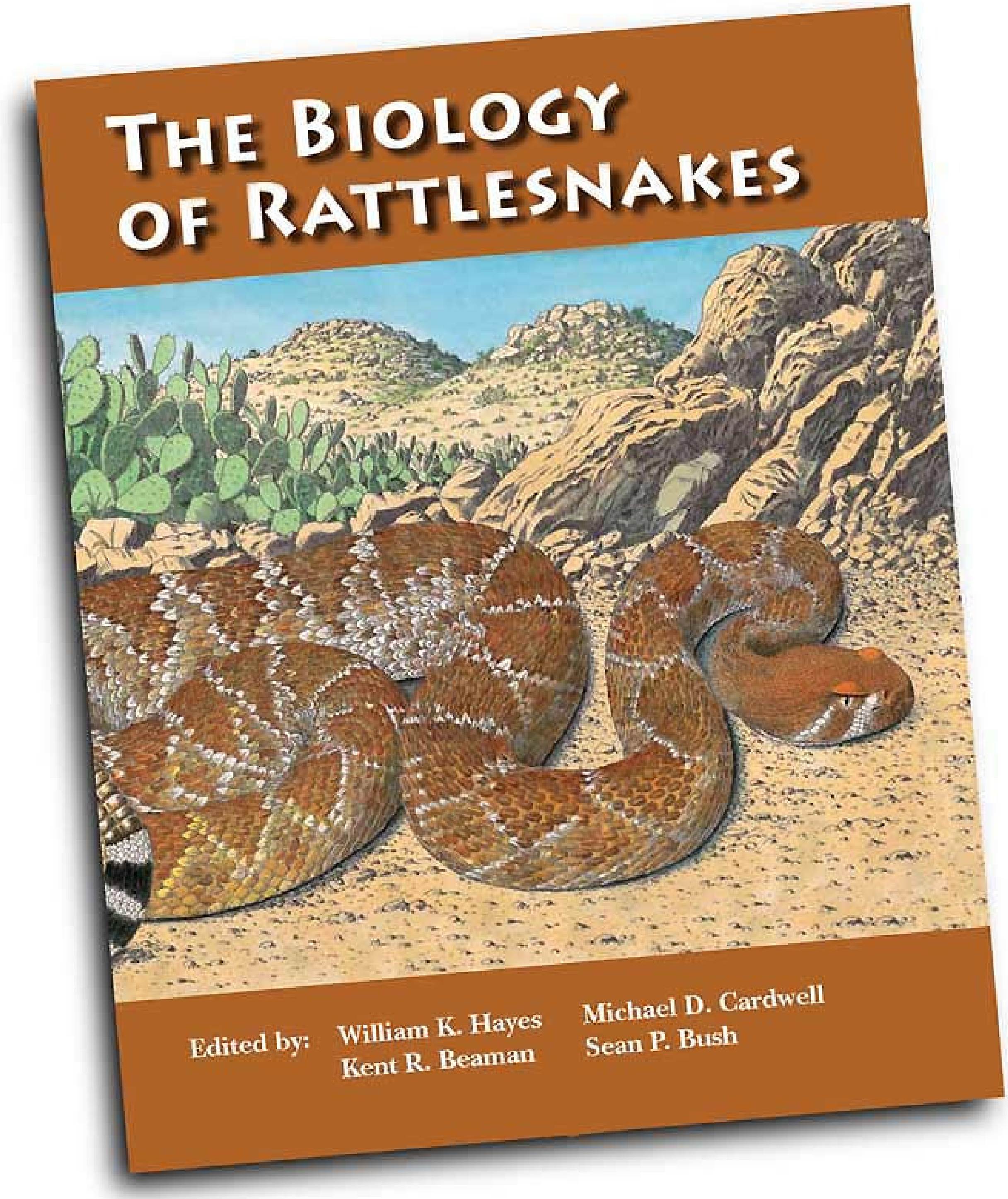
THE BIOLOGY
OF RATTLESNAKES
Edited by: William K. Hayes
Kent R. Beaman
Michael D. Cardwell
Sean P. Bush

Pp. 287-290 in W. K. Hayes, K. R. Beaman, M. D. Cardwell, and S. P. Bush (eds.),
The Biology of Rattlesnakes. Loma Linda University Press, Loma Linda, California.

Observations on the Thermal Ecology of Montane Mexican Rattlesnakes

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Abstract.—The thermal ecology of rattlesnakes inhabiting the high mountainous areas of Mexico is poorly known. We captured individuals of five taxa of montane *Crotalus* (*C. lepidus maculosus*, *C. l. morulus*, *C. p. pricei*, *C. p. miquihuanus*, and *C. t. triseriatus*) in Mexico and recorded cloacal and environmental temperatures at the time of capture. We assessed the relationship between cloacal and environmental temperatures and determined differences in body temperatures among taxa. We also described activity periods and body temperatures for each taxa. Overall, body temperatures were more closely associated with substrate temperatures than air temperatures. In addition, body temperatures of *C. t. triseriatus* were significantly warmer than other *Crotalus* examined when compared at a constant substrate temperature. Finally, no distinct patterns were observed in activity periods or the relationship between body temperatures and time of day.

Introduction

Nearly all aspects of snake ecology are potentially affected by body temperature, either directly (by changing the rate of biochemical reactions) or indirectly (because of costs associated with thermal regulation; Peterson et al., 1993). Understanding the relationship of body temperature to the environment is especially important in helping to understand the ecology of snakes occurring at high altitudes. The thermal ecology of montane *Crotalus* is known primarily from reports on species found within the United States (*C. lepidus*: Beaupre, 1995a,b; McCrystal et al., 1996; *C. pricei*: Prival et al., 2002; *C. willardi*: McCrystal et al., 1996). The only description of thermal relationships for montane Mexican *Crotalus* of which we are aware was reported by Lemos-Espinal et al. (1997) for *C. triseriatus* and *C. ravus*.

We measured cloacal and environmental temperatures of five taxa of montane *Crotalus* from the Mexican states of Chihuahua (*C. p. pricei*), Durango (*C. lepidus maculosus*, *C. p. pricei*), Coahuila (*C. p. miquihuanus*), Nuevo León (*C. p. miquihuanus*, *C. l. morulus*), México (*C. t. triseriatus*), Michoacán (*C. t. triseriatus*), and Morelos (*C. t. triseriatus*). Two of these species (*C. l. morulus* and *C. p. miquihuanus*) from Sierra Peña Nevada, Nuevo León, were sampled over a two-year period. Here we present the analysis of these measurements and provide an explanation of the observed interspecific variation.

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Materials and Methods

Snakes were collected with tongs and either partially restrained in clear acrylic tubes or with a gloved hand. Body temperatures (T_b) were taken with a cloacal quick-reading thermometer (Miller and Weber, Inc., Queens, New York). Care was taken to ensure that body temperatures were recorded quickly (typically within 10 sec after initial capture), especially with smaller snakes; measurements taken from snakes that required considerable time to restrain were discarded. Only temperatures from surface-active snakes (i.e., crawling or coiled on the surface, and not underneath surface cover) are reported herein. Searches were conducted during the daytime only. Air temperatures (T_a; 1.5 m above the location where each snake was found) and substrate temperatures (T_s; on the substrate where each snake was initially found) were recorded using a shaded bulb. All temperatures were recorded to the nearest 0.1°C. Time of collection was recorded in Central Standard Time (CST).

Linear regression was used to determine if T_a and T_s were significantly correlated to T_b for each species. In addition, analysis of covariance (ANCOVA) was used to determine which environmental temperatures (T_a, T_s, or both) were useful in the prediction of body temperature (model: $T_b = T_a + T_s$ + species, $\alpha = 0.05$ for predictor variable deletion). After removal of nonsignificant variables from the model, T_b was compared among the different species of *Crotalus* holding the environmental temperature constant (i.e., H_0: y-intercepts for each species are equal). Rejection of this null hypothesis was followed by pairwise comparisons of means. For ANCOVA, the assumption of equal slopes was tested by including a covariate-by-factor interaction term, determining it was not significant, and removing the

Table 1. Analysis of covariance statistics for test of predictors of cloacal temperature (T_b) in montane Mexican *Crotalus*. Predictors include air temperature (T_a), substrate temperature (T_s), and species.

Source	Type III Sum of Squares	df	Mean Square	*F*	*P*
T_a	24.9	1	24.9	2.5	0.120
T_s	182.1	1	182.1	18.3	<0.001
Species	190.2	4	47.6	4.8	0.002
Error	476.5	48	9.9		

term for subsequent analyses. The assumption of homogeneous variances was tested using Levene's test. For all tests, significance was assessed with $\alpha = 0.05$. Probabilities for pairwise comparisons of species were adjusted using the Bonferroni adjustment. In addition to the hypotheses tested, a graph of time of capture by T_b was plotted to visually assess activity periods and T_bs for each species. Analyses were conducted using SPSS software (SPSS, Inc., Chicago, Illinois, USA).

Results

Conditions of capture and significance of intraspecific temperature variation for each taxa are reported below.

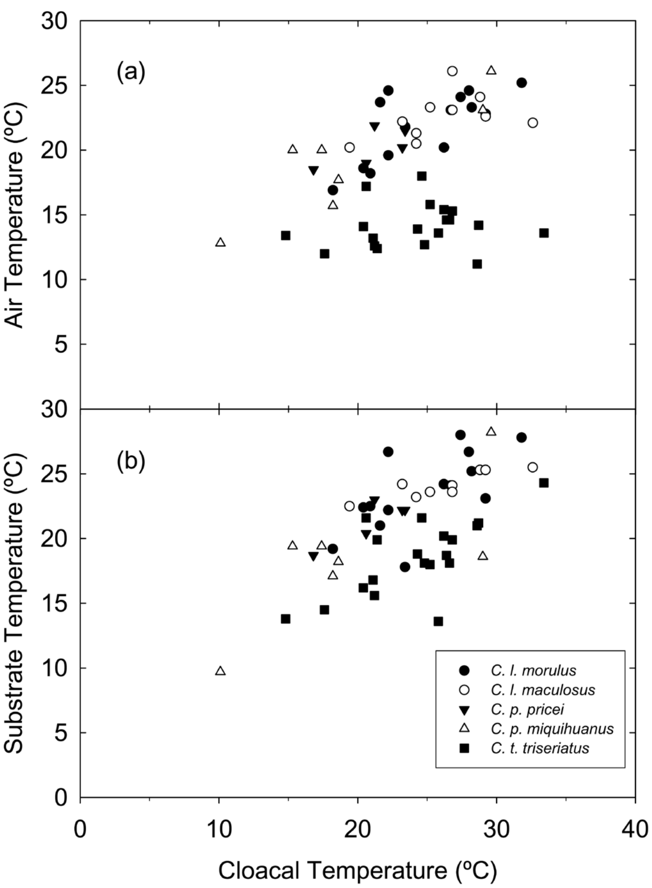

Figure 1. The relationship of cloacal temperature to (**a**) air temperature and (**b**) substrate temperature for five taxa of montane Mexican *Crotalus*. All data collected from active snakes.

Crotalus lepidus morulus.—Snakes ($N = 14$) were collected from Sierra Peña Nevada, Nuevo León, Mexico, from 2000-2001. Snakes were found among limestone rocks and thick clumps of agaves on flat to moderately-sloping hillsides with sparse canopy in pine/oak forests at elevations of 2,500-2,800 m. Most snakes were found within or near (within 1 m of) clumps of agaves, and typically attempted to escape into these clumps upon approach. Several inactive snakes were found embedded well within agave clumps under several layers of dead leaves. Active snakes were collected from 0922-1515 h. Active snakes were most commonly encountered during the latter part of the rainy season (August-September). The regressions of both T_b on T_a and T_b on T_s were statistically significant ($r^2 = 0.521$, $P = 0.004$, and $r^2 = 0.443$, $P = 0.009$, respectively).

Crotalus lepidus masculosus.—Snakes ($N = 10$) were collected near Hwy 40 along the Durango/Sinaloa border during late June 2000. Snakes were found at an elevation of 2,150 m on relatively flat hillsides in grassy, rocky areas near breaks in the pine/oak forest with little canopy. Active snakes were found from 0956–1442 h during breaks in the otherwise rainy weather. Only the regression of T_b on T_s was statistically significant ($r^2 = 0.779$, $P = 0.001$).

Crotalus pricei pricei.—Snakes were collected from the Sierra del Nido, Chihuahua, in July 2000, and from Rancho Santa Barbara, Durango, in August 2003. The snakes from the Sierra del Nido ($N = 3$) were found near a high elevation (2,700 m) grassy meadow in pine/oak forest at 0803, 1725, and 1750 h. The latter two snakes were found immediately after a light rain following reappearance of the sun. The snakes from Rancho Santa Barbara ($N = 2$) were found at 2,300 m in a dry, rocky creek bottom in pine/oak forest at 1258 and 1323 h. Although the regressions of both T_b on T_a and T_b on Ts were not statistically significant, T_s had a strong effect on T_b ($r^2 = 0.723$, $P = 0.068$).

Crotalus pricei miquihuanus.—Most snakes ($N = 6$) were collected from Sierra Peña Nevada, Nuevo León, from 2000-2001. Snakes were found at elevations of 2,500-3,100 m on flat to moderately-sloping hillsides in pine/oak forest with an abundance of agaves and low-growing shrubs. As with *C. l. morulus*, this species was frequently encountered in or near thick clumps of agaves. Several inactive snakes were found embedded well within agave clumps under several layers of dead leaves. At lower elevations (2,500-2,800 m), this snake was found in agave thickets shaded by a dense oak canopy. Higher-elevation sites were characterized by

Table 2. Variation in cloacal, air, and substrate temperatures among five taxa of montane Mexican *Crotalus*. All data collected from active snakes.

		Cloacal Temperature		Air Temperature		Substrate Temperature	
Taxon	***N***	**range**	**mean ± SE**	**range**	**mean ± SE**	**range**	**mean ± SE**
C. lepidus morulus	14	18.2-31.8	24.7 ± 1.0	16.9-25.2	21.9 ± 0.7	17.8-28.0	23.6 ± 0.8
C. lepidus maculosus	10	19.4-32.6	26.0 ± 1.1	20.2-26.1	22.5 ± 0.5	22.5-25.5	24.0 ± 0.3
C. p. pricei	5	16.8-23.4	21.0 ± 1.2	18.5-21.9	20.2 ± 0.7	18.7-23.0	21.3 ± 0.8
C. p. miquihuanus	7	10.1-29.6	19.7 ± 2.6	12.8-26.1	19.3 ± 1.6	9.7-28.2	18.6 ± 2.0
C. t. triseriatus	19	14.8-33.4	24.1 ± 1.0	11.2-18.0	14.1 ± 0.4	13.6-24.3	18.5 ± 0.7

thickets of low-growing shrubs and agaves with a relatively open canopy. Active snakes were found throughout the year. One snake was collected from Santa Rita, Coahuila, at 2,631 m on a steep hillside amongst thick manzanita and exposed limestone on 27 May 2001. Individuals were found active from 1026-1845 h. The regressions of both T_b on T_a and T_b on T_s were statistically significant ($r^2 = 0.771$, $P = 0.009$, and $r^2 = 0.593$, $P = 0.043$, respectively).

Crotalus triseriatus triseriatus.—Snakes were obtained from three different localities. Numerous snakes ($N = 14$) were collected off the Ajusco-Xalatlaco highway near the México/Distrito Federal border in 1993-1994 and 2001 at an elevation of 3,510 m in a grassy meadow. Snakes ($N = 3$) from Lagunas de Zempoala, Morelos, were found near the base of a steep slope in grassy, rocky pine/oak forest at 2,900-3,000 m. Snakes ($N = 2$) from Cerro Tancítaro, Michoacán, were found at 3,350-3,400 m on a steep slope in rocky pine/oak forest. Active snakes were found from 1030-1520 h. Although snakes were collected throughout the year, during the rainy season from late June to early September, snakes were only found active for short periods of time corresponding to breaks (typically from 1000-1300 h) in the rainy weather. Only the regression of T_b on T_s was statistically significant ($r^2 = 0.463$, $P = 0.001$).

When evaluating which environmental temperatures were most useful for predicting T_b, T_a and T_s were found to be highly correlated (adj. $r^2 = 0.812$). However, T_a was not significant as a predictor of T_b when T_s and species were included in the same model (Table 1). Thus, T_s was better than T_a as a predictor of T_b (Fig. 1).

After removing T_a from the model, significant differences were found in T_b among species ($P = 0.001$). Pair-wise comparisons at a constant T_s revealed that *C. t. triseriatus* was significantly warmer than *C. l. morulus* (difference = 4.6°C, $P = 0.007$), *C. p. pricei* (difference = 5.9°C, $P = 0.01$), and *C. p. miquihuanus* (difference = 4.5°C, $P = 0.02$). Mean T_b of *C. t. triseriatus* was 3.7°C warmer than *C. lepidus maculosus*, but that difference was not significant ($P = 0.15$).

Finally, no distinct patterns were observed in activity period or the relationship between T_b and time of day (Fig. 2). Temperature data are summarized in Table 2.

Discussion

The mean T_bs among montane Mexican *Crotalus* sampled in this study were generally similar to those reported for other taxa of montane *Crotalus*. The mean T_b of 25.2ºC for *C. lepidus* from the Huachuca and Patagonia Mountains of Arizona (McCrystal et al., 1996) was nearly identical to the mean T_b of *C. l. morulus* (24.7°C) and *C. l. maculosus* (26.0°C) from this study. The mean T_b of 26.1°C for *C. p. pricei* in the Chiricahua Mountains in Arizona (Prival et al., 2002) was much higher than the mean T_b for the two taxa of *C. pricei* sampled in our study (*C. p. pricei*: 21.0°C; *C. p. miquihuanus*: 19.7°C), but this difference may be an artifact of our small sample size. Lemos-Espinal et al. (1997) reported the mean T_b for *C. t. triseriatus* to be 26.2°C. Individual temperature measurements from the ten specimens sampled in their study were sent to us for use in the present study. The addition of nine samples of *C. t. triseriatus* from various localities (see Results) in our study changed the mean T_b reported by Lemos-Espinal et al. (1997) from 26.2 to 24.1°C. However, T_a and T_s remained remarkably similar (14.2°C and 18.7°C vs. 14.1°C and 18.5°C).

In our pooled analysis, T_s was better than T_a as a predictor of T_b. When evaluated for each individual species, T_a was

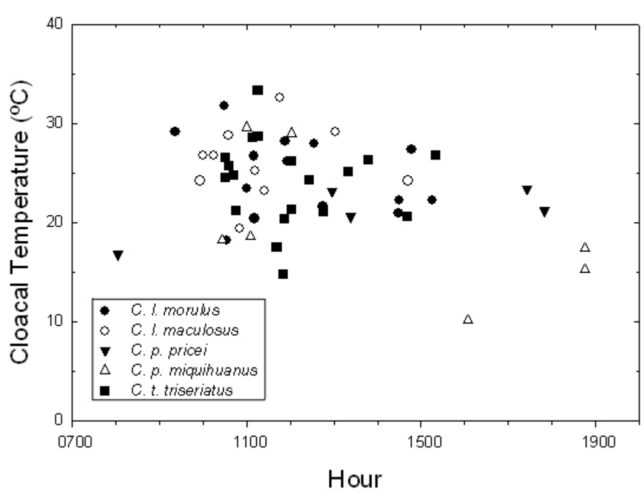

Figure 2. The relationship of cloacal temperature to time of collection for five taxa of montane Mexican *Crotalus*. All data collected from active snakes.

found to have a slightly stronger relationship to T_b than T_s for two species, *C. l. morulus* and *C. p. miquihuanus*. However, the validity of the functional relationship is uncertain due to multicollinearity; i.e., the predictor variables for T_b are themselves correlated. Solar radiation, whether direct or indirect (through warming of the substrate), is an important factor in the thermoregulation of the high-elevation species sampled. McCrystal et al. (1996) found that T_s was a better predictor of T_b for *C. lepidus*, but T_a was a stronger predictor of T_b for *C. willardi*. *Crotalus willardi* typically inhabits canyon bottoms and cooler areas with more canopy cover (McCrystal et al., 1996; Smith et al., 2000; Campbell and Lamar, 2004), which may explain this difference.

Specimens of *C. t. triseriatus* in this study had higher T_bs when adjusted for T_s than the other taxa of *Crotalus*. Does this indicate a difference in temperature preference or a difference in thermoregulatory behavior due to environmental conditions? *Crotalus t. triseriatus* specimens were collected from the highest elevations in this study. Further exploratory analysis of temperatures revealed that T_b did not differ among species ($P = 0.068$) when analyzed independent of covariates, but T_s did ($P < 0.001$). This suggests that the differences in T_bs observed in this study may reflect the relatively cool thermal environment of this species. *Crotalus t. triseriatus* individuals may elevate their body temperatures higher than in other species to compensate for the lower substrate and air temperatures present in their environment. Still, this is an important and easy to miss detail in the biology of montane *Crotalus*. Populations of *Crotalus* at higher, cooler elevations may face stronger evolutionary pressures related to achieving optimal body temperatures relative to low elevation species. Behavioral mechanisms, such as increased basking time when sunlight is available, could be the means by which individuals at higher elevations persist, and ecological studies of these snakes should test this prediction. Most captive *C. t. triseriatus* bask longer than most other species of montane *Crotalus* maintained under similar conditions (RWB, unpubl. data). In addition, morphological characteristics that would allow more rapid heating, such as smaller body size and darker coloration that enhance heat absorption, should be stronger selective pressures for effective thermoregulation in high, cool environments.

For the two sympatric species of montane *Crotalus* sampled from Sierra Peña Nevada, Nuevo León, *C. p. miquihuanus* were captured over a greater range of time of day and a wider range of temperatures than *C. l. morulus*. This trend is evident in Figure 2. The lower mean T_b of *C. p. miquihuanus* may, in part, be due to collection locations up to 300 m higher for several specimens as compared to collection locations for *C. l. morulus*.

Acknowledgments

We thank J. Lemos-Espinal for sharing his data on *C. triseriatus* with us, the numerous people that assisted in the field (X. Hernadez-Ibarra, J. Banda-Leal, G. Ulies de la Rosa-Lozano, D. Hartman, R. Queen, K. Peterson, and the many students at UANL), and several anonymous reviewers for providing comments that greatly improved the final manuscript. DL thanks A. Contreras Balderas for his academic guidance. Funding for research on the herpetofauna of Sierra Peña Nevada was supported in part by the San Antonio Zoo. Collecting was conducted under permits granted to RWB, DL, and J. Lemos-Espinal by SEMARNAT.

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