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Variation in Resting Metabolic Rate of the Eastern Massasauga (*Sistrurus catenatus*)

Sarah J. Baker[1,2], Steven J. Beaupre[3], Michael J. Dreslik[1], and Christopher A. Phillips[1]

[1] Illinois Natural History Survey, Prairie Research Institute, University of Illinois Urbana-Champaign, Champaign, Illinois 61820, USA
[3] Department of Biological Sciences, University of Arkansas, Fayetteville, Arkansas 72701, USA

ABSTRACT.—Physiological functions of reptiles are generally temperature-dependent, but variation exists among taxa in the magnitude of response. Pitvipers have been identified as low-energy specialists among the Squamata and exhibit characteristic metabolic responses related to this specialization. Previous studies have measured both field and resting metabolic rates in multiple species of *Crotalus* and *Agkistrodon piscivorous*, but no studies have been conducted for the third North American pitviper genus, *Sisturus*. We measured resting metabolic rates across an ontogenetic series of 28 individual Eastern Massasauga (*Sistrurus catenatus*) from Illinois to understand the magnitude and variability of their resting metabolic requirements. We found significant effects of sex, body mass, temperature, and the time-by-temperature interaction. Mass and temperature effects were expected, as larger warmer individuals will naturally have higher resting metabolic rates. The time-by-temperature interaction indicates the presence of a temperature-dependent circadian cycle in resting metabolic rate, and interpretation of the unexpected sex effect remains unclear. We compared our results to previous studies and conclude that, overall, *S. catenatus* does not differ greatly from other pitvipers, except with regard to the significant effect of sex. When data were extrapolated to include an entire active season, we found a 250-g female needs to ingest 2.5–8.5 individual rodents (depending on species consumed) per year to meet her resting energy requirements, further supporting their designation as low energy specialists.

INTRODUCTION

Ectothermy affords numerous energetic advantages for reptiles, including the ability to endure periods of low food availability and efficient biomass production (Pough, 1980). Within squamate reptiles, some taxa are adapted as low energy specialists. Such taxa include species in the families Anguidae, Gekkonidae, and Xantusiidae among lizards (Pough, 1983; Mautz and Nagy, 2000), and Achrochordidae (Shine, 1986), Boidae (Chappel and Ellis, 1987) and Viperidae among snakes (Beaupre and Duvall, 1998; Zaidan, 2003). Boids and viperids in particular share traits supporting a low energy model including sit-and-wait foraging and gut atrophy between meals (Secor et al., 1994). As low energy specialists, rattlesnakes are interesting model organisms for metabolic studies (Beaupre and Duvall, 1998). Metabolic studies allow us to determine the effects of the environment on physiological processes, which is important because the energy available to an organism is finite and must be apportioned among the competing functions of maintenance, growth, reproduction, and storage (Congdon et al., 1982). How energy is apportioned depends on factors such as age, reproductive status, and environmental influences. Simply meeting energetic needs for resting metabolism can comprise 10–45% of a reptile's annual energy budget (Congdon et al., 1982; Secor and Nagy, 1994; Beaupre, 1995). Measurement of resting metabolic rate allows for further analysis of an organism's energy use (Zaidan, 2003), and enables estimates of mass scaling relationships. Squamates express a high degree of variation in mass scaling relationships, the reasons for which remain unknown (Beaupre and Zaidan, 2001).

[2] Correspondence e-mail: sjbaker2@illinois.edu

Snake species are of special interest, as their populations may be experiencing rapid and sudden declines globally, the causes of which go beyond habitat loss (Reading et al., 2010). Studies describing resting metabolic rates for individual species or genera lay the framework for understanding snake metabolism on a broader scale. When combined with ecological data on diet, reproduction, and demographics, metabolic studies can assist in assessing the vulnerability of individual genera, species, or populations to potential causes of decline. For example, by modeling the potential impacts of climate change on energy requirements for species of interest, the consequences of those changes (more or less required energy) could be applied to life history traits, population carrying capacity (ability of prey populations to support increased predation), and even trophic dynamics (Brown et al., 2004). Currently, *S. catenatus* is a candidate for listing under the federal endangered species act (USFWS, 1999), and is listed as endangered in Illinois (Herkert, 1994). As populations decline range-wide, additional biological data aid in determining and combating threats. In Illinois, the historic range of *S. catenatus* formerly included the northern two-thirds of the state (Smith, 1961), but has contracted now to comprise only one extant population, located at Carlyle Lake in Clinton County (Dreslik, 2005). Given the threats to reptile populations globally and to *S. catenatus* locally, it is essential to have the most complete data possible for conservation. Because environmental stochasticity has profound impacts on reptile physiological processes, which are in turn linked to numerous larger-scale ecological processes (Brown et. al., 2004), physiological studies comprise an important, but underutilized component of conservation. Metabolic studies of species of both *Crotalus* and *Agkistrodon* have been conducted previously (Beaupre, 1993; Beaupre and Zaidan, 2001; Zaidan, 2003; Dorcas et al., 2004), as well as a few other vipers (*Bothrops moojeni*, Cruz-Neto and Abe, 1994; *Vipera berus*, Johansen and Lykkeboe, 1979; and *V. palaestinae*, Dmi'el, 1972), and the data suggest that viperids, specifically crotaline snakes, consistently emerge as low energy specialists (Zaidan, 2003). Studies of North American *Crotalus* and *Agkistrodon* species revealed a positive relationship between metabolism and both body size and temperature (Secor and Nagy, 1994; Beaupre, 1996; Beaupre and Duvall, 1998; Beaupre and Zaidan, 2001; Zaidan, 2003; Dorcas et al., 2004). Both *Crotalus* and *Agkistrodon* also have a metabolic circadian rhythm, with higher rates during certain times of day even under constant temperature (Beaupre and Zaidan, 2001; Zaidan, 2003). In addition, males and non-gravid females do not differ in resting metabolic rates in any snake species measured to date.

We used an ontogenetic series of *S. catenatus* to quantify mass and temperature scaling of metabolic rate, and to evaluate potential differences in metabolic expenditure between sexes, and throughout the day. We compared our results to those for other rattlesnakes (*Crotalus*) and pitvipers (*Agkistrodon*) to better understand metabolic patterns among North American vipers. In addition, we estimated the annual resting metabolic energy budget for *S. catenatus*, and calculated the number of prey items required to meet resting metabolic requirements. Our results provide data that can be used in future bioenergetic models to provide a greater understanding of trophic and population ecology. Moreover, our study site is located at the southern range limit for *S. catenatus*, a wide ranging species, and thus we provide initial data for future investigations into geographic variation in metabolic rates.

MATERIALS AND METHODS

Data collection.—We obtained 92 individuals from the Carlyle Lake population through visual encounter surveys conducted during the spring egress period from 9 March to 12 April 2007. We excluded reproductively active females undergoing secondary folliculogenesis (assessed using ultrasonography) and sick or injured individuals, because of the possibility they would display an elevated metabolic rate. We then randomly selected 28 snakes (mass range 8–495g) from the remaining 78 individuals to provide an equal sex ratio and an ontogenetic series. Before metabolic measurements began, we held snakes in captivity for a minimum of 10 days to ensure a post-absorptive state. This period was adequate for *C. horridus* (Zaidan and Beaupre, 2003), *C. cerastes,* and *Python molorus* (Secor and Nagy, 1994, Secor et al., 1994, Secor and Diamond, 1995).

We sexed all captured individuals by cloacal probing. We measured snout-vent length (SVL) to the nearest 0.1 cm using a flexible seamstress tape by taking repeated measurements of the snake while restrained in a snake tube and averaging three measurements within 1 cm. We measured tail length to the nearest 0.1 cm (posterior vent to rattle base) by gently stretching the tail and using a transparent plastic ruler. We measured mass using an electronic balance accurate to 0.001 g. Individuals were identified by: 1) unique blotch patterns via digital photographs, 2) painting rattle segments with unique color combinations, and 3) injecting individuals larger than 35 cm SVL with passive integrated transponders (PIT) inserted subcutaneously in the posterior third of their body.

Respirometry.—We determined metabolic rate by measuring CO_2 production in a Sable Systems TR-3 (Sable Systems International, Las Vegas, NV) configured as an open flow system, following the methods of Beaupre and Zaidan (2001), except that we used a Percival environmental chamber (Percival Scientific, Perry, IA) set to a 12L:12D photoperiod to maintain temperature rather

than immersion in a water bath. Eight 2500 cm^3 gas-tight chambers were available for use, enabling the simultaneous measurement of seven snakes, with one chamber left empty for baseline reference. Clean (scrubbed of CO_2 and H_2O) high-pressure air from an 80-psi line was provided by a Whatman Purge Gas generator (model FT-IR 75–45 purge-gas generator, Whatman, Haverhill, MA). The high-pressure gas was split into eight equal flows with a Sable Systems MF-8 airflow manifold. We matched flow rates through each line using the mass flow meter supplied with the Sable System and needle valves for each line of the MF-8 manifold. Flow rates used varied from 250–400 mL min^{-1} depending on snake size and temperature. A Sable System eight-channel multiplexer was used to subsample gas from each snake chamber for 6.7 minutes $hour^{-1}$ during each hour of sampling. The baseline chamber was sampled for 3.3 minutes at the beginning and end of each hour to allow block adjustment for any detected drift. Subsampled gas from respirometry chambers was routed through Drierite (W.A. Hammond Drierite Co. LTD, Xenia, OH) to remove any water before flowing to a Li-Cor CO_2 infrared gas analyzer (IRGA; Li-Cor, Lincoln, NE). Data from the IRGA were downloaded using the Sable Systems Universal Interface software.

Experimental design and analysis.—We measured CO_2 production rates for each individual at four different temperatures (17, 22, 27, and 32°C), which encompassed the range of observed body temperatures measured in the field by Dreslik (2005). We measured CO_2 production at each temperature for a continuous 24-hour period. We changed the temperature daily between 1200 and 1300 hours CST, and discarded measurements taken between 1300 and 1400 hours because of the possibility a change in chamber temperature could influence metabolic rate. We randomly assigned each of the 28 individual snakes to one of four groups, and randomized the order of temperatures within each group. Carbon dioxide (ppm) was recorded from each chamber every 5 sec for 6.7 min hr^{-1}, and measurements for each individual were averaged for each hour.

We processed raw data using Microsoft Excel 2010 Spreadsheets (Microsoft, Redmond, WA) and SPSS (ver. 16; IBM, Armonk, NY) for: individual number, mass, sex, time of day, temperature, and hourly averages of VCO_2. We calculated VCO_2 using the equation:

$$VCO_2 = (f_e - f_i) \cdot FR \cdot 60 \quad (1)$$

where VCO_2 is in mL hr^{-1}, f_e is the fractional concentration of CO_2 from the excurrent flow line, f_i is the fractional concentration of CO_2 from the incurrent flow line, FR is the flow rate in mL min^{-1}, and 60 converts to hourly rates.

Before analysis, data were linearized by $\log_{10}$ transformation of VCO_2 (mL min^{-1}) and body mass (g). We applied repeated-measures analysis of covariance (ANCOVA) using SAS (ver. 9.2; SAS Institute, Cary, NC) mixed models procedure (SAS, PROC MIXED), with $\log_{10}$ body mass (g) as a covariate, time and temperature as within-subjects factors, and sex as a between-subjects factor. The best fitting variance-covariance structure (unstructured in temperature, compound symmetry in time) for repeated measures was assessed by minimization of Akaike's Information Criterion (AIC_c). We tested homogeneity of slopes assumptions for ANCOVA by examining the interactions between $\log_{10}$ body mass and temperature, time, and sex. After passing homogeneity of slopes assessment, we ran ANCOVA to adjust data for body mass. Least squares means (adjusted for covariate) were estimated for all levels of significant effects and pair-wise comparisons were conducted using the GT2 method (Hochberg 1974), which is recommended when comparing means adjusted by covariance (Day and Quinn, 1989). Statistical significance was set at $\alpha = 0.05$, and means are presented +/- 95% CI, unless otherwise noted.

We used least squares regression to construct predictions of VCO_2 as a function of body mass and temperature for each statistically significant group (identified by repeated-measures analysis). The equation:

$$Log_{10}VCO_2 = X_1 log_{10}W + X_2T - X_3 \quad (2)$$

(where VCO_2 is CO_2 production rate in mL h^{-1}; X_1, X_2, and X_3 are fitted constants; W is mass in grams; and T is temperature in degrees C) was fitted to each group using SAS proc REG. For constants, X_1 is the mass scaling component, X_2 is the magnitude of the temperature effect, and X_3 is the intercept (Andrews and Pough, 1985). The equation converts to exponential form:

$$VCO_2 = aW^b \cdot 10^{cT} \quad (3)$$

where $a = 10^{X_3}$, $b = X_1$, and $c = X_2$ following Andrews and Pough (1985) and Beaupre and Zaidan (2001).

Comparative analysis.—We compared the mass-temperature scaling relationships of *S. catenatus* to *A. piscivorus* (Zaidan, 2003), *C. atrox* (Beaupre and Duvall, 1998), *C. horridus* (Beaupre and Zaidan, 2001), and *C. molossus* and *C. lepidus* (Beaupre, 1993). Due to differences in how metabolic rates were measured (VCO_2 or VO_2) across studies, we converted the data to common units before comparisons. We followed Beaupre and Zaidan (2001) by assuming a respiratory quotient (RQ) of 0.72, which equated to a conversion of 27.42 J mL^{-1} CO_2 (Gessaman and Nagy, 1988) and 19.68 J mL^{-1} O_2 (Brody, 1945). We then selected a similar period during the circadian cycle for each species, which included the 0700–1300 hr estimates

for *C. lepidus* and *C. molossus* (Beaupre, 1993; Beaupre and Zaidan, 2001). For *A. piscivorus*, we chose 0700–1000 hr, 0800–1100 hr for *C. atrox* (Beaupre and Duvall, 1998), and 0800–1100 hr for *C. horridus* (Beaupre and Zaidan, 2001). To examine the comparative mass effects, we calculated the metabolic rate (J hr^{-1}) for snakes at 27°C across masses of 50–1000g. To examine comparative temperature effects, we calculated the metabolic rate (J hr^{-1}) for a snake weighing 300 g across temperatures of 10–35°C.

Annual resting energy budget.—To estimate the annual resting energy budget, we used T_b for snakes we radio-located from 1999–2002 (Dreslik, 2005). We took the average daily body temperature across years for all non-gravid females and males. We then used the same time period as for the comparative analysis for the mass scaling equation (0800–1100 hrs) and calculated CO_2 production, as above, for the active season, 15 March to 31 October. We repeated this calculation for five size classes within the range observed for snakes at our site: 10, 50, 100, 250, and 500 g. We then calculated the mean minimum and mean maximum daily temperatures using historic data from the NOAA National Climate Data Center (http://www.ncdc.noaa.gov/cdo-web/search) for Carlyle Lake. This allowed us to visually examine if peaks in estimated resting metabolic rates simply tracked temperature. We converted the summed values to Kcals and estimated the mass and approximate number of individual prey items required for a snake of each size class to maintain its resting metabolic rate through the active season.

RESULTS

CO_2 production rates.—We recorded 2,618 temperature-by-hour individual measurements from 28 snakes. Slope heterogeneity tests revealed no significant interaction terms; thus, slopes between the covariate and levels of treatment variables were deemed homogeneous. Repeated-measures ANCOVA (Table 1) revealed that CO_2 production rates increased with snake mass ($F_{1,25}$ = 641.27, P < 0.001; Fig. 1). The mass scaling exponents for *S. catenatus* ranged from 0.834–0.863 for females and 0.893–0.949 for males (Table 2). We also found females had higher CO_2 production rates than males ($F_{1,25}$ = 14.13, P < 0.001). The mass-adjusted estimates of log CO_2 production rate were 0.355 (SE 0.025) for females and 0.227 (SE 0.023) for males. Thus, females showed a significant increase in CO_2 production rates compared to males (GT2 procedure, t = 3.76, df = 25, P = 0.001). Because we found no significant two-way interactions between sex and temperature ($F_{3,78}$ = 0.3, P = 0.79), sex and time ($F_{4,104}$ = 0.29, P = 0.89), and sex, temperature, and time ($F_{12,312}$ = 1.45, P = 0.14) in CO_2 production rates, the sex response was scalar (Fig. 1).

Table 1. Results of the ANCOVA using mass (g), sex, four temperatures, and five time periods on oxygen consumption (VCO_2) of Eastern Massasauga (*Sistrurus catenatus*) tested from Carlyle Lake, Clinton County, Illinois.

Effect	df	*F*	*P*
LogMass	**1,25**	**641.270**	**<0.001**
Sex	**1,25**	**14.130**	**<0.001**
Temp	**3,78**	**274.650**	**<0.001**
Sex*Temp	3,78	0.360	0.785
Time	4,104	1.100	0.360
Sex*Time	4,104	0.290	0.885
Temp*Time	**12,312**	**3.760**	**<0.001**
Sex*Temp*Time	12,312	1.450	0.144

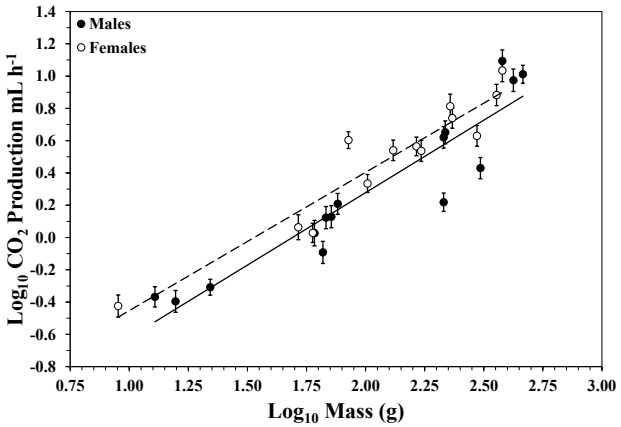

Figure 1. Relationships of log_{10} CO_2 production by log mass with means and 95% confidence intervals (with trend lines) for all temperature and time combinations for female and male Eastern Massasaugas (*Sistrurus catenatus*).

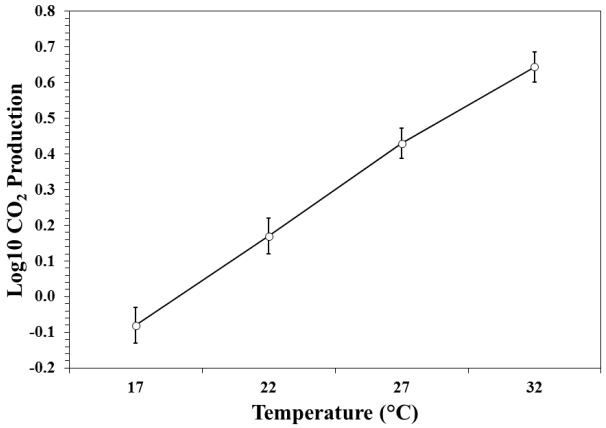

Figure 2. Relationship of log_{10} CO_2 production with means and 95% confidence intervals (with trendline) of each temperature pooled across time periods and sexes for *S. catenatus*.

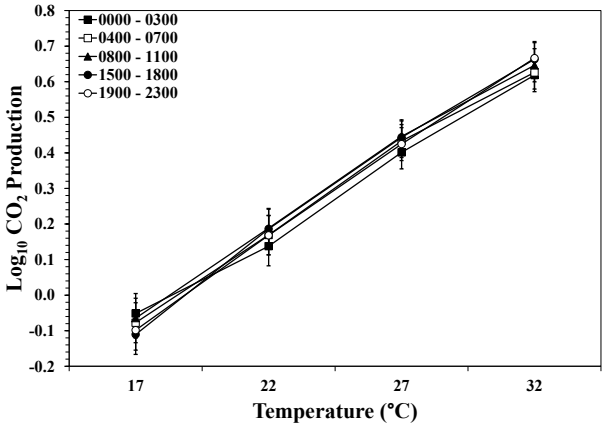

Figure 3. Relationship of $\log_{10}$ CO_2 production with means and 95% confidence intervals by temperature and time (hr) and pooled by sexes for *S. catenatus*.

We found that CO_2 production rates also increased with temperature ($F_{3,78}$ = 274.65, P < 0.001; Fig. 2). Mean CO_2 production rates were lowest at 17°C compared to 22°C (GT2 procedure, t = 9.16, df = 78, P < 0.001), 27°C (t = 20.98, df = 78, P < 0.001), and 32°C (t = 25.59, df = 78, P < 0.001). In addition, mean CO_2 production rates were lower at 22°C compared to 27°C (t = 10.69, df = 78, P < 0.001) and 32 °C (t = 18.63, df = 78, P < 0.001), and lower at 27°C compared to 32 °C (t = 8.67, df = 78, P < 0.001). Thus, CO_2 production rates increased nearly 400% from 17°C to 32°C (Fig. 2).

We found CO_2 production rates did not vary solely with time ($F_{4,104}$ = 1.10, P = 0.36); instead, we found that temperature and time interacted ($F_{12,312}$ = 3.76, P < 0.001; Fig. 3), suggesting a circadian rhythm that is temperature dependent. Thus, at 17°C no clear pattern in CO_2 production rates was apparent, with the lowest rates in the mid-afternoon, and highest rates in the very early morning. At both 22 and 27°C, CO_2 production rates were lowest in the late evening and very early morning, increasing to their highest levels in the mid-morning and late afternoon. At 32°C, CO_2 production rates mirrored a diel sequence where rates were lowest at early hours and highest in the late evening (Fig. 3).

Comparative analysis.—Of the species examined, the mass scaling exponents for female and male *S. catenatus*

Table 2. Regressions of $\log_{10}$ CO_2 produced (mL/h) on $\log_{10}$ body mass (g) and body temperature (°C) for males and females. W = weight, T = temperature. Parameter estimates for equations of the form $\log_{10} CO_2 = X_1 \log_{10} W + X_2 T + X_3$ are presented with standard error in parentheses (CST = central standard time, M = mass in grams, T = temperature °C).

Group	Time	X_1 (SE)	X_2 (SE)	X_3 (SE)	R^2	VCO_2 Equation
Males (df = 2,57 P <0.0001 for all models)	0000–0300 CST	0.915 (0.051)	0.044 (0.005)	-2.742 (0.153)	0.881	$0.0018M^{0.915*}10^{0.044T}$
	0400–0700 CST	0.949 (0.053)	0.047 (0.005)	-2.885 (0.159)	0.881	$0.0013M^{0.949*}10^{0.047T}$
	0800–1100 CST	0.893 (0.050)	0.049 (0.004)	-2.797 (0.151)	0.885	$0.0016M^{0.893*}10^{0.049T}$
	1500–1800 CST	0.911 (0.050)	0.053 (0.004)	-2.921 (0.150)	0.893	$0.0012M^{0.911*}10^{0.053T}$
	1900–2300 CST	0.926 (0.048)	0.051 (0.004)	-2.907 (0.143)	0.901	$0.0012M^{0.926*}10^{0.051T}$
Females (df= 2,49 P <0.0001 for all models)	0000–0300 CST	0.834 (0.049)	0.047 (0.004)	-2.517 (0.140)	0.900	$0.0030M^{0.834*}10^{0.0471T}$
	0400–0700 CST	0.848 (0.051)	0.048 (0.004)	-2.550 (0.143)	0.899	$0.0028M^{0.848*}10^{0.0478T}$
	0800–1100 CST	0.837 (0.046)	0.046 (0.003)	-2.484 (0.129)	0.911	$0.0033M^{0.837*}10^{0.0464T}$
	1500–1800 CST	0.863 (0.047)	0.051 (0.004)	-2.651 (0.132)	0.918	$0.0022M^{0.863*}10^{0.0507T}$
	1900–2300 CST	0.837 (0.047)	0.051 (0.004)	-2.626 (0.132)	0.916	$0.0024M^{0.837*}10^{0.0513T}$

Table 3. Resting metabolic rate regression equations (during similar circadian periods) for six species of pitvipers derived from the literature and from this study. Populations of *A. piscivorous* were from three different locations (Arkansas, Louisiana, Missouri).

	Time	VCO_2 or VO_2	Production	Source
Agkistrodon piscivorous (AR)	0700–1000	VCO_2	$0.0038M^{0.7099}10^{0.0468T}$	Zaidan, 2003
Agkistrodon piscivorous (LA)	0700–1000	VCO_2	$0.0027M^{0.6954}10^{0.0577T}$	Zaidan, 2003
Agkistrodon piscivorous (MO)	0700–1000	VCO_2	$0.0062M^{0.5416}10^{0.0518T}$	Zaidan, 2003
Crotalus atrox - Females	0800–1100	VO_2	$0.0025M^{0.916}10^{0.0491T}$	Beaupre and Duvall, 1998
Crotalus atrox - Males	0800–1100	VO_2	$0.0075M^{0.676}10^{0.0482T}$	Beaupre and Duvall, 1998
Crotalus horridus	0800–1100	VCO_2	$0.0012M^{0.777}10^{0.0590T}$	Beaupre and Zaidan, 2001
Crotalus lepidus & *C. molossus*	0700–1300	VO_2	$0.00331M^{0.646}10^{0.0532T}$	Beaupre, 1993
Sistrurus catenatus - Females	0800–1100	VCO_2	$0.0033M^{0.837}10^{0.0464T}$	This study
Sistrurus catenatus - Males	0800–1100	VCO_2	$0.0016M^{0.893}10^{0.049T}$	This study

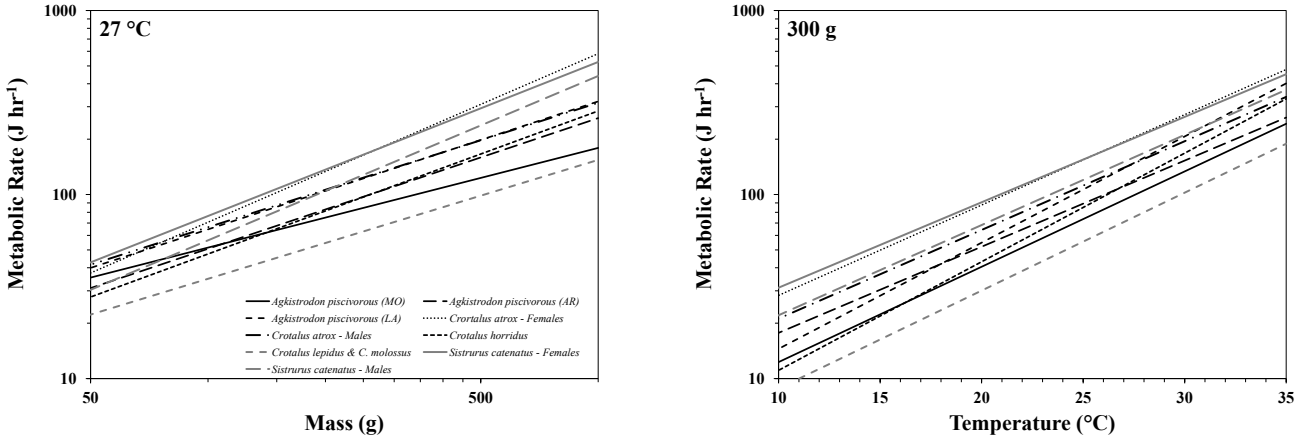

Figure 4. Comparative patterns in metabolic rates of pitvipers by mass and temperature evaluated at 27°C and 300 g mass. Data for species other than *S. catenatus* were derived from the literature. Only the slopes for regression equations are shown.

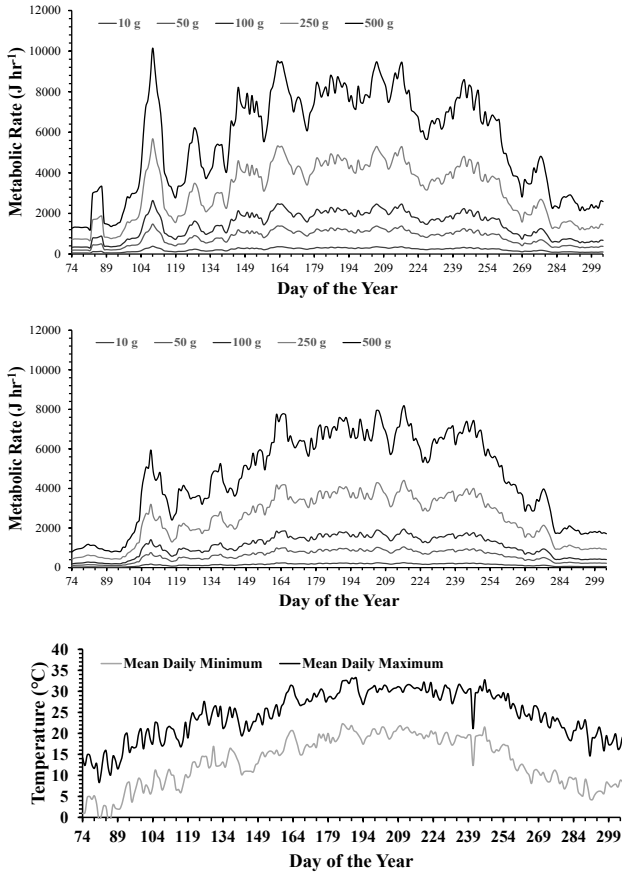

Figure 5. Predicted resting metabolic energy budget for *Sistrurus catenatus* during the active season by sex and using 10, 50, 100, 250, and 500 g masses of snakes (lines bottom to top). T_b's were derived from average daily body temperatures for non-gravid females and males from 1999–2002 (Dreslik, 2005). We used the mass scaling equations for 0800–1100 hrs, assumed a respiratory quotient of 0.72, and thus converted VCO_2 (ml hr^{-1}) to joules (J hr^{-1}) using 27.42 as a conversion factor. Julian days are indicated.

from 0800–1100 hrs were broadly overlapped by *Crotalus* species, but the exponents were on the higher end (Table 3). The exponents for *S. catenatus* were also greater than the three populations of *A. piscivorus* studied (Table 3). Conversely, for the temperature scaling exponent, *S. catenatus* was on the low end, with females having the lowest temperature scaling coefficient of the taxa examined (Table 3). At 50 g, the metabolic rates of all species are tightly clustered, but as mass increases, rates spread out (Fig. 4). Compared to other species, female *S. catenatus* have higher metabolic rates at lower masses, whereas male *S. catenatus* display more average metabolic rates at lower masses (Fig. 4). By 500 g, we observed some shifting in which female *S. catenatus* had relatively high metabolic rates (Fig. 4). When examining the effects of temperature at a constant size (300 g), we still found female *S. catenatus* had higher metabolic rates than all other groups examined (Fig. 4).

Annual resting energy budget.—The overall estimated daily resting metabolic expenditures fluctuate greatly, with snakes of lower mass showing lower estimated expenditures (Fig. 5). In addition, the sex difference detected between females and males is illustrated well, as females have much higher peaks and overall higher estimated expenditures (Fig. 5). Of note, it does not appear that all peaks and troughs in metabolic rate occur in conjunction with environmental temperature, as peaks from roughly days 100–120 (mostly April) are estimated to be higher for both sexes suggesting possible thermoregulation during spring emergence. Similarly, peaks in metabolic rate are seen later in the year from days 269–284 (late September to early October), prior to ingress when environmental temperatures are falling (Fig. 5). Overall females and males, respectively, are estimated to require 49.0–1,295.3 KJ and 32.4–1,065.6 KJ of energy annually depending on size with larger snakes estimated to require more energy (Table 4). When equated to estimates of rodent mass or rodent number, we observe *S. catenatus*

Table 4. Estimated annual resting energy budget (in J and Kcal) and trophic equivalents* across the active season (15 March–31 October) for both sexes and five body size classes of Eastern Massasaugas (*Sistrurus catenatus*) at Carlyle Lake, Clinton County, Illinois, based on daily average T_b from snakes radio-located from 1999–2002 (Dreslik, 2005).

	Females (g body mass)					Males (g body mass)				
	10	**50**	**100**	**250**	**500**	**10**	**50**	**100**	**250**	**500**
Estimated Annual Resting Energy Budget										
Joules	49,017	188,531	336,779	725,137	1,295,335	32,391	136,334	253,176	573,830	1,065,621
Kcal	11.72	45.06	80.49	173.31	309.59	7.74	32.58	60.51	137.15	254.69
By Rodent Mass										
P. leucopus	8.81	33.88	60.52	130.32	232.79	5.82	24.50	45.50	103.13	191.51
M. pennsylvanicus	9.38	36.07	64.43	138.73	247.81	6.20	26.08	48.44	109.78	203.87
B. brevicauda	10.20	39.23	70.08	150.90	269.55	6.74	28.37	52.68	119.41	221.75
Estimated Number of Rodents										
P. leucopus	0.42	1.61	2.88	6.21	11.09	0.28	1.17	2.17	4.91	9.12
M. pennsylvanicus	0.19	0.74	1.31	2.83	5.06	0.13	0.53	0.99	2.24	4.16
B. brevicauda	0.57	2.20	3.94	8.48	15.14	0.38	1.59	2.96	6.71	12.46

*Estimates for five size classes were obtained using the mass scaling equation (0800–1100 hrs); energy expended was calculated by assuming a respiratory quotient (RQ) of 0.72 and a conversion of 27.42 J mL^{-1} CO_2 (Gessaman and Nagy, 1988). Estimates of how much prey mass and number of prey items are required, on average, to achieve the estimated energetic costs for three of the most common prey items used the following estimates of dry mass caloric content and mean mass from the literature: *Peromyscus leucopus*, 5.51 Kcal/g (Powers et al., 1989), 21 g; *Microtus pennsylvanicus*, 5.16 Kcal/g (Davison et al., 1978), 49 g; *Blarina brevicauda*, 4.75 Kcal/g (Davison et al., 1978), 17.8 g. All mass values were from Damuth (1987), and metabolizable energy content was assumed 80.6% (Beaupre and Zaidan, 2012).

at Carlyle Lake require few meals to meet their estimated resting energetic demands (Table 4).

DISCUSSION

The significant effects of mass, temperature, and the temperature-by-time interaction are consistent with previous results for other North American pitvipers (Beaupre and Zaidan, 2001; Beaupre, 1993; Beaupre and Duvall, 1998; Zaidan, 2003). As these genera are closely related (Castoe and Parkinson, 2006), it is logical that their physiological responses would share similarities through common ancestry and would be influenced by similar ecological factors. All three genera share the same basic ecology, being relatively thick-bodied ectotherms relying on behavioral regulation of body temperature and using a "sit-and-wait" foraging strategy. Thus, they are affected similarly by factors such as ambient temperature. As with all chemical processes, the rates of metabolism increase with increasing temperature (McNab, 2002). In ectothermic organisms whose body temperatures may not remain constant, this results in a direct correlation between temperature and metabolic rate.

Our finding of a significant effect of sex is not consistent with previous studies. The possibility that we included vitellogenic females in the analysis is low because our ultrasonography, performed during the first two weeks of April, showed no indication of vitellogenesis. Enlarged vitellogenic oocytes were visible in *S. catenatus* using ultrasonography during March and April (Jellen, 2005; Aldridge et al., 2008).

There is the possibility that a source of unknown bias existed in the individuals chosen for study, which lead to a statistically significant sex effect that is not actually present. Adult males and females in this population showed no evidence of sexual size dimorphism (SSD) in SVL when examining the overall average of all adults (Dreslik, 2005). Thus, size alone should not be the factor causing the sexual differences. However, recent growth analysis has shown the presence of age-specific SSD, with female snakes being slightly longer than males at birth, and exhibiting a relatively accelerated growth rate (Dreslik et al. this volume), which could account for the higher metabolic rate. Several individual males used in this study did exhibit metabolic rates that are lower than their body mass would predict (Fig. 1), but, the animals used in this study were fasted and presumably not growing at the time metabolic measurements were taken.

It is possible that the time of year the study was conducted may impact the measurements. Male and female *Thamnophis sirtalis parietalis* exhibited different metabolic rates immediately following hibernation (Crews et al., 1987), with males exhibiting higher metabolism during the 40 days immediately following emergence. However,

sex was not a significant factor when metabolism was measured in fasted *T. s. sirtalis* during the active season (Birchard et al., 1984), indicating there may be a seasonal component to metabolic rate. The *S. catenatus* used in our study were collected immediately following hibernation during the spring emergence period, and the sexes possibly exhibit different metabolic rates during this part of the year. However, unlike *S. catenatus*, *Thamnophis* are slender-bodied active-foraging snakes, which influences their energetics (Secor and Nagy, 1994). Also unlike *S. catenatus*, *Thamnophis* begin metabolically costly mating activity in the spring, immediately post-emergence (Ernst and Ernst, 2003), and thus these results may not be applicable to our study. Alternatively, the significant sex effect could merely be a side effect of small sample size and the random chance some individuals selected for study all had naturally low or high metabolic rates, or had some undetectable condition which artificially lowered or inflated their metabolic rates. To be certain the significant sex effect is real, sample size would need to be increased.

Other rattlesnake species (Beaupre, 1993; Beaupre and Duvall, 1998; Beaupre and Zaidan, 2001) and *A. piscivorus* (Zaidan, 2003) exhibit temporal effects on resting metabolic rates, and we found a similar temporal biorhythm in *S. catenatus*, whereby the temporal cycling in metabolic rate differed depending on the temperature the snake is experiencing. The presence, degree, and/or order of the circadian cycle can all be affected by temperature, which is why time of day alone is not a significant factor. In general, cycles are reduced or absent at low temperatures and become more pronounced as temperatures increase. We did find that variance in metabolic rate increases with temperature (Fig. 3), meaning the cycle is more variable at warmer temperatures. We also found the rank order of the time periods changes between 17 and 22°C, and again between 27 and 32°C, but does not change between 22 and 27°C (Fig. 3), which encompasses the range of preferred body temperatures of *S. catenatus* at Carlyle Lake, as measured in the field by Dreslik (2005). Additionally, CO_2 production appears to be highest at 22 and 27°C during the 1500–1800 hr time block, the time of day when *S. catenatus* is likely to be active (Ernst and Ernst, 2003).

Comparative analysis.—When converted to common units, the mass and temperature scaling of *S. catenatus* appears typical of other crotaline snakes (Fig. 4). The variability in mass and temperature scaling within North American pitvipers (both intra- and interspecies) has also been documented in other studies (Beck, 1995; Beaupre, 1996; Beaupre and Zaidan, 2001; McCue and Lillywhite 2002), and while the sources of variation remain unclear, they could be the result of the geographic location the animals came from, disposition of animals used (field versus lab acclimated), maternal effects, adaptation, and/or random error. Plots such as Fig. 4, while interesting to examine for patterns, should also be interpreted with caution when extrapolating outside of the species' normal size range. For example, there are very few 300 g *C. lepidus* or 500 g *S. catenatus*.

As with other crotaline snakes, *S. catenatus* exhibits similar resting metabolic rates to boids, and below the average for squamates. For comparison, resting metabolic rates are as follows for a 250-gram individual at 25°C: male *S. catenatus*, 2,447 J hr^{-1}; female *S. catenatus*, 3,190 J hr^{-1}; *C. lepidus*, 1,183 J hr^{-1} (Beaupre, 1993); boid snakes, 2,602 J hr^{-1} (Chappell and Ellis, 1987); squamates, 4,534 J hr^{-1} (measured from 34 snake and 60 lizard species; Andrews and Pough, 1985). The documented similarity in metabolic rates between boids and viperids (Beaupre and Zaidan, 2001; McCue and Lillywhite, 2002) is likely a reflection of ecological and behavioral similarities between the groups, (both employ energetically conservative sit-and-wait foraging modes; Huey and Pianka, 1981), as they are not closely related evolutionarily (McCue and Lillywhite, 2002; Pyron et al., 2013). Foraging mode has been identified as the key factor explaining differences in field metabolic rate between the sympatric desert species *Masticophis flagellum* (an active foraging colubrid) and *C. cerastes* (Secor and Nagy, 1994), and therefore it could also drive similarities.

Annual resting energy budget.—Calculations of annual resting energy budgets and associated number of prey items needed to fulfill resting energy requirements further support the designation of *S. catenatu*s as a low energy specialist, along with the other pitvipers. Our calculations indicate that a 250-g female only needs to ingest 130–150 g of prey (2.5–8.5 individual rodents, depending on species) per year to meet her resting energy requirements, and a male of the same size can subsist on slightly less. Energy requirements vary ontogenetically, with 10-g snakes needing to consume 58–102% of their body mass per year, dropping to 45–70% for a 250-g snake, and 39–54% for a 500-g snake. Similar results have been reported for *Crotalus* species, showing that several sympatric desert species require only 2–3 meals per year (Beck, 1995), and adult *C. ruber* require as little as 1 large meal per year (Dugan and Hayes, 2012). While our calculations represent the minimum energy required to merely remain alive, and do not account for the energetic demands of growth or reproduction, from a conservation standpoint it does appear that prey availability is not a limiting factor for *S. catenatus* population growth at Carlyle Lake. Measurements of individual growth rates in the population further support that prey is not a limiting factor, as individuals in the population are able to double their length in just one year (Dreslik et al. this volume), rather than the 2–3 years required for many other viper species (Fitch, 1949; Heyrend and Call, 1951; Barbour, 1956; Gibbons, 1972; Klauber, 1972; Gannon and

Secoy, 1984; Fitch, 1985; Martin, 1988).

To loosely approximate the required energy input for *S. catenatus* to reach sexual maturity, we performed the following calculations. A female snake born at 10 g must gain 126 g to reach the minimum size of reproduction (determined as 48 cm SVL [Dreslik, unpubl. data], average mass of snakes 47–50 cm SVL = 136 g). Assuming the energy density of snake tissue is 6.637 kJ/g wet mass (23.287 kJ/g dry mass (Vitt, 1978) and a fractional water content of 0.715; Beaupre, 2008), a snake must consume 836.262 kJ to gain 126 g of mass. Using a value of 116.85 kJ of energy in an average mouse *(Peromyscus*, 21g; Powers et al., 1989), and assuming the metabolizable energy content of a mouse is 80.6% (calculated for *C. horridus*; Beaupre and Zaidan, 2012), we calculate a minimum of 7.2 mice needed for growth to sexual maturity. When accounting for the energetic cost of growth (2.98 kJ/g; Beaupre and Zaidan, 2012), and resting metabolism (this study), we conclude that about 13.25 mice would be needed for a female *S. catenatus* to reach the minimum size of sexual maturity. While this is clearly an over-simplified underestimate that does not account for cost of movement or temperature fluctuations, we feel it may still be informative at a management level, for example, to determine if an adequate prey base exists at sites being considered for reintroduction programs.

Conclusions.—Metabolically, the data from *S. catenatus* fits with what has been observed for other closely related pit-vipers. Their resting metabolic rate is closely tied to temperature and body size. The significant effect of sex on resting metabolic rate appears rare among pitvipers and should be investigated to confirm its validity, and then to determine the underlying proximate and ultimate causes of this difference and why similar results have not been seen in the closely related genera *Crotalus* and *Agkistrodon*. Mass scaling exponents were within the expected range when compared to other pitvipers that have been studied. Keeping with the designation of pit-vipers as low energy specialists, *S. catenatus* requires few prey items to meet minimum maintenance requirements.

Further research into the physiological ecology of pitvipers will expand our knowledge of these processes and increase our understanding of the ecology of these organisms. These studies should include range-wide investigations to document potential latitudinal variation, assessment of the impacts of climate change on pitviper populations, and measurements of field metabolic rate to determine more accurate energy budgets for use in conservation. Additionally, environmental acclimatization in metabolic response (exhibiting higher or lower metabolic rates than predicted when acclimatized to a particular temperature range) is not well studied, and could introduce significant error into the calculation of annual energy budgets. Acclimatization has been documented at low temperatures in both *A. piscivorus* and *C. horridus* (Zaidan, 2003; Agugliaro, 2011), but the direction of the response differs, and future studies should seek to document if environmental acclimatization in metabolic rate is present in additional taxa and investigate the triggers of this response.

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