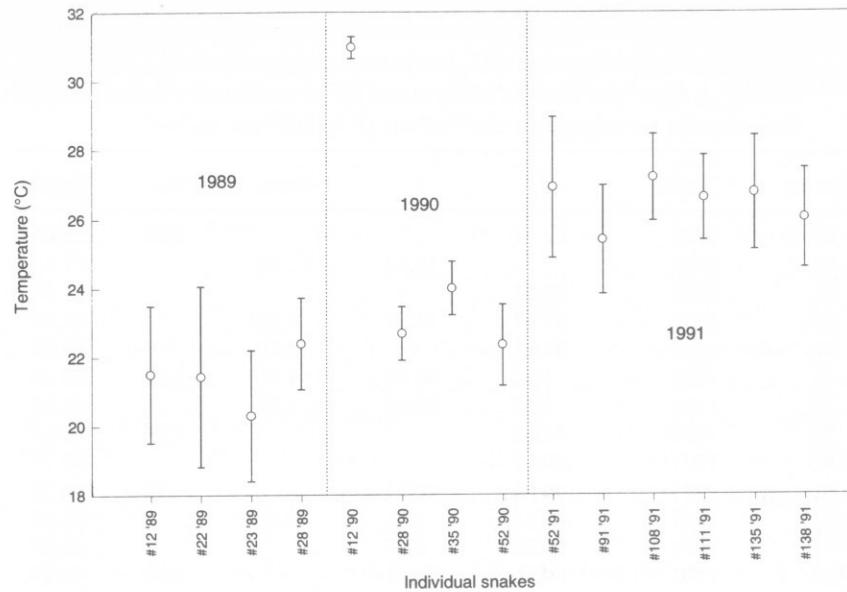


Fig. 5. Body temperature ($\bar{x} \pm 95\%$ CI) of 11 snakes during the incubation period of 12 in 1990 (25 May to 10 August) 1989, 1990, or 1991. Three snakes were each monitored in 2 consecutive years. In 1990, snake 12 had a higher mean T_b (body temperature) for this period than any other snake, including its own T_b in 1989.

and minimum temperatures (measured at the visitor center), and were spread throughout the range. In 1991, most T_b values were still within the visitor center maximum–minimum temperature range but were clustered near the maximum line much more than in 1989 or 1990. In 1991, snake T_b 's followed T_s more closely than in 1989 or 1990 (Figs. 2–4). This is also evident from the results of regression analyses where T_s accounted for most of the explained variation in T_b 's in all snakes followed in 1991 (Table). Body temperatures of snakes tracked more than 1 year (12, 28, 52) all differed between years. Differences in T_b between years were due to differences each year in snake thermoregulatory behavior.

Snakes radio-tagged in 1989 were first captured in the residence area. In 1990, two snakes tagged in 1989 (12 and 28) were tracked from their dens, and two were captured in the residence area and tagged. All of the snakes followed in 1989 and 1990—except snake 12 in 1990—had home ranges in or near the residence area. In 1991, we captured snakes at the den, implanted radios, and

released them at the den. Five of these snakes moved southeast and did not visit the residence area. One (32) was killed a few days after release. The only snake to include the residence area in its home range in 1991 was 52, first captured and tagged in the residence area in 1990.

In 1991, snakes occupied habitat that was subjectively different from habitat near the residence area used by snakes tracked in 1989 and 1990. Habitat used in 1991 was rockier and more open with less tree-and-shrub cover and more exposed bedrock. Microhabitats selected in 1991 probably received more solar radiation than the area around the residences. Whereas air and substrate temperatures in 1991 were comparable to 1989 and 1990, snakes in more open habitats could reach high T_b 's more rapidly in the morning and keep T_b 's higher during the day with less effort and perhaps fewer costs (Lillywhite 1987). The warmest snake in 1989 (23) spent most of his time in the open locations bordering parking lots in the residence area. Snake 35 had the warmest average T_b of any nongravid snake in 1990. This snake, a male, was more active than the three females tracked in 1990, and spent more time in the open in full sun than the other three snakes (unpublished data from authors' observations—not part of this study). Snake 12 selected similar rocky, open habitat for incubation instead of more densely vegetated habitats available nearby.

Snake 12 carried a radio from 15 June 1989 to 17 August 1990. She was gravid in 1990, providing an opportunity to contrast T_b and behavior of the same snake under different physiological constraints. We had radios in males and nongravid females—including snake 28—both years, with data encompassing the entire period that snake 12 was tracked. Because of this, we can compare snake 12's behavior and resulting T_b to the other snakes to assess whether there were deviations from the normal range by snake 12 in either year. Figures 1 and 5 indicated that snake 12's T_b in 1989 did not differ from the other snakes monitored in 1989 nor from nongravid snakes in 1990, but in 1990 her T_b was much higher. The differences between snake 12's T_b during incubation in 1990 and all other snake T_b 's emphasize the importance of thermoregulating to keep T_b high, even at the expense of other physiological needs.

The behavior of snake 12 in 1990 was different from her own behavior in 1989 and different from that of all other snakes observed during the 3 years. Her behavior was similar to gravid female rattlesnakes in other studies (Brown et al. 1982; Reinert 1984; Graves et al. 1986; Reinert and Zappalorti 1988; Graves and Duvall 1993; Peterson et al. 1993). The few differences between environmental temperatures at snake 12's locations in 1990 and at other snake locations

indicate that snake 12's T_b was maintained by active thermoregulation rather than thermoconformity with the microhabitats each snake selected.

Moves by snake 12 in 1989 were extensive. She was first captured on 5 June 1989 in the residence area, and her home range in 1989 was estimated to be more than 5 ha (unpublished data from authors' observations—not part of this study). In 1990, she moved only approximately 325 m (straight line distance) from the den and remained in a 30-m² area for 79 days until parturition. In 1989, snake 12 ate at least twice—we did not detect her feeding at all in 1990. Even during the spring migration from the den in 1990, snake 12 maintained a higher T_b than snake 28 ($T_{b12} = 15.15 \pm 6.96$, $T_{b28} = 12.43 \pm 5.91$, $t_{139} = 2.54$, $P = 0.012$).

Charland and Gregory (1990:1090) identify "at least two factors that influence thermoregulatory behavior of a free-ranging snake: its preferred T_b and the priority it places on thermoregulation (i.e., thermoregulation may conflict with other activities)." The difference in T_b between 1989 and 1990 for snake 12 reflects a shift in the priority the snake placed on thermoregulation between the 2 years; this shift was generated by pregnancy. In 1989, snake 12's priorities were probably related primarily to foraging, whereas in 1990, maintaining a high T_b superseded other needs. Maintaining a high T_b at Natural Bridges is apparently not compatible with other activities. Graves and Duvall (1993) suggested foraging conflicts with efficient thermoregulation in the cool Wyoming environment of the population they studied. Gravid females do not undergo the extensive vernal migrations in search of dense populations of small rodents that males and nongravid females do (Duvall et al. 1985, 1990).

Gravid female snakes have been documented to aggregate in rookeries in some populations (Brown et al. 1982; Reinert 1984; Reinert and Zappalorti 1988; Graves and Duvall 1993). We did not observe this at Natural Bridges. No other snakes were observed near snake 12's rookery at any time during 1990. We believe this difference reflects a greater abundance of thermally suitable microhabitats for gestation at Natural Bridges relative to these other studies.

An organism's maximum metabolic rate occurs at a specific temperature, considered to be its optimum or preferred temperature (Dawson 1975; Huey 1982). Ectotherms thermoregulate to maintain body temperature as near optimum temperatures as possible (Huey and Stevenson 1979; Pough 1980; Huey 1982). Various metabolic processes (e.g., digestion, locomotion, gestation, etc.), however, could have different temperature optima (Regal 1966; Pough 1980; Slip and Shine 1988; Peterson et al. 1993). Ectotherms may regulate T_b to

optimize one process at the expense of other activities or compromise efficiency among a variety of metabolic needs (Dawson 1975).

Environmental constraints, physical and biological, can prevent ectotherms from maintaining their T_b 's near optimum temperature (DeWitt 1967; Muth 1977; Magnuson and Beitingger 1978; Magnuson et al. 1979; Peterson 1987; Gier et al. 1989). Body temperatures may also deviate from optimum because thermoregulatory behavior is too costly in terms of predation risk, loss of foraging time, energetic costs, competition, or social interactions (Regal 1967; Huey 1974; Huey and Slatkin 1979; Huey 1982; Charland and Gregory 1990).

Snakes have needs (e.g., thermoregulation, food, shelter, mates) that must be balanced in a heterogenous environment. Beck (1991) found that thermoregulatory response varied with time of year; basking occurred only when ambient temperatures were low. Basking is not without costs because snakes are more exposed to predators, are not able to actively forage, and can't search for mates. In fact, snakes may bask only when the need to raise T_b is greater than other physiological needs (Huey 1974; Beck 1991).

Western rattlesnakes at NABR are capable of maintaining high, constant T_b 's, at least in summer. Ambient temperatures at NABR are high enough for snakes to be active without basking but not high enough to maintain high T_b 's without basking. At NABR, males and nonincubating females sacrifice high T_b 's to perform other necessary activities. Pregnant females such as snake 12 in 1990 must maintain a high, constant T_b for normal development of embryos and do so at the expense of other needs.

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