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Ecological Study of Oxygen Consumption in Three Species of Rattlesnake, Crotalus atrox, C.lepidus and C. molossus (VIPERIDAE) from the Northern Chihuahuan Desert

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Abstract

The purpose of this study was to compare oxygen consumption of three species of rattlesnakes, *Crotalus atrox*, *C. lepidus* and *C. molossus*, that inhabit the Chihuahuan Desert within the Indio Mountain Research Station (IMRS), Hudspeth County, Texas. The resting metabolic rates (RMR) of 39 rattlesnakes (*C. atrox*, N = 17; *C. lepidus*, N = 8; and *C. molossus*, N = 14) were determined at four experimental temperatures (20°, 25°, 30°, and 35°C). The body masses ranged from 47 to 660 g for all three rattlesnake species.

The temperature coefficient of metabolism (Q_{10}) averaged 2.8 between temperatures of 20°-30°C and 2.15 between temperatures of 25°-35°C, these are similar to other coefficients reported for large rattlesnakes such as *C. adamanteus*. The Q_{10} values for *C. atrox* ranged from 1.77 to 2.35, *C. lepidus* ranged from 2.54 to 3.32, and *C. molossus* ranged 2.13 to 2.75 from temperatures that ranged from 20°C through 35°C Interspecific differences in Q_{10} were slight or insignificant. A multiple regression relating oxygen consumption (VO_2) to mass and temperature indicated that RMR increased with body mass and temperature. Interspecific oxygen consumption was statistically significant between the three species. Oxygen consumption varied between the three species due to size differences. Metabolic rates of males and females at comparable body mass for the three species of rattlesnakes were found to have no significant differences.

The results indicate oxygen consumption is greatly affected by temperature and body mass. Incremental increases in temperature resulted in increased resting metabolic rates, with Q_{10} values within the range reported for most squamates. Assessing how environmental parameters affect physiological processes is critical to further understand the ecology and natural history of these organisms.

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Chapter 1

General Introduction

1.1 Introduction

Arid regions demonstrate limitations in resources, and the organisms that inhabit them are well known to reduce their usage of resources in several ways. These organisms exhibit a series of biological modifications in response to limitations associated with these arid regions, such as deserts. Over evolutionary time, endothermic organisms respond to such restrictions by reducing demanding behaviors, morphological, and physiological characteristics to decrease total energy expenditure (McNab, 1994). Although ectothermic organisms require less energy than do similar sized endotherms by virtue of lower resting metabolic rates (RMR), it is reasonable to expect that ectotherms might respond to periodic limitations in resources by reducing energy expenditure in similar ways (Pough, 1980; Bennett, 1980).

Energy expenditure in ectotherms can be reduced in a number of ways. Andrew and Pough (1985) suggested that prey type and foraging strategies influence metabolic rates in serpents. The most obvious effects are changes in body temperature, body size, sexual activity, acclimation to temperature, and time of their activity period (Bennett and Dawson, 1982; Andrews and Pough, 1985; Patterson and Davies, 1989). For example, large-heavy bodied snakes from different families, including viperidae, have evolved a series of morphological and behavioral characteristics that enable them to ambush prey successfully (Ayers and Shine, 1997). Beaupre (1995a) indicates energy budgets in rock rattlesnakes, *Crotalus lepidus*, varied in relation to energy acquisition and allocation between two populations in the Big Bend region, Texas. Intraspecific differences, such as sexual dimorphism in many squamates, are also affected by energy acquisition and expenditure. Non-reproductive and vitellogenic females of western diamondbacks, *Crotalus atrox*, from the Sonoran Desert were shown to differ in metabolic rates (Beaupre and Duvall, 1998a), yet there were no differences between non-reproductive females and

males. They hypothesize that the adult female body may represent a compromise between selections for increased frequency of producing offspring as previously suggested for other ectotherms.

Snakes also have different behavior and activity capacities directly influenced by physiology and morphology. Studies comparing metabolic physiology of prey acquisition and escape in racers, rattlesnakes, and boas show that they depend on different metabolic capacities (Ruben, 1976). Racers tend to be fast, highly mobile snakes during prey pursuit and escape. Rattlesnakes cannot attain high speeds to pursue their prey and escape predators, but rely on a "sit and wait" ambush strategy with intense striking behavior (Ruben, 1976; Beaupre and Duvall, 1998b; Bennett, 1980). Rosy boas, *Lichanura travirgata*, are slow moving snakes that rely on constriction to immobilize and kill their prey. However, they rely on an escape defense such as rolling into a ball and releasing secretions from their cloaca (Ruben, 1976). These type of behavioral and activity patterns are evident in other ectotherm group, such as amphibians (Andrews and Pough, 1985).

Knowledge of snake temperature relationships to their environments contribute to understanding many aspects of their behavior, physiology, development, ecology and evolution (Peterson *et al*., 1993). Snake body temperature are regulated by heat obtained directly from the physical environment and can be constrained by the range of thermal conditions present. One of the direct effects of body temperature on the physiology of the snake is the rate of oxygen consumption, which is also affected by physical activity and body mass. The thermal ecology of pit vipers, especially the effects on oxygen consumption and metabolic rates has experienced a renewed interest in recent years through the work of Dorcas, *et. al.* (2006), Beaupre (1993), McCue and Lillywhite (2002), and Zaidan (2003), among others. In those studies, oxygen consumption was used as the estimation of the resting metabolic rate and the terms are often used interchangeably. In practice, measuring oxygen consumption is the standard choice in estimating metabolic rates in reptiles. The significant periods of activity used predominately for these measurements are if the organism is at a "resting" state.

The most thoroughly investigated aspect of reptilian physiology is thermobiology; which studies the thermal acclimation strategies of ectotherms and endotherms (Gans and Dawson, 1976; Ayers and Shine, 1997; Beaupre, 1995a; Peterson *et al*., 1985; Rice et al., 2006; Zimmerman *et al*., 1994). Despite the abundance of data, there are difficulties in the interpretation of the adaptive patterns reptiles have in conjunction with their environment. One of the main correlations between thermoregulation and physiological factors is oxygen consumption that is often used as an equivalent for metabolic rate (Gans and Dawson, 1976; McCue, 2007). The term metabolism encompasses all the chemical reactions occurring in an organism. Measurements of metabolism come in two forms: basal and resting (standard) rates. Basal metabolic rate (BMR) is the minimal rate of energy metabolism after fasting measured despite body temperature. Resting metabolic rate (RMR) is the equivalent of BMR at a given body temperature. These measurements are important baseline indicators of energy requirements and can be used to create a relationship between an ectotherm's thermo-environment and physiological activity.

Crotalus lepidus is a small rattlesnake that inhabits portions of the Chihuahuan Desert (Figure 1.1). It exhibits in a variety of background colors ranging from pale gray to pinkish (Werler and Dixon, 2000). Adult males are typically 600-700 mm snout-vent, with females being smaller (Werler and Dixon, 2000; Campbell and Lamar, 1989; Klauber, 1972). The chief prey of the rock rattlesnake is lizards, but small mammals, snakes and frogs are also eaten (Werler and Dixon, 2000; Klauber, 1997). However, arthropods, once considered secondary prey eaten by consumed lizards, are now known to be normal prey items for this species. *Crotalus lepidus* has been found in rocky gorges, hillsides with boulder fields and talus slopes (Werler and Dixon, 2000; Beaupre, 1993). Beaupre (1995a) studied the snake's ecology at two distinct sites within the Big Bend National Park; one locality consisted of limestone gorges while the second consisted of several volcanic extrusions associated with several boulder fields. Ernst (1992) suggested that this small rattlesnake may also be found in low lying desert habitats where it occurs in rocky flats and mesquite-grassland associations. At Indio Mountain Research

Station (IMRS), located in the Chihuahuan Desert, Hudspeth County, Texas, this species has been found in various habitats such as rocky outcrops and along arroyos provided there is enough vegetation cover.

Figure 1.1 A photograph of a rock rattlesnake, *Crotalus lepidus* from IMRS.

Crotalus molossus is an olive green to gray colored rattlesnake with a distinctive black tail (Figure 1.2). Adult males of this species range from 700-1100 mm snout-vent length. This large rattlesnake is found in rocky habitats with rock crevices and stony ridges and also mesquite-creosote flats with sufficient vegetation to provide protective cover (Werler and Dixon, 2000). Beck (1995) reported that in the late summer and fall, this rattlesnake species frequents arroyos and creosote flats in the Sonoran Desert. The activity season for this species of rattlesnake normally extends from early April to at least November, and seems to be more tolerant toward cool temperatures than most other rattlesnakes (Beck, 1995). In a field study of the black-tailed rattlesnake's food habits, Reynolds and

Scott (1982) indicated fewer species of rodents are available to this rattlesnake in its rocky habitat than found in the more diverse environments occupied by the western diamondback rattlesnake.

Figure 1.2. Photograph of a Black-tailed Rattlesnake, *Crotalus molossus* at IMRS.

The most important prey in that study were rodents such as rock pocket mice (*Chaetopidus intermedius*), cactus mice (*Peromyscus eremicus*), and Merriam's kangaroo rats (*Dipodomys merriami*). Other species making up its diet included wood rats (*Neotoma* spp.), and deer mice (*Peromiscus* spp.), but also include a large number of birds, mostly consisting of ground nesting species.

Figure 1.3. Photograph that shows a western diamondback rattlesnake, *Crotalus atrox* at IMRS.

Perhaps the most abundant rattlesnake species at IMRS is the Western Diamondback, *Crotalus atrox* (Figure 1.3). It is one of the most widespread venomous serpents in the United States (Werler and Dixon, 2000; Campbell and Lamar, 2004). This rattlesnake species is only exceeded in size by the eastern diamondback rattlesnake (*C. adamanteus*). Adult individuals of *C. atrox* are 1200-1500 mm in size (Werler and Dixon, 2000; Campbell and Lamar, 2004). It commonly occurs in less elevated areas when compared to *C. lepidus* and *C. molossus*, which prefer rockier habitats. In some areas of its range, it ascends mountains to considerable heights (Werler and Dixon, 2000). It lives in a wide variety of ecosystems which may include desert flats, brush land, and along arroyos, just to mention a few. *Crotalus atrox* exhibits considerable color diversity ranging from gray to dull red and is distinguished by its prominent black and white tail bands. This rattlesnake preys mostly on small mammals ranging in size from shrews and pocket mice to full grown wood rats, cottontail rabbits and rock squirrels (Beavers, 1976). Reynolds and Scott's (1982) study of diamondback food habits in Mexico's northwestern

Chihuahuan Desert found that the most abundant rodent species in an area made up the majority of its diet; Merriam's kangaroo rats and deer mice were also frequently consumed by *C. atrox* during that study. Birds are also preyed upon by the western diamondback, primarily ground dwelling species such as doves and quail. Lizards are occasionally consumed by smaller diamondbacks. Texas banded geckos (*Coleonyx brevis*), side blotch lizards (*Uta stansburiana*), earless lizards (*Cophosaurus*) and horned lizards (*Phrynosoma* spp.) have also been reported in the diet of *C. atrox*. Klauber (1997) indicated bird eggs, amphibians, and even lubber grasshoppers have been consumed by this rattlesnake.

1.2 Objectives

The subject of this study was to determine if there are differences in the RMR as indicated by O_2 consumption of *Crotalus atrox*, *C. lepidus*, and *C. molossus* at IMRS. This study investigated the functional relationships among body size and temperature with resting metabolic rates by measuring oxygen consumption at four different temperatures (Dorcas *et al.*, 2004), and attempted to answer the following questions: 1) Do males and females of each species demonstrate variations in oxygen consumption? 2) How does body mass affect metabolic rates and oxygen consumption of each species? 3) How does body temperature affect metabolic rates of each species? 4) How do metabolic rates differ between the 3 species?

Chapter 2.

Methods and Materials

2.1 Study Area

The three species of rattlesnake were collected from IMRS centered on 30°16´ 45” N and 105°00´55” W, 1215 m, which is approximately 16000 hectares (ca. 40000 acres) of Chihuahuan Desert landscape owned and administered by the University of Texas at El Paso. It is located in southeastern Hudspeth County, Texas, approximately 40 km southwest of Van Horn. The topography at IMRS is a diverse mixture of rocky outcrops, arroyos, and bajadas covered by different association of Chihuahuan Desert scrub vegetation (Johnson, 2000). IMRS facilities allowed for onsite experimentation (Figure 2.1), which enabled snakes to be housed on site, thereby reducing unnecessary stress associated with moving them offsite. IMRS was developed under NSF grants specifically to provide high quality field research facilities in the Chihuahuan Desert.

Figure 2.1. Photograph of the headquarters facilities at IMRS.

Vegetation on IMRS is typical of Chihuahuan Desert scrubland containing plants such as (Creosote, *Larrea tridentate*), Lechuguilla (*Agave lechuguilla*), Ocotillo (*Fouquieria splendens*), Eve's needle, *Yucca faxioniana*, White thorn acacia (*Acacia constricta)*, Catclaw (*Acacia greggi*) and desert grassland represented by Black Gramma (*Bouteloua eriopoda)* and Fluff grass (*Erioneuron pulchellum*) (Figure 2.2). The flora is affected by the Rio Grande corridor which allows plants to ascend from the Big Bend area into the Rio Grande Valley (Johnson, 2000). Typical Chihuahuan Desert grasslands surround the northern side of the Indio Mountains in which the remnants of grassland that can be found at IMRS might have originated. The annual precipitation in IMRS is on average less than 25 cm per year, with most falling during the summer monsoon season (from June through September). The average annual temperature is 18.6 C.

Figure 2.2. Photograph of typical geomorphology and vegetation found at IMRS

2.2 Sampling and Processing

The initial objective of the study was to obtain approximately 30 specimens (10 from each species) from the IMRS landscape. In total, 39 rattlesnakes were captured and used to conduct this study; eight *C. lepidus*, 17 *C. atrox*, and 14 *C. molossus* during May 2007 to June 2008.

Snakes were located either by active searching areas known to be inhabited by particular species, either on foot or by "road cruising," which requires driving on IMRS roads. Snakes can be easily spotted on roads and more areas can be covered by this technique. Once a snake was located, either snake tongs or a snake hook was used to safely place the specimen into a 18. 9 liter bucket or into large cotton bag. Date of capture and GPS location of capture snakes were recorded and then they were taken to the laboratory at IMRS for processing.

Prior to conducting the experiment, snakes were housed in 18.9 liter gallon plastic buckets with screw-on Gamma Seal lids. Each snake was measured for mass and snout-vent length. For permanent identification, pit tags (passive integrated transponder; AVID Inc.; Dixon and Camper, 1988) were inserted subdermally into the right dorsolateral section of the body, previously disinfected with 70% ethanol, approximately 20 cm from the cloaca using a sterile pit-tagging syringe. After implantation, first aid antiseptic "new skin," liquid bandage was applied to seal the small needle punctures and induce healing and for infection prevention.

Snakes were fasted for 10 to 14 days to obtain standard metabolic rates (Dorcas *et al*., 2004; Beaupre, 1993, 1995a; Beaupre and Duvall, 1998a; Beaupre and Zaidan, 2001; McCue and Lillywhite, 2002; Zaidan, 2003; Wills and Beaupre, 2000). The process of fasting animals provided a highly reproducible function indicative of maintenance cost. In order to achieve an informative maintenance cost, animals were required to be in the dark in the inactive phase of their diurnal cycle. Other metabolic studies of similar species required the snakes to clear most food from their digestive tract in order to record RMR (Dorcas *et al*., 2004; Beaupre, 1993, 1995a; Beaupre and Duvall, 1998a; Beaupre and

Zaidan, 2001; McCue and Lillywhite, 2002); therefore they were not fed before commencing the experiment. Snakes remained from two to eight hours, depending on the snake size, in a chamber to ensure acclimation to the temperature at which the animals were tested (Coulson and Hernandez, 1980). All measurements of RMR were made on fasted animals during the inactive (diurnal) phase of their diel cycle (Andrews and Pough, 1985). For each animal, basal Volume of Oxygen (VO_2) consumed was measured at four experimental temperatures (20°, 25°, 30°, and 35°C). These temperatures reflect active thermal conditions in most desert reptiles (Bennett, 1982).

2.3 Respirometry

To collect metabolic data, snakes were placed into metabolic respirometry chambers. Large specimens were placed in a 3.2 l chamber that was made of translucent acrylic to accommodate observation. Smaller snakes were placed in a 2 l chamber. Both chambers have an opening in order to place snakes into the chambers, which were then sealed. Each chamber was tested for gas leakage or carbon dioxide absorbance with the use sodium hydroxide (NaOH). The translucent acrylic allowed observation of behavior during experiments while also reducing the intensity of light entering chambers. A centigrade thermometer was placed inside the chamber to monitor temperature. Before the snakes were placed into the respirometry chamber, 30 g NaOH were placed at the bottom of the chamber to absorb CO_2 and H_2O. The gas scrubbing material was replaced daily. A calibrated tube was inserted into a rubber stopper which was placed into the metabolic chamber. The tube was sealed by applying a soap film solution to the end of the pipette.

The chambers were placed into a temperature controlled water-bath in order to increase and decrease the temperatures within the chambers to measure the oxygen consumption (VO_2) of each snake at prescribed temperatures. Snakes were allowed to adjust to the metabolic chambers and experimental temperatures for 2-8 hr, depending on the size of the animal (Coulson and Hernandez, 1980). Four levels of temperature were used (20°, 25°, 30° and 35°C) during four random time periods throughout the

normal 24 hour cycle. The chamber temperature never fluctuated more than $\pm$ 0.1°C. The experimental temperatures matched those during the activity periods of the species within their natural environments (Bennett, 1982).

As oxygen was consumed by the snake, released CO_2 and H_2O vapor were absorbed by the NaOH. As pressure dropped from the removal of oxygen by the snake's respiration inside the chamber, a soap bubble was drawn down the calibrated tube in the direction of the chamber. The difference between the starting and ending measurements was recorded and divided by time, in this case 60 minutes. For each snake, resting VO_2 was measured three to four times for at least an hour at each of the four experimental temperatures between 0600 and 2300 hrs. Barometric pressure used in the calculation of VO_2 was recorded by a weather station located near the IMRS headquarters.

Measurements were made only when snakes were judged to be resting by visual inspection and minimal VO_2 data were collected as the animals acclimated to the chambers. Most of the animals remained coiled and inactive for the duration of the experiments, except when first placed into the chambers. Each snake was noted for either remaining motionless, alert with head up but remaining motionless, or actively moving in the chamber. Data was not used if snakes were continuously active in the chamber at particular temperatures. Metabolic measurements on reptiles can be performed at known phases of the circadian cycle (Pough and Andrews, 1985; Dorcas *et al.*, 2004; Beaupre and Duvall, 1998), however for this study sampling was conducted throughout a normal 24 h cycle, and results indicate oxygen consumption is not significantly different during this cycle at a given temperature.

2.4 Measurement of Oxygen Consumption

The use of a stopwatch determined the time required for the soap bubble to move along the graduated pipette. To calculate oxygen consumption (VO_2), the following formulas were used:

VO_2 = ml O_2 / h and

$V^* O_2$= ml O_2 / h g^{-1}

Where h represents hours and g represents grams or the mass of the organism.

A modified equation was used to calculate oxygen consumption on site where variables such as pressure and temperature are constantly changing. This equation allowed to compare results of trials performed under different conditions. In order to calculate some corrections, gas volume were corrected to the volume that would have been observed under conditions of standard temperature (°C) and pressure (760 mm Hg). The corrected measurement of oxygen values (ml / h) were determined by the formula:

$$V_{corr} = V_{obs} \times 273Kelvin/(273Kelvin + T) \times (B.\ P. / 760mm\ Hg)$$

Where V_{corr} represents the corrected volume in mls which indicate the oxygen consumed under standard conditions and V_{obs} represents the observed volume of oxygen consumed in ml per hour (ml / h). Temperature is recorded in °C and B.P. represents barometric pressure.

2.5 Temperature Dependence

Temperature dependence of metabolic rate was determined by using the so-called Q_{10} which was calculated by using the van't Hoff equation (Eckert, 1988):

$$Q_{10} = (k_2 / k_1)^{10/(t_2 - t_1)}$$

Where k_1 and k_2 are velocity constant of reaction at temperatures t_1 and t_2, respectively. The following form of the formula was most appropriate:

$$Q_{10} = (n_2 / n_1)^{10/(t_2 - t_1)}$$

in which n_1 and n_2 are the metabolic rates at temperatures t_1 and t_2. For temperature intervals of 10°C, the following form of the van't Hoff equation was used in this study:

$$Q_{10} = n_{(t + 10)} / n_t$$

Where n_t is the metabolic rate at the lower temperature and $n_{(t + 10)}$ is the metabolic rate at the higher temperature (Eckert, 1988). For given enzymatic reactions, respiratory quotients differ over different temperatures (Fleharty, 1963).

2.6 Data Analysis

Prior to analysis, oxygen consumed (ml O_2 / h) and body mass (g.) were $\log_{10}$ transformed to linearize the relationship between the variables. To examine the relationship among body mass, temperature, and VO_2 (ml O_2 / h), multiple regression analysis were used (Andrews and Pough, 1985; Beaupre and Zaidan, 2001). To examine the effects of body mass and temperature on RMR (ml O_2 / h g^{-1}), we used repeated measures regression with snake body mass (g.) as covariate. A one way ANOVA was used to determine any differences between species, temperature and mass. A two sample t-test was used to determine significance between sexes and oxygen consumption. Statistical significance was assessed at $P < 0.05$ and was performed by MINITAB release 14 Software.

Chapter 3

Results

3.1 Morphology

A total of 39 specimens were collected and oxygen consumption measured for this study; 17 *C. atrox*, 14 *C. molossus* and eight *C. lepidus*. In total there was 25 males and 14 females collected for all three species; 10 males and seven females of *C. atrox*, five males and three females of *C. lepidus*, 10 males and four females of *C. molossus*. Of the females collected, four of the seven females of *C. atrox* were gravid females. The remainder of the females from the three species were not gravid.

Snakes were observed in chambers a total of 156 times and exhibiting varying degrees of activity during respiratory measurements. The mean mass of the 39 snakes for all three species in this study was 290.29 g (range = 47.0 – 660.0 g). The mean masses of the three species were; 17 *C. atrox* was 362.01 g (range 159.2 – 660.0 g) (Table 3.1), for 8 *C. lepidus* was 133 g (range 47.0 -200.0 g) (Table 3.2), and 14 *C. molossus* was 293 g. (range 48.0 – 596.0 g) (Table 3.3). *Crotalus atrox* males ranged in size (SVL) from 470 mm to 1000 mm , whereas female *C. atrox* ranged from 604 mm to 835 mm (Table 3.4). Males of *C. lepidus* ranged from to 388 mm to 656 mm in size and females ranged from 407 mm to 508 mm (Table 3.5). As for the males of *C. molossus*, their size ranged from 446 mm to 923 mm and females ranged from 470 mm to 773 mm (Table 3.6).

Table 3.1. Mean of adult specimens of *Crotalus atrox* (N = 17) with maximum and minimum of Body Mass (g) of males (N = 10) and females (N = 7) from IMRS, Hudspeth County, Texas. The statistical test used was a Mann Whitney U test (P < 0.05)

Variable	N	Mean	StDev	SE Mean	95% CI	Z	P
Body Mass	17	362.012	160.980	0.049	(361.917, 362.107)	-0.00	0.996
Male	10	452.200	150.541	0.063	(452.076, 452.324)	1426.00	0.001
Female	7	233.029	46.005	0.076	(232.880, 233.177)	-1706.29	0.001

Table 3.2. Mean of adult specimens of *Crotalus lepidus* (N = 8) with maximum and minimum of body mass (g) of males (N = 5) and females (N =3) from IMRS, Hudspeth County, Texas. The statistical test used was a Mann Whitney U test (P < 0.05)

Variable	N	Mean	StDev	SE Mean	95% CI	Z	P
Body Mass	8	133.000	56.846	0.707	(131.614, 134.386)	185.26	0.001
Male	5	155.400	61.525	0.894	(153.647, 157.153)	171.51	0.001
Female	3	95.6667	19.8578	1.1547	(93.4035, 97.9298)	81.12	0.001

Table 3.3. Mean of adult specimens of *Crotalus molossus* (N = 14) with maximum and minimum body mass (g) of male (N = 10) and females (N = 4) from IMRS, Hudspeth County, Texas. The statistical test used was a Mann Whitney U test (P < 0.05)

Variable	N	Mean	StDev	SE Mean	95% CI	Z	P
body mass	14	293.000	191.274	0.535	(291.952, 294.048)	544.41	0.001
Male	10	343.170	197.127	0.632	(341.930, 344.410)	539.44	0.001
Female	4	167.575	112.233	1.000	(165.615, 169.535)	165.58	0.001

Table 3.4. Mean of maximum and minimum values of morphological characteristic snout-vent length (SVL) of adult male and female specimens of *C. atrox* IMRS, Hudspeth County, Texas. The statistical test used was a Mann Whitney U test (P < 0.05)

Variable	N	Mean	StDev	SE Mean	95% CI	Z	P
Females	7	729.857	70.829	0.076	(729.709, 730.005)	4866.13	0.001
Males	10	807.600	146.533	0.063	(807.476, 807.724)	7045.36	0.001

Table 3.5. Mean of maximum and minimum values of morphological characteristic snout-vent length (SVL) of adult male and female specimens of *C. lepidus* IMRS, Hudspeth County, Texas. The statistical test used was a Mann Whitney U test(P < 0.05).

Variable	N	Mean	StDev	SE Mean	95% CI	Z	P
Male	5	563.400	103.333	0.894	(561.647, 565.153)	627.66	0.001
Female	3	485.667	19.858	1.155	(483.403, 487.930)	418.87	0.001

Table 3.6. Mean of maximum and minimum values of morphological characteristic snout-vent length (SVL) of adult male and female specimens of *C. molossus* from IMRS, Hudspeth County, Texas. The statistical test used was a Mann Whitney U test ($P < 0.05$).

Variable	N	Mean	StDev	SE Mean	95% CI	Z	P
Male	10	751.100	148.342	0.632	(749.860, 752.340)	1184.43	0.001
Females	4	623.000	144.100	1.000	(621.040, 624.960)	621.00	0.001

3.2 Oxygen consumption

Results of oxygen consumption (RMR) show *C. atrox*, *C. lepidus*, and *C. molossus* being influenced by body mass and temperature (Figure 3.1 – 3.5). Multiple regression analysis indicated the RMR increased with increasing body mass and temperature in this study. The effect of temperature on all three species on VO2 is illustrated in Figure 3.1 at all four experimental temperatures.

Examination of temperature by oxygen consumption (ml / h g^{-1}) for all species (Figure 3.6) suggests a consistent increase in oxygen consumption with temperature increments. This significance of temperature by mass interaction arises from differences in slope in the effect of temperature increases among different oxygen consumption by each species

Figure 3.1 shows oxygen consumption for all three species (*C. atrox, C. lepidus* and *C. molossus*), at four experimental temperatures (20°, 25°, 30°, 35°C) compared to body mass (g) ($df = 4$; $r^2 = 0.87$; $P < 0.001$). Multiple regression analysis indicates that RMR increased with body mass and temperature. An analysis for all three species for oxygen consumption (ml / h g^{-1}) and temperature (°C) indicates a strong correlation between the two ($df = 4$; $r^2 = 0.92$; $P < 0.001$). At 20°C, there is significant differences in $\log_{10} VO_2$ for the three rattlesnake species ($r^2 = .048$; $p < 0.001$; ANOVA). A one way ANOVA at 25°C, also indicated significant differences in $\log_{10} VO_2$ between the three species ($r^2 =$

0.43; $P < 0.001$) as well as at 30°C ($r^2 = 0.25$; $P < 0.005$). At 35°C, there is significant differences in oxygen consumption for the three species ($r^2 = 0.28$; $P < 0.003$) (Table 3.7).

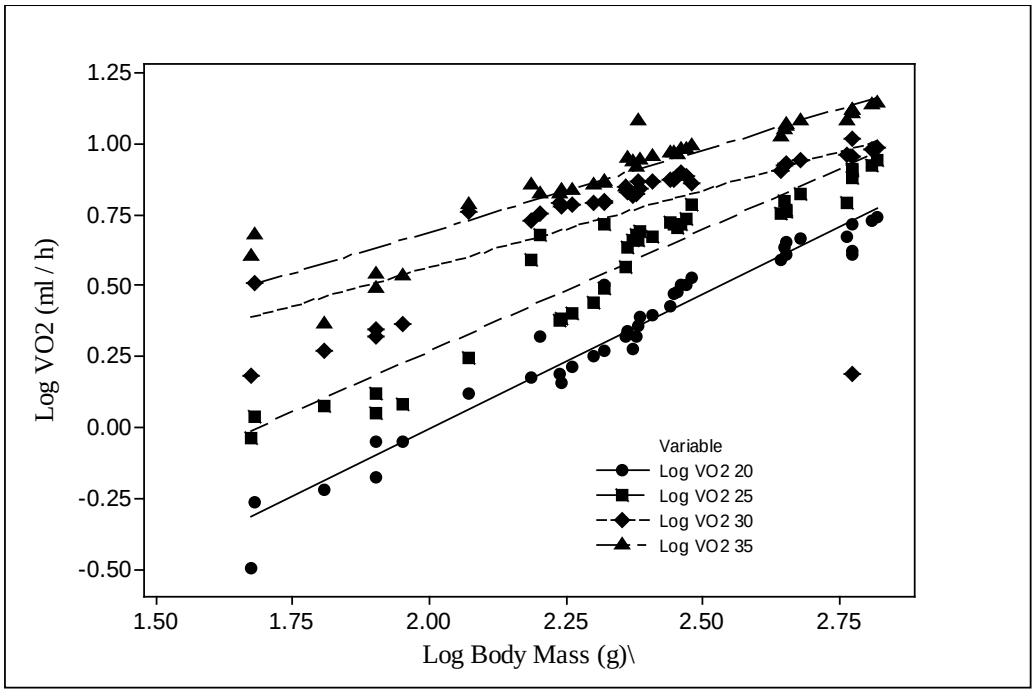

Figure 3.1. Relationship of of Log_{10} VO_2 (ml / h) and Log_{10} body mass (g) for all *Crotalus* species combined from IMRS, Hudspeth County, Texas. In total 39 specimens were used. Each plot depicts allometric relationships of all snakes at four experimental temperatures (20°, 25°, 30° and 35°C). Symbols depict the mean of individual snakes. Circles represents snakes at 20°C, squares at 25°C, diamonds at 30°C and triangles at 35°C.

Figure 3.2 shows a comparison of oxygen consumption for all three rattlesnake species from IMRS at 20°C. Slopes of the relationship between Log_{10} VO_2 and Log_{10} body mass (g) were approximately comparable between the three species of rattlesnakes (Table 3.8). Figure 7 shows the residual Log_{10} VO_2 and body mass for *C. atrox* (N = 17), *C. lepidus* (N = 8), and *C. molossus* (N = 14)

at 20°C. There is significant relationship between Log_{10} VO_2 (ml / h) and Log_{10} body mass (g) (ANOVA, F = 10.6, df = 2, 36, P < 0.001) (Table 3.7).

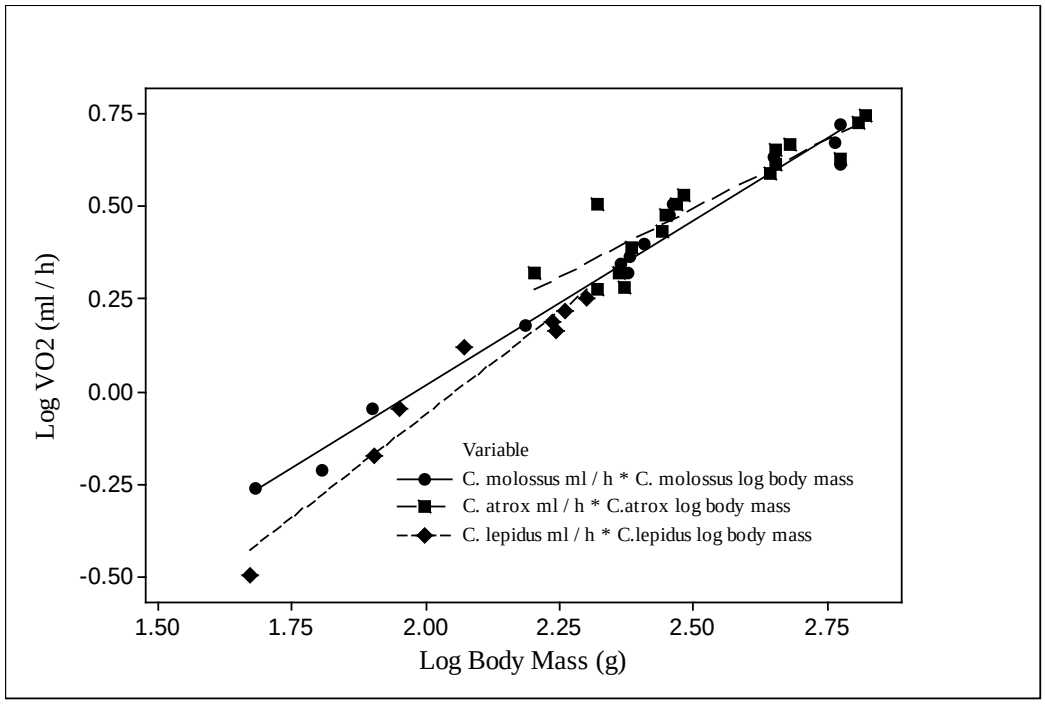

Figure 3.2. Comparison of Log_{10} VO_2 (ml / h) and Log_{10} body mass (g) at 20°C for the three species of rattlesnakes, *C. atrox, C. lepidus*, and *C. molossus* from IMRS, Hudspeth County, Texas. Each symbol represents the mean of oxygen consumption for individual snakes.

Figure 3.3 illustrates a comparison of oxygen consumption for all three rattlesnake species from IMRS at 25°C. Slopes of relationship between Log_{10} VO_2 (ml / h) and Log_{10} body mass (g) were comparable between *Crotalus atrox* (N = 17), *C. lepidus* (N = 8) and *C. molossus* (N = 14) at the experimental temperature (Table 8). There was significant between Log_{10} VO_2 (ml / h) and Log_{10} body mass (g) (ANOVA, F = 15.53, df = 2, 36, P < 0.001) (Table 3.7).

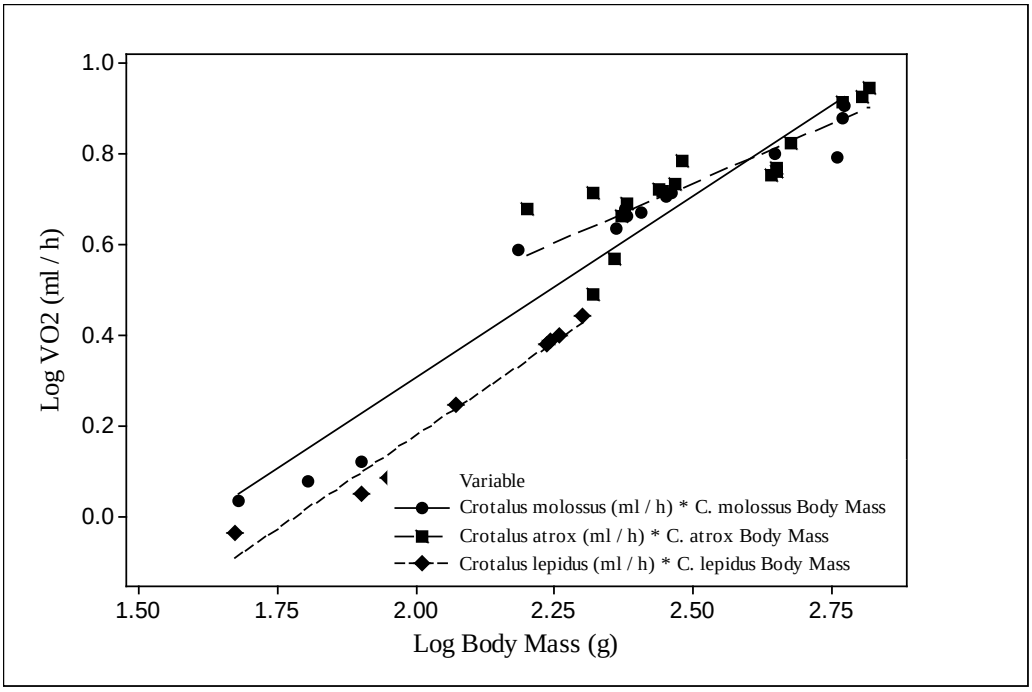

Figure 3.3. Comparison of Log_{10} VO_2 (ml / h) and Log_{10} body mass (g) at 25°C for the three species of rattlesnakes, *C atrox*, *C. lepidus*, and *C. molossus* from IMRS, Hudspeth County, Texas. Each symbol represents the mean of oxygen consumption for individual snakes.

Figure 3.4 shows a comparison of oxygen consumption for all three rattlesnake species from IMRS. Slopes of relationship between Log_{10} VO_2 (ml / h) and Log_{10} body mass (g) were comparable between *C. atrox* (N = 17), *C. lepidus* (N = 8) and *C. molossus* (N = 14) at 30°C (Table 3.8). There is significant relationship between Log_{10} VO_2 (ml / h) and Log_{10} body mass (g) for all three species (ANOVA, $F = 5.67$, $df = 2, 36$, $P < 0.001$) (Table 3.7).

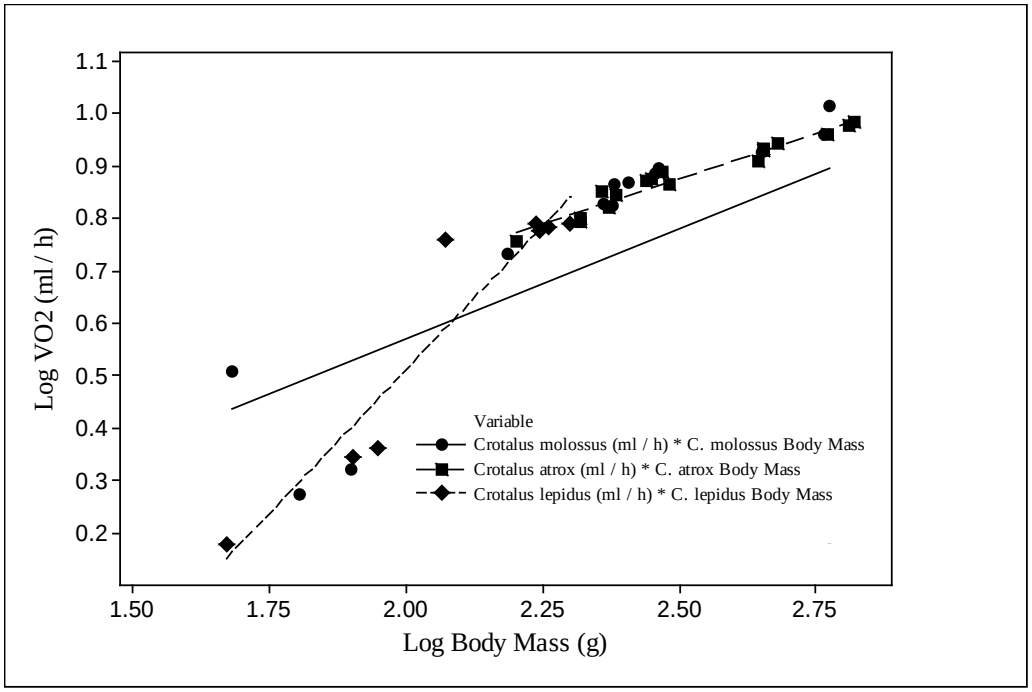

Figure 3.4. Comparison of Log_{10} VO_2 (ml / h) and Log_{10} body mass (g) at 30°C for the three species of rattlesnakes, *C. atrox*, *C. lepidus*, and *C. molossus* from IMRS, Hudspeth County, Texas. Each symbol represents the mean of oxygen consumption for individual snakes.

Figure 3.5 shows oxygen comparison of oxygen consumption for all three rattlesnake species from IMRS at 35°C. Relationships of slopes between Log_{10} VO_2 (ml / h) and Log_{10} body mass (g) for all three species of snakes were comparable (Table 3.8). There is a significant relationship between Log_{10} VO_2 (ml / h) and Log_{10} body mass (g) for all three species at 35°C (ANOVA, $F = 7.19$, $df = 2, 36$, $P < 0.002$) (Table 3.7).

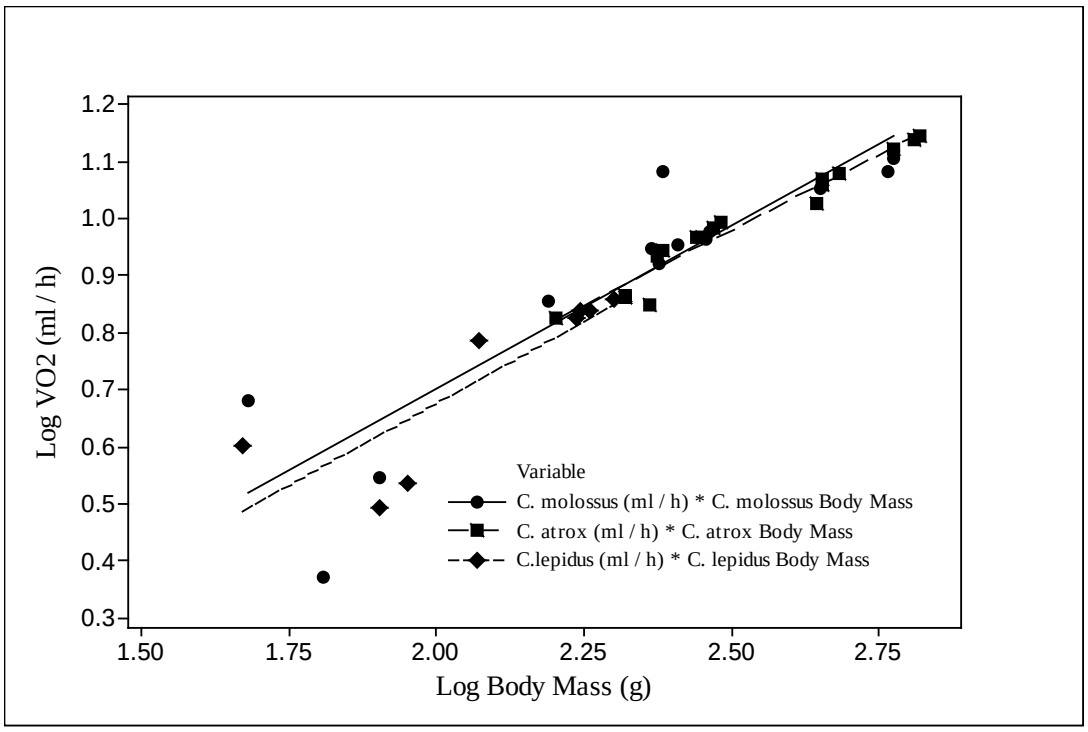

Figure 3.5. Comparison of Log_{10} VO_2 (ml / h) and Log_{10} body mass (g) at 35°C for the three species of rattlesnakes, *C. atrox, C. lepidus*, and *C. molossus* from IMRS, Hudspeth County, Texas. Each symbol represents the mean of oxygen consumption for individual snakes.

Table 3.7. Analysis of variance for Log_{10} VO_2 (ml / h) of the three species of rattlesnakes, *C. atrox*, *C. lepidus*, and *C. molossus* from IMRS, Hudspeth County, Texas at four experimental temperatures (20°, 25°, 30°, 35°C). Tukey's test was used for confidence intervals.

T(°C)	N	df	S.S.	F-ratio	P
20°C	39	2, 36	1.26332	10.6	0.001
25°C	39	2, 36	1.3570	15.53	0.001
30°C	39	2, 36	0.4808	5.67	0.001
35°C	39	2, 36	0.3942	7.19	0.002

Table 3.8. Regression coefficients and statistics for the relations of Log_{10} VO_2 (ml / h) to Log_{10} body mass (g) for *C. atrox, C. lepidus* and *C. molossus* from IMRS, Hudspeth County, Texas.

	N	T (°C)	Slope	Intercept	SE of slope	r^2
C. atrox	17	20	1.122	1.947	0.0689	0.82
	17	25	1.364	1.503	0.2214	0.70
	17	30	2.752	0.008	0.1384	0.95
	17	35	1.804	0.731	0.1029	0.95
C.lepidus	8	20	0.849	2.055	0.0804	0.94
	8	25	1.172	1.791	0.0897	0.96
	8	30	0.883	1.573	0.0626	0.96
	8	35	1.099	1.319	0.0789	0.93
C. molossus	14	20	1.102	1.985	0.0446	0.97
	14	25	1.172	1.661	0.0860	0.93
	14	30	1.224	1.432	0.1060	0.91
	14	35	1.307	1.222	0.0933	0.93

3.3 Sex Differences

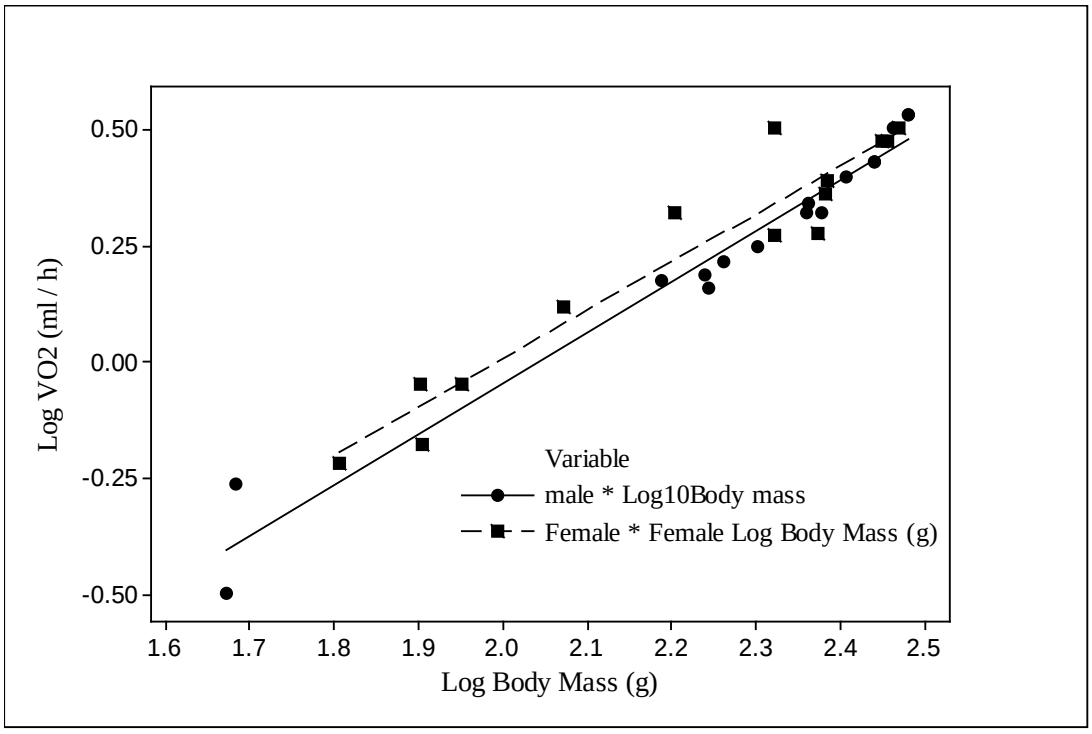

Figure 3.6. Residual Log_{10} VO_2 of female and male rattlesnakes in relation to Log_{10} body mass at 20°C from IMRS, Hudspeth County, Texas. Squares represent females (N = 14) and circles represent males (N = 16).

Slopes of the relationship between Log_{10} VO_2 and Log_{10} body mass were almost comparable between the two sexes at a certain body mass (Table 3.9). Figure 3.6 shows the residual Log_{10} VO_2 and Log_{10} body mass for male (N = 16) and females (N = 14) of the three species at a temperature of 20°C. Oxygen consumption by females of the three rattlesnake species is similar to males of comparable body size. Regression analysis for males rattlesnakes indicate a significant correlation ($r^2 = 0.72$; $P < 0.01$). Females at similar temperature has a correlation of $r^2 = 0.86$; $P < 0.001$. A two sample t-test between both sexes indicated no significant difference between sexes at a comparable mass ($T = 0.23$; $P = 0.816$).

For males of greater masses, there is significant differences in oxygen consumption, (T = 0.63; P = 0.0001).

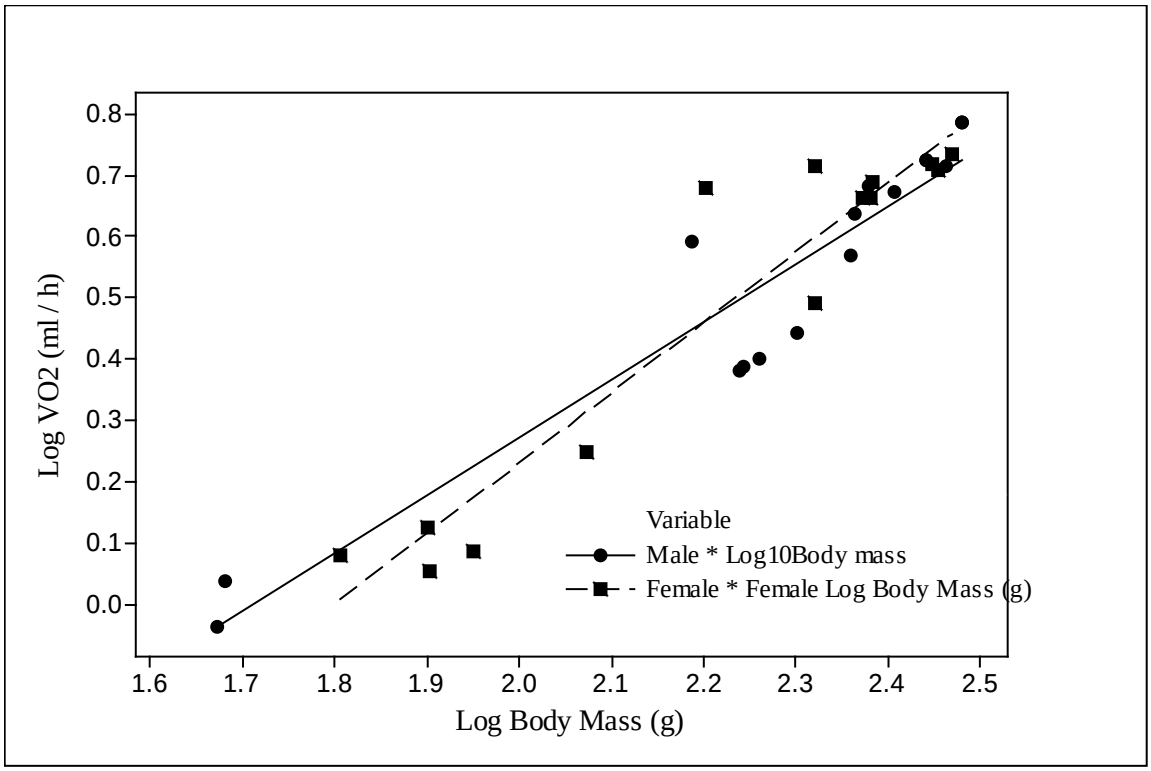

Figure 3.7. Residual Log_{10} VO_2 of female and male rattlesnakes in relation to Log_{10} body mass at 25°C. Squares represent females (N = 14) and circles represent males (N = 16) from IMRS, Hudspeth County, Texas.

Figure 3.7 shows residuals of Log_{10} VO_2 and Log_{10}body mass of male and female rattlesnakes of all three species at 25°C. Regression analysis for male rattlesnakes (N = 16) also indicate significance between the two factors (r^2 = 0.74; P < 0.001). Regression coefficients of slopes are comparable (Table 3.10). As for females (N = 14) at this same temperature, regression analysis indicated significance between oxygen consumption and body mass (r^2 = 0.86; P < 0.001). A two sample t-test between of both sexes at 25°C indicated no significance at comparable body masses (T = 0.57; P = 0.60). Males of

greater body mass have elevated oxygen consumption (T = 0.87; P = 0.001) than females at a lower body mass.

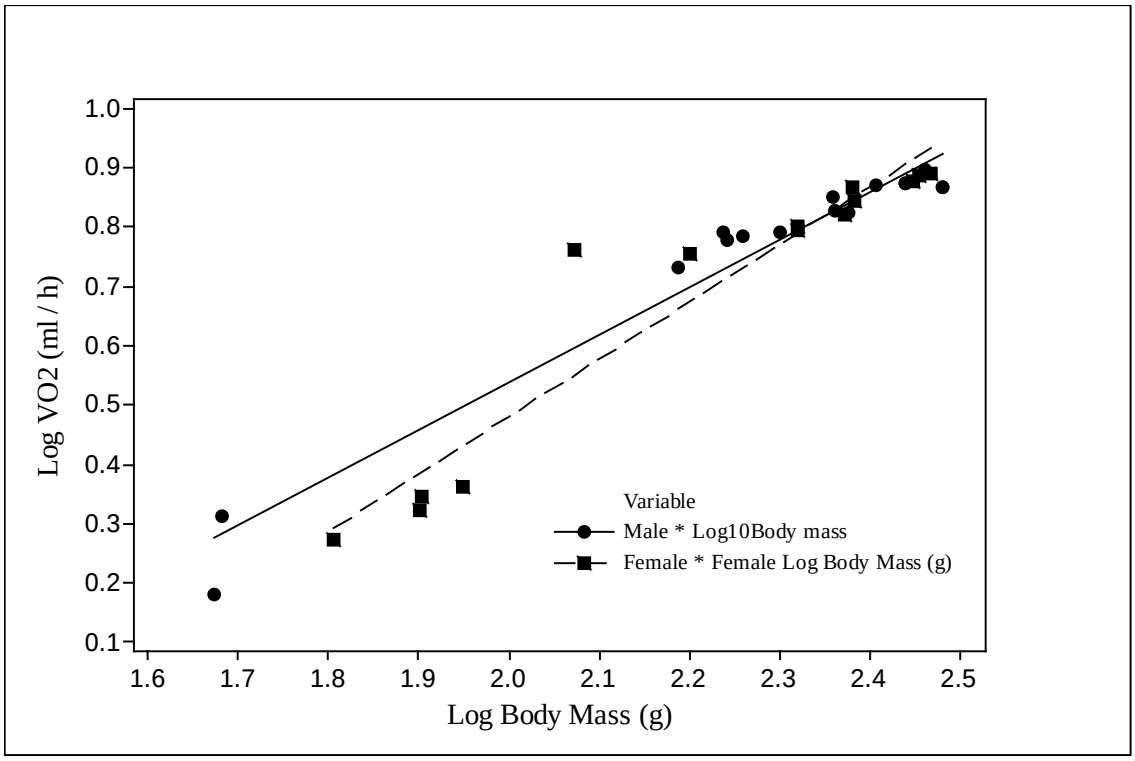

Figure 3.8. Residual Log_{10} VO_2 of female and male rattlesnakes in relation to Log_{10} body mass at 30°C. Squares represent females (N = 14) and circles represent males (N = 16) from IMRS.

Residuals in Figure 3.8 of Log_{10} VO_2 and Log_{10} body mass for males (N = 16) is (r^2 = 0.60; P < 0.001). For similar temperature of 30°C, females (N = 14) showed a significance differences when compared to males at this experimental temperature (r^2 = 0.83; P < 0.001). Slopes of both regressions are heterogeneous as body mass increases for both male and female at this experimental temperature. If compared to snakes with similar body masses, the slopes for both males and females rattlesnakes are almost homogeneous (Table 3.10). A two sample t-test indicated no differences between both sexes at comparable masses (T = 0.87; P = 0.39) (Table 3.9). A dissimilar correlation can be distinguished for males with larger body masses than females with lower body masses (T = 0. 67; P = 0.001).

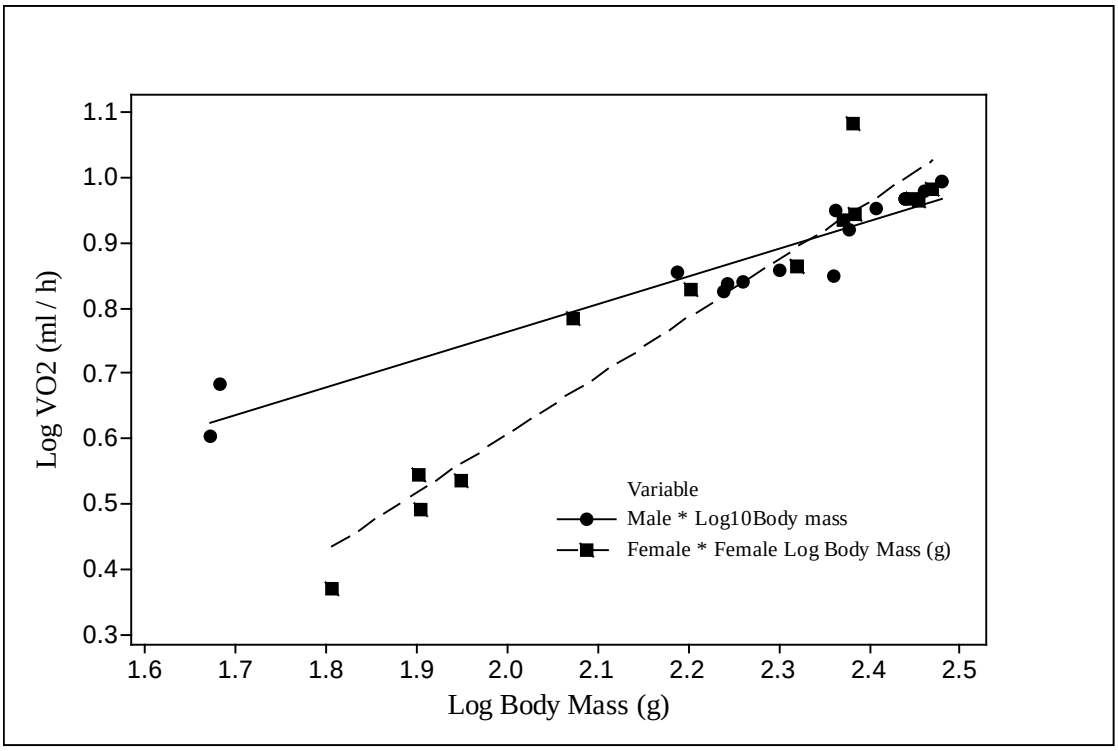

Figure 3.9. Residual Log_{10} VO_2 of female and male rattlesnakes in relation to Log_{10} body mass at 35°C. Squares represent females (N = 14) and circles represent males (N = 16) from IMRS.

Figure 3.9 shows residuals of Log_{10} oxygen consumption and Log_{10}body mass of male (N = 16) and female (N = 14) rattlesnakes. Residuals were plotted in scatterplots based on means of oxygen consumption at 35°C with regression. Male rattlesnakes residuals are significant and show a correlation between Log_{10} VO_2 and body mass (r^2 = 0.88; P <0.001). As for female residuals, Figure 3.9 shows a correlation between both factors (r^2 = 0.86; P < 0.001). Similar to the other figures, slopes of regression for both sexes are heterogeneous, however, they are almost similar when compared to the same body mass (Table 3.10). A two sample t-test indicates no significant differences between both sexes at comparable mass (T = 1.27; P = 0.221) in Table 3.9. At 35°C, the oxygen consumption is higher in males of larger mass than females (T = 0.90; P = 0.001).

Table 3.9. A two sample t-test comparison (P = 0.05) of male (N = 16) and female (N = 14) rattlesnakes from IMRS, Hudspeth County, Texas at the four experimental temperatures.

T (°C)	VO_2 (ml / h)	T	P
20°C			
Male	0.253553	0.23	0.816
Females	0.230656		
25°C			
Male	0.531367	0.57	0.60
Female	0.475200		
30°C			
Male	0 . 757469	0.87	0.39
Female	0.685896		
35°C			
Male	0.880123	1.27	0.221
Females	0.797310		

Table 3.10. Regression coefficients and statistics for the relations of Log_{10} VO_2 (ml / h) to Log_{10} body mass (g) for male (N = 16) and female (N =14) rattlesnakes from IMRS, Hudspeth County, Texas.

	N	T (°C)	Slope	Intercept	SE of slope	r^2
Male	16	20	0.884	2.0503	0.071	0.96
Female	14	20	0.889	2.0081	0.076	0.91
Male	16	25	0.956	1.7664	0.084	0.90
Female	14	25	0.793	1.836	0.072	0.90
Male	16	30	1.193	1.3706	0.068	0.95
Female	14	30	0.943	1.5658	0.084	0.91
Male	16	35	2.136	0.3945	0.176	0.90
Female	14	35	1.035	1.3877	0.840	0.92

3.4 Temperature and Oxygen Consumption

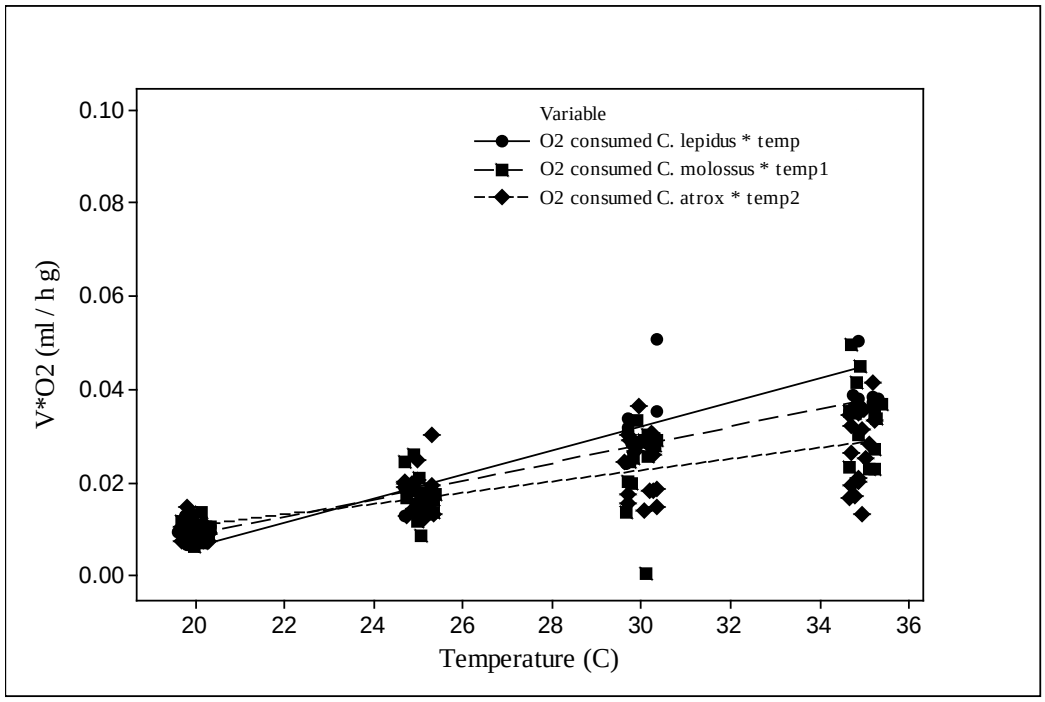

Figure 3.10. Temperature profile of oxygen consumption $V*O_2$ (ml / h g^{-1}) for all three species of rattlesnake (N = 39), *C. atrox*, *C. lepidus*, and *C. molossus* from IMRS, Hudspeth County, Texas at four experimental temperatures (20°, 25°, 30° and 35°C). Each symbol represents the mean of an individual snake's oxygen consumption at the four temperatures.

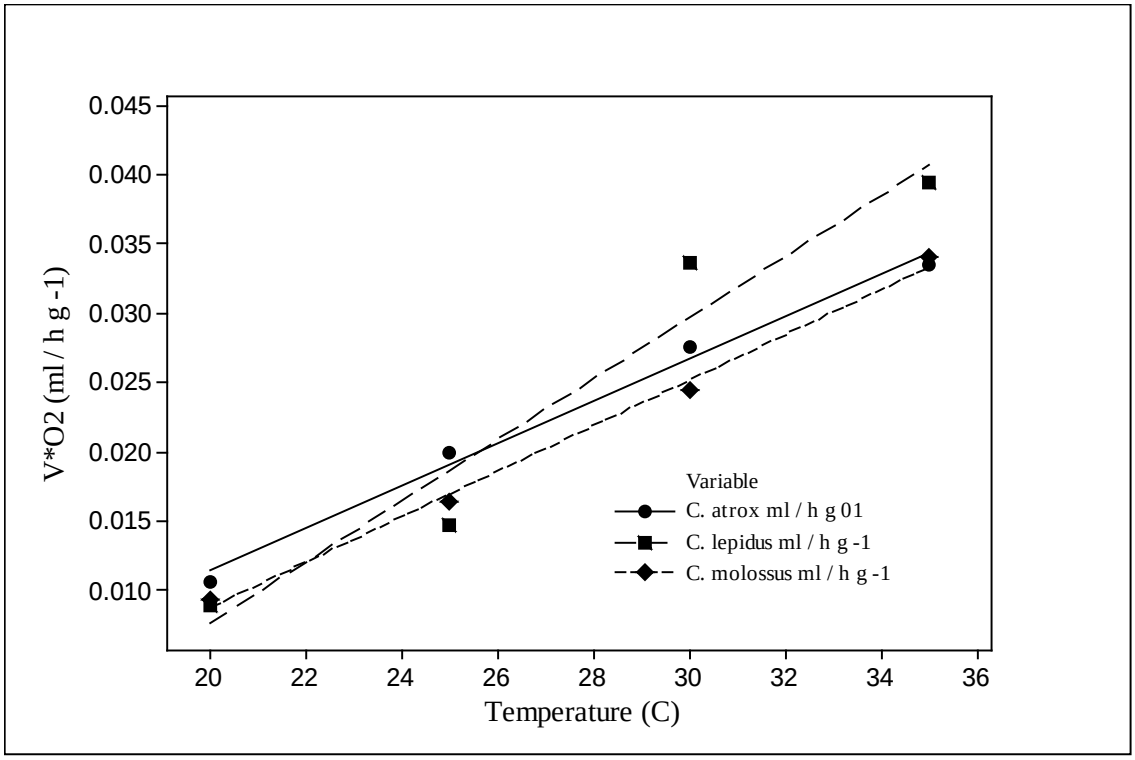

Figure 3.11. Temperature profile of mean oxygen consumption $V*O_2$ (ml / h g $^{-1}$) for all three species of rattlesnake (N = 39), *C. atrox*, *C. lepidus*, and *C. molossus* from IMRS, Hudspeth County, Texas at four experimental temperatures (20°, 25°, 30° and 35°C).

Figures 3.10 and 3.11 show oxygen consumption $V*O_2$ (ml / h g $^{-1}$) affected by temperature for *C. atrox*, *C. lepidus* and *C. molossus*. Figure 15 represents a linear correlation of mean residuals for individual snakes of the three specimens at the four experimental temperatures, 20°, 25°, 30° and 35°C.

Figure 3.11 represents a linear correlation of mean residuals for the three rattlesnakes, *C. atrox, C. lepidus* and C. *molossus* for each of the four experimental temperatures ($r^2 = 0.85$; $P < 0.001$). This regression analysis shows a correlation between temperature and VO_2.

An analysis for all three species for oxygen consumption $V*O_2$ (ml / h g $^{-1}$) and temperature (°C) indicates a strong correlation between the two (df = 4; $r^2 = 0.92$; $P < 0.001$). At 20°C, there is significant differences in $V*O_2$ for the three rattlesnake species ($r^2 = .048$; $p < 0.001$; ANOVA). A one way

ANOVA at 25°C, also indicated significant differences in $\log_{10} VO_2$ between the three species (r^2 = 0.43; P < 0.001), as well as at 30°C (r^2 = 0.25; P < 0.005). At 35°C, there is significant differences in oxygen consumption for the three species (r^2 = 0.28; P < 0.003).

Table 3.11. The mean values of $V*O_2$ (ml / h g^{-1}) and temperature (°C) for all four experimental temperatures for *C. atrox*, *C. lepidus* and *C. molossus* from IMRS, Hudspeth County, Texas.

	N	T(°C)	(ml / h g^{-1})
C. atrox	17	20°C	0.0099
		25°C	0.012
		30°C	0.023
		35°C	0.027
C. lepidus	8	20°C	0.0089
		25°C	0.0149
		30°C	0.033
		35°C	0.041
C. molossus	14	20°C	0.0096
		25°C	0.017
		30°C	0.027
		35°C	.038

3.5 Respiratory Quotient

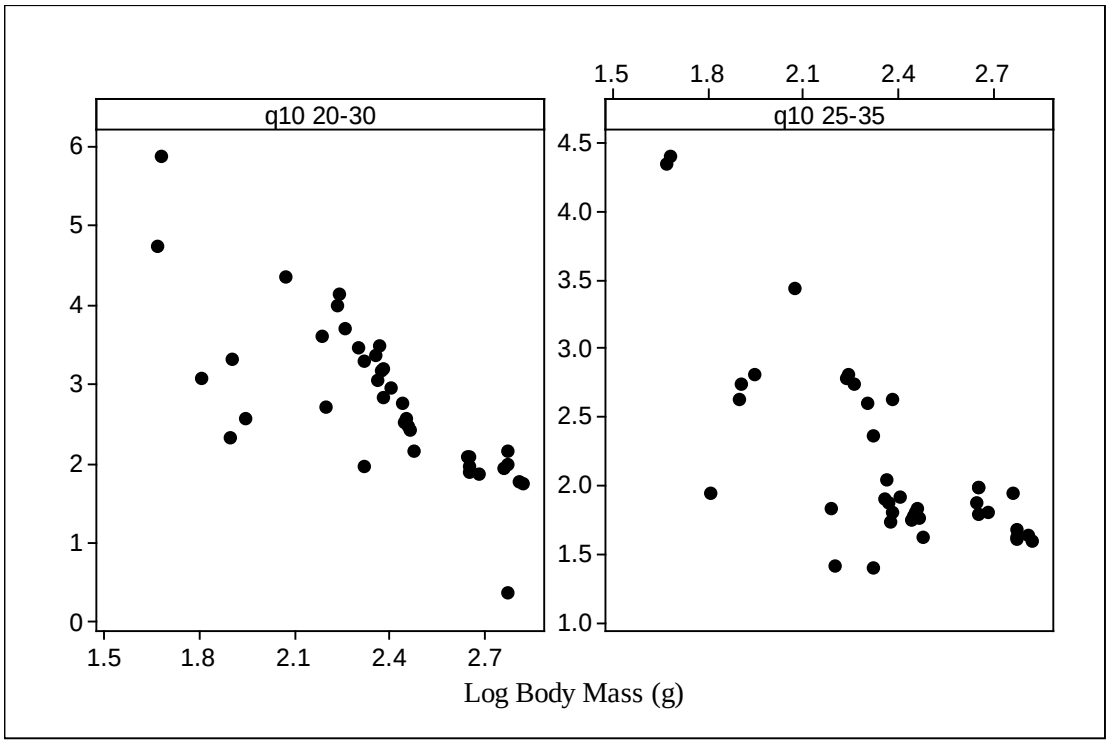

Figure 3.12. Temperature coefficients (Q_{10}) of oxygen consumption (ml / h) of mass over ambient temperature, 20°C to 30°C and 25°C to 35°C, for all three species of rattlesnakes from IMRS, Hudspeth County, Texas.

The Q_{10} data (Figure. 3.12) was distributed normally throughout; therefore the data was not logged in all three species when combined. There was no significant differences between values of Q_{10} between 20° to 30°C and 25° to 35°C (2.80 $\pm$ 0.09 (N = 39) and 2.15 $\pm$ 0.86 (N = 39). A regression of Q_{10} and body mass (g) was significant ($P < 0.001$) but the relationship was weak ($r^2 = 0.51$). A similar regression for the 25° to 35°C data was also significant ($P < 0.001$), however the relationship was also weak ($r^2 = 0.27$). No intraspecific differences in Q_{10} were observed in the three species in the 20° to 30°C and 25° to 35°C and were of no significance ($r^2= 0.69$; $P > 0.71$). The mean of Q_{10} for the 14 *C.*

molossus at 20° to 30°C was 2.75 and at 25° to 35°C, the mean was 2.13. As for *C. lepidus*, Q_{10} was 3.32 at 20° to 30°C and 25 to 35°C, the mean of Q_{10} for all eight was 2.54. As for the 17 *C. atrox*, Q_{10} for 20° to 30°C was 2.35. At temperature 25° to 35°C, Q_{10} for *C. atrox* was 1.77.

Table 3.12. Reported Q_{10} values of rattlesnake species from IMRS, Hudspeth County, Texas.

Temperature	20°C - 30°C	25°C - 35°C	Range	Source
C. atrox	2.35	1.77	1.77-2.35	this study
C. lepidus	3.32	2.54	2.54-3.32	this study
C. molossus	2.75	2.13	2.13-2.75	this study
C. adamantus	3.30	2.60	2.60-3.30	Dorcas *et al*., 2004
C. molossus & *C. lepidus*	not indicated	not indicated	2.19-3.55	Beaupre, 1993
C. horridus	not indicated	not indicated	3.7-4.8	Beaupre and Zaidan, 2001
C.atrox	not indicated	not indicated	1.7-3.1	Beaupre and Duvall, 1998

Chapter 4

Discussion

4.0 Discussion

Oxygen consumption or metabolic rate of *C. atrox*, *C. lepidus* and *C. molossus* at Indio Mountain Research Station was influenced by both body mass and temperature. Except for the amount of oxygen consumed, these three snakes demonstrated the same trend of increased oxygen consumption. Dorcas *et al*. (2004), Beaupre (1993), also demonstrate this general trend within *Crotalus* species. Other vipers such as *Agkistrodon,* which also belong to the Viperidae, have shown that oxygen consumption and metabolic rates are affected by body mass and temperature (McCue and Lillywhite, 2002; Zaidan, 2003). Compared to other snakes such as boids and colubrids, vipers have lower metabolic rates and oxygen consumption. Boids have low oxygen consumption and metabolic rates also, but not as low as those of vipers (Chappell and Ellis, 1987; Canjani *et al*, 2001). One suggestion may be the life style of ambush predation for these two groups of snakes compared to active foraging behavior found in colubrids.

The effects of temperature on VO_2 consumption in these three species for this study increased over the range of temperatures tested (Figures 3.1 - 3.5). A similar trend is indicated from several studies on other *Crotalus* species. For example, *Crotalus adamantus*, perhaps the largest of all rattlesnake species has a very low metabolic rate for a snake of its size (Dorcas *et al*., 2004). Other studies of metabolic rates of rattlesnakes (Beaupre, 1993a; Secor and Nagy, 1994; Beck, 1995; Beaupre and Duvall, 1998a) uniformly suggest that these organisms have very low energy expenditure relative to other snake species with the exception of boids (Chappell and Ellis, 1987; Ayers and Shine, 1997; Canjani *et al*, 2001). The observation's of *C. atrox*, *C. lepidus*, and *C. molossus* in this study supports this general trend. Beaupre and Duvall (1998a) indicated the metabolic rates are slightly higher for *C. atrox* than those reported for *C. lepidus* and *C. molossus* (Beaupre, 1993a). In this study, *C. atrox* also

has a higher metabolic rate than *C. lepidus* and *C. molossus*, however the values of oxygen consumption are higher than those reported by Beaupre (1993) and Beaupre and Duvall (1998a). Secor and Nagy (1998) suggested that low metabolic rates in rattlesnakes or boids may be associated with infrequent feeding which may represent an adaptation to a low energy life style. These parameters such as feeding and thermoregulation strategies can account for snakes having a low metabolic rate.

Because RMR vary with temperature in reptiles, thermal dependence represents a parameter that influences the physiological activities of these snakes. The regression analysis in this study indicated a strong relationship between metabolism and temperature. However, studies in other squamates have produced a mixture of results of temperature in oxygen consumption and metabolism. To determine sensitivity of thermal dependence in squamates, for example in this study of rattlesnake oxygen consumption, is to compare Q_{10} values. Q_{10} values in snakes usually range from 1.5 to 3.0 (Lillywhite, 1987; Zaidan, 2003). In boids, it has been shown that Q_{10} values have a mean of 2.6. The Q_{10} values of 1.77-2.35 for *C. atrox* in this study (Table 3.11) mostly fall below the squamate mean of 2.4 (Andrews and Pough, 1985), but are comparable to Beaupre and Duvall's (1998) Q_{10} values of 1.7-3.1 for *C. atrox* from the Sonoran Desert. Reported values for *C. lepidus* and *C. molossus* are around 3.4 (Beaupre, 1993; Beaupre and Zaidan, 2001). In this study, the Q_{10} values for *C. lepidus* range from 2.54 to 3.32, and as for *C. molossus*, the values are 2.13-2.75 (Table 3.10). These values fall within the suggested values of Andrews and Pough's (1985). However, the Q_{10} values for Beaupre's (1993a) study for both *C. lepidus* and *C. molossus* are higher than the values in this study for the same two species. Another notable study of Q_{10} values reported that *C. horridus*'s values ranged from 3.7 to 4.8 (Beaupre and Zaidan, 2001). These values are high compared with those normally reported. It has also hypothesized that cold adaptation can be implicated for high Q_{10} values (Davies and Bennett, 1981). Thus, high Q_{10} values in snakes are not fully understood. It has also implied that differential selection on the

temperature-metabolic rate relationship may be based on different operative temperature availability (Beaupre and Zaidan, 2001).

Sex differences in oxygen consumption or metabolic rates were insignificant in this study. Previous studies indicate that non-gravid females tend to have lower metabolic rates than males of their own species; however some studies of sex differences in metabolic rates of reptiles have produced unclear results. Bennett and Dawson (1982) summarized data from several studies of squamates comparing metabolic rates of male and females and reported that females have lower metabolic rates (60-80%) than males. Other studies in squamates have produced equivocal results. In two studies on the lizard *Sceloporus occidentalis*, indicated males from three different populations tend to have higher oxygen consumption compared to females (Jamison *et al*., 1976). However according to Heusner and Jamison (1981), *S. occidentalis* had no difference in oxygen consumption between sexes. Likewise in a study of *C. lepidus* and *C. molossus*, Beaupre (1993) concluded that significant differences between sexes were dependent on temperature and origin of population. However, in a comparative study of males, non-reproductive females and vitellogenic females of *C. atrox*, Beaupre and Duvall (1998a) found that vitellogenic females had significantly higher oxygen consumption than non-reproductive females. Males and non-reproductive female diamondbacks had similar metabolic rates during inactivity. In my study, females of the three species of rattlesnake had similar oxygen consumption as males at comparable body mass. However, there are significant differences between males and females when body mass is not comparable. Large males of *C. atrox* and *C. molossus* had higher metabolic rates than smaller female snakes. This is consistent with other studies of viviparous squamates, such as *Thamnophis sirtalis* were no differences were found between males, post-partum females, and non-reproductive females (Bichard *et al*., 1984). This has been supported by previous work on *C. atrox* (Beaupre and Duvall, 1998a), *C. lepidus* and *C. molossus* (Beaupre, 1993).

Although there have been a variety of techniques used to measure metabolic rates in other studies, some of these techniques do not adequately describe VO_2 patterns. Determining how environmental factors (e.g., temperature) affect physiological processes such as metabolism has always been critical in understanding processes such as energy expenditure and the ecology of an organism (Bennett, 1982; Bennett and Gleeson, 1979; Congdon, 1989; D'meil, 1986; Willis and Beaupre, 2000; Secor and Nagy, 1994; Rice *et al*,¸2006;). For example, western diamondback rattlesnakes demonstrate physiological and biochemical strategies for tolerating prolonged starvation in which the snakes continue to grow without been feed for almost two years (McCue, 2007). The effects of meal size on snake metabolism have also been explored and bring further details of rattlesnake metabolism (Andrade, *et al.,* 1997, McCue and Lillywhite, 2002). Such studies have allowed and understanding of energetics in rattlesnakes (Secor and Nagy, 1994; Beaupre, 1995a; Beaupre, 1996). The study of metabolism in rattlesnakes has thus allowed new questions to be raised such as the impact the effects of climatic changes in reptile energetics (Patterson *et al.*, 1993).

The present study was an attempt to decipher affects of one of the major environmental factors such as temperature on the oxygen consumptions. However there are many factors that need to be explored to fully comprehend the natural history of these snakes'. One is the variation of oxygen consumption of rattlesnake species throughout their geographical range. Another is the effects of circadian rhythms on of metabolic rates in rattlesnakes, as well as other reptiles. It would also be of interest to determine if any metabolic increment is associated with aging in reptiles. This would require a deep understanding of thermoregulation and its effects on oxygen consumption. This can be accomplished by comparing metabolic rates between juvenile and adult snakes (Beaupre and Zaidan, 2001). There is also little information available on metabolism and its effect on growth of embryos, especially in rattlesnakes. How venom production is influenced by metabolism further needs exploration. Because survival and reproduction success of rattlesnakes are strongly dependent on

opportunities to thermoregulate by selecting macro- and microhabitats, investigating such habitat selection and its associated thermal characteristics adds to the further understanding of the natural history of *C. atrox*, *C. lepidus* and *C. molossus*. Thus, understanding energy acquisition that influence's life history characteristics is an important factor for rattlesnake conservation.

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Appendix

APPENDIX A

Morphology data of *C. atrox* (SVL = snout-vent length, TL = tail length, BM = Body Mass).

Sex	BM	SVL	TL
male	449.6	860	75
female	209.8	710	50
male	644	1000	90
male	275.5	762	67
male	660	878	80
female	159.2	604	43
female	209.2	780	40
female	280.7	835	50
female	294.5	720	55
female	235.7	740	40
male	592.6	836	70
male	229	720	65
male	479	920	75
male	441.1	890	80
female	242.1	720	50
male	302.6	740	60
male	448	470	64

APPENDIX B

Morphology data of *C. lepidus* (SVL = snout-vent length, TL = tail length, BM = body mass).

Sex	BM	SVL	TL
male	175	565	60
male	200	656	59
male	182	610	62
male	173	598	58
female	118	508	48
female	80	470	60
female	89	479	40
male	47	388	42

APPENDIX C

Morphology of data of *C.molossus* (SVL = snout-vent length, TL = tail length, BM = body mass).

sex	BM	SVL	TL
male	289.6	767	68
male	255.2	790	85
male	154	640	70
female	285.8	773	58
male	591.1	885	77
male	48	446	41
male	580.5	849	80
male	230.5	630	63
female	79.7	534	51
male	238.9	701	64
female	64	470	25
male	593.5	923	72
male	448	880	70
female	240.8	715	45

APPENDIX D

Oxygen consumption of *C. atrox* at 20°C. (BM = body mass)

Sex	BM	LogBM	$AVGVO_2$	$LOGVO_2$	ml/ h g^{-1}	LOG ml/ h g^{-1}
Male	229	2.359835482	2.1	0.322219295	0.009170306	-2.037616188
Male	275.5	2.440121603	2.7	0.431363764	0.009800363	-2.008757839
Male	302.6	2.480868924	3.4	0.531478917	0.011235955	-1.949390007
Male	441.1	2.644537058	3.9	0.591064607	0.008841533	-2.053472451
Male	449.6	2.652826303	4.5	0.653212514	0.010008897	-1.999613789
Male	449.6	2.652826303	4.1	0.612783857	0.009119217	-2.040042446
Male	479	2.680335513	4.67	0.669316881	0.009749478	-2.011018633
Male	592.6	2.772761647	4.234	0.626750854	0.007144786	-2.146010793
Male	644	2.808885867	5.34	0.727541257	0.008291925	-2.08134461
Male	660	2.819543936	5.55	0.744292983	0.008409091	-2.075250952
Female	242.1	2.383994789	2.456	0.390228362	0.010144568	-1.993766427
Female	235.7	2.372359583	1.9	0.278753601	0.008061095	-2.093605982
Female	294.5	2.469085299	3.2	0.505149978	0.010865874	-1.963935321
Female	280.7	2.448242413	2.98	0.474216264	0.010616316	-1.974026149
Female	209.2	2.32056168	1.88	0.274157849	0.008986616	-2.046403831
Female	159.2	2.201943063	2.1	0.322219295	0.013190955	-1.879723769
Female	209.2	2.32056168	3.2	0.505149978	0.015296367	-1.815411702

APPENDIX D Continued

Oxygen consumption of *C. atrox* at 25°C

$AVGVO_2$	$LOGVO_2$	ml/ h g^{-1}	LOG ml/ h g^{-1}
3.7	0.568201724	0.016157205	-1.791633758
5.3	0.72427587	0.01923775	-1.715845734
6.1	0.785329835	0.020158625	-1.695539089
5.7	0.755874856	0.01292224	-1.888662202
5.8	0.763427994	0.012900356	-1.889398309
5.9	0.770852012	0.013122776	-1.881974291
6.65	0.822821645	0.01388309	-1.857513868
8.2	0.913813852	0.013837327	-1.858947795
8.435	0.926085087	0.013097826	-1.88280078
8.8	0.944482672	0.013333333	-1.875061263
4.9	0.69019608	0.02023957	-1.693798709
4.6	0.662757832	0.019516334	-1.709601751
5.44	0.7355989	0.018471986	-1.733486399
5.23	0.718501689	0.018631991	-1.729740724
3.1	0.491361694	0.014818356	-1.829199986
4.76	0.677606953	0.029899497	-1.524336111
5.2	0.716003344	0.024856597	-1.604558337

APPENDIX D Continued

Oxygen consumption of *C. atrox* at 30°C.

$AVGVO_2$	$LOGVO_2$	ml/ h g^{-1}	LOG ml/ h g^{-1}
7.1	0.851258349	0.031004367	-1.508577134
7.45	0.872156273	0.027041742	-1.56796533
7.33	0.865103975	0.024223397	-1.615764949
8.12	0.909556029	0.018408524	-1.734981029
8.55	0.931966115	0.019016904	-1.720860188
8.56	0.932473765	0.019039146	-1.720352538
8.77	0.942999593	0.018308977	-1.73733592
9.11	0.959518377	0.015372933	-1.81324327
9.54	0.979548375	0.014813665	-1.829337493
9.67	0.985426474	0.014651515	-1.834117461
6.99	0.844477176	0.028872367	-1.539517614
6.63	0.821513528	0.028128978	-1.550846054
7.76	0.889861721	0.026349745	-1.579223578
7.54	0.877371346	0.026861418	-1.570871067
6.21	0.7930916	0.029684512	-1.52747008
5.7	0.755874856	0.03580402	-1.446068208

6.33	0.80140371	0.030258126	-1.51915797

APPENDIX D Continued

Oxygen consumption of *C. atrox* at 35°C.

$AVGVO_2$	$LOGVO_2$	ml/ h g^{-1}	LOG ml/ h g^{-1}
7.067	0.84923509	0.030860262	-1.510600391
9.31	0.96894968	0.028431942	-1.546193475
9.88	0.99475694	0.026768011	-1.572383898
10.675	1.02836788	0.020630243	-1.685495657
11.5	1.06069784	0.024882117	-1.604112672
11.76	1.07040732	0.020240214	-1.6937849
12.01	1.07954301	0.017327766	-1.761257426
13.24	1.12188799	0.013555518	-1.867883882
13.77	1.13893394	0.01863354	-1.72970463
14.02	1.14674801	0.016818182	-1.774220952
8.82	0.94546859	0.036431227	-1.438526204
8.61	0.93500315	0.036529487	-1.437356431
9.63	0.98362629	0.032699491	-1.485459012
9.31	0.96894968	0.033167082	-1.479292732
7.34	0.86569606	0.035086042	-1.45486562
6.72	0.82736927	0.042211055	-1.37457379
7.31	0.86391738	0.034942639	-1.456644303

APPENDIX E

Oxygen consumption of *C. lepidus* at 20°C. (BM = body mass)

Sex	BM	LogBM	$AVGVO_2$	$LOGVO_2$	ml/ h g^{-1}	LOG ml/ h g^{-1}
Male	175	2.243038049	1.45	0.161368002	0.008285714	-2.081670046
Male	200	2.301029996	1.78	0.250420002	0.0089	-2.050609993
Male	182	2.260071388	1.65	0.217483944	0.009065934	-2.042587444
Male	173	2.238046103	1.55	0.190331698	0.008959538	-2.047714405
Female	118	2.071882007	1.32	0.120573931	0.011186441	-1.951308076
Female	80	1.903089987	0.67	-0.17392519	0.008375	-2.077015184
Female	89	1.949390007	0.9	-0.04575749	0.01011236	-1.995147497
Male	47	1.672097858	0.32	-0.49485002	0.006808511	-2.16694788

APPENDIX E Continued

Oxygen consumption of *C. lepidus* at 25°C

$AVGVO_2$	$LOGVO_2$	ml/ h g^{-1}	LOG ml/ h g^{-1}
2.44	0.387389826	0.013942857	-1.855648222
2.78	0.444044796	0.0139	-1.8569852
2.52	0.401400541	0.013846154	-1.858670847
2.41	0.382017043	0.013930636	-1.856029061
1.77	0.247973266	0.015	-1.823908741
1.13	0.053078443	0.014125	-1.850011544
1.22	0.086359831	0.013707865	-1.863030176
0.92	-0.03621217	0.019574468	-1.708310031

APPENDIX E Continued

Oxygen consumption of *C. lepidus* at 30°C

$AVGVO_2$	$LOGVO_2$	ml/ h g^{-1}	LOG ml/ h g^{-1}
6.01	0.778874472	0.034342857	-1.464163577
6.19	0.791690649	0.03095	-1.509339347
6.1	0.785329835	0.033516484	-1.474741553
6.2	0.792391689	0.03583815	-1.445654414
5.76	0.760422483	0.048813559	-1.311459524
2.22	0.346352974	0.02775	-1.556737013
2.31	0.36361198	0.025955056	-1.585778027
1.52	0.181843588	0.032340426	-1.49025427

APPENDIX E Continued

Oxygen consumption of *C. lepidus* at 35°C

$AVGVO_2$	$LOGVO_2$	ml/ h g^{-1}	LOG ml/ h g^{-1}
6.88	0.83758844	0.039314286	-1.40544961
7.22	0.8585372	0.0361	-1.44249279
6.91	0.83947805	0.037967033	-1.42059334
6.7	0.8260748	0.038728324	-1.4119713
6.1	0.78532984	0.051694915	-1.28655217
3.1	0.49136169	0.03875	-1.41172829
3.43	0.53529412	0.038539326	-1.41409588
4	0.60205999	0.085106383	-1.07003786

APPENDIX F

Oxygen consumption of *C. molossus* at 20°C. (BM = body mass)

Sex	BM	LogBM	$AVGVO_2$	$LOGVO_2$	ml/ h g^{-1}	LOG ml/ h g^{-1}
Male	289.6	2.461798558	3.2	0.505149978	0.011049724	-1.956648579
Male	255.2	2.40688067	2.5	0.397940009	0.009796238	-2.008940661
Male	154	2.187520721	1.5	0.176091259	0.00974026	-2.011429462
Female	285	2.45484486	3	0.477121255	0.010526316	-1.977723605
Male	593.5	2.773420723	4.1	0.612783857	0.006908172	-2.160636867
Male	48	1.681241237	0.55	-0.25963731	0.011458333	-1.940878548
Male	580.6	2.763877031	4.7	0.672097858	0.008095074	-2.091779174
Male	230.5	2.36267093	2.2	0.342422681	0.009544469	-2.020248249
Female	79.7	1.901458321	0.9	-0.04575749	0.011292346	-1.947215812
Male	238.9	2.37821615	2.1	0.322219295	0.008790289	-2.055996855
Female	64	1.806179974	0.61	-0.21467016	0.00953125	-2.020850139
Male	596	2.77524626	5.23	0.718501689	0.008775168	-2.056744571
Male	448	2.651278014	4.3	0.633468456	0.009598214	-2.017809558
Female	240.8	2.381656483	2.3	0.361727836	0.009551495	-2.019928647

Oxygen consumption of *C. molossus* at 25°C

$AVGVO_2$	$LOGVO_2$	ml/ h g^{-1}	LOG ml/ h g^{-1}
5.2	0.716003344	0.017955801	-1.745795214
4.7	0.672097858	0.018416928	-1.734782812
3.9	0.591064607	0.025324675	-1.596456114
5.1	0.707570176	0.017894737	-1.747274684
7.6	0.880813592	0.012805392	-1.892607131
1.09	0.037426498	0.022708333	-1.643814739
6.2	0.792391689	0.010678608	-1.971485342
4.345	0.637989781	0.018850325	-1.724681149
1.33	0.123851641	0.016687578	-1.77760668
4.8	0.681241237	0.020092089	-1.696974912
1.2	0.079181246	0.01875	-1.726998728
8.1	0.908485019	0.013590604	-1.866761241
6.3	0.799340549	0.0140625	-1.851937465
4.6	0.662757832	0.01910299	-1.718898651

APPENDIX F Continued

Oxygen consumption of *C. molossus* at 30°C

$AVGVO_2$	$LOGVO_2$	ml/ h g^{-1}	LOG ml/ h g^{-1}
7.9	0.897627091	0.027279006	-1.564171466
7.4	0.86923172	0.028996865	-1.53764895
5.4	0.73239376	0.035064935	-1.455126961
7.7	0.886490725	0.027017544	-1.568354135
1.56	0.193124598	0.002628475	-2.580296125
3.23	0.509202522	0.067291667	-1.172038715
9.14	0.960946196	0.015742336	-1.802930836
6.73	0.828015064	0.029197397	-1.534655866
2.1	0.322219295	0.026348808	-1.579239027
6.67	0.824125834	0.027919632	-1.554090316
1.88	0.274157849	0.029375	-1.532022125
10.4	1.017033339	0.017449664	-1.75821292
8.43	0.925827575	0.018816964	-1.725450439
7.34	0.86569606	0.030481728	-1.515960423

Oxygen consumption of *C. molossus* at 35°C

$AVGVO_2$	$LOGVO_2$	ml/ h g^{-1}	LOG ml/ h g^{-1}
9.53	0.9790929	0.032907459	-1.482705657
9	0.95424251	0.035266458	-1.452638161
7.167	0.8553374	0.046538961	-1.332183316
9.21	0.96425963	0.032315789	-1.49058523
12.8	1.10720997	0.021566976	-1.666210754
4.81	0.68214508	0.100208333	-0.999096161
12.1	1.08278537	0.02084051	-1.681091661
8.9	0.94939001	0.038611714	-1.413280923
3.5	0.54406804	0.04391468	-1.357390277
8.344	0.9213743	0.034926748	-1.456841854
2.34	0.36921586	0.0365625	-1.436964117
13.2	1.12057393	0.022147651	-1.654672329
11.3	1.05307844	0.025223214	-1.598199571
12.1	1.08278537	0.050249169	-1.298871112

Vita

Luis Miranda Jr. was born on July 29, 1977 in Socorro, Texas. The only son born to Luis O. Miranda and Manuela S. Miranda in a family of nine, Luis attended the University of Texas at El Paso and obtained his Bachelors in Science Degree in Biological Sciences in 2001. Since the fall 2006, he has studied as a Masters Candidate under the guidance of Dr. Jerry D. Johnson, in the Department of Biological Sciences at the University of Texas at El Paso. Luis has worked as a Teaching Assistant at the University of Texas at El Paso. Before being admitted to graduate school, Luis was a middle school science teacher. He also participated in a National Science Fellowship grant that allowed teachers to develop lesson using the Chihuahuan Desert as a natural laboratory.

Luis is a member of the Society of Advancing Hispanic/Chicanos & Native Americans in Science, Society of Sigma Xi, and the Association of Southwestern Naturalists.

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