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PHYSIOLOGICAL RESPONSES TO TEMPERATURE IN THE PATCH-NOSED SNAKE, *SALVADORA HEXALEPIS*

ELLIOT R. JACOBSON AND WALTER G. WHITFORD

ABSTRACT: *Salvadora hexalepis* had a mean preferred body temperature in the laboratory of 33.0 C, a mean critical thermal minimum of 7.0 C, and a mean critical thermal maximum of 43.8 C. Oxygen consumption and heart rate increased with temperature, with greatest changes in these parameters at high and low temperature extremes. Cardiac and metabolic responses are what would be predicted for a reptile the size of *S. hexalepis*. A wide range of thermal tolerance is suggested as an important adaptation for a snake that is primarily a lizard predator.

MANY recent studies have been concerned with physiological responses to temperature in lizards (Dawson and Templeton, 1963, 1966; Bartholomew and Tucker, 1963; Dawson, 1967; Licht et al., 1966; Kour and Hutchison, 1970). However, there are a limited number of studies in which there are data on physiological responses to temperature in snakes. Brattstrom (1965) reviewed the data on body temperatures of snakes, and the limited studies dealing with ophidian metabolism were recently reviewed by Biukema and Armitage (1969). These reviews point to a lack of information concerning hot desert inhabiting snakes and especially species that are diurnal.

Salvadora hexalepis inhabits open scrub desert areas in the southwestern United States and northern Mexico. *S. hexalepis* is a diurnal snake that feeds on lizards (Stebbins, 1966). Therefore, we decided to study physiological responses to temperature in this snake in order to make comparisons with the large body of information available on thermophilic lizards.

MATERIALS AND METHODS

Three *Salvadora hexalepis deserticola* were collected during August in Dona Ana Co., New Mexico at an elevation of about 4500 ft. Nine *Salvadora hexalepis hexalepis* were secured from a supplier in Tucson, Arizona. The snakes were housed in a terrarium maintained at 27 ± 1 C and 14 hr light—10 hr dark photoperiod. The snakes were fed small lizards at five day intervals but were not fed four days prior to the experiments.

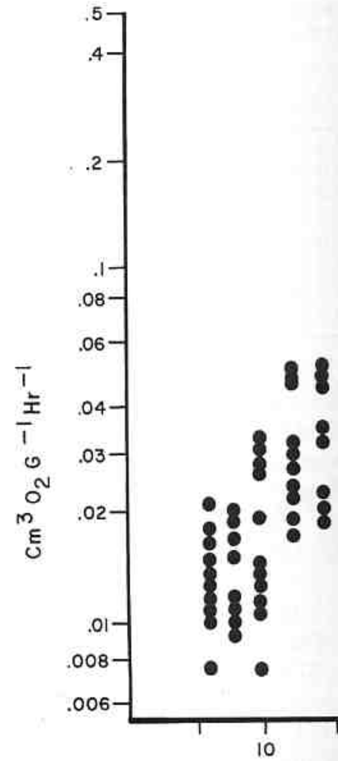
Studies of the mean preferred temperatures (MPT) in *S. hexalepis* were conducted in a thermal gradient box which was kept in a 16 C temperature-controlled room. A temperature gradient from 16 C to 80 C was provided by banks of 300 w, 100 w and 75 w incandescent bulbs spaced above the box. Studies of the MPT of individual snakes or groups of three to five animals were made by placing the animals in the gradient in the morning (between 0800 and 0900 hr) and measuring body temperatures over a 5-hr period. Body temperatures were recorded with a Schultheis quick-reading thermometer at 30-min intervals. The groups of snakes studied included untested and previously tested individuals. Attempts to continuously record body temperatures with a thermistor were unsuccessful because the snakes coiled around the lead wire which resulted in an absence of normal movements.

The critical thermal minimum (CTMin) was determined in a 1-gal jar containing 3 cm dry sand in which the temperature could be lowered at a desired rate by pumping a mixture of ethylene glycol and water precooled to below 0 C through copper coils wrapped around the jar. The flow rate was adjusted to cool the snake at a rate of about 1 C per min. A patch-nosed snake with a Yellow Springs Instrument (YSI) thermistor inserted in the cloaca was placed in the jar and the temperature of the jar lowered. Body temperature, air and substrate temperatures were monitored with a YSI telethermometer. The behavior of the snake was closely observed and the body temperature at which an animal lost its righting response was recorded as the CTMin.

The critical thermal maximum (CTMax) was determined in a 1-gal jar fitted with a wire top holding a 100 w incandescent bulb with the height adjusted to provide heating at about 1 C per minute. The body temperature was monitored at 1-min intervals with a cloacal thermistor and YSI telethermometer until the snake lost its righting response. This body temperature was recorded as the CTMax.

Oxygen consumption was measured in a respirometer modified from that used by Whitford and Hutchison (1963). The respirometers were paired Erlenmeyer flasks connected by a manometer. One served as a thermobarometer while the other contained the animal and was fitted with an oxygen filled syringe. Containers of NaOH in each flask absorbed CO_2. A volume of water equal to that of the animal as determined by displacement was added to the thermobarometer. Oxygen was injected into the respirometer to compensate for movement of the manometer column and oxygen consumption was read directly from the syringe. One-hour measurements of oxygen consumption were made at 2 C increments between 6 C and 40 C. A 30-min temperature equilibration at the desired test temperature was used between measurements. This equilibration period was sufficient to eliminate movement and allowed measurements to be made on resting animals. Gas volumes were corrected to STP.

Electrocardiograms were recorded at 5-min intervals simultaneously with oxygen consumption measurements at each temperature. Electrocardiograms were recorded on an E and M Physiograph. Leads were made of thumb tack heads soldered to fine wire which



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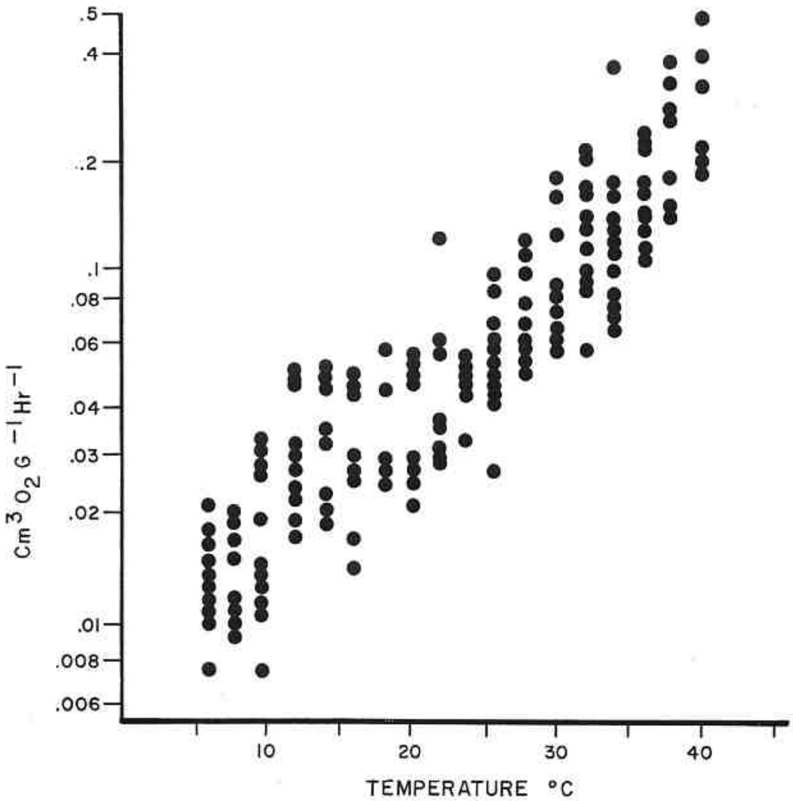


FIG. 1.—The effect of temperature on oxygen consumption in *Salvadora hexalepis*. Each point represents the calculated oxygen consumption for 1 hr for an individual snake.

were placed directly cephalad and caudad to the heart. "EKG Sol" was placed on the leads for maximum contact. The wires were sealed into the top of the respirometer and connected to a high gain preamplifier in series with the physiograph.

RESULTS

The mean preferred body temperature (MPT) in *Salvadora hexalepis* was 33.0 C with a range of observed body temperatures of 30.2 C–34.5 C. The mean MPT and 95% confidence interval of snakes studied individually was 33.2 C ± 0.63 and in groups was 32.8 C ± 0.50.

The mean CTMin and 95% confidence interval of 10 *S. hexalepis* was 7.0 ± 0.3 C with a range of 6.5 C–8.0 C. When the air temperature dropped below 20 C, the snakes attempted to burrow in the layer of soil in the bottom of the jar.

TABLE 1.—Oxygen consumption, heart rate, oxygen pulse and Q_{10} for oxygen consumption and heart rate in *Salvadora hexalepis* at various temperatures.

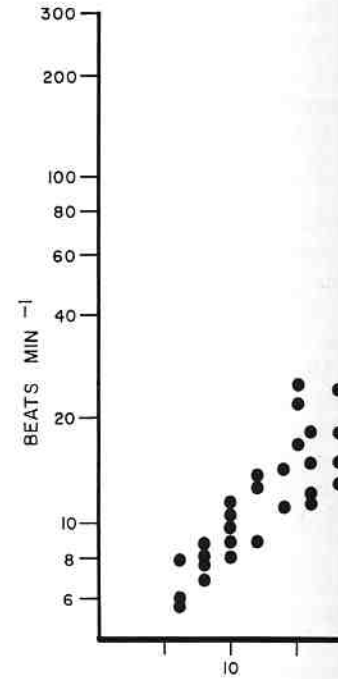
Temperature (°C)	Mean O_2 consumption ($cc\ O_2\ g^{-1}hr^{-1}$)	Mean heart rate ($beats\ hr^{-1}$)	O_2 pulse ($cc\ O_2\ beat^{-1}g^{-1}hr^{-1}$)	Q_{10} oxygen consumption	Q_{10} heart rate
6	.015	396	3.8×10^{-5}		
10	.023	630	3.6×10^{-5}	2.6	3.2
15	.040	1002	4.0×10^{-5}	3.2	2.5
20	.046	1440	3.1×10^{-5}	1.3	2.1
25	.065	2172	2.9×10^{-5}	2.0	2.3
30	.107	3216	3.3×10^{-5}	2.7	2.2
35	.122	4548	2.6×10^{-5}	1.3	2.0
40	.277	7860	3.5×10^{-5}	5.2	3.0

The mean CTMax and 95% confidence interval of 10 *S. hexalepis* was 43.8 ± 0.6 C with a range of 42.5 C–45.0 C. At body temperatures between 33 and 37 C the snakes became hyperactive, and at body temperatures above 39 C they attempted to burrow. Panting was observed in some *S. hexalepis* at body temperatures greater than 41 C. There was no difference in the CTMin and CTMax between the subspecies of *S. hexalepis*.

Oxygen consumption increased from a mean of 0.02 cc $g^{-1}hr^{-1}$ at 6 C to 0.28 cc $g^{-1}hr^{-1}$ at 40 C (Fig. 1). The snakes were inactive in the respirometers at temperatures below 37 C, and oxygen consumption values at these temperatures represent resting rates. At temperatures above 35 C the animals were active by moving around in the chambers, and at 40 C the snakes became extremely active. This activity accounts for the marked increase in oxygen consumption at temperatures above 35 C. The heart rate increased from a mean of 6.6 beats/min^{-1} at 6 C to 131 beats/min^{-1} at 40 C (Fig. 2). The Q_{10} values for heart rate were relatively stable with high values at the extremes. The Q_{10} values for oxygen consumption were more variable but also were highest at the temperature extremes (Table 1). The oxygen pulse was relatively constant at all temperatures. There

TABLE 2.—The mean P-R and R-T intervals in *Salvadora hexalepis* at different temperatures.

Temperature (°C)	P-R	R-T
6	1.63	2.72
10	1.45	1.90
15	.79	1.30
20	.57	.97
25	.32	.61
30	.24	.44
35	.18	.23
40	.12	.18



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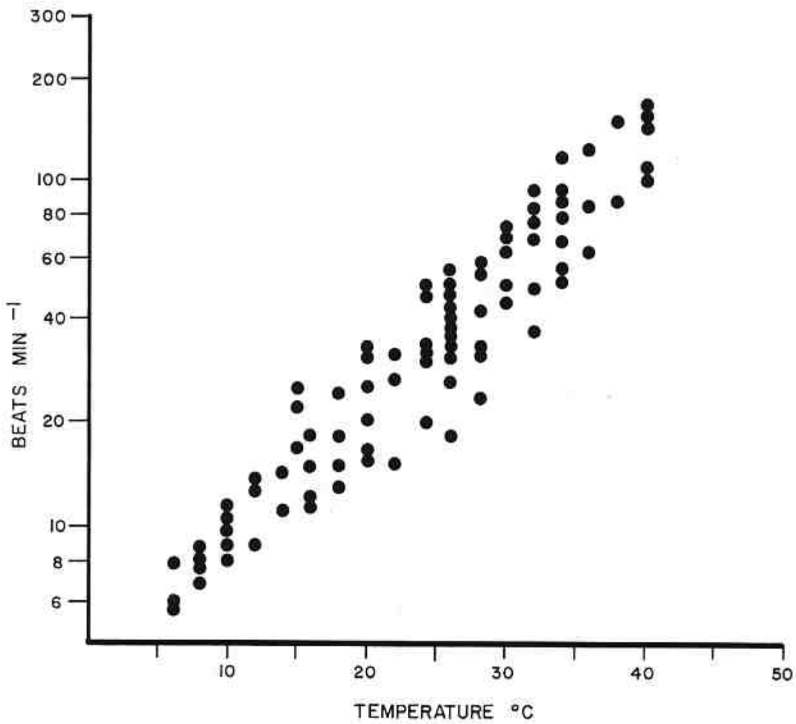

FIG. 2.—The effect of temperature on heart rate in *Salvadora hexalepis*. Each point represents mean heart rate for an individual snake.

was a decrease in both P-R and R-T intervals with an increase in temperature (Table 2).

Discussion

The MPT and CTMax in *S. hexalepis* was higher than any of the snakes reviewed by Brattstrom (1965) except another diurnal, desert-inhabiting snake, *Masticophis flagellum*, which also feeds on lizards. The MPT and CTMax of *S. hexalepis* are comparable to those of many of the iguanid lizards that serve as its principle food source. The CTMin is about 3 C lower than the desert-inhabiting lizards that have been studied by comparable methods (Kour and Hutchison, 1970; Whitford, unpubl.), but it is approximately the same as that of *Natrix rhombifera* and *Thamnophis proximus* acclimated at 30 C (Jacobson and Whitford, 1970). The thermal tolerance range (CTMax-CTMin, 36.8 C) is greater than all lizards and snakes that have been studied except for *Phrynosoma douglassii* (Prieto and Whitford, 1971). The thermal tolerance range, low CTMin, and high MPT of this species are important factors in its ecology. The low CTMin and wide thermal tolerance range allow *S. hexalepis* to emerge from a cool retreat and bask to raise its body temperature to a level allowing maximal activity in search of lizards during their active period, and its high CTMax protects *S. hexalepis* from thermal damage if it is forced to remain exposed to high temperatures for an extended period.

The oxygen consumption and heart rate of *S. hexalepis* are lower than *Thamnophis proximus* but higher than *Natrix rhombifera* and *Pituophis catenifer* (Jacobson and Whitford, 1970; Greenwald, 1971). The oxygen consumption in *S. hexalepis* at 30 C is 64% of that predicted by the general equation for lizards: $ml\ O_2\ g^{-1}hr^{-1} = 0.82W^{-.38}$ (Bartholomew and Tucker, 1964) where W is body weight in grams. According to this equation, a 65-g lizard would consume 0.167 ml $O_2\ g^{-1}hr^{-1}$, whereas the patch-nosed snake at 30 C consumes 0.107 ml $O_2\ g^{-1}hr^{-1}$. This supports the observation of Greenwald (1971) that where oxygen consumption of a snake and lizard of the same body size and temperature differ, the snake has a lower rate of oxygen consumption than the lizard.

The oxygen pulse in *S. hexalepis* varied little with temperature indicating that the increased demand for oxygen at higher temperatures was met by increased heart rate with essentially no increase in stroke volume and/or increased difference in oxygen content of arterial and venous blood.

The changes in P-R and R-T intervals with temperature in *S. hexalepis* were similar to those in *Natrix rhombifera* and *Thamnophis proximus* (Jacobson and Whitford, 1970). Mullen (1967) stated that the average P-R interval for snakes and lizards was 0.26 and 0.16 respectively which was fairly close to the value obtained in this study at 30 C. Both *N. rhombifera* and *T. proximus* have greater P-R and R-T intervals at all temperatures than *S. hexalepis*. We suggest that these differences in depolarization pattern in part account for oxygen pulse differences and are related to activity and ecological adaptations of the species of snake or lizard being considered.

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