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Effects of Body Mass and Temperature on Standard Metabolic Rate in the Eastern Diamondback Rattlesnake (*Crotalus adamanteus*)

MICHAEL E. DORCAS, WILLIAM A. HOPKINS, AND JOHN H. ROE

Determining the consequences of body size and body temperature (T_b) variation is critical to understanding many aspects of snake ecology, because size and temperature play such important roles in the biology of ectotherms. Here, we investigate the effects of body size and temperature variation on the energetics of the largest species of rattlesnake, the Eastern Diamondback Rattlesnake (*Crotalus adamanteus*). Specifically, we measured oxygen consumption to estimate the standard metabolic rate (SMR) of five *C. adamanteus* (mass range 800–4980 g) at 5-degree increments from 5–35 C. A multiple regression model indicated that SMR increased with body size and temperature. Q_{10}s were generally high (range 1.82–4.20) compared to other squamates but were similar to the high values calculated for other large rattlesnakes. An energy balance model for *C. adamanteus* predicted that as T_b increases, so must prey consumption to meet annual SMR energy demands. Thus, T_b variation likely affects patterns of energy acquisition and use and, in turn, influences processes such as growth and reproduction.

BODY size and temperature affect nearly every aspect of the biology of ectotherms (Pough, 1980; Huey, 1982; Peterson et al., 1993). Body temperature influences locomotion (Stevenson et al., 1985), digestive function (Dorcas et al., 1997), development (Osgood, 1978), growth (Arnold and Peterson, 1989), and metabolic rate (Bennett and Dawson, 1976). Body size affects metabolic rate (Andrews and Pough, 1985) and the roles that an organism plays within trophic systems (Pough, 1980). Given the importance of both body size and temperature, it is vital to understand their effects on basic biological functions to gain a thorough understanding of an ectotherm's biology (Huey, 1982; Lillywhite, 1987; Peterson et al., 1993).

Knowledge of the relationships among metabolic rate, body size, and temperature can be used to develop models explaining overall energy requirements (Porter and Tracy, 1974; Secor and Nagy, 1994; Beaupre, 1995a). Rattlesnakes provide a particularly suitable species for examining the relationships between temperature and energy expenditure in ectotherms (Beaupre and Duvall, 1998). Because they are primarily ambush predators, they spend extended periods of time motionless awaiting potential prey. Thus, understanding the effects of temperature on resting metabolic rate will contribute substantially to predicting their energy expenditure while foraging (Waldschmidt et al., 1987; Secor and Nagy, 1994) and, thus, provide an estimate of a large portion of their annual energy expenditure (Beaupre, 1996).

The Eastern Diamondback Rattlesnake (*Crotalus adamanteus*) is the largest species of rattlesnake in the world and is imperiled over much of its former geographic range, primarily because of effects of habitat destruction and indiscriminant killing by humans (Klauber, 1972; Martin and Means, 2000). Studies examining the ecology and physiology of *C. adamanteus* are lacking but are essential in developing a complete understanding of its natural history, a critical first step in conservation. In this study, we describe the functional relationship among body size, temperature, and standard metabolic rate (SMR) in *C. adamanteus* by measuring oxygen consumption of five *C. adamanteus* at seven temperatures. From our results, we predict the energy needed to meet annual SMR requirements of typically sized snakes at various body temperatures.

MATERIALS AND METHODS

We used five *C. adamanteus* to determine the effects of body mass and temperature on SMR (masses = 800, 954, 1504, 2626, and 4980 g). We estimate SMR as the baseline metabolic rate of a quiescent, postabsorptive snake at a given temperature (Bennett and Dawson, 1976; Andrews and Pough, 1985). Three snakes (two males and one female) were obtained from the Riverbanks Zoo in Columbia, South Carolina, and the other two snakes (one male and one female) were acquired from the Savannah River Ecology Laboratory, Aiken, South Carolina. All snakes were captive bred offspring of snakes captured in South Carolina. Prior to metabolic measurements, snakes were fasted for at least 10 days at 25 C to ensure that they were postabsorptive. Each snake was transferred to a respiratory chamber (described below) and allowed to acclimate to 25 C for 24 h in an environmental cabinet (in which all subsequent measures were taken).

We measured SMR of *C. adamanteus* as rates of oxygen consumption (VO_2) using a computer-controlled open-flow respirometry system (Oxymax with Equal Flow Capabilities, Columbus Instruments, Columbus, OH). Each snake was placed into a sealed plastic respiratory chamber (7.8 liters for smaller snakes and 16.0–19.0 liters for larger snakes) and maintained within a temperature-controlled environmental cabinet. Within each chamber, snakes rested upon a screen grate suspended 7 cm above the base of the chamber. Beneath the support grate, ambient air was pumped (0.3–0.6 ml/min) using an external fresh air pump controlled by an equal flow meter at 0.60 L/min (Oxymax, Columbus Instruments, Columbus, OH) into the base of the chamber and circulated within the chamber with a 4-cm fan. The equal flow meter distributed incoming air evenly among all chambers. Airflow was reduced to 0.30 L/min at lower temperatures to increase sensitivity of respiration measures. Air circulated past the snake within each chamber and exited through a constricted port in the chamber lid. An additional port in each chamber lid, connected by an airline to the respirometer sample pump, was used for all air sampling. Air samples were collected approximately 5 cm above each resting snake.

We determined the SMR of each snake at 5 C increments between 5 and 35 C, a range of body temperatures experienced by free-ranging *C. adamanteus* throughout the year as determined by temperature-sensitive radiotelemetry (M. E. Dorcas, A. F. Bennett, and W. Kalinowsky, unpubl.). The order of experimental temperatures was randomized to reduce any potential effects of temperature acclimation (Waldschmidt et al., 1987; Beaupre and Duvall, 1998). Thus, the order of temperatures encountered by snakes in the respiratory trials was 25, 15, 10, 20, 30, 35, and 5 C. At 0915 h each day, the environmental cabinet temperature was changed to the target temperature and a new respiratory trial was initiated. For each VO_2 measurement, the respirometry system sample pump removed an air sample from each chamber, which then circulated over a water absorbent (Drierite) column before passing through the oxygen sensor. Oxygen consumption rates were calculated by the respirometer software (Oxymax, vers. 6.08, Columbus Instruments, Columbus, OH) as the difference between oxygen content of the ambient air and the oxygen content of the sample from each respiratory chamber. Thereafter, VO_2 was determined every 24 min for 24 h. All measures were corrected for standard temperature and pressure by the Oxymax software.

We acquired 58 VO_2 measurements for each snake at each temperature treatment. We removed the initial 6 hours of measurements to allow metabolic rates to stabilize after each temperature change (Roberts, Rice, and M. E. Dorcas, unpubl.). We estimated SMR as the lower quartile VO_2 (the value that marks the boundary between the lowest two quarters of the dataset) of the remaining measurements for each snake at each temperature. Snakes periodically exhibited activity during respiratory trials. Using the lower quartile VO_2 as an estimate of SMR reliably removed these activity-induced elevations in metabolism from the dataset (Fig. 1; Hopkins et al., in press).

To examine the effects of body mass and temperature on SMR (ml O_2/h), we used a repeated measures ANCOVA with snake body mass (g) as the covariate in the model (PROC MIXED Model, SAS, vers. 8.1, SAS Institute, Cary, NC; Petraitis et al., 2001). To examine the functional relationship among body mass, temperature, and SMR, we used multiple regression analysis (Andrews and Pough, 1985; Beaupre and Zaidan, 2001). Both body mass and SMR were $\log_{10}$-transformed prior to ANCOVA and regression analysis to linearize their relationship. Statistical significance was assessed at $P < 0.05$. We calculated Q_{10}-values for each snake over every 10 C increment using their SMR at each temperature. We report mean Q_{10} values ($\pm$ 1 SE) for each 10 C increment.

We assessed the energy costs of maintaining SMR at various body temperatures by estimating annual metabolic costs (kJ/yr) for a small (1 kg) and a large (4 kg) snake by assuming an average conversion factor of 19.87 J/ml oxygen consumed (Gessaman and Nagy, 1988). We then estimated the number of prey items equal to 30% of each snake's body mass needed to meet annual costs of SMR at different body temperatures, assuming an 80% assimilation efficiency (Secor and Nagy, 1994; Andrade et al., 1997). Energy content of prey (5.9 kJ/g wet mass) used in our model was based on values for wild rodents (Kaufman et al., 1975).

RESULTS

Snakes exhibited varying degrees of activity during respiratory measurements, with the

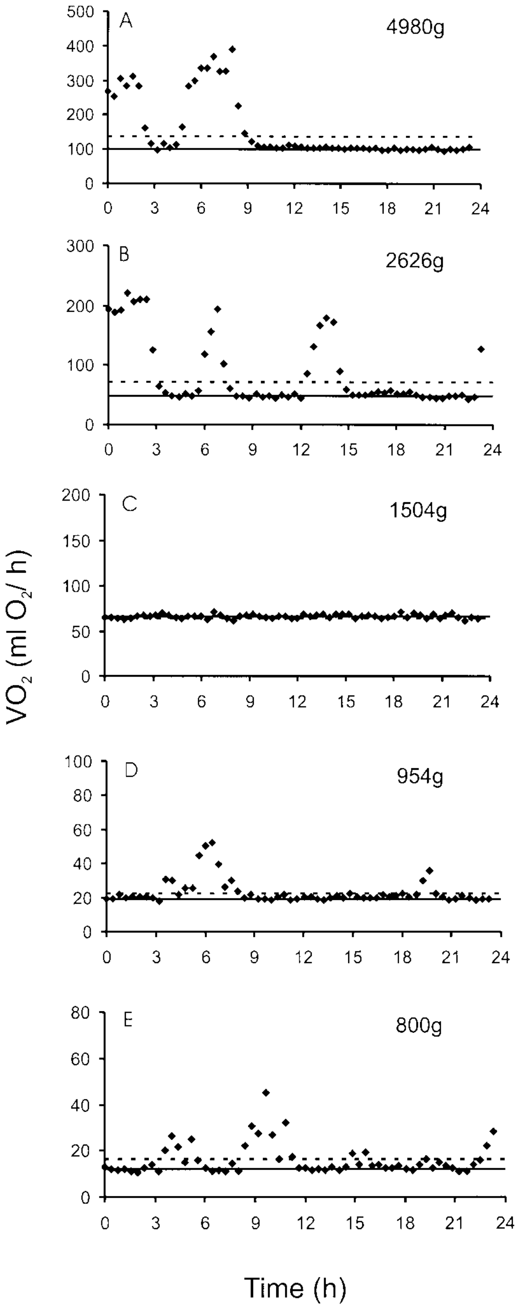

Fig. 1. Examples of oxygen consumption (ml O_2/h) measurements of *Crotalus adamanteus* measured at 25 C using a computer-controlled, open-flow respirometry system, which sampled every 24 min. Note the sporadic activity exhibited by most snakes, as well as the differential ability of the two estimation techniques (average [dashed line] vs lower quartile [solid line]) to reduce the influence of elevated VO_2 rates from SMR estimates. Time zero equals 0915 h.

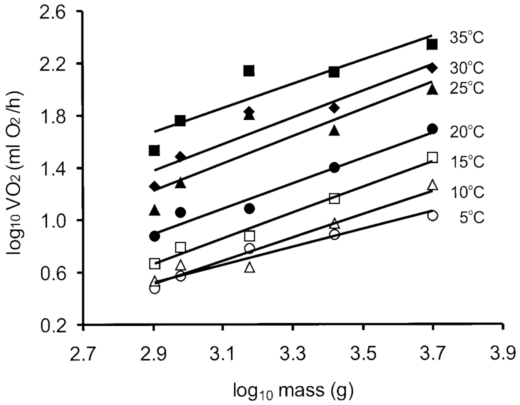

Fig. 2. Relationship between SMR and body mass in five *Crotalus adamanteus* at seven experimental temperatures. Each symbol represents a different temperature. At all temperatures, body mass significantly affected SMR (mean $R^2 = 0.91$, range = 0.79–0.98; all P-values < 0.05).

greatest peaks in activity observed at 25 and 35 C. Our lower quartile estimate of SMR transects the majority of data points that represent resting, baseline metabolism (Fig. 1). The effectiveness of our technique is clearly illustrated when the lower quartile VO_2 is compared to the overall mean VO_2 for individual snakes, an alternative estimation technique that would be highly influenced by activity (Fig. 1).

As expected, SMR of *C. adamanteus* was influenced by body mass and temperature (ANCOVA; log mass: $F_{1,3} = 212.11$, $P < 0.001$; temperature: $F_{6,24} = 92.89$, $P < 0.001$; Figs. 2–3). Multiple regression analysis indicated that SMR in-

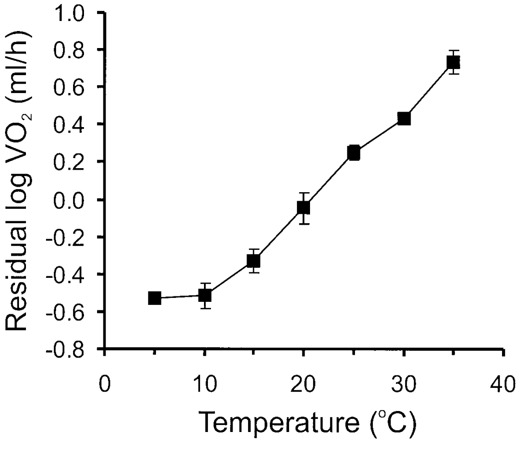

Fig. 3. Residual $\log_{10}$ VO_2 (adjusted for body mass) of *Crotalus adamanteus* at temperatures ranging from 5–35 C. To obtain residuals, all $\log_{10}$-transformed mass and SMR data were combined into a single linear regression model. Values are presented as mean ± 1 SE.

TABLE 1. ESTIMATED SMR, ANNUAL ENERGY COSTS OF SMR, AND NUMBER OF PREY REQUIRED TO MEET ANNUAL ENERGY COSTS OF SMR. Model is based upon a 1 kg and a 4 kg *Crotalus adamanteus* ingesting prey items equal to 30% of their body mass.

	SMR (ml O_2/h)		kJ/year		Prey items/year*	
Temperature (C)	1 kg	2 kg	1 kg	2 kg	1 kg	2 kg
5	2.64	9.59	461	1672	0.33	0.30
10	4.39	15.92	764	2775	0.54	0.49
15	7.28	26.42	1269	4605	0.90	0.81
20	12.08	43.84	2106	7643	1.49	1.35
25	20.04	72.76	3494	12684	2.47	2.24
30	33.27	120.76	5799	21051	4.10	3.72
35	55.21	200.41	9624	34936	6.80	6.17

* Calculations based on 80% assimilation efficiency (Andrade et al., 1997; Secor and Nagy, 1994) and meal energy content of 5.9 kJ/g (Kaufman et al., 1975).

creased with increasing body mass and temperature ($R^2 = 0.95$; $P < 0.001$). The effect of temperature on residual VO_2 (adjusted for body mass) is illustrated in Figure 3. The functional relationship among body mass, temperature, and SMR is described by the following equation:

$$\mathrm{Log_{10}SMR} = (0.930 \times \mathrm{Log_{10}mass}) + (0.044 \times \mathrm{Temp}) - 2.589$$

Standard errors for the mass coefficient, temperature coefficient, and constant were 0.071, 0.002, and 0.235, respectively. Q_{10}-values were 1.82 ± 0.25 (5–15 C), 2.57 ± 0.11 (10–20 C), 4.20 ± 1.10 (15–25 C), 3.30 ± 0.58 (20–30 C), and 2.60 ± 0.18 (25–35 C).

Models of daily energy expenditures using meals equal to 30% of snake mass over the range of experimental temperatures indicate that a 1-kg snake would need to consume between 0.33 and 6.80 rodent meals (at 5 and 35 C, respectively) to meet its annual SMR costs. A 4-kg snake would require between 0.30 (5 C) and 6.17 (35 C) rodent meals per year to meet its SMR costs (Table 1).

DISCUSSION

As expected, SMR of *C. adamanteus* was influenced by body mass and temperature. The mean mass exponent (0.930) describing the allometric relationship between SMR and body mass in *C. adamanteus* is higher than the range of exponents reported for other rattlesnakes, boid snakes, and other squamates (Table 2). Although the mass range of *C. adamanteus* in this study was wide, we did not measure SMR of neonate snakes, a group that has typically been included in investigations of SMR and body mass. Additionally, our small sample size makes our analysis potentially sensitive to unusually high or low values that can skew the relationship between body mass and SMR. Incremental increases in temperature also resulted in increased SMR, with Q_{10}-values above those of most squamates but generally within the range reported for other rattlesnakes (Beaupre and Duvall, 1998; Beaupre and Zaidan, 2001). Explanations for the high Q_{10}-values in rattlesnakes remain elusive (Beaupre and Zaidan, 2001).

The SMR of *C. adamanteus* was generally lower than that reported for many other squamates (Table 2), but was above SMR documented in other snakes using ambush foraging tactics (e.g., Boids and other Crotaline snakes). Based on our regression equation, SMR of a 1-kg *C. adamanteus* is 20.0 mlO_2/h at 25 C, whereas SMR of a similar-sized, typical squamate is estimated to be 29.1 mlO_2/h at 25 C (Andrews and Pough, 1985). A comparably sized *Agkistrodon piscivorus*, *C. horridus*, and a typical boid have estimated SMR's of 4.5, 10.7, and 16.8 mlO_2/h at 25 C, respectively (based on equations in Chappell and Ellis, 1987; Beaupre and Zaidan, 2001; McCue and Lillywhite, 2002). Comparisons with other species were prevented because of the large body sizes of the animals in our study. Compared to most squamates, the low SMR of *C. adamanteus* and other snakes using ambush foraging strategies allows conservation of energy during long periods of gut down-regulation between meals by reducing daily energy requirements (Table 2; Secor and Diamond, 2000).

Our study raises methodological considerations when estimating metabolic parameters in animals. Even highly sedentary species such as *C. adamanteus* may exhibit periodic activity bouts during VO_2 measurements, although there was no evidence of a circadian cycle in VO_2 for *C. adamanteus*. Activity or even subtle

TABLE 2. RELATIONSHIPS BETWEEN SMR, BODY MASS, AND TEMPERATURE FOR TAXONOMIC GROUPS.

Taxonomic group	X_1	X_2	X_3	R^2	Mass range (g)	Source
Agkistrodon piscivorus leucostoma (VCO_2)	0.580	0.054	−2.383	0.72	17–286	Zaidan, 2003
	0.694	0.049	−2.447	0.73	12–693	
	0.690	0.063	−2.708	0.89	12–579	
Agkistrodon piscivorus conanti (VO_2)	0.760	0.041	−2.635	0.93	70–2700	McCue and Lillywhite, 2002
Crotalus horridus (VCO_2)	0.777	0.059	−2.908	0.81	22–1080	Beaupre and Zaidan, 2001
Crotalus atrox (VO_2)	0.676	0.482	−2.122	0.86	14–643	Beaupre and Duvall, 1998
Crotalus lepidus and *Crotalus molossus* (VO_2)	0.646	0.532	−2.480	0.88	5–612	Beaupre, 1993
Crotalus adamanteus (VO_2)	0.930	0.440	−2.588	0.95	800–4980	This study
Boid snakes (VO_2)	0.806	0.415	−2.229	0.97	10–67800	Chappell and Ellis, 1987
Squamates (VO_2)	0.80	0.038	−1.87	0.96	0.3–25600	Andrews and Pough, 1985

Note: Parameter estimates refer to the regression equation of the form $\log_{10} VO_2$ or $VCO_2 = X_1 \times \log_{10}$ mass $+ X_2 \times$ temperature $+ X_3$. Parameters of *Agkistrodon piscivorus leucostoma* are for three populations during late scotophase.

variation in metabolism based on changes in alertness have been observed in other rattlesnakes (Beaupre and Duvall, 1998; Beaupre and Zaidan, 2001) and can greatly influence estimates of SMR and other metabolic parameters. Thus, techniques must be adopted to remove elevations in metabolism attributable to sporadic activity from estimates of metabolic parameters that assume a resting state (Hopkins et al., in press). Compared to traditional SMR estimation procedures based on fewer and less frequent respiratory measurements (e.g., 1–3 metabolic measurements per day over several days; Ruben, 1976; Secor, 1995; Secor and Diamond, 2000), our techniques clearly reveal activity bouts by documenting VO_2 at frequent intervals (Fig. 1). Our lower quartile estimate of SMR eliminated obvious periods of activity during each respiratory trial and appears to accurately represent the resting, baseline metabolism of each snake at a given temperature (Fig. 1).

Assessing how environmental factors (e.g., temperature) affect physiological processes (e.g., metabolism) is critical to understanding the energy expenditure and ecology of an organism. For example, our energy expenditure model predicts that T_b variation in *C. adamanteus* would greatly influence resource acquisition and use (Table 1). Higher selected body temperatures would require snakes to ingest more prey items if they are to continue allocating energy to growth, storage, and reproduction. Because the amount of energy available for growth, reproduction, and storage is related to the difference between harvested energy and the energy expended for maintenance costs, assessing how T_b variation and associated resting energy expenditure affects whole-body energy balance can help in our understanding of life-history traits (Congdon et al., 1982). For example, growth rate and adult body size are factors that influence relative clutch mass, offspring size, and frequency of reproduction in snakes (Seigel and Ford, 1987). Consequently, such factors may be related to the influence of the thermal environment on energy expenditure of *C. lepidus* (Beaupre, 1995a,b). Determining the extent to which resting energy expenditure varies with temperature in *C. adamanteus* yields a better understanding of the consequences of T_b variation for growth, reproduction, and survival, all of which have population-level implications. Our model is not an attempt to describe the annual energy requirements of a free-ranging *C. adamanteus*, because body temperature in snakes varies both daily and seasonally (Peterson et al., 1993). Additionally, our model does not consider costs related to food processing (e.g., specific dynamic action, SDA) or movement. However, coupled with annual T_b profiles of wild snakes, our models may serve as a useful framework for studies that attempt to more completely describe energy costs for resting, postabsorptive snakes (Secor and Nagy, 1994). Determining and incorporating the temperature-dependence of VO_2 during activity and digestion would allow more comprehensive models predicting energy requirements of free-ranging snakes.

Developing a comprehensive knowledge of the natural history of animals is a first essential step in effective conservation strategies. For snakes, having suitable opportunities to thermoregulate is likely as important as having essential resources such as adequate food and suitable habitat (Magnuson et al., 1979; Mushinsky et al., 1980). Because survival and reproductive success of snakes may be ultimately dependent on opportunities to thermoregulate, most terrestrial ectotherms behaviorally thermoregulate by selecting macro- and microhabitats offering appropriate thermal environments (Lillywhite, 1987; Huey et al., 1989; Robertson and Weatherhead, 1992; Reinert, 1993). Investigating habitat selection (e.g., foraging sites, refugia) and the associated thermal characteristics of habitats would be especially enlightening in assessing whole-body energy balance of *C. adamanteus.* Because T_b variation affects energy acquisition and allocation patterns, which in turn may influence life-history traits, identifying habitats critical for thermoregulatory needs of *C. adamanteus* is ultimately important for their conservation.

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(MED) DEPARTMENT OF BIOLOGY, DAVIDSON COLLEGE, DAVIDSON, NORTH CAROLINA 28035; AND (WAH, JHR) UNIVERSITY OF GEORGIA'S SAVANNAH RIVER ECOLOGY LABORATORY, DRAWER E, AIKEN, SOUTH CAROLINA 29803. E-mail: (MED) midorcas@davidson.edu; (WAH) hopkins@srel.edu; and (JHR) roe@srel.edu. Send reprint requests to MED. Submitted: 1 April 2003. Accepted: 1 Oct. 2003. Section editor: M. E. Douglas.