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Ecophysiology of the Eastern Massasauga

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Prepared for: Illinois Department of Natural Resources

Project Name: Ecophysiology of the Eastern Massasauga
Grant / Project Number: 08-034W

Access Restriction: Access Restricted

INHS Technical Report 2009 (#)
Date of issue: 20 October 2009

ILLINOIS NATURAL HISTORY SURVEY

Abstract

Energy available to organisms is finite and must be partitioned between competing life functions. Metabolic studies give information about the energy requirements of a species, which can provide insight into possible limiting factors in their environment. I measured CO_2 production rates of 28 individual Eastern Massasaugas (*Sistrurus catenatus catenatus*) to quantify the response of resting metabolic rate (RMR) to sex, body mass, temperature, and time. I found that unlike other pit vipers for which these measurements are available, *S. c. catenatus* exhibits a significant difference in resting metabolic rate between the sexes. Their RMR increases with increasing body mass and temperature, and varies temporally, suggestive of a metabolic circadian rhythm. These results are similar to what has been found in other pit viper species. Female *S. c. catenatus* have a steeper mass scaling relationship, however more variation is seen in the mass scaling of males. Q_{10} values for both sexes are similar and within the range of what has been reported for other pit vipers.

Introduction

Energy available to an organism in a given system is finite and distributed among the competing costs of maintenance, growth, reproduction, and storage (Congdon et al 1982). Individuals partition energy to these competing functions differently depending on factors such as age and reproductive status. An individual must meet its minimum maintenance requirements before allocating energy to any other function. Simply meeting energetic requirements for resting metabolism is demanding and can comprise 10-45% of a reptile's yearly energy budget (Condon et al 1982; Secor and Nagy 1994; Beaupre 1995). Snakes such as *Crotalus lepidus*, *C. cerastes*, *Masticophis flagellum,* and *Thamnophis sirtalis* spend as much as 19-35% of their annual energy budget meeting the demand of resting metabolism (Beaupre 1996; Peterson et al. 1998; Secor and Nagy 1994). Thus, energetic limitations and meeting minimum maintenance requirements can cause differences in energy expenditure. Such energetic expenditures can influence everything from

growth and reproduction to sexual size dimorphism (SSD) (Beaupre and Duvall, 1998). Therefore, quantification of resting metabolism is necessary before conducting further analysis of an organism's energy use (Zaidan 2003). Calculation of resting metabolism also enables the estimation of temperature coefficients (Q_{10} values) and mass scaling relationships of organisms, values which can be easily compared across taxa. Q_{10} is a unit-less value that describes the effect of temperature on a function being studied (here metabolism). To calculate Q_{10}, rates of metabolism are compared at temperature T and T-10 degrees C and the ratio describes the temperature sensitivity of the reaction, with higher values indicating greater temperature sensitivity. For most biological processes, Q_{10} values normally range between 2-3 (Willmer et al. 2000). Mass scaling exponents provide information on the relationship between mass and metabolic rate by quantifying the rate of increase in metabolism with increasing mass. Squamates express a high degree of variation in Q_{10} and mass scaling relationships, the reasons for which remain obscure (Beaupre and Zaidan 2001).

Previous studies on squamate reptiles have investigated metabolic rates and energy budgets for many lizard genera including: *Sceloporus, Anolis,* and *Uta* (see Congdon et al. 1982 for a review). These studies have investigated the effects of behavior on energy budgets and energy assimilation and partitioning. One study found *Sceloporus* used approximately 61% of their assimilated energy for metabolism (Mueller 1970). Previous studies on Colubrid snakes include the quantification of the metabolic costs of growth in *Thamnophis* (Peterson et al. 1998) and metabolic circadian rhythms in *Nerodia* (Hopkins et al. 2004). Extensive ecophysiological studies of the genus *Python* have also been conducted by Secor and Diamond (1995; 1998) focusing heavily on the physiology of digestion. Among the North American pit vipers, both *Crotalus* (Secor and Nagy 1994; Beaupre 1996; Beaupre and Duvall 1998; Beaupre and Zaidan 2001), and *Agkistrodon* (Zaidan 2003) have been studied metabolically. These studies have found that metabolism is most affected by body size and temperature. A circadian rhythm has been reported for both genera, and sex does not influence metabolism when males are tested against non-reproductive females.

Metabolic studies are especially important for endangered or declining species. An understanding of how the organism uses energy can result in more precise conservation measures. For example, if we construct energy budgets for the various reproductive states, and determine the prey density of the area, we can attempt to predict if augmenting the prey base would increase population size and fitness. Before inferences such as this can be made, a solid understanding of the ecology of a species is also needed. The Eastern Massasauga Rattlesnake (*Sistrurus catenatus catenatus*) is an ideal model for these types of ecophysiolgical studies because we currently have a large body of knowledge detailing its ecology and its status as a candidate species on the federal endangered species list (USFWS 1999) makes it a priority for conservation. However, no studies quantifying resting metabolic rate have been conducted on the genus *Sistrurus*.

For this study, an ontogenetic series of *S. c. catenatus* was used to quantify mass and temperature scaling of metabolic rate and evaluate potential differences in metabolic expenditure between sexes, and temporally. Based on previous work conducted with *Crotalus* spp. and *Agkistrodon piscivorus*, I would not expect to see a metabolic difference between sexes in *S. c. catenatus*, given that only non-reproductive females were used in this study. However, I would expect time to be a significant factor, with metabolic rates being lowest during the night time hours. Mass scaling exponents are variable among squamates, with previous studies reporting values of 0.5 - 0.9 for *Crotalus* and *A. piscivorus*, I would therefore expect *S. c. catenatus* to fall within this range. The average Q_{10} value reported for squamates is 2.4 (Andrews and Pough 1985), with reported values for snakes between 1.6-4.7. I expect *S. c. catenatus* to fall within this range.

Materials and Methods

Study Animals

The Eastern Massasauga (*S. c. catenatus*) is a small thick-bodied rattlesnake rarely exceeding 100cm in total length and characterized by a light brown to grayish dorsal background color and 21-50 dark brown saddle-shaped dorsal blotches (Ernst and Ernst, 2003). The range of *S. c. catenatus* extends from southern

Ontario, Canada and central New York to northwestern Pennsylvania, west to eastern Iowa and as far south as Illinois and Missouri (Ernst and Ernst, 2003). Historically in Illinois, the species was found throughout the northern two-thirds of the state, and population declines have been documented since 1866 (Atkinson and Netting, 1927). The precipitous decline of *S. c. catenatus* in Illinois has been attributed to the settlement and subsequent conversion of prairie habitats into an agricultural landscape. The range of *S. c. catenatus* in Illinois is now made up of only 3-5 extant populations, the largest of which is located at Carlyle Lake in Clinton County (Dreslik 2005). *S. c. catenatus* was listed as state endangered in 1994 (Herkert 1994) and is currently a candidate for listing under the federal endangered species act (USFWS 1999). Studies by Dreslik (2005) and Jellen (2005) using radio telemetry have expanded our knowledge and afforded insight into growth, thermal biology, movement patterns, and reproductive biology. Prevalence of disease within the population (Allender 2006) and genetic population structure (Andre 2003) have also been investigated, however, our knowledge of the ecophysiological aspects of the species is lacking.

I obtained study animals from the Carlyle Lake population through visual encounter surveys conducted during the spring egress period (March – April) 2007. From 9 March to 12 April 2007 I captured 92 snakes, and selected 28 individuals for this study (Table 1). Selection was based on the following criteria: 1) equal number of each sex 2) ontogenetic series 3) no obvious sickness or injury 4) no gravid females. Before metabolic measurements began, I held snakes in captivity for a minimum of 10 days to ensure a postabsorptive 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). While in captivity, I maintained snakes in individual plastic tubs on a 12L:12D photoperiod, and at an ambient temperature of 21-23 degrees C.

I sexed all captured individuals by cloacal probing, and measured snout-vent length (SVL) and tail length to the nearest 0.1 centimeter using a flexible seamstress tape (for SVL) and transparent ruler (for tail

length), and also recorded the number of subcaudal scales and rattle segments. I measured mass of all individuals on day of capture using Pescola spring scales, and then re-measured it for individuals selected for the study on the first day of metabolic measurements using an electronic balance accurate to 0.001 grams. I multiply marked all individuals: 1) took diagnostic photographs using a digital camera, 2) all rattles were painted with a unique color combination using permanent markers for easy field identification, and 3) individuals larger than 35cm SVL were injected with a passive integrated transponder (PIT) tag inserted subcutaneously in the posterior 1/3 of their body. I evaluated female reproductive state using ultrasonograms preformed by Dr. Randy Junge at the Saint Louis Zoological Park. Females were judged to be gravid if follicles were visible in the reproductive tract.

Respirometry

I determined metabolic rate by measuring CO_2 production in a Sable Systems TR-3 configured as an open flow system, following the methods of Beaupre and Zaidan (2001). I placed snakes in appropriately sized gas-tight chambers. Eight chambers were available for use, enabling the simultaneous measurement of seven snakes, with one chamber left empty for baseline reference. Clean high-pressure air from an 80 psi line was split into eight equal flows with a Sable Systems MF-8 airflow manifold. I 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 to 400 mL min^{-1} depending on snake size and temperature. I connected each line to one port of the sealed respirometry chambers and a second line carried excurrent gas to a barrel syringe for subsampling. Subsampling was controlled using a Sable System eight channel multiplexer. The multiplexer subsampled each snake chamber for a total of 6.7 minutes per hour, each hour of sampling, and the baseline chamber for 3.3 minutes at the beginning and end of each hour. Subsampled gas passed through Drierite to remove any water before flowing to a Li-Cor CO_2 infrared gas analyzer (IRGA). Data from the IRGA were downloaded using the Sable Systems Universal Interface software. To maintain a stable temperature, I placed chambers in a Percival environmental chamber, set to a 12L:12D photoperiod.

Experimental Design

I measured CO_2 production rates for each individual at four different temperatures (17, 22, 27, and 32 degrees C), which encompass the range of preferred body temperatures measured in the field by Dreslik (2005). I measured CO_2 production at each temperature level for 6.7 minutes each hour for a continuous 24 hour period. Temperatures in the environmental chamber were changed daily between 1200 and 1300 hours CST. Because of the possibility that a change in chamber temperature could influence metabolic rate, I discarded measurements taken between 1300 and 1400 hours. I randomly assigned each of the 28 individual snakes to one of four groups, and randomized the order of temperatures within each group of measurements. CO_2 ppm was recorded from each chamber every 5 seconds for 6.7 min/h, and measurements for each individual were averaged for each hour.

Statistical Analyses

I processed raw data using a Microsoft Quick Basic program designed to use values in the output file to create a text file containing columns for: individual number, mass, sex, time of day, temperature, and hourly averages of VCO_2. Where VCO_2 is calculated using the equation:

$$VCO_2 = (f_e - f_i) \text{ x FR x } 60$$

where VCO_2 is in mL/h, 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, and 60 converts to hourly rates.

I analyzed the data in a repeated measures design using SAS GLM procedure, and REG procedure for regression analysis. Statistical significance was set at alpha = .05. Before analysis, I $\log_{10}$ transformed CO_2 production rates and body mass to linearize the relationship between them. To adjust the data set for the known relationship between metabolic rate and body mass (Kleiber, 1975), I regressed $\log_{10}CO_2$ production

on $\log_{10}$body mass, and used the residuals from this regression in the analysis as the mass adjusted response variables.

I 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:

$$\text{Log}_{10}VCO_2 = X_1 * \log_{10}W + X_2 * T - X_3$$

(where VCO_2 is CO_2 production rate in mL/h; 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. The equation reduces to:

$$VCO_2 = aW^b * 10^{cT}$$

(where $a = 10^{X_3}$, $b = X_1$, and $c = X_2$ following Andrews and Pough 1985; Beaupre and Zaidan 2001). I used metabolic rates calculated using this equation to estimate Q_{10} values for each significant group. Q_{10} is defined as the metabolic rate at temperature T, divided by metabolic rate at temperature T-10 degrees C. For these calculations, I estimated Q_{10} as the ratio of VCO_2 at 30 degrees C to VCO_2 at 20 degrees C, assuming a 200 gram snake.

Results

I recorded 2,618 temperature by hour individual measurements. My preliminary analysis indicated that one individual (snake #502) exhibited an abnormally high metabolic rate for its size. Further investigation revealed I collected this snake from an area where other individuals had been observed in poor body condition, thus I assumed the individual was unhealthy and it was excluded from further analysis.

Repeated Measures

Repeated measures MANOVA indicates non-gravid females maintain a higher metabolic rate than males ($p=0.0065$; Figure 1), and there is a positive relationship between temperature and metabolic rate ($p= <.0001$; Figure 2). Additionally, metabolic rates differed with time of day ($p= <.0001$; Figure 3); rates were lowest during 0-0300 hours and highest from 0800-1100 hours CST. There is also an interaction between

time and sex (p= .0177; Figure 4) indicating that time of day does not affect each sex in the same way, and we therefore cannot interpret the effect of time without considering sex of the individual. The interaction between temperature and time (p = < .0001; Figure 2) was also significant indicating the effect of temperature cannot be interpreted without also considering what time the measurement was taken. Between 17-22 degrees and 27-32 degrees, metabolic rate increases more slowly during the 1900-2300 and 0000-0300 hours time blocks (See Table 2).

Mass Scaling and Q_{10}

The mass scaling exponent for *S. c. catenatus* differs between males and females. Average value for males is 0.51 while for females the average value is 0.79 (See Table 3 for complete list of values). This shows a much steeper rate of metabolic increase with increasing mass in females compared with males.

Q_{10} values were calculated for each statistically significant group (sex and time block). Male Q_{10} ranged from 2.775 - 3.413 (average 3.155), and female Q_{10} ranged from 2.829 – 3.227 (average 3.043; Table 3) which indicates males and females share the same degree of temperature sensitivity.

Discussion

The significant effects of temperature, time, and the temperature by time interaction are all consistent with what has been reported for other North American pit viper species (Beaupre and Zaidan 2001; Beaupre 1993; Beaupre and Duvall 1998; Zaidan 2003). As these genera appear to be closely related evolutionarily (Castoe and Parkinson 2006), it is logical that their physiological responses would be influenced by similar factors. All three genera share the same basic ecology, being relatively thick bodied ectotherms which rely on behavioral means to regulate their body temperature and utilize a “sit and wait” foraging strategy. Thus, they are affected similarly by factors such as ambient temperature and time of day. 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. The increase in metabolic rate at higher temperatures seen in *S. c. catenatus* was expected for this reason.

Not consistent with the findings of previous studies is the significant effect of sex and the time by sex interaction. All females used in this study were judged non-gravid by ultrasonogram performed during the first 2 weeks of April. It may be possible that during this time period, follicles are not developed well enough to be detected using this method. However, Jellen (2005) was able to locate enlarged vittelogenic oocytes using ultrasonograms during March and April so it is unlikely that enough gravid females were missed to account for the sex difference. Alternatively, assuming all adult females were indeed non-gravid, and that *S. c. catenatus* exhibits a biennial reproductive cycle (Seigel 1986; Jellen 2005) the sex difference could indicate a higher metabolic rate present in postpartum females when they emerge from hibernation. Although this result would still be unique among pit vipers for which metabolic rates have been quantified. It could be that the smaller body size of *Sistrurus* when compared to most *Crotalus* and *Agkistrodon* species forces females to maintain higher metabolic rates to offset the high costs of reproduction

A significant effect of time has been observed in other rattlesnake species (Beaupre 1993; Beaupre and Duvall 1998; Beaupre and Zaidan 2001) as well as in *A. piscivorus* (Zaidan 2003) and was expected in *S. c. catenatus*, indicating the presence of a circadian rhythm. Ambient temperatures are typically lowest during the night which could produce a decrease in metabolism under field conditions, however the persistence of this change under constant lab conditions indicates it is not caused solely by temperature. Metabolic rates are lowest during 0000 – 0300 hours, and highest during daytime hours. This corresponds with activity patterns found by Seigel (1986) in Missouri showing that during the spring, most snakes are active from 1200 – 1600 hours. What does not correspond to observations in other rattlesnakes is the timing of the low point in the metabolic cycle. In species of the genus *Crotalus*, the lowest metabolic rates are typically

observed between 0800 – 1100 hours CST (Beaupre and Zaidan 2001). In *A. piscivorus*, lowest metabolic rates are observed between 0100-0600 hours CST (Zaidan 2003), which more closely matches *S. c. catenatus*. The difference in timing of the low point in the metabolic cycle perhaps indicates a difference in thermoregulatory abilities based on habitat type. *C. horridus* exhibits its lowest metabolic period in the morning hours, perhaps due to the shady forested areas they typically inhabit. The sun may not heat these areas in the morning as quickly as it does in the more open habitats occupied by *A. piscivorus* and *S. c. catenatus*, resulting in a shift of their circadian rhythm to have the lowest metabolic rate during the morning hours instead of at night. The significant interaction between temperature and time shows that from 17 degrees to 22 degrees and from 27 degrees to 32 degrees, metabolism does not increase at the same rate at all times. It is slower to increase during the 1900-2300 and the 0000-0300 hour blocks. This result further supports the finding of circadian variation in metabolic rate.

Mass scaling exponents give us information regarding the steepness of the relationship between mass and metabolic rate. The higher mass scaling exponent seen in females indicates that as body mass increases, metabolic rate increases at a faster rate than seen in males. This could be an effect of the higher cost of reproduction to females. Perhaps to offset the costs of producing offspring, females must increase their metabolism at a faster rate as they grow. This would represent a unique adaptation seen in *S. c. catenatus*, perhaps due to their small body size, compared with *C. horridus* and *A. piscivorus*. Male *S. c. catenatus* show more variability in their mass scaling exponents as indicated by their lower R^2 values (Table 3). More variation in males could be an indication of their ability to maintain lower metabolic rates once they reach sexual maturity, but requiring higher metabolic rates before sexual maturity to increase body size at a more rapid rate to allow mating to begin at an earlier age.

Reported Q_{10} values for pit vipers range from 1.65 – 4.78 (Table 4), indicating that *Crotalus*, *Agkistrodon* and *Sistrurus* vary interspecifically in their temperature sensitivity. Values for *S. c. catenatus* range from 2.775 – 3.413 (average 3.099) which falls approximately in the middle of the range that has been reported

for other pit vipers. Boids also show a considerable amount of variability, with Q_{10} values ranging from 1.5-4 (Chappell and Ellis 1987). It is therefore necessary when conducting studies of ecophysiology to determine temperature sensitivity on a species by species basis, rather than relying on published values for related species.

Metabolically, *S. c. catenatus* fits well with what has been observed for other closely related pit vipers. Their metabolic rate is closely tied to temperature and body size, but also varies throughout the day on a circadian rhythm. The significant effect of sex on metabolic rate is potentially unique and should be investigated to determine the underlying causes of this difference and why we do not see the same results in studies of the closely related genera *Crotalus* and *Agkistrodon*. The similarity in circadian rhythm to *A. piscivorus* rather than to members of the genus *Crotalus* is also notable and may reflect differences in habitat. Future metabolic studies should examine other members of the genus *Agkistrodon*, such as *A. contortrix* which occupies habitat similar to *C. horridus* to further investigate this hypothesis. Intraspecific differences in mass scaling exponents have not been previously observed for pit vipers, and may reflect the discrepancy in reproductive costs between the sexes. Further research into the physiological ecology of pit vipers will expand our knowledge of these processes and increase our understanding of the ecology of these organisms.

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Tables and Figures

Table 1: Individual *S. c. catenatus* used in this study. Mass is in grams, snout-vent length (SVL) in centimeters. Capture site abbreviations: HR3-W = SSSP West, F3 = EHSP Field #3, DamE = ACOE Dam East, DamW = ACOE Dam West, AR = EHSP Archery Range, KT= EHSP Kaskaskia Trail, WC = EHSP Wetland Corner

Snake #	Sex	Mass	SVL	Capture Site
95	M	462.91	76.9	HR3-W
431	M	378.92	69.2	F3
466	M	422.11	71.4	F3
479	F	358.06	67.1	HR3-W
481	F	378.93	68.3	F3
501	M	94.49	49.8	DamE
502	M	22.01	32.2	DamE
503	M	68.00	43.9	DamE
505	M	12.84	26.9	DamW
506	F	8.98	26.4	DamW
507	F	101.89	49.2	DamW
508	M	306.19	69.7	DamE
512	M	15.70	24.9	DamE
514	M	76.19	44.7	DamW
515	M	65.96	46.6	DamW
516	F	51.91	43.0	DamW
517	F	296.03	62.1	HR3-W
520	F	59.76	41.4	DamE
521	F	84.64	48.5	DamE
522	M	71.59	45.2	DamE
524	M	60.78	41.5	DamW
525	F	232.81	55.8	F3
526	M	217.35	54.7	F3
527	F	130.84	49.0	AR
528	F	164.12	56.5	KT
530	M	213.88	60.6	WC
531	F	171.94	57.2	F3
532	F	228.03	64.3	F3

Table 2: Results of repeated measures analysis of variance

Source	df	Type III Sum of Squares	*F* Value	*P*
Between Subjects				
Sex	1	15.401	8.8	0.0065
Error	25	43.754		
Within Subjects	df	Wilks' λ	*F* Value	*P*
Temperature	3, 23	0.0085	892.5	<.0001
Temp*Sex	3, 23	0.8881	0.97	0.4255
Time	4, 22	0.0248	216.29	<.0001
Time*Sex	4, 22	0.5936	3.76	0.0177
Temp*Time	12, 14	0.0102	112.98	<.0001
Temp*Time*Sex	12, 14	0.5635	0.9	0.5651

Table 3: Regression of $\log_{10}CO_2$ produced (mL/h) on $\log_{10}$body mass (g) and body temperature (C) for males versus females. W=weight (g) T=temperature (C) Q_{10} is calculated as the ratio of V_{co2} produced at 30 to V_{co2} produced at 20, assuming a 200 gram snake.

Male

Time (HoursCST)	X_1 (SE)	X_2 (SE)	X_3 (SE)	Adj R^2	Equation for V_{CO2} (mL/h)	Q_{10}
1500-1800	.51879 (.04672)	.05331 (00399)	-2.27452 (.13820)	0.5733	$.005315W^{.51879}$ $10^{.05331T}$	3.413
1900-2300	.52855 (.04209)	.05183 (.00360)	-2.25226 (.12451)	0.5656	$.005594W^{.52855}$ $10.^{.05183T}$	3.298
0000-0300	.48580 (.04941)	.04433 (.00422)	-2.01356 (.14615)	0.4788	$.009692W^{.48580}$ $10^{.04433T}$	2.775
0400-0700	.53435 (.04891)	.04828 (.00418)	-2.20391 (.14467)	0.5293	$.006253W^{.53435}$ $10^{.04828T}$	3.039
0800-1100	.49689 (.05022)	.05119 (.00431)	-2.17605 (.14787)	0.5556	$.006667W^{.49689}$ $10^{.05119T}$	3.250

Female

Time (Hours CST)	X_1 (SE)	X_2 (SE)	X_3 (SE)	Adj R^2	Equation for V_{CO2} (mL/h)	Q_{10}
1500-1800	.83326 (.03955)	.05088 (.00301)	-2.53216 (.11224)	0.7786	$.002936W^{.83326}$ $10^{.05088T}$	3.227
1900-2300	.81890 (.03599)	.05084 (.00274)	-2.51835 (.10213)	0.7687	$.003031W^{.81890}$ $10^{.05084T}$	3.224
0000-0300	.77160 (.04117)	.04728 (.00313)	-2.32636 (.11684)	0.7361	$.004716W^{.77160}$ $10^{.04728T}$	2.970
0400-0700	.79473 (.04283)	.04719 (.00326)	-2.35588 (.12154)	0.7274	$.004406W^{.79473}$ $10^{.04719T}$	2.964
0800-1100	.75907 (.04368)	.04517 (.00341)	-2.21510 (.12444)	0.7366	$.006093W^{.75907}$ $10^{.04517T}$	2.829

Table 4: Taxonomic comparisons of SMR regression and Q_{10} values. *Note: Q_{10} reported as values or ranges as published by the source, and therefore may not have been calculated using a uniform temperature range.

Species	X_1	X_2	X_3	R^2	Q_{10}	Source
Sistrurus catenatus (Male)	0.486	0.044	-2.013	0.48	2.775-3.413	This Study
(Female)	0.772	0.047	-2.326	0.74	2.97-3.227	This Study
Agkistrodon piscivorus	0.58	0.054	-2.383	0.72	2.754-3.467	Zaidan 2003
	0.694	0.049	-2.447	0.73	2.239-3.09	
	0.69	0.063	-2.708	0.073	3.236-4.266	
Crotalus adamanteus	0.93	0.44	-2.588	0.95	3.3	Dorcas et al. 2004
Crotalus atrox	0.676	0.482	-2.122	0.86	1.65-3.02	Beaupre and Duvall 1998
Crotalus cerastes	n/a	n/a	n/a	n/a	2.6	Secor and Nagy 1994
Crotalus horridus	0.777	0.059	-2.908	0.81	3.89-4.78	Beaupre and Zaidan 2003
Crotalus lepidus and Crotalus molossus	0.646	0.0532	-2.4797	0.88	3.4	Beaupre 1993
Boids	0.806	0.0415	-2.229	0.97	1.5-4	Chappel and Ellis 1987
Squamates	0.8	0.038	-1.87	0.96	2.4	Andrews and Pough 1985

Figure 1: Graph showing Log_{10} CO_2 production by mass for male versus female *S. c. catenatus*

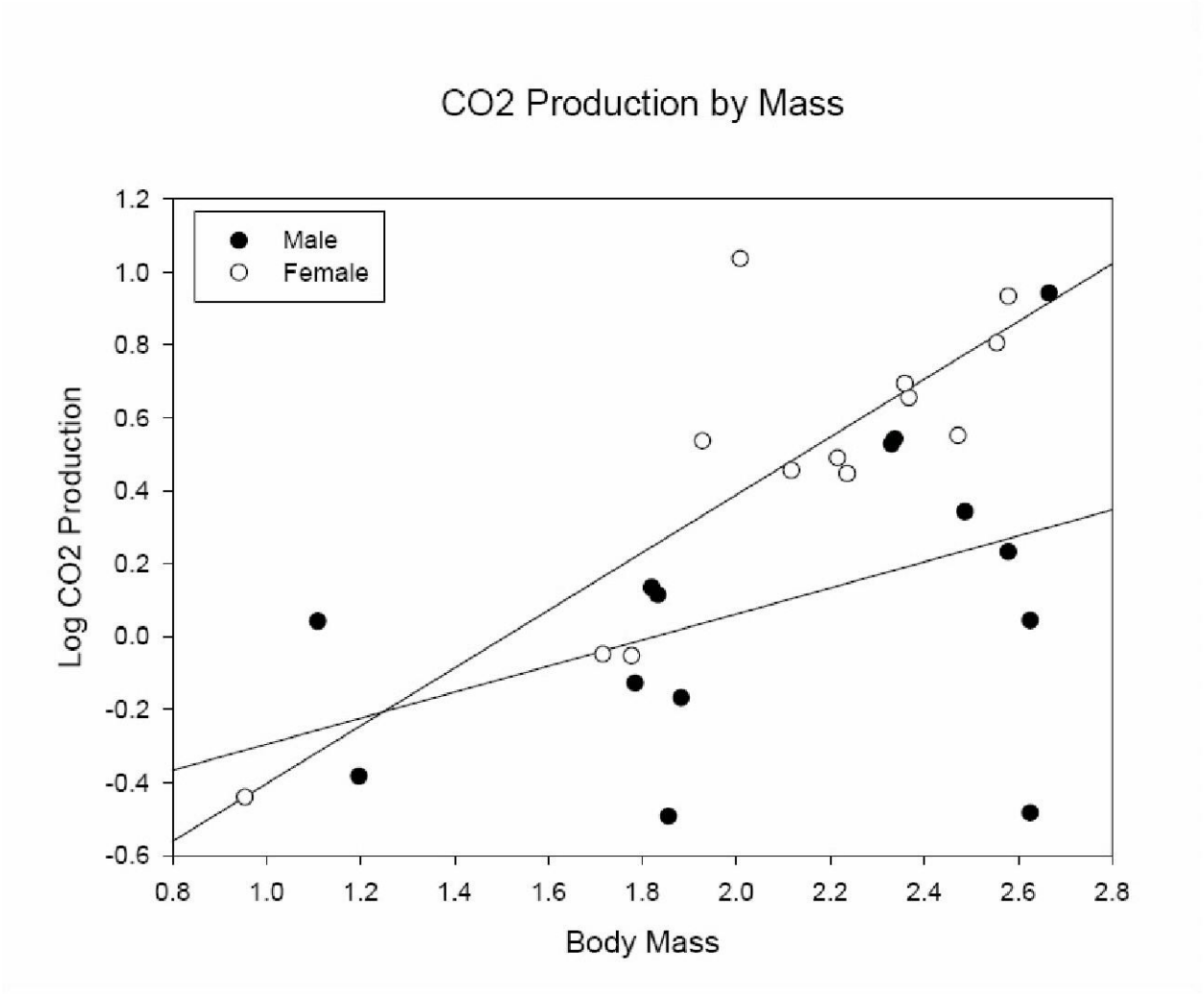

Figure 2: Graph of mean VCO_2 production by temperature and time. Where Time 1= 1500-1800, Time 2= 1900-2300, Time 3= 0000-0300, Time 4= 0400-0700, and Time 5= 0800-1100 hours CST.

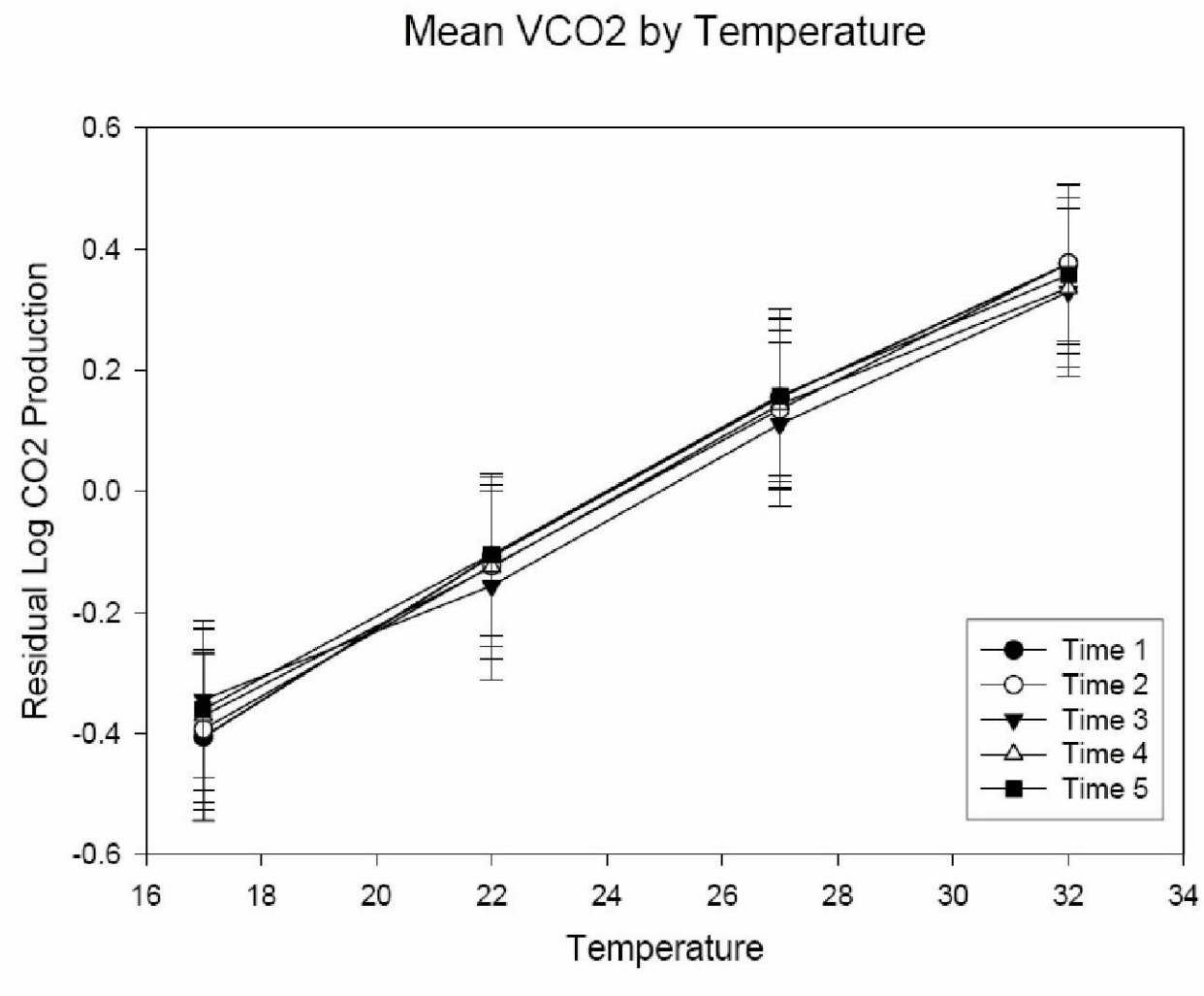

Figure 3: Graph of Log VCO_2 by time where Time 1= 1500-1800, Time 2= 1900-2300, Time 3= 0000-0300, Time 4= 0400-0700, and Time 5= 0800-1100 hours CST.

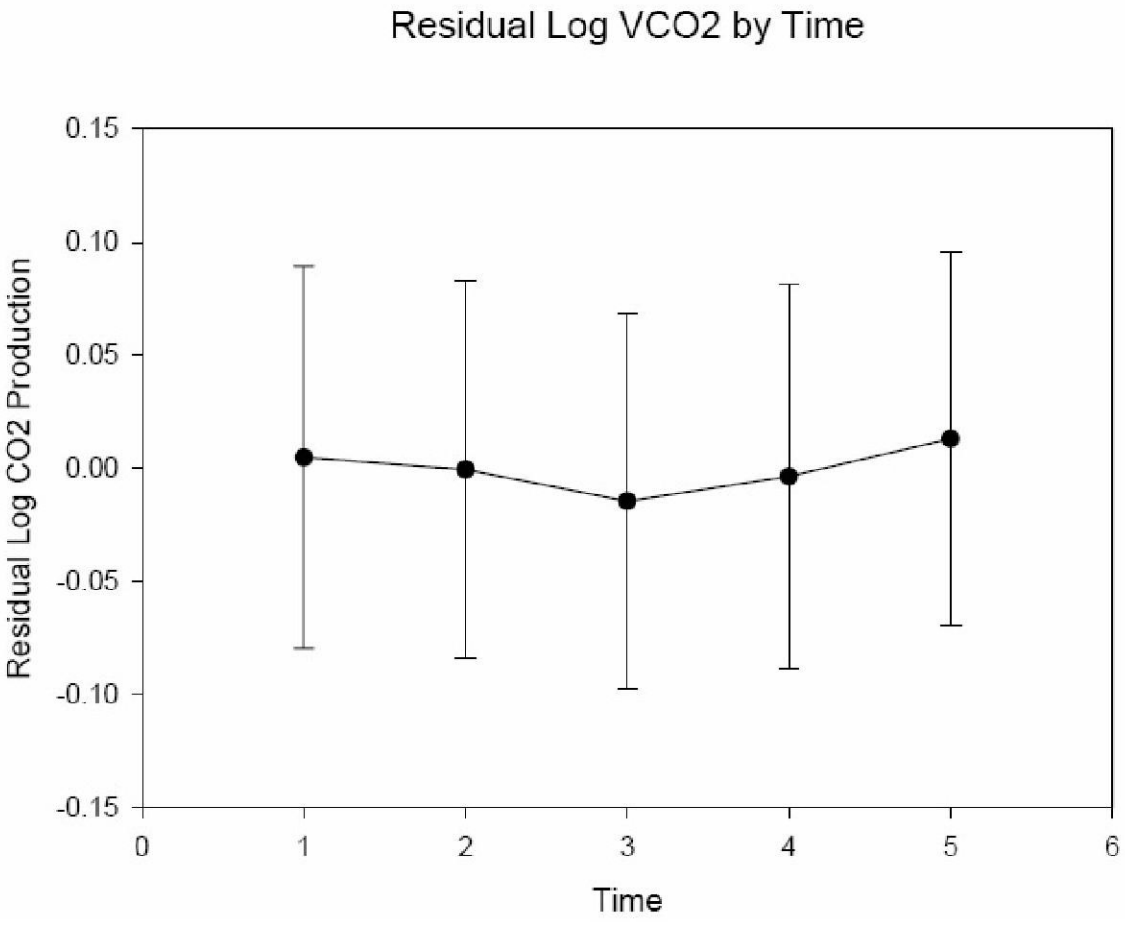

Figure 4: Graph of Log VCO_2 by Time and Sex where Time 1= 1500-1800, Time 2= 1900-2300, Time 3= 0000-0300, Time 4= 0400-0700, and Time 5= 0800-1100 hours CST