A STUDY OF FACTORS AFFECTING SCALE ROUGHNESS IN THE WESTERN DIAMONDBACK RATTLESNAKE (*CROTALUS ATROX*)

by

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ABSTRACT

A STUDY OF FACTORS AFFECTING SCALE ROUGHNESS

IN THE WESTERN DIAMONDBACK RATTLESNAKE

(CROTALUS ATROX)

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Reptilian scales may seem simple to the naked eye, but under a microscope they are very complex with multiple patterns across their surface that are much like a human fingerprint. These patterns have been shown to be species specific but there has been no way to quantify these differences. A new technique has been found using the confocal microscope that allows a measurement of the roughness of a surface. The roughness of the scales of *Crotalus atrox* were measured and compared with factors such as sex, age, clade, and various environmental variables to help determine if this technique may be useful to taxonomists in determining species, or if it is simply a measure that is dependent on the environment. *Crotalus atrox* was chosen for this study because it is a very widespread species spanning across the southwestern United States and encompassing many different biomes. The results found that the roughness of a scale decreased as the snake aged, and was significantly different between the two clades, with the Eastern clade being much rougher. When these factors were controlled in the analysis of the environmental factors, it was found that a higher temperature seasonality and a higher maximum temperature in the warmest month both caused an increase in scale roughness.

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CHAPTER 1

INTRODUCTION

Scales are an important adaptation and one that is very well known in reptiles, but why are they there? What purpose do they serve? We have only scratched the surface in understanding these questions.

When reptilian scales are viewed under a scanning electron microscope at high magnifications, a number of different patterns can be seen that appear to be species specific. Scale patterns vary greatly from species to species and include lines, ridges, spicules and pits. These patterns are more commonly called microornamentation or microdermaglyphics. There have been many hypotheses' throughout the years as to why such patterns evolved, but none have proven terribly convincing. Most recently, it has been suggested that these patterns aid in pheromone dispersion and retention (Smith et al., 1982). Previous studies hypothesized that these scale patterns played a role in locomotion by creating or minimizing friction according to the behavior and habitat of the species in question (Stewart and Daniel, 1973). Yet another study gave evidence supporting the hypothesis that the radiation emitted from the sun was converted to heat by these structures (Porter, 1967). Arnold (2002) concluded that the more primitive ornamentations were those that were smooth to reduce friction and promote dirt-shedding while the more derived patterns were those that were rougher and favored a reduction in shine for camouflage purposes.

A study conducted by Burstein *et al.* found these patterns to be species specific and thought that they would be very useful in phylogeny (1974). However, another study in 1976 by Cole and Van Devender showed there was too much variation on a single specimen between body regions for these patterns to be of any use to taxonomists. A later study was conducted on 40 species of snakes to determine whether there was a correlation between the scale patterns and the habitat in which the animal lived (Price, 1982). The results of this study would answer questions as to whether this ornamentation of the scales could be useful in classifying species taxonomically or only as an indicator for habitat selection. In the end it was found that these patterns did show a phylogenetic relationship and had no real correlation to habitat or environment.

There are also many different factors that can cause snakes of the same species to be of different sizes that may cause differences in scale sizes and therefore cause differences in the roughness of the scales. The most obvious factor would be age. Snakes have a fixed number of scales from when they are born until they die. They do not gain more scales as they age; the scales simply grow larger as the snake grows larger. A snake grows longer as it ages, and while there are no set formulas for finding the age of a specimen from it's length alone, length can be used to compare ages in individuals of the same species from the same locality.

Snakes taken from different localities may have size differences caused by differences in food availability, however, so this comparison is not as reliable when specimens are from different locations. Studies on *Crotalus atrox* found that snakes that were supplied with food grew and gained mass faster than control snakes that were left to find food on their own (Taylor el al., 2005). This same study found that food availability also increased the number of litters per year, but not the number of offspring in each litter or the mass of the offspring. Therefore, we can assume that each snake starts out relatively the same size and there are no significant differences in scales as a result. A study using the chuckwalla lizard, *Sauromalus obesus,* had different results however. When juvenile chuckwallas from different populations with different environments, habitats and elevations, were raised under controlled conditions in a lab, they seemed to show genetic differences in size and growth (Tracy, 1999). Chuckwallas from populations with large adults grew faster after maturity while those from populations with small adults grew the fastest before reaching maturity. It was also noted that the populations with the large adults and the faster growth rates after maturity were from higher elevation sites than the populations with smaller adults.

Another factor that can cause individuals to be of different sizes is their geographic location and the environment in which they live. The area in which an animal lives has a unique elevation, range of temperatures, amount of rainfall, and latitude and longitude. These factors all act together to make the "perfect habitat" for the animals that are found there. A single species with a wide distribution may have many different habitats in which it can live comfortably. The elements of these habitats all act upon the animal in their own way, possibly causing a single species to show differences across its distribution. Bergmann's rule says that warm-blooded species in cool environments are usually larger than those in warmer environments. Studies have shown that while turtles follow this rule, squamate reptiles tend to follow the opposite

(Ashton, 2001a). When *Crotalus viridis*, which has two very different phylogenetic clades, was examined it was found that in one clade individuals were smaller in cooler environments while they were larger in the same environments in the other clade (Ashton, 2001b). Another study using the chuckwalla lizard, when examined with many different rainfall and temperature variables, found that the body size of the species was very highly correlated with the average winter rainfall (Case, 1976). It is hypothesized that this was an indirect correlation resulting from the winter rainfall increasing the growth rate of the plants that the chuckwalla feeds upon.

Sex is another factor that can cause size differences in a species. When one sex is typically larger than the other, this is known as sexual size dimorphism. Darwin's hypothesis was that in species where females are the larger sex, size might be advantageous in reproduction (Darwin, 1871). He also hypothesized that in species where males were the larger sex, size may provide an advantage in competition amongst other males. Males are usually the larger sex in birds and mammals (Andersson, 1994) while the females are typically larger in reptiles (Fitch, 1981). *Crotalus atrox* is an exception in reptiles, typically showing male-biased sexual dimorphism (Klauber, 1972). One study using *Crotalus atrox* observed the snakes in the wild and found that the sexes started to diverge at sexual maturity (Beaupre et al., 1998). This same species was used in a study to determine if the cause of the size differences was an effect of higher food intake in males (Taylor and DeNardo, 2005). When living in laboratory conditions and eating the same diet, there was found to be no difference in growth or mass between sexes. This finding seems to show that the size differences seen in

Crotalus atrox were a result of differences in food availability rather than a fixed effect. Are these differences between the sexes that are seen in nature enough to create a difference in the roughness of the scales?

Ongoing research findings suggest that there is a difference in scale pattern and roughness between different species of reptiles. There is question to whether this difference should be attributed to species' differences, or just a result of the species living in different environments. It is possible that factors such as age, sex, temperature, altitude, or precipitation are the causes of these differences. Testing a single species with a wide distribution that includes many different climates, weather patterns and elevation ranges would be beneficial in solving this puzzle. The problem with previous studies is there was no way to quantify the differences in scale surface patterns using the scanning electron microscope that was most commonly used (Price, 1982; Smith et al., 1982; Peterson, 1984; Chaisson and Lowe, 1989; Arnold, 2002). The laser scanning confocal microscope has a software package that allows the user to find measures of roughness, or surface area, of a given specimen. This software will be used in this study as a means of quantifying differences in scale surface patterns.

Crotalus atrox was the species chosen for this study. It was chosen because of its wide distribution across many different habitats. The range of this species was illustrated by Campbell and Lamar (2004) and an adapted version is shown in Figure 1.1. It occurs east to west from Arkansas to California and from Kansas to as far south as Veracruz, Mexico. The altitudes range from below sea level to 2,440m, though most individuals of the species do not occur above 1,500m (Campbell and Lamar, 2004). The terrain varies widely also, from gulf coastal plains, to deserts, to rocky hillsides.

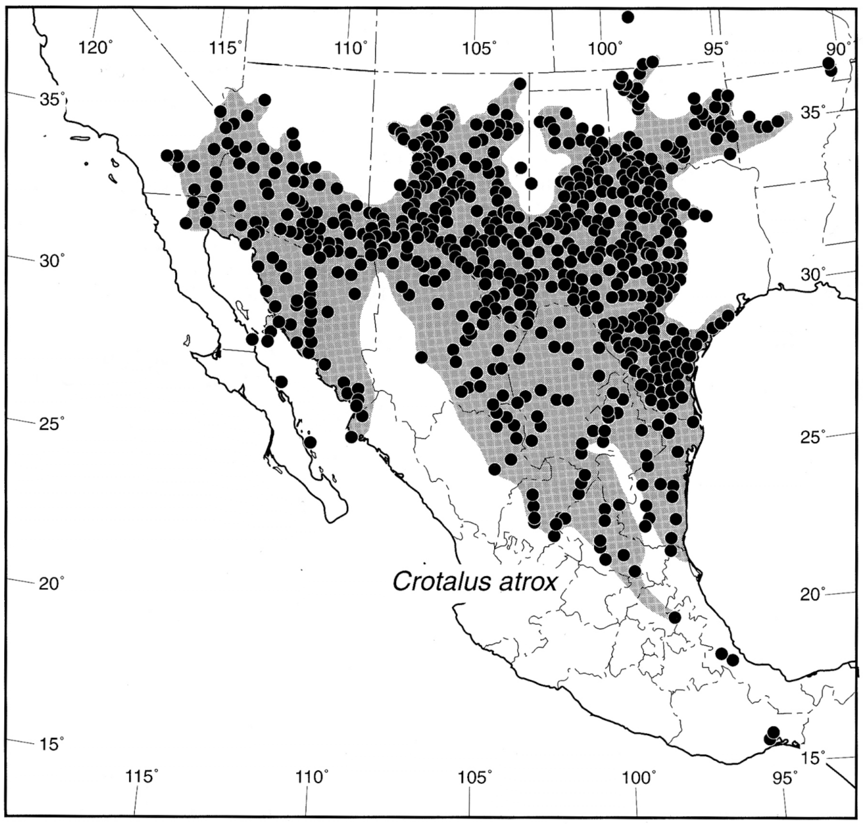

Figure 1.1: Distribution of *Crotalus atrox*
(Adapted from Campbell and Lamar, 2004)

There are no recognized subspecies in *Crotalus atrox*, but two clades have been established that have been geographically separated by the Sierra Madre Occidental (also known as the Cochise Filter Barrier or Continental Divide) since its uplift in the pre-Pleistocene era 3 million years ago (Castoe et al., in press). Scale roughness will be examined between the Eastern and Western clades to determine if there are differences in scale roughness between the clades.

Since *Crotalus atrox* has been found to be sexually dimorphic with the males being larger than the females (Klauber, 1972). This could possibly cause a difference in scale size and roughness for individuals of the opposite sexes that appear to be of the same length, but are actually of different ages because of sexual dimorphism.

Finally, altitude at which each specimen was found and many variables of temperature and rainfall will also be compared with scale roughness to determine if roughness changes as a result of differences in any of these factors.

CHAPTER 2

MATERIALS AND METHODS

2.1 Scale Collection

All scales were removed from preserved specimens of *Crotalus atrox* in the collection at the Amphibian and Reptile Diversity Research Center at the University of Texas at Arlington. The specimens were collected over a period of many years by many different people covering nearly the entire range of the species. Snakes were chosen randomly from the counties represented in the collection throughout the distribution of the species. California, Oklahoma and Arkansas, though in the range of *Crotalus atrox*, were not represented in the collection so these populations were not included in this study. States represented are Arizona, New Mexico, and Texas, as well as the Mexican states of San Luis Potosi, Sonora, Tamaulipas, Veracruz, Hidalgo, and Nuevo Leon.

Sex was determined in specimens by the eversion of the hemipenes in males, and the absence of these in females. Snout vent length was used to approximate age, assuming that shorter specimen were younger than longer specimen. Specimen were measured with only a metric ruler unless they were coiled, in which case their lengths were marked with string and the string was measured. Measurements were recorded in centimeters. Neonates were not used as their scales proved to be too small to be comparable using the same objective on the microscope without including the keel. The two clades that have been established for *Crotalus atrox* (Castoe et al., in press) were determined for each specimen by their position relative to the Cochise Filter Barrier. Those specimens found east of the barrier were grouped in the Eastern clade and those found west of the barrier were grouped in the Western clade.

Scales were removed from each specimen by gently rubbing the mid-dorsal surface, about mid-way down the length of the specimen. Once scales were removed, they were placed in 95% ethanol until ready for slide preparation. When ready for viewing, scales were placed on depression slides with the external surface exposed, covered with immersion oil, and coverslipped.

2.2 Confocal Microscopy

An Axioplan 2 LSM 510 META (Zeiss, Jena, Germany) was used for image data acquisition. The microscope was equipped with three lasers: a 30mW Ar laser (458, 477, 488, 514 nm), a 1mW He/Ne laser (543 nm), and a 5mW He/Ne laser (633 nm). A Plan-Apochromat 20x/0.75 objective was used and the final area measurement was 212,244.49μm^2. The program was set to take z-stack sections in 1μm increments. The specimen was excited with the 488 nm laser and the autofluorescence was measured with a FITC filter at 518 nm.

Three scales were chosen per snake, and three sites per scale, for a total of nine measurements of scale roughness per snake. A median filter was applied to each image before roughness was calculated. The Topo for LSM software was used to find a measure of roughness for each site on each scale. This feature gives a 3D display of the site and a number of different measures of roughness. The measure chosen for statistical purposes was the S_z measure for the average roughness depth. This finds the depth in microns at 25 areas on the surface and averages them for a measure of the homogeneity of the surface.

2.3 Environmental Data Collection

The location at which each snake was originally found is on file in the collection at the Amphibian and Reptile Diversity Research Center at the University of Texas at Arlington. These locality data were used in ArcGIS (v. 9.1, Environmental Systems Research Institute, Redlands, CA, USA) to pinpoint the locations at which the environmental data were taken for each specimen. ArcGIS compatible layers with data for counties, cities and roads were found for Arizona, New Mexico, Texas and Mexico. Each county or Mexican state that was represented by a snake was searched for the corresponding location data using the select by attributes feature. The measure tool was used to measure distances from intersections and cities for the best possible accuracy. Figure 2.1 shows the map that was produced of the snake data points that were used in this study.

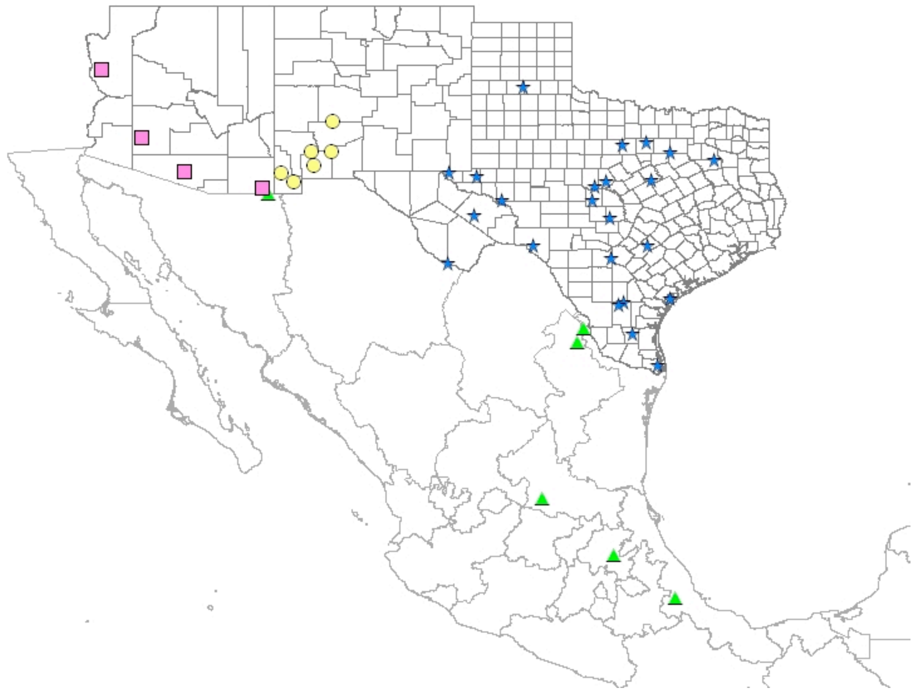

Figure 2.1: Snake Data Points

The environmental map layers were downloaded from Worldclim (v.1.4, University of California, Berkeley, Berkeley, CA, USA). These global climate layers have a spatial resolution of 30 arc-seconds, which is equal to 0.86 km^2 at the equator, and is the best possible resolution for finding environmental variability (Hijmans et al., 2005). Maps were available for altitude and 19 different bioclimatic variables that are all derived from monthly temperature and rainfall data. These maps are available for download at www.worldclim.com. Table 2.1 gives the code name and description of each of the bioclimatic variables that were used in this study, as taken from the Worldclim website. These code names shall be used as abbreviations throughout this paper. All temperature measurements were recorded in degrees Celsius x 10, precipitation amounts were recorded in millimeters, and altitude was recorded in meters. Each climatic layer was paired individually with the snake locations layer and then map tips was used to find the exact value at each point.

Table 2.1: Explanation of Bioclimatic Variables

Variable	Description
BIO1	Annual Mean Temperature
BIO2	Mean Diurnal Range (Mean of monthly (max temp - min temp))
BIO3	Isothermality ((BIO1/BIO7) *100)
BIO4	Temperature Seasonality (Standard Deviation *100)
BIO5	Max Temperature of Warmest Month
BIO6	Min Temperature of Coldest Month
BIO7	Temperature Annual Range (BIO5-BIO6)
BIO8	Mean Temperature of Wettest Quarter
BIO9	Mean Temperature of Driest Quarter
BIO10	Mean Temperature of Warmest Quarter
BIO11	Mean Temperature of Coldest Quarter
BIO12	Annual Precipitation
BIO13	Precipitation of Wettest Month
BIO14	Precipitation of Driest Month
BIO15	Precipitation of Seasonality (Coefficient of Variation)
BIO16	Precipitation of Wettest Quarter
BIO17	Precipitation of Driest Quarter
BIO18	Precipitation of Warmest Quarter
BIO19	Precipitation of Coldest Quarter

2.4 Statistical Analysis

Statistical analysis was performed using SAS (v. 9.1.3, SAS Institute Inc., Cary, NC, USA). A test for normality was run and the data was not normally distributed, so a natural log transformation was performed before any analyses' were run to give a normal distribution. A generalized least squares analysis was used which accounted for the correlations between responses on the same snake. This analysis was first run with sex, clade, and age, as represented by snout-vent-length, as factors and roughness as the dependent variable. If there were found to be a correlation between the roughness and any of these three factors, the factors in question would be controlled through the analysis of the altitude and the 19 environmental factors. Each of these factors was added into the model individually to keep the power of the analysis high. The SAS code that was used is included in Appendix A.

CHAPTER 3

RESULTS

The data that was collected for each individual specimen is shown in Appendix B. The raster data layers for altitude and each environmental factor are shown for the given snake localities in Appendix C. The environmental data that was collected at each snake locality is found in Appendix D. The results of the SAS analysis are also shown in Appendix E. The final model for the analysis is shown below.

$$\mu = \beta_0 + \beta_1 * svl + \beta_2 * clade + \beta_3 * BIO4 + \beta_4 * BIO5 + \beta_5 * svl * BIO4 + \beta_6 * svl * BIO5 + \beta_7 * clade * BIO4 + \beta_8 * clade * BIO5 + \beta_9 * BIO4 * BIO5$$

After the first statistical analysis was run in SAS to see if there was any initial correlation between sex, clade, or age, the results showed that there was a very high correlation between the age and clade of the snake with the roughness of the scale. The Pvalue for the age/roughness correlation was 0.0056 and the Pvalue for the Clade/roughness correlation was 0.0024. There was no correlation between the sex of the snake and the roughness of the scale.

The estimator for Clade demonstrated that the Eastern Clade had rougher scales than the Western Clade by a factor of 2.1822. The estimator for age demonstrated that as the length of the snake increased by 1 cm, the roughness decreased by a factor of 0.05388.

When the environmental analyses were run, the clade and the age of the snake were controlled while each variable was added into the model individually. After the altitude and all 19 environmental variables were run, only two of the variables were significant at a Pvalue of 0.1, which were Bio4 (Pvalue = 0.0797) and Bio5 (Pvalue = 0.0616), or the temperature seasonality and maximum temperature of the warmest month, respectively. It appears that the main causes of differences in snake scale roughness are the clade and the age of the snake.

It has been shown that these factors affect the scale roughness, but how do they affect it? In order to see this, we must hold all factors constant except for the one that we want to see the effect of. The model equation was rearranged so that all the constant factors are knocked out and only the ones that had the variable in question were kept. When the derivative was found for the remaining equation by factoring out the term in question, what you are left with is the slope. The other factors can then be filled into the equation to find the slope of the log roughness and the variable in question, with all other variables held constant. Where the other variables are set constant can make a difference, however. For instance, temperature seasonality (Bio4) might have a greater effect on longer snakes versus shorter snakes. Figures 3.1, 3.2, 3.3, and 3.4 show how the slope of the log roughness changes with each variable, with all other variables held constant. Each point on each graph represents a different calculation of the slope, using different variations of the constant variables. The variables were held constant at the 25^{th} percentile, average, and 75^{th} percentile to show the effects for the average, as well as the greater and lesser values of each variable.

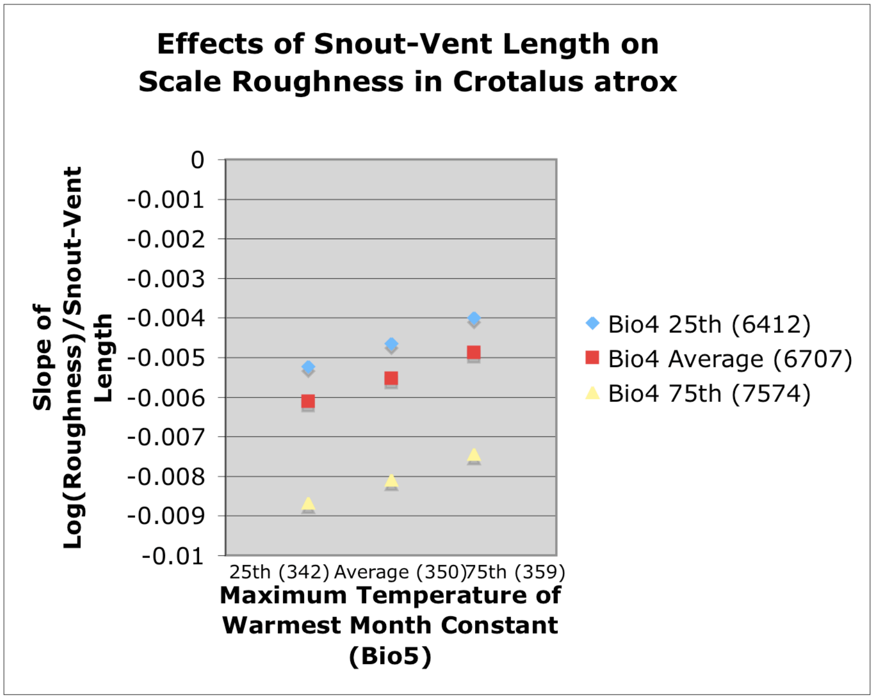

Figure 3.1: Effects of Snout-Vent Length on Scale Roughness in *Crotalus atrox*

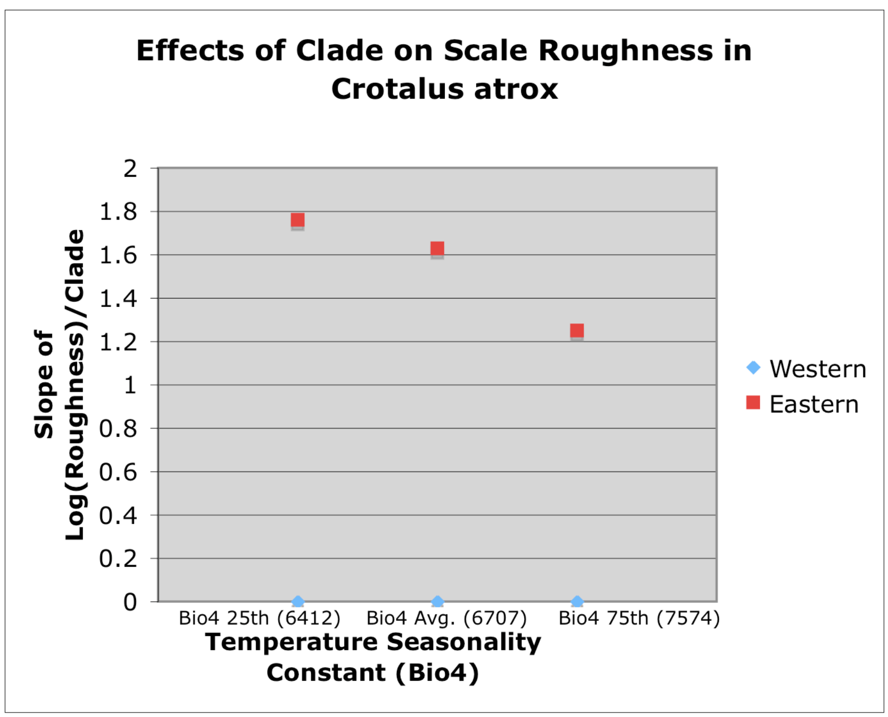

Figure 3.2: Effects of Clade on Scale Roughness in *Crotalus atrox*

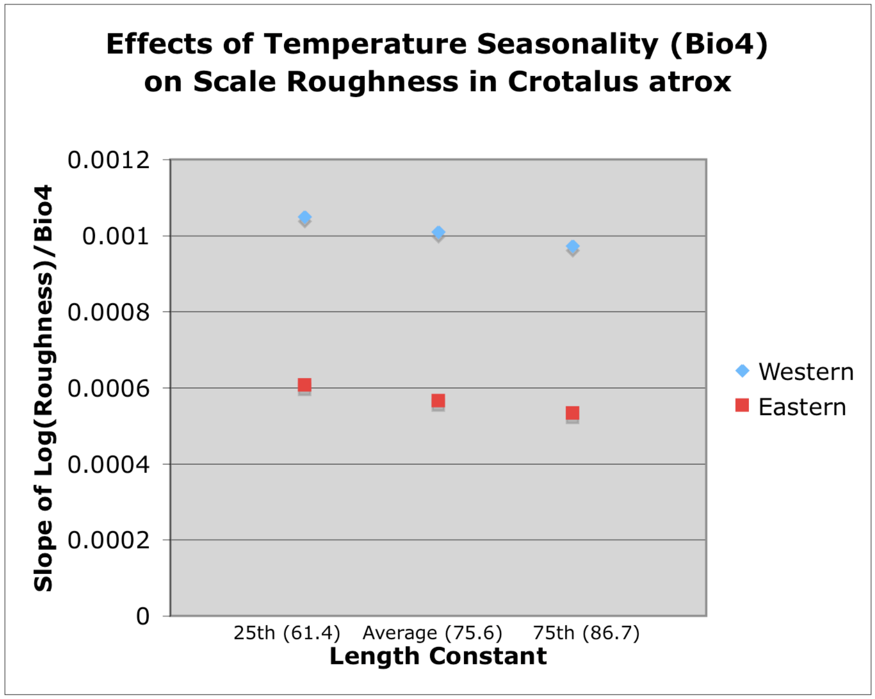

Figure 3.3: Effects of Temperature Seasonality (Bio4) on Scale Roughness in *Crotalus atrox*

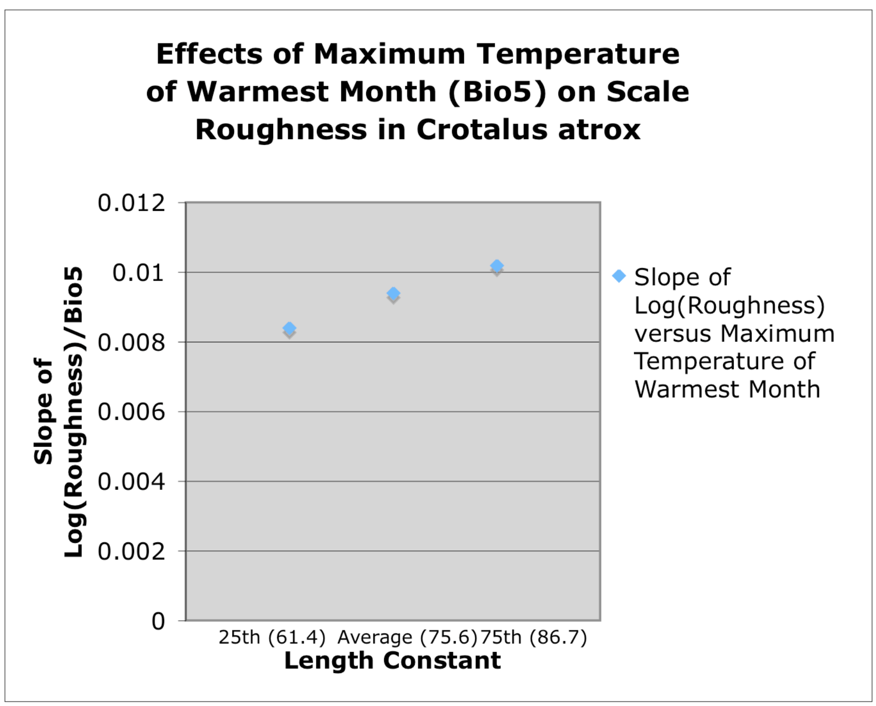

Figure 3.4: Effects of Maximum Temperature of Warmest Month (Bio5) on Scale Roughness in *Crotalus atrox*

CHAPTER 4

DISCUSSION

The first program run in SAS found that there was a very high correlation between the age and clade of the snake with the roughness of the scales but found no correlation with the sex of the snake. The second set of statistics that included altitude and the environmental factors found that only two factors correlated with scale roughness, the temperature seasonality and the max temperature of the warmest month.

Age seems to be the only factor that causes the scales to decrease in roughness, as shown by the negative slopes. This could be a result of scales being smoothed by rough objects that the snake comes into contact with throughout its lifetime. However, this correlation may also simply be a result of older snakes being longer and having larger scales. The same objective was used for viewing on all scales, large or small. This causes the viewing area to be the same size in each image, as opposed to being proportional to the size of the scale. This area would cover a greater proportion of the scale on small scales than it would on large scales. If scales keep the same pattern and only get larger as the snake ages, it might make sense that older snakes seem to have scales that are less rough since the scale pattern has gotten larger though the area stayed the same size. Further studies might measure size of scales and control for this difference in the statistics to determine if this is a real correlation.

When the slopes were calculated and graphed for the age of the snake as shown in Figure 3.1, the interactions of the temperature seasonality and the maximum temperature of the warmest month had to be taken into account. This graph of the slopes found that scales increased in roughness as the temperature of the warmest month increased and decreased in roughness as a result of increasing temperature seasonality (a measure of how much variance there is in the temperature in a year).

The differences seen between the clades in scale roughness were quite frankly a surprise as they were only thrown into the statistics as an afterthought. The Eastern clade was determined to be 2.1822 times rougher than the Western clade, which could be a result of other environmental factors not represented in this study. (It should be noted however, that the numbers for clade versus roughness are only arbitrary as clade is a qualitative factor that was represented in the statistics by 0 and 1 rather than unique values. This results in the Western clade, represented by the 0, to have all slope values equal to 0.) If *Crotalus atrox* were classified as a single species before the uplift of the Sierra Madres Occidental, there must be some factor that is acting upon them that has caused them to diverge. Further research on the differences between these two clades might benefit from more equal sample sizes.

This seems to show that even the slightest change in phylogenetics can be detected by the differences in scale roughness, which could be of large importance to taxonomists. This could mean that a species could be determined by a single scale and those that have closer measures of scale roughness might be closer in relation than others. Further study is needed to determine exactly how useful this technique might be.

The final model produced showed that the clade and the max temperature of the warmest month had no effect on each other. This must mean that the temperatures were relatively the same over the distributions of both clades, which would make sense because they cover the same latitudes, only different longitudes. As demonstrated in Figure 3.2, the temperature seasonality was the only environmental factor from the study that was shown to act upon the clades differently. This factor caused the Eastern clade to decrease in roughness with increasing variance of the temperature.

The sex of the snakes was not found to have any effect on the roughness of the scales. Apparently the male-biased sexual dimorphism does not carry over to the pattern of the scales, even though it has been shown to cause differences in size.

The next factor found to effect the scale roughness was the temperature seasonality, which is a measure of how much variance there is around the average temperature. The results showed that as the variance of the temperature increased, the scale roughness also increased. This factor was also shown in Figure 3.3 to have a greater effect on the Western clade than on the Eastern clade, resulting in rougher scales in the Western clade. This factor must not be terribly important however, because the Eastern clade was still shown to be rougher than the Western clade. There must be another variable that is more important that was not available in this study that has a greater role in causing the divergence of these two clades. Figure 3.3 also demonstrated that the temperature seasonality had less effect on scale roughness in longer snakes than shorter snakes. Further study would be needed to investigate this phenomenon.

The final factor found to affect the scale roughness in this study was the maximum temperature of the warmest month. This factor was found to increase the scale roughness with higher maximum temperatures. This finding seems to support studies that implicate the scale patterns in reflection of solar radiation because higher temperatures would imply more sunlight, so perhaps previous studies were on the right track. This factor was also found to affect the roughness more in longer snakes, as shown in Figure 3.4. The model for the analysis showed that the clades were not affected differently by this variable, so they were not included in the model.

It is surprising that no other factors were found to have an effect on the scale roughness. It would seem that precipitation would play some role since it would come into direct contact with each scale, but it is possible that the sample size available in this study was not large enough to detect every correlation. A larger sample size would probably be beneficial in detecting these variables.

This new technique of quantifying the pattern differences seen in reptile scales using the confocal microscope has proved to be very useful and may prove even more so for further research. It seems that the results of this technique are species specific as seen by the differences in roughness between the two clades, but it also appears to be somewhat dependent on the environment. A more in depth study and the analysis of many other factors would be beneficial in determining just how this new technique might be of use.

Future studies might focus on the variability of the scale roughness on an individual specimen. It is well known that scale patterns and sizes vary on different parts of the body, but how does the roughness vary? Benefit might also be gained from looking at other environmental factors such as soil types or solar radiation. It is likely that there are many more factors that all play their own role in determining scale roughness.

APPENDIX A

SAS CODE

```
*data one; *set Skach.AmberData;


libname skach 'C:\Min\Stat Lab\Snake data';
data one ; set skach.amberData;
svl=1*svl__cm_;
lr=log(roughness);
*proc print; *var svl svl__cm_;
run;

data two; set one;
if site='A' then site1=1;
if site='B' then site1=2;
if site='C' then site1=3;
sex1=(sex='M');  **sex index: M=1, F=0;
Clade1=(Clade='Eastern');  **Clade index: Eastern=1, Western=0;

*proc print data=two; *var sex1 Clade1;

**first consider sex svl and clade is important to roughness, the model is
   roughness=mu+scale(i)+site(j)+scale*site(i,j)+e where scale and site
  are random ;

**Full model: including interaction effects;
proc mixed data=two empirical ;
classes Scale site1 snake;
model lr= svl Clade1    /solution;
*random Scale site1 Scale*site1/ subject=snake type=vc  ;
repeated / subject=snake type=cs r;
run;

**Reduced model: no interaction effects;
proc mixed data=two empirical ;
classes Scale site1 snake;
model lr=  svl Clade1   BIO19/solution;
*random Scale site1 Scale*site1/ subject=snake type=vc  ;
repeated / subject=snake type=cs r;
run;

***add other factors into the model one by one; *the BIO4 and Bio5 affect roughness;
******then put them into the model and consider the interaction;
proc mixed data=two empirical ;
classes Scale site1 snake;
```

```
model lr= svl Clade1 BIO4 BIO5 svl*BIO4 svl*BIO5 Clade1*BIO4 Clade1*BIO5
BIO4*BIO5/solution;
*random Scale site1 Scale*site1/ subject=snake type=vc  ;
repeated / subject=snake type=cs r;

/******* reduced model **************;
proc mixed data=two empirical ;
classes Scale site1 snake;
model lr= svl Clade1 BIO4 BIO5 svl*BIO4 svl*BIO5 Clade1*BIO4 Clade1*BIO5
/solution;
*random Scale site1 Scale*site1/ subject=snake type=vc  ;
repeated / subject=snake type=cs r;
run;*/
proc glm data=two  ;
*classes Scale site1 snake;
model lr= svl Clade1 BIO4 BIO5 svl*BIO4 svl*BIO5 Clade1*BIO4 Clade1*BIO5
BIO4*BIO5;
*random Scale site1 Scale*site1/ subject=snake type=vc  ;
*repeated / subject=snake type=cs r;
output out=new residual=r;
proc univariate normal plot data=new; var r;
proc univariate data=new; var svl;
run;
```

APPENDIX B

SNAKE SCALE LOCALITY DATA

#	State	County	Clade	Sex	SVL (cm)	Latitude	Longitude
1	San Luis Potosi		Eastern	M	skin only	22.098	-100.892
2	Sonora		Western	M	92	31.312	-109.179
3	Tamaulipas		Eastern	M	61.4	27.26	-99.612
4	Veracruz		Eastern	M	84.2	19.083	-96.833
5	Hidalgo		Eastern	M	51.5	20.382	-98.722
6	Nuevo Leon		Eastern	F	61.3	26.832	-99.839
7	Arizona	Mohave	Western	M	46.5	35.042	-114.247
8	Arizona	Cochise	Western	M	62.5	31.472	-109.375
9	Arizona	Pima	Western	M	53.3	31.949	-111.751
10	Arizona	Maricopa	Western	F	68.5	33.002	-113.042
11	New Mexico	Dona Ana	Eastern	M	67.2	32.578	-107.289
12	New Mexico	Socorro	Eastern	M	109.2	33.51	-107.245
13	New Mexico	Luna	Eastern	F	78.3	32.177	-107.831
14	New Mexico	Hidalgo	Western	M	83.5	31.916	-108.796
16	New Mexico	Hidalgo	Eastern	M	122.2	31.656	-108.449
17	New Mexico	Grant	Eastern	M	69.5	32.578	-107.896
19	Texas	Aransas	Eastern	M	55	28.16	-97.006
23	Texas	Bexar	Eastern	M	51.5	29.363	-98.781
24	Texas	Bosque	Eastern	M	82.7	31.75	-97.577
25	Texas	Brewster	Eastern	M	84.8	29.241	-103.738
26	Texas	Brooks	Eastern	F	72.7	27.099	-98.149
27	Texas	Briscoe	Eastern	M	90.9	34.545	-101.474
28	Texas	Brown	Eastern	M	46	31.709	-98.944
29	Texas	Caldwell	Eastern	F	86.7	29.771	-97.699
30	Texas	Cameron	Eastern	M	57	26.14	-97.373
32	Texas	Coleman	Eastern	M	75.9	31.546	-99.291
35	Texas	Duval	Eastern	M	96.5	27.976	-98.577
36	Texas	Val Verde	Eastern	M	82.1	29.771	-101.168
39	Texas	Winkler	Eastern	M	79.4	31.852	-102.882
40	Texas	Pecos	Eastern	M	91.3	30.689	-102.943
42	Texas	Llano	Eastern	F	87.4	30.608	-98.821
43	Texas	Loving	Eastern	M	decapitated	31.954	-103.718
44	Texas	Upton	Eastern	F	83.4	31.138	-102.106
46	Texas	McCulloch	Eastern	F	85	31.138	-99.373
47	Texas	McMullen	Eastern	M	69.8	28.037	-98.414
48	Texas	Palo Pinto	Eastern	M	80.5	32.791	-98.455
49	Texas	Van Zandt	Eastern	F	87	32.342	-95.68
52	Texas	Dallas	Eastern	M	52.1	32.587	-97.006
60	Texas	Parker	Eastern	M	90	32.872	-97.741

APPENDIX C

ENVIRONMENTAL FACTOR DATA MAPS

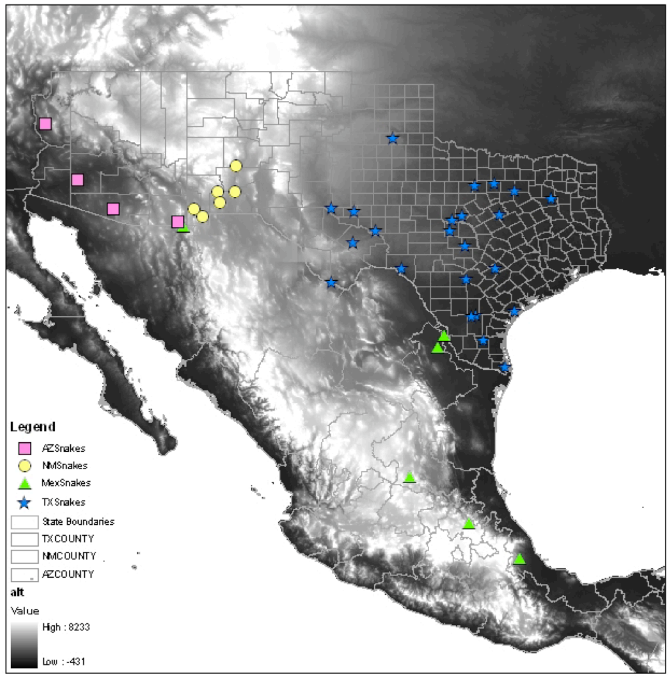

Figure C.1: Altitude Data Map

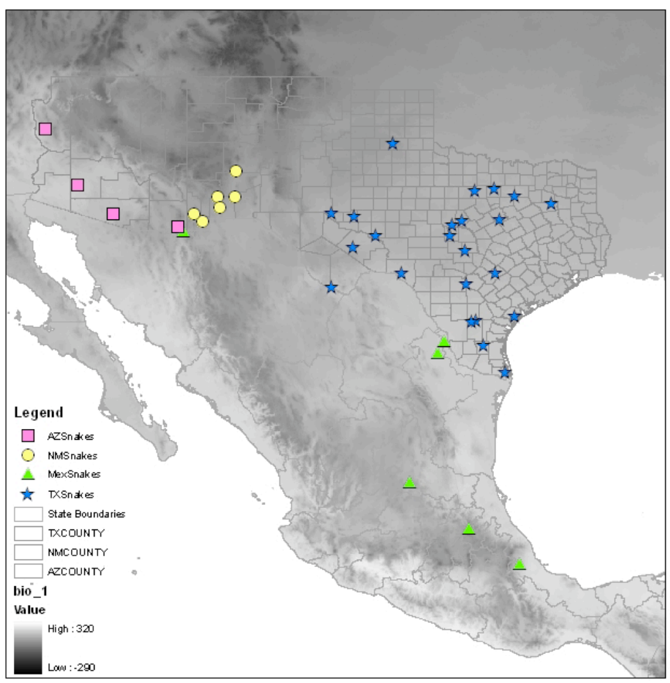

Figure C.2: Annual Mean Temperature Data Map (Bio1)

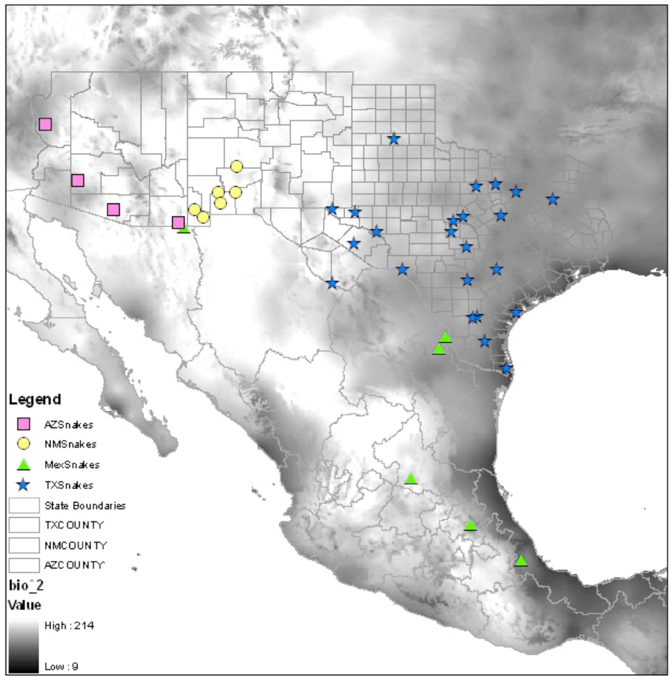

Figure C.3: Mean Diurnal Range Data Map (Bio2)

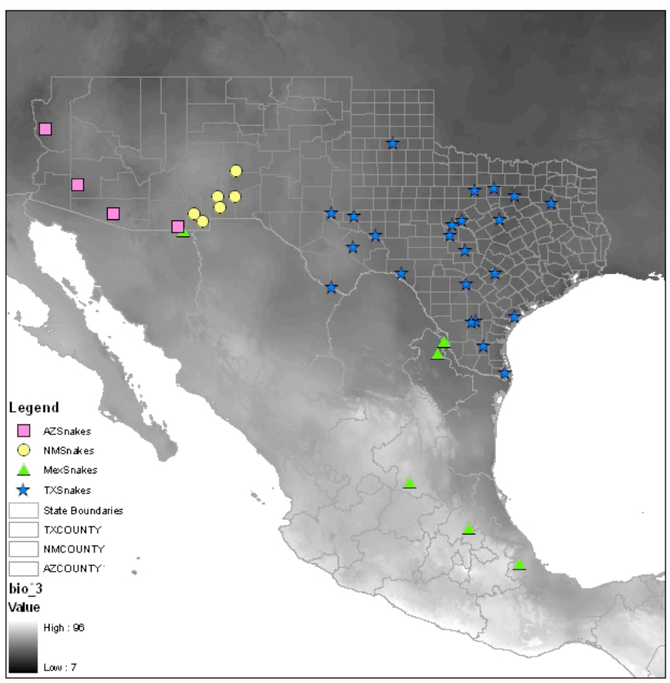

Figure C.4: Isothermality Data Map (Bio3)

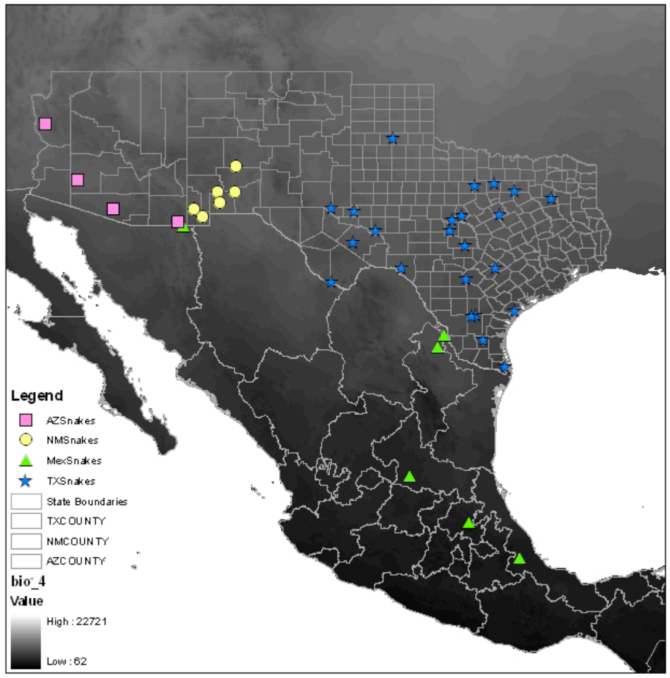

Figure C.5: Temperature Seasonality Data Map (Bio4)

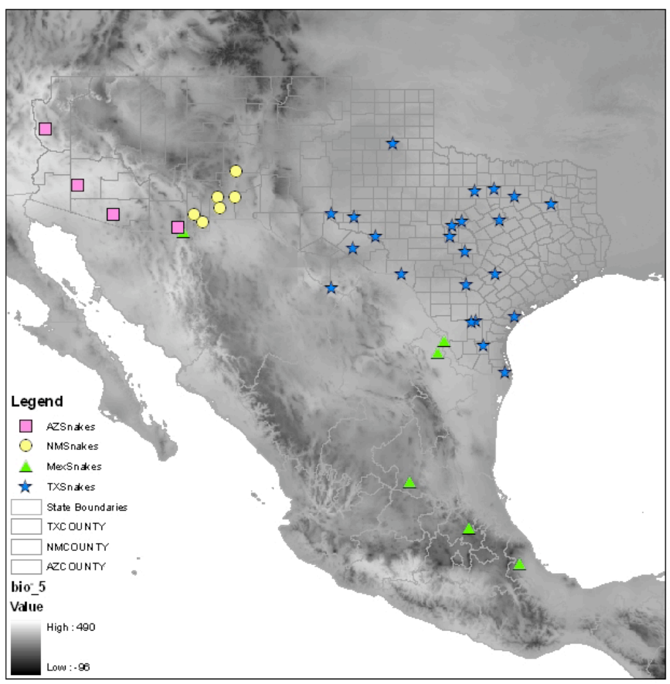

Figure C.6: Max Temperature of Warmest Month Data Map (Bio5)

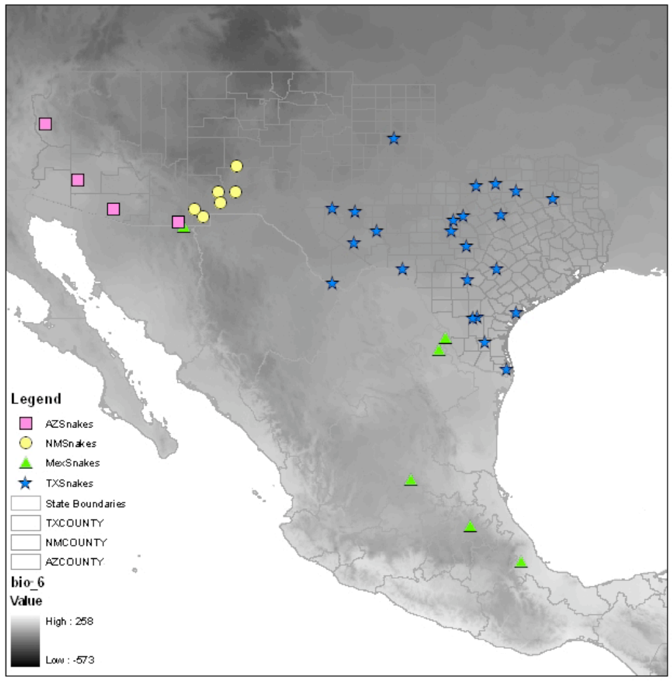

Figure C.7: Min Temperature of Coldest Month Data Map (Bio6)

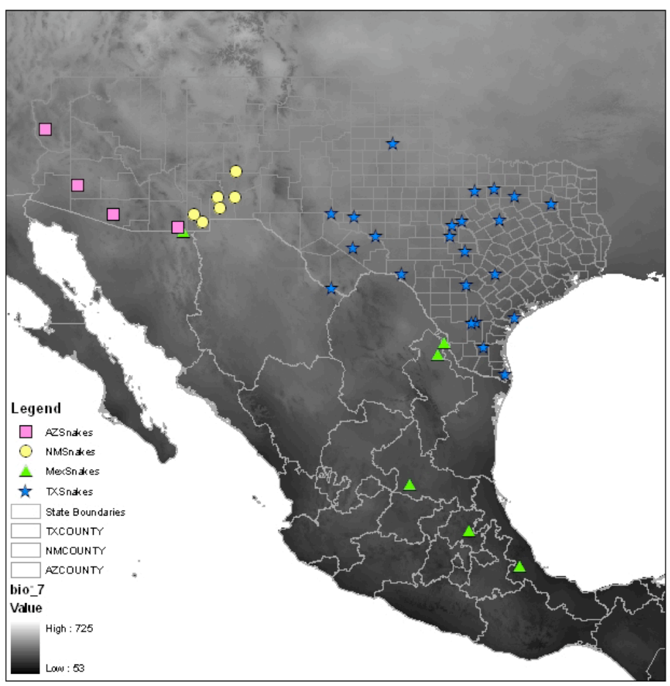

Figure C.8: Temperature Annual Range Data Map (Bio7)

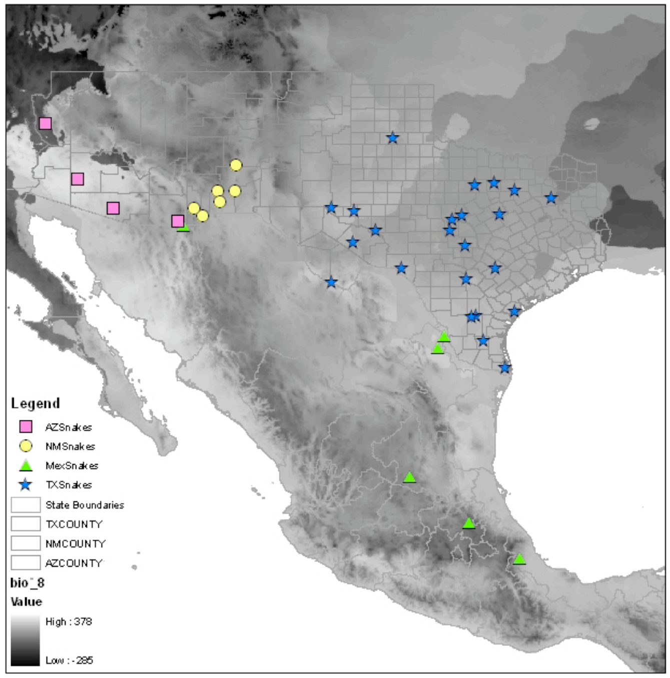

Figure C.9: Mean Temperature of Wettest Quarter Data Map (Bio8)

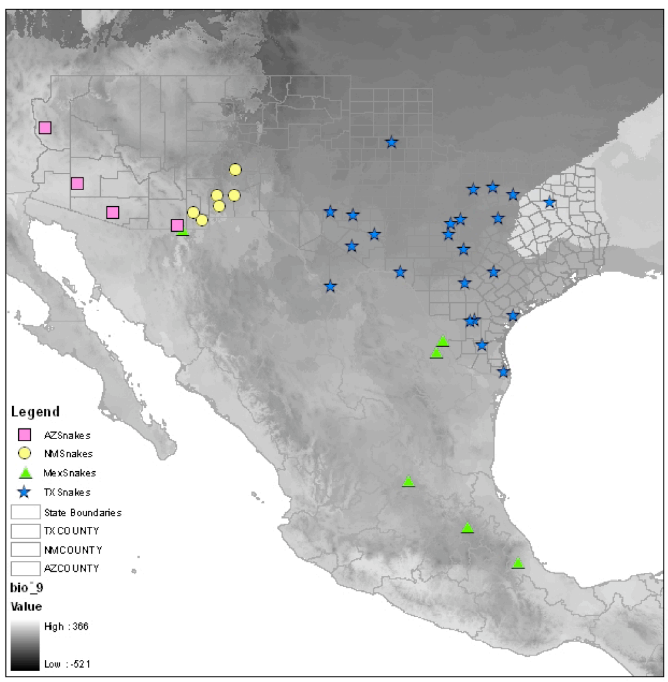

Figure C.10: Mean Temperature of Driest Quarter Data Map (Bio9)

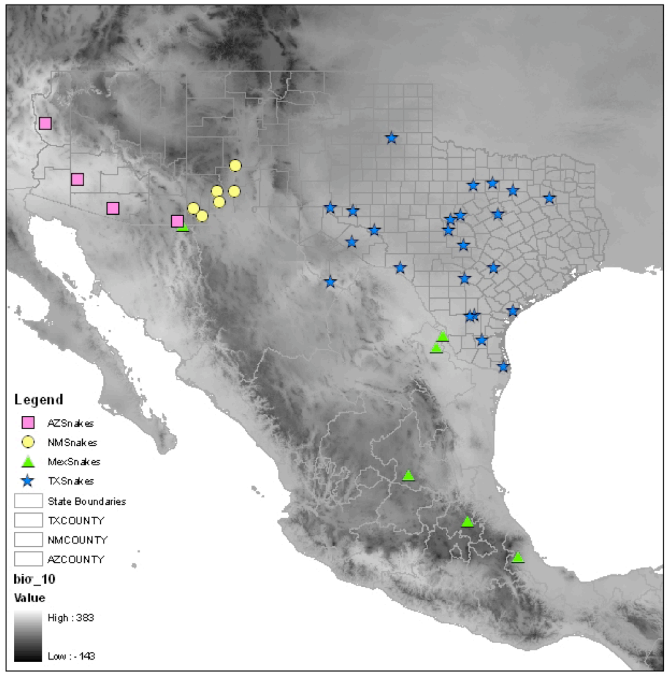

Figure C.11: Mean Temperature of Warmest Quarter Data Map (Bio10)

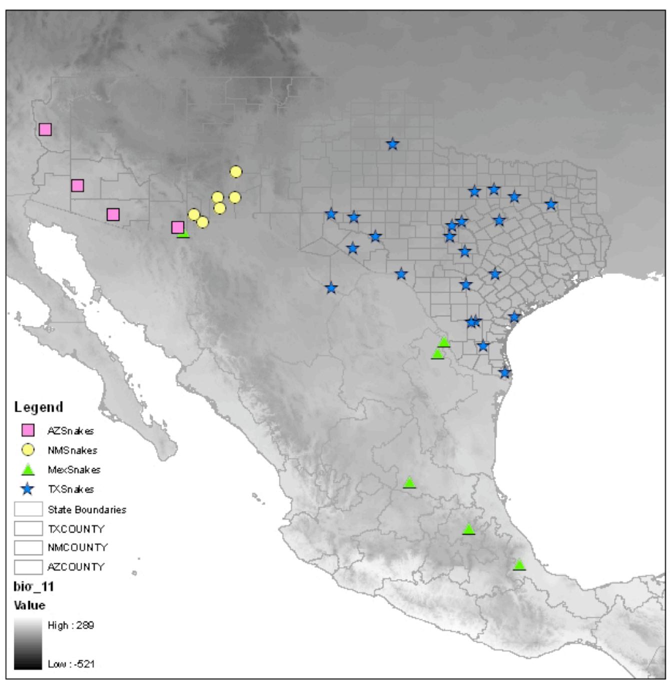

Figure C.12: Mean Temperature of Coldest Quarter Data Map (Bio11)

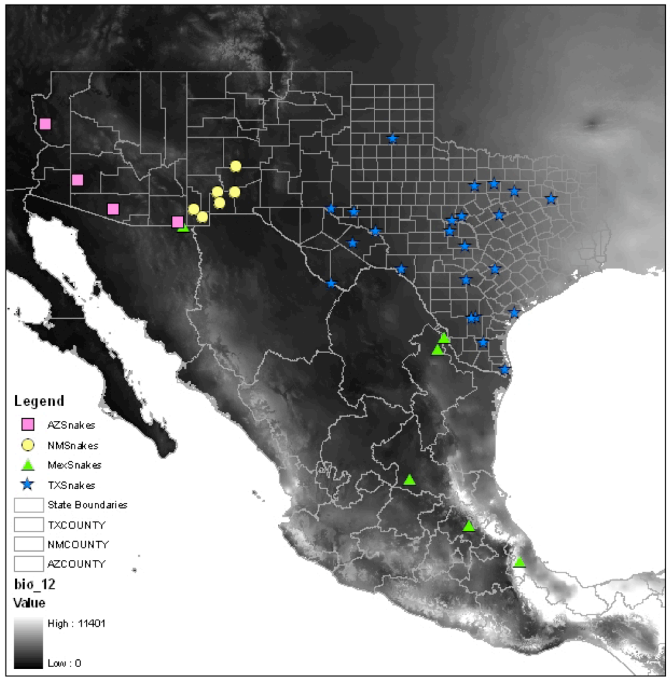

Figure C.13: Annual Precipitation Data Map (Bio12)

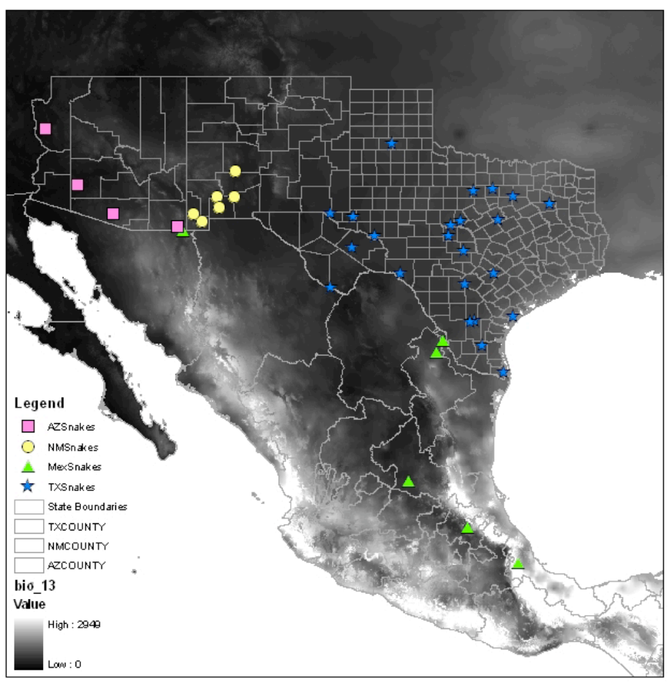

Figure C.14: Precipitation of Wettest Month Data Map (Bio13)

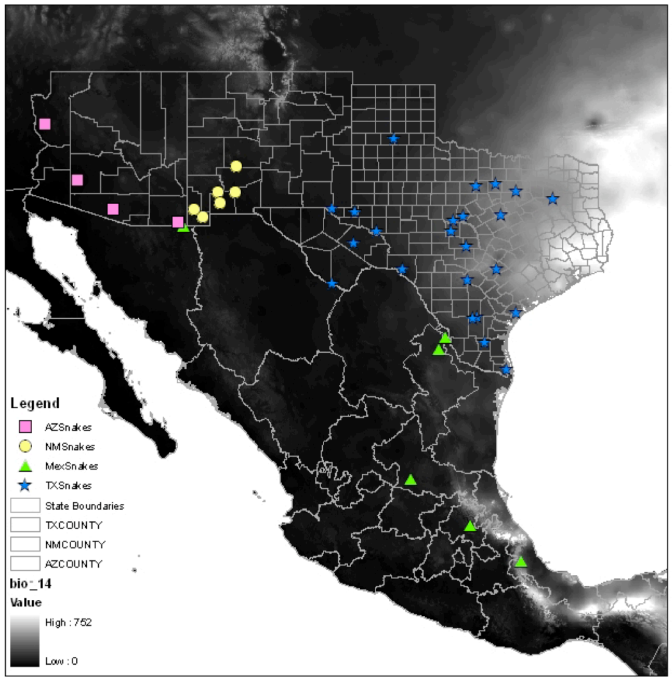

Figure C.15: Precipitation of Driest Month Data Map (Bio14)

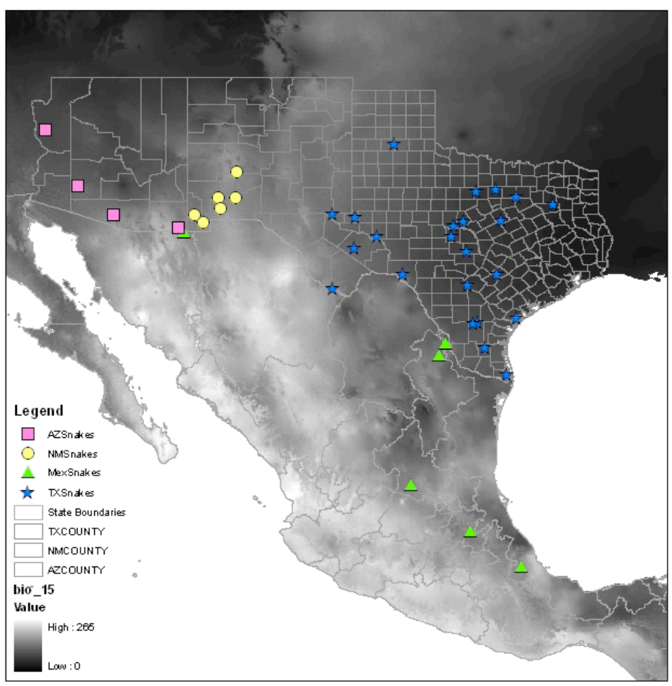

Figure C.16: Precipitation of Seasonality Data Map (Bio15)

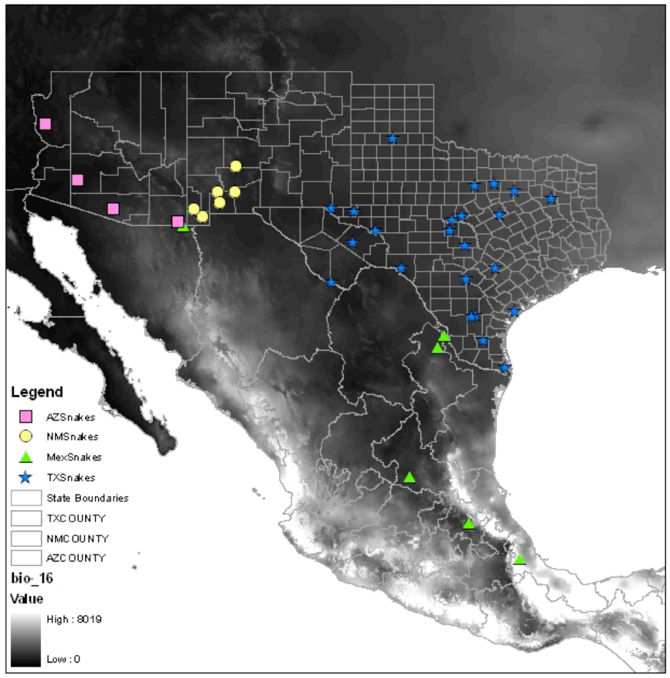

Figure C.17: Precipitation of Wettest Quarter Data Map (Bio16)

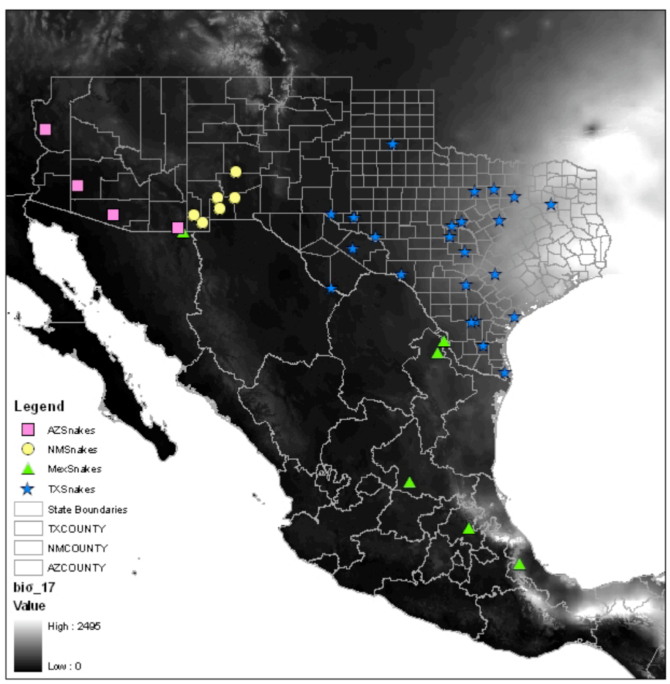

Figure C.18: Precipitation of Driest Quarter Data Map (Bio17)

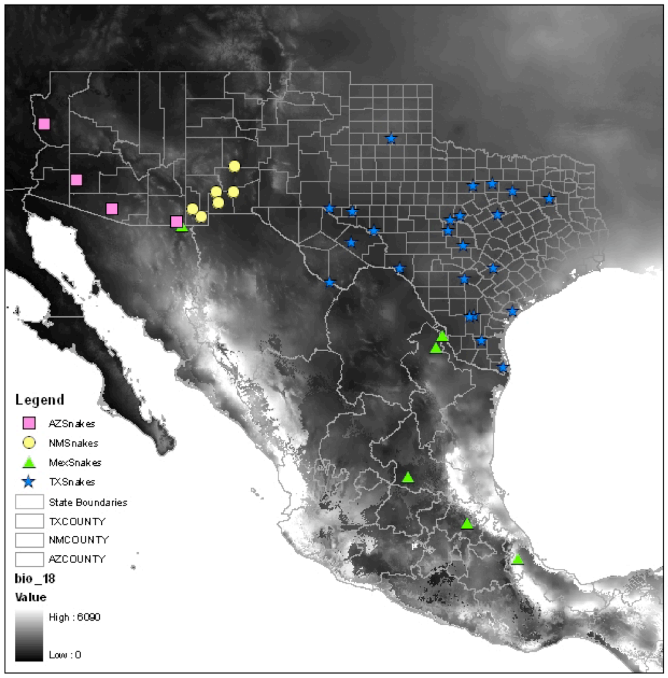

Figure C.19: Precipitation of Warmest Quarter Data Map (Bio18)

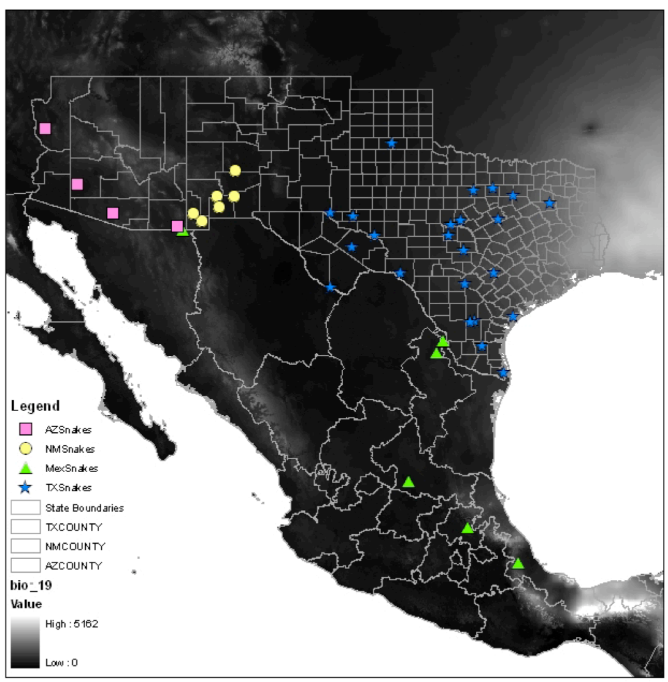

Figure C.20: Precipitation of Coldest Quarter Data Map (Bio19)

APPENDIX D

ENVIRONMENTAL LOCALITY DATA

#	Altitude (m)	BIO 1	BIO 2	BIO 3	BIO 4	BIO 5	BIO 6	BIO 7	BIO 8	BIO 9	BIO 10
1	1856	180	164	65	2571	300	50	250	202	156	207
2	1202	169	191	50	6913	358	-20	378	247	209	255
3	134	235	134	42	6321	382	69	312	283	164	308
4	810	214	114	63	2073	305	123	182	229	191	235
5	1966	152	144	65	2077	263	42	219	164	126	178
6	178	230	133	42	6275	381	68	313	275	161	304
7	700	190	142	39	7978	384	24	360	107	224	296
8	1375	158	184	50	6709	339	-23	362	233	192	241
9	829	192	174	49	6953	374	17	357	278	222	282
10	198	227	161	43	7686	416	48	368	325	260	328
11	1386	145	187	48	7445	342	-47	384	236	142	246
12	1676	137	180	46	7492	326	-53	378	221	89	231
13	1319	155	187	48	7638	349	-36	385	245	150	256
14	1361	154	188	49	7246	348	-33	381	238	194	247
16	1332	161	191	49	7214	354	-28	382	239	200	250
17	1556	140	182	48	7245	331	-42	372	226	131	234
19	8	216	91	35	5706	328	74	255	262	180	283
23	221	206	129	41	6503	355	43	312	244	128	285
24	219	186	135	37	7665	358	0	358	225	81	277
25	846	206	169	46	7113	362	12	350	268	123	279
26	40	226	125	43	5656	361	77	285	268	162	293
27	955	143	158	40	8228	334	-58	392	249	34	249
28	409	180	142	40	7569	353	-3	356	225	92	275
29	134	201	130	40	6752	357	33	324	238	126	282
30	10	228	88	38	4928	330	100	230	267	199	284
32	452	184	148	41	7495	355	-4	360	227	95	276
35	175	215	137	43	6175	361	49	312	261	145	287
36	584	198	138	42	6794	348	20	330	247	114	279
39	916	175	164	43	7645	351	-23	373	260	93	270
40	1053	175	166	47	6887	342	-8	349	252	102	263
42	421	186	143	41	7067	350	8	344	228	92	274
43	915	178	173	45	7578	359	-19	378	262	97	273
44	774	187	152	42	7530	354	-4	358	240	107	280
46	517	180	149	41	7316	350	-8	358	222	92	269
47	161	215	134	43	6159	360	50	310	260	145	289
48	297	175	139	38	7952	355	-15	367	219	69	275
49	158	185	130	37	7342	351	10	341	222	274	274
52	191	187	122	35	7773	355	10	345	227	96	284
60	307	179	134	36	7914	352	-7	358	218	71	275

#	BIO 11	BIO 12	BIO 13	BIO 14	BIO 15	BIO 16	BIO 17	BIO 18	BIO 19
1	143	360	69	7	71	176	26	123	28
2	80	314	79	4	82	180	21	154	60
3	146	468	99	12	60	194	49	128	55
4	184	1712	327	40	80	891	122	453	123
5	125	793	159	13	76	375	45	239	57
6	143	468	108	11	67	195	48	146	53
7	92	161	22	2	43	56	14	40	51
8	72	357	90	5	84	204	24	172	67
9	106	340	71	5	72	177	19	143	83
10	132	133	25	1	54	55	7	42	40
11	51	274	57	4	76	152	19	126	45
12	37	262	61	6	83	155	20	127	30
13	59	240	52	4	78	138	16	113	46
14	62	306	66	5	73	165	22	137	59
16	67	281	65	4	77	160	19	133	53
17	49	323	68	5	75	177	22	147	57
19	136	929	160	35	41	339	142	264	168
23	118	692	94	34	35	228	114	177	117
24	82	828	115	46	29	285	150	195	150
25	105	287	62	6	76	173	21	153	21
26	147	625	112	19	49	240	87	184	99
27	32	508	96	11	61	220	41	222	41
28	80	700	97	34	34	246	113	183	114
29	109	867	116	40	33	296	158	199	163
30	159	681	152	20	57	286	97	167	118
32	82	658	94	31	38	230	98	181	99
35	128	624	102	24	46	229	90	177	91
36	105	430	78	11	54	177	43	131	49
39	73	326	60	8	57	140	32	120	32
40	85	366	65	10	56	155	35	134	39
42	92	711	104	31	37	244	111	187	111
43	78	305	59	9	65	144	28	128	30
44	87	371	68	12	55	157	40	115	43
46	80	652	92	28	38	219	94	187	96
47	127	645	104	24	44	233	97	180	98
48	69	774	108	38	32	265	121	199	124
49	84	1053	129	48	24	327	195	197	240
52	83	893	128	47	31	308	164	189	165
60	72	841	119	41	31	289	137	200	137

APPENDIX E

SAS RESULTS

The scale and site are random variables, at the beginning, just consider the effect of sex, svl and clade, the model is: $y_{ijk} = \mu + scale_i + site_j + (scale * site)_{ij} + \varepsilon_{ijk}$ where

$y_{ijk} = \ln(r_{ijk})$

$\mu = \beta_0 + \beta_1 * sex + \beta_2 * svl + \beta_3 * clade + \beta_4 * sex * svl + \beta_5 * sex * clade + \beta_6 * svl * clade$

where i: index of scale, j: index of site, k: index of snake.

Fit Statistics

-2 Res Log Likelihood	1624.2
AIC (smaller is better)	1628.2
AICC (smaller is better)	1628.2
BIC (smaller is better)	1631.4

Solution for Fixed Effects

Effect	Estimate	Standard Error	DF	t Value	Pr > |t|
Intercept	11.1848	4.5826	30	2.44	0.0208
sex1	1.3665	4.0792	30	0.34	0.7400
svl	-0.02986	0.06690	30	-0.45	0.6586
Clade1	0.4395	2.6837	30	0.16	0.8710
sex1*svl	-0.03052	0.05877	30	-0.52	0.6074
sex1*Clade1	1.5191	0.8557	30	1.78	0.0860
svl*Clade1	0.006719	0.03890	30	0.17	0.8640

We tried several reduced models, finally we keep svl and clade in the model, $y_{ijk} = \mu + scale_i + site_j + (scale * site)_{ij} + \varepsilon_{ijk}$ where $\mu = \beta_0 + +\beta_1 * svl + \beta_2 * clade$ since :

Fit Statistics

-2 Res Log Likelihood	1623.3
AIC (smaller is better)	1627.3
AICC (smaller is better)	1627.3
BIC (smaller is better)	1630.5

Solution for Fixed Effects

Effect	Estimate	Standard Error	DF	t Value	Pr > |t|
Intercept	12.2317	1.4188	34	8.62	<.0001
svl	-0.05388	0.01821	34	-2.96	0.0056
Clade1	2.1822	0.6649	34	3.28	0.0024

Then, we keep adding the factor in the model one by one.

Altitude:

Type 3 Tests of Fixed Effects

Effect	Num DF	Den DF	F Value	Pr > F
svl	1	33	8.05	0.0077
Clade1	1	33	12.30	0.0013
Altitude	1	33	1.10	0.3028

BIO1

Type 3 Tests of Fixed Effects

Effect	Num DF	Den DF	F Value	Pr > F
svl	1	33	7.27	0.0109
Clade1	1	33	10.34	0.0029
BIO1	1	33	0.10	0.7481

BIO2

Type 3 Tests of Fixed Effects

Effect	Num DF	Den DF	F Value	Pr > F
svl	1	33	4.75	0.0365
Clade1	1	33	6.49	0.0157
BIO2	1	33	0.02	0.8951

BIO3

Type 3 Tests of Fixed Effects

Effect	Num DF	Den DF	F Value	Pr > F
svl	1	33	7.70	0.0090
Clade1	1	33	11.90	0.0016
BIO3	1	33	2.10	0.1571

BIO4

Type 3 Tests of Fixed Effects

Effect	Num DF	Den DF	F Value	Pr > F
svl	1	33	5.57	0.0243
Clade1	1	33	6.71	0.0142
BIO4	1	33	3.27	0.0797

BIO5

Type 3 Tests of Fixed Effects

Effect	Num DF	Den DF	F Value	Pr > F
svl	1	33	7.94	0.0081
Clade1	1	33	5.89	0.0209
BIO5	1	33	3.75	0.0616

BIO6

Type 3 Tests of Fixed Effects

Effect	Num DF	Den DF	F Value	Pr > F
svl	1	33	4.89	0.0340
Clade1	1	33	8.28	0.0070
BIO6	1	33	0.32	0.5752

BIO7

Type 3 Tests of Fixed Effects

Effect	Num DF	Den DF	F Value	Pr > F
svl	1	33	4.41	0.0434
Clade1	1	33	4.96	0.0329
BIO7	1	33	2.32	0.1377

BIO8

Type 3 Tests of Fixed Effects

Effect	Num DF	Den DF	F Value	Pr > F
svl	1	33	7.05	0.0121
Clade1	1	33	10.84	0.0024
BIO8	1	33	0.37	0.5452

BIO9

Type 3 Tests of Fixed Effects

Effect	Num DF	Den DF	F Value	Pr > F
svl	1	33	8.39	0.0067
Clade1	1	33	3.56	0.0681
BIO9	1	33	0.27	0.6053

BIO10

Type 3 Tests of Fixed Effects

Effect	Num DF	Den DF	F Value	Pr > F
svl	1	33	8.38	0.0067
Clade1	1	33	9.59	0.0040
BIO10	1	33	2.23	0.1447

BIO11

Type 3 Tests of Fixed Effects

Effect	Num DF	Den DF	F Value	Pr > F
svl	1	33	5.38	0.0267
Clade1	1	33	8.61	0.0060
BIO11	1	33	0.33	0.5669

BIO12

Type 3 Tests of Fixed Effects

Effect	Num DF	Den DF	F Value	Pr > F
svl	1	33	6.93	0.0128
Clade1	1	33	6.27	0.0174
BIO12	1	33	0.04	0.8430

BIO13

Type 3 Tests of Fixed Effects

Effect	Num DF	Den DF	F Value	Pr > F
svl	1	33	6.87	0.0131
Clade1	1	33	6.36	0.0167
BIO13	1	33	0.61	0.4392

BIO14

Type 3 Tests of Fixed Effects

Effect	Num DF	Den DF	F Value	Pr > F
svl	1	33	7.45	0.0101
Clade1	1	33	9.11	0.0049
BIO14	1	33	0.24	0.6280

BIO15

Type 3 Tests of Fixed Effects

Effect	Num DF	Den DF	F Value	Pr > F
svl	1	33	7.80	0.0086
Clade1	1	33	11.87	0.0016
BIO15	1	33	0.89	0.3521

BIO16

Type 3 Tests of Fixed Effects

Effect	Num DF	Den DF	F Value	Pr > F
svl	1	33	7.37	0.0104
Clade1	1	33	6.69	0.0143
BIO16	1	33	1.29	0.2649

BIO17

Type 3 Tests of Fixed Effects

Effect	Num DF	Den DF	F Value	Pr > F
svl	1	33	7.50	0.0099
Clade1	1	33	9.78	0.0037
BIO17	1	33	0.35	0.5573

BIO18

Type 3 Tests of Fixed Effects

Effect	Num DF	Den DF	F Value	Pr > F
svl	1	33	7.68	0.0091
Clade1	1	33	5.78	0.0220
BIO18	1	33	1.11	0.2988

BIO19

Type 3 Tests of Fixed Effects

Effect	Num DF	Den DF	F Value	Pr > F
svl	1	33	8.02	0.0078
Clade1	1	33	12.55	0.0012
BIO19	1	33	0.89	0.3521

So, if we choose $\alpha = 0.1$, then only svl, clade, BIO4 and BIO5 (since their p-value<0.1) would affect roughness, so if we put then in the model, the model would be

$y_{ijk} = \mu + scale_i + site_j + (scale*site)_{ij} + \varepsilon_{ijk}$ where

$\mu = \beta_0 + \beta_1 * svl + \beta_2 * clade + \beta_3 * BIO4 + \beta_4 * BIO5 + \beta_5 * svl * BIO4 + \beta_6 * svl * BIO5 + \beta_7 * clade * BIO4 + \beta_8 * clade * BIO5 + \beta_9 * BIO4 * BIO5$

Solution for Fixed Effects

Effect	Estimate	Standard Error	DF	t Value	Pr > |t|
Intercept	-3.0121	2.7355	27	-1.10	0.2806
svl	-0.01087	0.02686	27	-0.40	0.6890
Clade1	4.5835	1.7988	27	2.55	0.0168
BIO4	0.001230	0.000449	27	2.74	0.0108
BIO5	0.003985	0.008893	27	0.45	0.6576
svl*BIO4	-0.000002959	0.00000116		-2.55	0.0111
svl*BIO5	0.000072411	0.00007220		1.00	0.3166
Clade1*BIO4	-0.000440370	0.00014982		-2.94	0.0035
Clade1*BIO5	-0.003554240	0.00309844		-1.15	0.2522
BIO4*BIO5	-0.000001830	0.00000066		-2.77	0.0059

Then consider the reduced model without interaction term, the reduced model is:

$y_{ijk} = \mu + scale_i + site_j + (scale*site)_{ij} + \varepsilon_{ijk}$ where

$\mu = \beta_0 + \beta_1 * svl + \beta_2 * clade + \beta_3 * BIO4 + \beta_4 * BIO + \beta_5 * svl * BIO4 + \beta_6 * clade * BIO4$

Solution for Fixed Effects

Effect	Estimate	Standard Error	DF	t Value	Pr > |t|
Intercept	0.2940	1.0361	30	0.28	0.7785
svl	0.01619	0.007274	30	2.23	0.0337
Clade1	2.3279	0.9928	30	2.34	0.0259
BIO4	0.000511	0.000148	30	3.46	0.0017
BIO5	-0.00394	0.001480	30	-2.66	0.0123
svl*BIO4	-3.18E-6	1.198E-6	30	-2.66	0.0126
Clade1*BIO4	-0.00030	0.000135	30	-2.20	0.0356

So the final model is

$y_{ijk} = \mu + scale_i + site_j + (scale * site)_{ij} + \varepsilon_{ijk}$ where

$\mu = \beta_0 + \beta_1 * svl + \beta_2 * clade + \beta_3 * BIO4 + \beta_4 * BIO5 + \beta_5 * svl * BIO4 + \beta_6 * svl * BIO5 +$
$\beta_7 * clade * BIO4 + \beta_8 * clade * BIO5 + \beta_9 * BIO4 * BIO5$

```
                         The UNIVARIATE Procedure
                              Variable:  r

     Stem Leaf                                        #             Boxplot
        9 0                                            1               0
        8 12                                           2               |
        7 13                                           2               |
        6 01116                                        5               |
        5 0013446                                      7               |
        4 22255677789                                 11               |
        3 000000122233344456777789999                 27               |
        2 0000001111111222333334455556666677888889    40            +-----+
        1 01111122233344444555566667778888999         35            |     |
        0 0000013333334444445556677788888899          34            |  +  |
       -0 999998888888776666655555444443332222111111110 45           *-----*
       -1 99998887777666655544443333322111000         35            |     |
       -2 99988888776655444422222211110000            32            +-----+
       -3 9777666554432222111111                      22               |
       -4 988765332221000                             15               |
       -5 76555554210                                 11               |
       -6 9876522                                      7               |
       -7 3                                            1               |
       -8 1                                            1               |
          ----+----+----+----+----+----+----+----+----+
      Multiply Stem.Leaf by 10**-1
```

Normal Probability Plot

```
  0.95+
      |                                  **
      |                                 **++
      |                               ***+
      |                              ***
      |                            ***
      |                         *****
      |                       *****
      |                     ****
  0.05+                      ****
      |                 ****
      |               ****
      |             ***
      |          ****
      |        +***
      |      ****
      | ******
      |*++
-0.85+*
       +----+----+----+----+----+----+----+----+----+----+
           -2       -1        0       +1       +2
```

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BIOGRAPHICAL INFORMATION

Amber Skach began her academic career at the University of Texas at Arlington in 2000. She participated in Undergraduate research with Paul Ustach in the Amphibian and Reptile Diversity Research Center in which she learned many things about the different species of reptiles. She graduated in 2003 with her Bachelor's degree in Biology and began the dreaded job hunt. After working for over a year at Howard Hughes Medical Institute, in January 2005, she decided to go back to school part-time to pursue her Master's degree. Her studies led her to the lab of Dr. Howard Arnott, in whose lab she learned many new microscopy techniques. Her interest in herpetology and microscopy led her to a project that allowed her to learn new things about both herpetology and microscopy. Amber enjoyed her time in school and all the people she has come to know, but she now plans to take some time off to enjoy life before returning for her PhD one day.