

PREDATION AND THE EVOLUTION OF COLOR POLYMORPHISM IN THE  
MOTTLED ROCK RATTLESNAKE (*CROTALUS LEPIDUS LEPIDUS*)

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## ABSTRACT

### PREDATION AND THE EVOLUTION OF COLOR POLYMORPHISM IN THE MOTTLED ROCK RATTLESNAKE (*CROTALUS LEPIDUS LEPIDUS*)

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Questions regarding the origin and maintenance of biodiversity are key topics of evolutionary biology, including in particular, polymorphism. The mottled rock rattlesnake (*Crotalus l. lepidus*) is a montane species that exhibits striking levels of color polymorphism associated with two distinct substrate types separated by lowland desert, a habitat not used by *Crotalus l. lepidus*. I hypothesized that selective predation on high contrast color and blotching patterns maintains the distinct races (phenotypes).

To test this hypothesis I performed a predation experiment using model snakes made of urethane foam, at 12 sites in the west Texas portion of the species range. The sites were split between the two regions in which the contrasting races are found including the eastern region composed primarily of light colored limestone and the

western region composed primarily of dark volcanic rocks. Two color treatments were used; one mimicking the light colored eastern race and one the dark colored western race. Additionally, these models varied in their blotching pattern. Half had no blotching to simulate the eastern race which has high proportions of anterior blotch fading. The other half of the models were painted with complete blotching to simulate the western race resulting in four total treatments. Forty models were placed at each site (N=10 per treatment). Photographs were taken of all models when they were placed at their respective sites as well as when the models were retrieved two weeks after placement. The number and location of non-predator disturbances and avian attacks of models were recorded. Attack and disturbance data were analyzed with a general linear model under a Poisson distribution with a reciprocal link function with number of avian attacks and non-predator disturbances as the response variable. Attack location data was analyzed with a one-way ANOVA comparing distance from head (computed as a percentage of total length) as the response variable and type of damage (Avian attack or non-predator disturbance) as the independent variable. I found that high contrast color models were attacked significantly more often; however there was no difference in the frequency of attacks on the different blotching treatments. Additionally, there were no significant differences in non-predator disturbances between the different color or blotching patterns. Predation attempts occurred significantly closer to the anterior end of models than did non-predator disturbances. These results are consistent with the hypothesis that color pattern has been maintained by selective predation.

## INTRODUCTION

Central to evolutionary biology are questions concerning the origin and maintenance of biodiversity. As all species have arisen out of previously existing taxa, investigations often seek to explain morphological variation within species. Color polymorphism is documented in a wide range of taxa including invertebrates (Cain and Sheppard 1950; Hairston 1979; Hughes and Jones 1985; Reid 1987; Byers 1990; Oxford and Gillespie 1998; Sandoval and Crespi 2008), plants (Brown and Clegg 1984; Stanton et al. 1989; Clegg and Durbin 2000; Schemske and Bierzychudek 2001) and vertebrates (Brodie 1992; Sinervo et al. 2001; Wente and Phillips 2003; Hoekstra et al. 2004; Olendorf et al. 2006). Color polymorphic species prompt a basic question: Why have multiple phenotypes within one species evolved and how are these phenotypes maintained? Heterogeneous habitat and substrates within/across a species' distribution can facilitate selection that contributes to color polymorphism (Byers 1990; Hoekstra et al. 2004; Rosenblum 2006). Cain and Sheppard's (1950) seminal work on polymorphism in the snail, *Cepaea nemoralis*, indicated that selection by predation could favor different color morphs in different habitats. Since this early work a multitude of competing hypotheses have been proposed concerning the maintenance of color polymorphism through selective predation on *C. nemoralis*. Additionally, Cowie and Jones (1985) proposed climatic selection as another force maintaining dark and light colored phenotypes in *C. nemoralis* and *C. hortensis*. Climate and genetic drift have also been

proposed to maintain color and banding polymorphism in marginal populations of *C. nemoralis* (Honek 1995). These multiple hypotheses, within this single genus, indicate the complexity behind color and pattern polymorphism.

One of the most well known examples of selective predation maintaining color polymorphism is that of the peppered moth, *Biston betularia*. This species exhibited a dramatic increase in the frequency of the melanistic phenotype during the onset of the industrial revolution which was accompanied by high levels of soot making the typical white and black color morph less cryptic (Clarke and Sheppard 1966; Bishop 1972; Lees and Creed 1975). Selective predation is one of many aspects of a species' ecology that can influence color polymorphism. Multiple studies have shown that color polymorphism can be maintained by a combination of selective predation and sexual selection (Slagsvold et al. 1995; Maan et al. 2008). Other aspects of behavior have been shown to influence color morph such as in red backed salamanders (*Plethodon cinereus*) which are found in two morphs that exhibit two different defense mechanisms (Venesky and Anthony 2007). Color morphs can also be maintained by differential predator types demonstrated by Caldwell (1982) who found that tadpoles of cricket frogs (*Acris crepitans*) exhibited two different tail colorations based on whether the primary predators in its environment were dragonfly larvae or fish. Behavioral and ecological factors need to be considered when addressing questions of color polymorphism rooted in selective predation.

Mottled rock rattlesnakes (*Crotalus lepidus lepidus*) of the desert southwest exhibit pronounced levels of color and pattern polymorphism throughout their geographic range (Vincent 1982). Individuals are typically less than 64 cm in length with strongly

variable dorsal color and pattern throughout their range, but appear to exhibit strong background color matching (Klauber 1972; Vincent 1982; Forstner et al. 1997).

*C. l. lepidus* is found from southern New Mexico, through west Texas, southward into central Mexico (Dixon and Werler 2005). This species has been documented at elevations ranging from 556 m to 2073 m (Dixon and Werler 2005). Much of their range is composed of isolated populations found on montane “islands” in “seas” of lowland desert (Gelbach 1981). These localized populations within two distinct regions of the species range in west Texas (Fig. 1), which also correspond with contrasting substrate type, have been described as two distinct races rooted in differing coloration and blotching frequency (Vincent 1982; Fig. 2). For the purposes of this study the term race will have only this meaning, it will refer to the two distinct phenotypic groups present in eastern and western regions of west Texas (Vincent 1982). Region refers to the distribution of *C. l. lepidus* in eastern and western portions of west Texas.

The two races of *C. l. lepidus* are distinguished by both color and blotch density (dorsal blotches contrasting with the predominant dorsal color). The eastern race located in the Stockton and Edwards plateau is characterized by blue- and light- gray coloration (Fig. 3), and is associated with lighter soil, limestone and uniform substrate (Vincent 1982). Additionally, this race has anterior fading of blotches resulting in a very uniform pattern on the anterior section of their body. The western race located from the Davis Mountains westward and southward through the Big Bend region, exhibits more color variation with typically pink or buff coloration (Fig. 4) and is associated with darker soils, volcanic rocks, and polymorphic substrate. The western race has a higher blotch density resulting in more distinct blotching than the eastern race (Vincent 1982). Forstner

el al. (1997) indicated that the races are not always restricted to the idealized ranges of the two races presented by Vincent (1982), but that the color morphs appear to be present when the corresponding substrate is available; however deviation from the dominant substrate only occurs in certain pockets of the respective regions. This observation gives credibility to the association of color morphs with substrate type. Additionally, rattlesnake species in general have many known, visually oriented, predators including many birds of prey. Red-tailed hawks (*Buteo jamaicensis*) and greater roadrunners (*Geococcyx californianus*) are well known snake hunters (Klauber 1972; Alemeida-Santos et al. 2000; Holycross et al. 2001; Vanderpool et al. 2005; Dugan et al. 2006). Predation events may maintain the color polymorphism observed in *C. l. lepidus*. This situation provides an excellent opportunity to investigate the role of predation in maintaining color and pattern polymorphisms of a vertebrate taxa.

Understanding the maintenance of the polymorphism in color and blotching in *C. l. lepidus* is the subject of this investigation. There are three proposed general hypotheses for the maintenance of color polymorphism which are applicable to *C. l. lepidus*. First, color variation could help to maximize thermoregulation when in different habitats with different substrates. This mechanism has been demonstrated in other species particularly insects and mollusks (Kavaliers 1992; Goulson 1994; Forsman et al. 2002; Bots et al. 2008). The remaining two hypotheses are based largely on crypsis which has been studied extensively (Reimchen 1979; Endler 1981; Reid 1987; Kark et al. 1997; Bond and Kamil 2002; Bond and Kamil 2006; Bond 2007). The second hypothesis states that the most cryptic coloration is prevalent in a given area as a result of foraging success of cryptic predators, which in this case refers to *C. l. lepidus*. The third hypothesis proposes

that the color pattern prevailing in a given area is the one that most effectively reduces potential predation of snakes from visually oriented predators. *C. l. lepidus* are vulnerable when moving to a new location as well as exposing themselves to thermoregulate which reveals the snakes to potential predators, mainly birds which rely on visual cues to find prey. These three hypotheses are not necessarily mutually exclusive. The focus of my studies will be on two variations of the third hypothesis.

I tested two specific hypotheses regarding the color variation of *C. l. lepidus*: (1) differential predation plays a role in the maintenance of different color morphs in *C. l. lepidus* based primarily on substrate type; (2) differential predation plays a role in the maintenance of blotch intensity variation in *C. l. lepidus* based primarily on substrate type.

These hypotheses were tested using model snakes in a predation experiment. Models are commonly used in predation studies (ex. Caldwell 1981; Caldwell 1986; Fitzpatrick et al. 2009) and while they are not as desirable as real organisms, they facilitate larger sample sizes and allow for more manipulation and isolation of specific traits. In particular, artificial snakes have been used in a variety of predation studies involving Batesian mimicry and/or aposematism (Madsen 1987; Brodie 1993; Brodie and Janzen 1995; Hinman et al. 1997; Wuster et al. 2004). The technique of deploying models has also been used to look at predation rates of garter snakes (*Thamnophis sirtalis*) with different color patterns (Bittner 2003). However, it was not until recently that artificial snakes were used to test survival rates based on habitat type (Wilgers and Horne 2007). My study examines the interaction of color and pattern polymorphism with

substrate type to determine: (1) if differential predation is occurring; (2) if selection on each color morph differs between the two dominant habitat types.

A major problem of testing hypotheses rooted in the interpretation of color is that not all animals see colors the same way, and our human perceptions can influence how we view color and hence its role in nature. Although data of the color vision of individual avian species are scarce, color vision may not be as important in predation as it is in other behaviors (i.e., courtship and mate choice; Bennett 1994 ) because the interaction occurs at further distances. For the purposes of this study I quantified contrast differences of models and substrate in an attempt to confirm the preconceived notion that the different color morphs are differentially cryptic.

## MATERIALS AND METHODS

### Model Construction

To test for selective predation of *C. l. lepidus* based on color and blotch pattern between varying substrates, I conducted a manipulative experiment using model snakes made from Foam-iT 3 urethane foam (Smooth-On; Easton, PA). The decision to use urethane foam over other commonly used materials such as modeling clay and rubber was clarified after preliminary evaluation of each (Appendix A). Models were constructed by first creating a mold which was made using a deceased adult broad banded Copperhead (*Agkistrodon contortrix laticinctus*) which exhibits the typical desired viper shape. The deceased snake was secured by its venter with double sided tape to the bottom of an aluminum pan previously sprayed with Ease Release<sup>®</sup> 200 (Smooth-On; Easton, PA) to ensure a smooth release of the urethane rubber. Reoflex 40 urethane rubber (Smooth-On; Easton, PA) was then poured into the aluminum pan and allowed to set for two hours before being de-molded. This mold was used to produce rubber snakes which were then used to create additional molds in order to increase model production efficiency. All molds were rubbed with Ease Release<sup>®</sup> 2831 (Smooth-On; Easton, PA) which acts as both a sealant and a release agent and is specific for use with urethane foam. Foam iT! 3 urethane foam was then poured into the molds and allowed to set for two hours. Models were painted using acrylic paint to represent two variations of the species natural color combined with two pattern types (no blotching or complete

blotching) to represent relative phenotypic extremes within this species (Fig. 5). Color of models were based on photos of multiple specimens from known localities as well as comments from individuals with extensive experience with *C. l. lepidus*. Blotch density per snake was taken from Vincent (1982) who found an average blotch number of 18.9 for the western region and 17.7 for the eastern region of *C. l. lepidus*. I used an average of the two for 18 total blotches on all blotched models. The four alternative color and banding patterns were representative of relative extremes within the species. Mottling, which refers to a variegated color pattern, of the models was noticeably absent despite the common name of the species they mimic, the mottled rock rattlesnake. This was done to simplify the models to present phenotypic attributes that are proposed to be most important (Vincent 1982) in affecting predation rates, base color and blotching which appear to be the most variable feature among individuals of varying substrate types. Thus models were not intended to be photo realistic but rather exhibit extremes of *C. l. lepidus* variation present at local scales.

### **Field Sites**

A total of twelve sites, equally allocated between the eastern and western regions of the range of *C. l. lepidus* in Texas, were used (Table 1; Fig. 1). The eastern and western regions were split into northern and southern groups resulting in four sections: Northeast, Northwest, Southeast, and Southwest. Each section contained three sites (replicates) within relatively close proximity but with enough separation to avoid as much individual predator overlap as possible. A minimum of 10 km and a maximum of 100 km separated field sites within each section while a minimum of 113 km and a maximum of 333 km separate different sections. This design allowed me to test for differences in

response variables of the eastern and western regions which have contrasting phenotypes, as well as northern and southern sites within each region which do not have the contrasting phenotypes of *C. l. lepidus*. Finally, the distribution of field sites throughout each region was intended to provide insight into the degree of predation occurring on differing phenotypes over a large portion of the species range.

### **Predation Experiment**

To test the hypotheses that snakes with less cryptic color and blotching pattern are selectively preyed upon based on substrate type I set out groups of 40 models (N=10 per treatment) at each site. Models were placed in both regions, therefore the model color and banding type were designated as high or low contrast depending on the region (rooted in the differed substrate types) in which they were placed (*e.g.*, light gray models would be high contrast in the western region and low contrast in the eastern region; banded models would be high contrast in the eastern region and low contrast in the western region), and this is how models are described in the remainder of the paper. These designations were based on general knowledge of the species and Vincent (1982). As the banding differences among snakes from different regions are rooted in less defined and more complex aspects of substrate composition, no further analysis was done to confirm the presumed differences. However, *a priori* assumptions of color contrast were confirmed through the analysis of photographs. Models were placed at 12 locations for two-week durations. Individual models were secured to rocks with adhesive backed Velcro at approximately 10 m intervals within a designated area in typical *C. l. lepidus* habitat with model type randomly assigned for each placement. When possible, models were placed along a linear transect; and multiple transects were used to accommodate all 40 models

when a single linear transect was not possible. Models were placed on rocks with the lowest amount of overhead obstruction as possible. A total of 480 models were deployed.

Experiments were initiated during two time frames, between May 13<sup>th</sup> and May 18<sup>th</sup> and then between June 4<sup>th</sup> and June 10<sup>th</sup> of 2009. The first placement included all northern sites in both the eastern and western region while the second placement included all the southern sites. This was done to reduce the chance of extremes in weather influencing potential predation attempts more heavily in one region. Models were left in position for two-week periods at each site; therefore models were removed for analysis from May 27<sup>th</sup> to June 1<sup>st</sup> and from June 18<sup>th</sup> to June 24<sup>th</sup>.

Photos were taken of each model at the site of placement and when retrieved using either a Canon PowerShot SD600 or a Canon Digital Rebel XT. All models were numbered sequentially and their location marked on a Garmin 60Cx handheld GPS unit to ensure all model locations were easily found for retrieval. If potential predation was suspected, additional photos were taken and the model was set aside for further inspection. Damage to models was scored as breaks (Fig. 6A), pecks (Fig. 6B), bites (Fig. 6C), or questionable marks corresponding to any physical damage to the model that did not fit into the bite, peck, or break categories (Fig. 6D). Suspected avian attacks were characterized by breaks or pecks which were defined as triangle or circular punctures, as well as broken models when devoid of obvious bite marks. Non-predator disturbances included all damage to models that was not considered a predation attempt which included bites and questionable marks. The location of damage to the models was quantified by measuring the distance from the anterior end of the model to each damage instance on the model. In the case of a single mark on a model I measured from the tip of

the head to the predation mark. In the case of multiple marks on a model, I made the same measurement for each mark and then averaged the distances. To compensate for variations in model size, due to the few instances of tail breaks that had occurred pre-deployment and moderate shrinkage that occurred following molding, I divided attack distance for each model by the total length. Therefore, the lower the proportion, the closer to the head the attack occurred.

Region, section, replicate, color, and blotching type were the independent variables used in analysis. Replicate refers to individual field sites and was nested within section and region. Section refers to the four major areas in which field sites were located (a northern and southern area within the eastern and western regions) and was nested within region. Both color and blotching were crossed together as well as being crossed with region. Attack and non-predator disturbance data were analyzed with a general linear model under a Poisson distribution with a reciprocal link function with number of avian attacks and non-predator disturbances as the response variables (McCullagh and Nelder 1989). This analysis was used in order to ensure normality of reciprocals as a typical log transformation was not possible given the nature of count data and therefore a standard ANOVA was inappropriate. The Poisson distribution is ideal for analyzing rare events such as in this predation study where only a small percentage of the total number of models were attacked. A separate analysis of attack location data used a one-way ANOVA comparing distance of attack from the head as a proportion of the total length as the response variable and type of damage (Avian attack or Non-predator disturbance) as the independent variable. All analyses were done using JMP (Version 7.0.1. SAS Institute Inc., Cary, NC, 1989-2007). The Burro Mesa site located in Big Bend National Park

(BBNP) incurred damage to all 40 models. This damage was presumably inflicted by arthropods because all models incurred similar damage and damage was consistent with small bites encompassing the entirety of each model therefore, no data were used from this site during any analysis. Additionally, 19 missing models at the Point of Rocks site appeared to indicate human interference. This was assumed because loss of models did not occur at any other site, and Point of Rocks was the most publicly accessible of all the sites. I conservatively assumed that all missing models were undisturbed and the site was included in all analyses.

### **Photograph Analysis**

Photographs taken of models directly after deployment were analyzed in order to estimate contrast between models and the surrounding substrate. Photos from the Burra Mesa site which were not included in the predation experiment analysis were excluded, as were eight additional photos that were obstructed. In order to account for variation in lighting at the time each photo was taken, a S.I. Photonics 400 series UV/Vis Spectrophotometer (Model 420) with a single channel fiber optic reflectance probe was used to record the 8-bit RGB color values for the four treatments of model snake. RGB color values are presented as a series of three number values ranging from 0 to 255 for red (R), green (G), and blue (B). The spectrophotometer was calibrated with a 99% Spectralon diffuse reflectance standard to ensure accurate readings (SRS-99). Color was measured for the four model treatments at the head, mid-section, and tail and then averaged. These values were used to calibrate the color values of the photos. The 8-bit RGB color values of the models and substrate were estimated from photos using Adobe Photoshop CS4 (Adobe Systems; Mountain View, CA). Points on the photo,

corresponding to approximately the same location on the model as during the spectrophotometry analysis, were used to find an average color value of the model. Points used for the color values of the substrate were taken directly adjacent to the points on the model. Areas of shade or intense light that was noticeably different from the remainder of the photo were avoided.

In order to calibrate the photos, the color value for all models was replaced with the known color value found during the spectrophotometry analysis. The average color value of the substrate for each photograph was then scaled to the color value of the corresponding model, using the color values obtained from the photographs and the spectrophotometry analysis. An average value was obtained for the model and substrate based on the three readings. In order to determine contrast between the model and substrate I totaled the values of R, B, and G which resulted in a value range between 0 (black) to 765 (white). Although this value does not give an indication of the actual color it does give a single value representing the lightness or darkness of the color. Finally, I took the absolute value of the difference of the combined color value for the model and the substrates. The treatments were designated as either expected or unexpected based on what region the model was placed. A one-way ANOVA was performed using JMP (Version 7.0.1. SAS Institute Inc., Cary, NC, 1989-2007). The expected or unexpected designation was used as the independent variable and the difference of the model and substrate combined color values were used as the dependent variable. Additionally, color values of a live *C. l. lepidus* as well as a representative rock from the specimens locality were obtained (Appendix B).

## RESULTS

### Photograph Analysis

Analysis of 432 photographs indicated that models mimicking the race of the region in which they were placed were significantly more similar to the substrate than were models mimicking the alternate race ( $df=1$ ,  $F = 535.4733$ ,  $P < 0.0001$ ). There was no significant difference between each site or between the four sections (Northeast, Northwest, Southeast, and Southwest). There was however a significant difference between the eastern and western region ( $df=1$ ,  $F=262.0648$ ,  $P < 0.0001$ ).

### Predation Experiment

There were a total of 27 avian attacks and 28 non-predator disturbances on the 440 models over the 14 days of exposure. This equates to 12% of all models being attacked by either attacked by avian predators (6%) or disturbed by non-predators (6%). There were significantly more avian attacks when models exhibited high color contrast with substrate (Table 2, Fig. 9). No significant differences were found in the frequency of avian attacks or non-predator disturbances among any of the regions, sections, or sites (Table 1). There was no significant difference in avian attack or non-predator disturbance rates for the high and low contrast banding patterns (Table 2 and 3; Fig. 9). Additionally, there was no difference in non-predator disturbances of the high and low contrast models for color and blotching treatments (Table 3, Fig. 8 and 9). All 27 avian attacks and were used in the attack location analysis. Four of the 24 total non-predator disturbances were

excluded from analysis due to excessive damage to the models that made it difficult to determine attack location. Models that were determined to be attacked by avian predators were attacked significantly closer to the head than models damaged by non-predator (df = 1,  $F = 4.1549$ ,  $P = 0.0469$ ; Fig. 11).

## DISCUSSION

Results from the predation experiment indicate that there is a strong level of selective avian predation which favors color morphs of *C. l. lepidus* that closely match the surrounding substrate. This supports the hypothesis that selective predation maintains the varying color morphs. This however, does not refute the other hypotheses presented by Vincent (1982) but does indicate that selective predation likely plays a key role in the maintenance of this color polymorphism. In contrast, there was no indication that differences in blotching are affected by avian predation.

The substrates in both regions differed noticeably (Fig. 10). Additionally, the photograph analyses indicated that the models represented two significantly contrasting color morphs in relation to the distinct regions of differing substrate type. The contrast values comparing the model and substrate were also significantly different between the two regions. Given there was no statistical difference in predation attempts between the regions, and when the regions were analyzed independently, there was still a significant difference between expected and unexpected models, therefore this result should have no effect on the interpretation of the predation data.

Trail cameras, personal observations, and communications with other researchers studying *C. l. lepidus* allowed me to determine the presence of potential predators and non-predator disturbers at study sites. At least one predator was seen at each site during the course of model setup or retrieval, which encompassed at most six hours total, at any

one site. Predators observed included red-tailed hawks (*Buteo jamaicensis*), Swainson's hawk (*Buteo swainsoni*), common black hawk (*Buteogallus anthracinus*), and greater roadrunners (*Geococcyx californianus*). Non-predator species and species unlikely to attack rattlesnakes were also observed first hand or captured on trail cameras (Appendix C) at each site including gray fox (*Urocyon cinereoargenteus*), common ringtails (*Bassariscus astutus*), raccoons (*Procyon lotor*), Barbary sheep (*Ammotragus lervia*), porcupine (*Erethizon dorsatum*), black-tailed jack rabbit (*Lepus californicus*) and domestic goats (*Capra aegagrus*). It was apparent that some questionable damage to models was caused by Barbary sheep that had left hoof imprints in the foam (Fig. 6D). Some bite marks were chisel shaped that correspond with rodent teeth (Fig. 7). Avian predation attacks were also identifiable by marks left in the foam including defined beak marks and broken sections of models when no signs of non-predator disturbances were present such as bite marks. Unfortunately, identifying marks to particular predator species was not possible.

As previously mentioned, this study does not address two alternative hypotheses proposed for color polymorphism in *C. l. lepidus*. Although, this study cannot refute either hypothesis, I offer reasoning for why neither hypothesis is likely to be a primary factor contributing to color polymorphism of this species in light of the results of this study. Thermoregulatory effects, although possible, would ultimately be rooted in predation. If no risk of predation was present, then individuals would be free to move between hot and cool locations to best thermoregulate regardless of coloration. Detection by prey items is also unlikely to be a primary factor in the maintenance of color and pattern polymorphism due to the ambush technique utilized by many rattlesnake species

(Reinert et al. 1984). It is reasonable to assume detection by prey items would be of less importance to individuals hunting from hidden locations.

A main caveat of this study is that the level of confidence in distinguishing between predation attempts and non-predator disturbances cannot be assessed. However, the peck marks left in the models are similar to marks made on clay models in other artificial snake studies (Brodie 1993; Brodie and Janzen 1995; Bittner 2003). It is also unlikely that these marks would be made by other animals consistently given they are single or double strikes without additional damage. An animal such as a raccoon would most likely cause more damage, rodents have distinctly shaped teeth that were clearly identifiable on two models, and animals such as ungulates do not have the teeth or claws to make such marks.

The analysis of attack location indicated that marks noted as avian attacks were significantly closer to the head than marks made by non-predator disturbers. This result supports the distinction between predators and non-predator disturbers, as predators would be more likely to attack the head region in an attempt to kill the snake, whereas non-predators would make marks randomly. Additionally, an unpublished radio telemetry study with *C. l. lepidus* reported the death of three study animals between fall 2007 and fall 2009. One snake was found 2 m from a burrow the snake was found in two days prior with both his head and tail removed (Fig. 12). The investigator witnessed muscle contractions of the snake indicating a relatively recent death. The other two snakes were not found, but the implanted transmitters were located, indicating the snakes were killed and possibly eaten (Vincente Mata personal communication). These snake deaths occurred in an area where human contact is very unlikely. This indicates that *C. l. lepidus*

are preyed upon, and the nature of the attacks are consistent with the damage observed on models that were broken.

The absence of differing attack rates on the banding treatments raises additional questions. Given the sizeable difference in predation rates on the low and high contrast color treatments, it would appear likely that if selective predation was a cause of the different banding patterns in the two regions that some signal would have been observed, especially given the extremes in banding pattern which were used. However, one major variable not accounted for in this study was differences in snake behavior. All models were placed in open areas on rocks that corresponded with exposure that would occur during the course of movement between sites or basking in the sun for thermoregulation. This design does not account for exposure during varying amounts of time or at differing times of day. The differences in blotching patterns may be a product of selective predation, but if so the selection is rooted in differential behaviors or activity levels in the eastern and western regions. The correlation of differing behaviors and selective predation has been suggested in other taxa, but in experiments focusing more on varied micro-habitat selection particularly between sexes rather than large scale habitat difference over a species range (Forsman and Shine 1995). Additionally, it has been shown that different habitats, even in close proximity, can affect aspects of the ecology of *C. l. lepidus*. Beaupre (1995a, b, 1996) showed that energy budgets were notably different at two sites within BBNP with different habitat types which in turn affected the snake's behavior due to the different levels of energy available for the different populations. If Beaupre's studies hold true over the entirety of their range, especially in areas that have markedly different habitat types in both substrate and elevation, then

varied behavior in the different regions could, in conjunction with selective predation, be a factor contributing to the differential banding patterns.

While the maintenance of color polymorphism through sexual selection is widely documented (Seehausen et al. 1999; Maan et al. 2008) the maintenance of distinct color morphs through increased fitness of nonsexual behaviors has been demonstrated less often. Much work concerning evolutionary interactions of behavior and color polymorphism has focused on invertebrates (Kavaliers 1992; Forsman et al. 2002; Punzalan et al. 2005) with a smaller number of studies indicating this process in vertebrates (Brodie 1992; Forsman and Appelqvist 1998; Venesky and Anthony 2007).

Varying patterns have been shown to coincide with different escape mechanisms such as differing patterns on garter snakes (*Thamnophis ordinoides*) which cause optical illusions when undergoing certain movements aiding in escape potential (Brodie 1992). However, there is also the possibility that color and behavior interact in an analogous manner that increases the success of predation attempts. Animals such as rattlesnakes which are typically ambush predators may be more cryptic in a stationary position because their colors and patterns have evolved with a predominately sedentary behavior.

Isolation can also play heavily in this process. For example slight differences in behavior in *C. l. lepidus* may play a more pivotal role in their color polymorphism than in a more widespread species such as *C. atrox* which is found over a greater geographic range and in varying habitat types. Level of geographic isolation in conjunction with intra-species behavioral differences may play a major role in determining the level of color polymorphism present in a species. This concept is particularly relevant to poikilothermic organisms which often require being exposed to regulate body

temperature. Poikilotherms not only need to regulate their body temperature which can influence color to allow for optimum thermoregulation, particularly in species that bask in sun light, but they must also face predation risks while regulating their body temperature and therefore must modify their behavior for optimal survival depending on their particular process of thermoregulation (Downes and Shine 1998; Angilletta et al. 2002).

In summary, the work by Beaupre (1993, 1995a, b, 1996) indicates that behavioral as well as physiological differences are present between different habitat types along with Forstner et al.'s (1997) comments on the presence of varying color pattern based on habitat type rather than the clear cut defined regions presented by Vincent (1982) indicate that a combination of behavior, habitat, and isolation likely play a role in the banding polymorphism.

Table 1. Field sites for the artificial predation study; including location as well as dates for placement and retrieval of model snakes at each site. All field sites were located within the state of Texas and the experiment was completed within the year 2009. Sections refer to geographic orientation within West Texas, Northeast (NE), Northwest (NW), Southwest (SW), and Southeast (SE). CDRI = Chihuahuan Desert Research Institute; BBNP = Big Bend National Park.

Name (Section)	Location (County; Latitude, Longitude)	Start Date	End Date
Sonora I-10 (NE)	Sutton; 30.5766°, -100.6308°	13-May	27-May
Iraan 190 (NE)	Crocket; 30.8678°, -101.6384°	14-May	28-May
Sheffield 290 (NE)	Crocket; 30.6743°, -101.6757°	15-May	29-May
Dixon Property (NW)	Jeff Davis; 30.6132°, -104.1108°	16-May	30-May
Point of Rocks (NW)	Jeff Davis; 30.5350°, -104.0651°	17-May	31-May
CDRI (NW)	Jeff Davis; 30.5353°, -103.8444°	18-May	1-June
BBNP Burra Mesa (SW)	Brewster; 29.2341°, -103.3836°	4-June	18-June
BBNP Pine Canyon (SW)	Brewster; 29.2519°, -103.1940°	5-June	19-June
BBNP Grapevine (SW)	Brewster; 29.4039°, -103.1957°	6-June	20-June
Seminole Canyon (SE)	Val Verde; 29.7032°, -101.3125°	8-June	22-June
Amistad Rock Quarry (SE)	Val Verde; 29.4710°, -101.0262°	9-June	23-June
Amistad Hunt Area 5 (SE)	Val Verde; 29.4900°, -100.9125°	10-June	24-June

Table 2. Results of a general linear model under a Poisson distribution with a reciprocal link function with avian attacks as the response variable. Region = eastern and western areas designated by Vincent (1982). Section = the two regions broken into northern and southern groups. Replicate = individual field sites. Color = the coloration of models. Blotching = the presence or absence of blotching.

Source	DF	$\chi^2$	Prob > $\chi^2$
Region	1	0.1024	0.7489
Section [Region]	2	0.9427	0.6242
Replicate [Section, Region]	7	3.6146	0.8229
Color	1	18.2971	<0.0001*
Blotching	1	0.0848	0.7709
Color*Region	1	0.0974	0.7550
Blotching *Region	1	0.0514	0.8206
Color* Blotching	1	0.0749	0.7844

Table 3. Results of a general linear model under a Poisson distribution with a reciprocal link function with non-predator disturbances as the response variable. Region = eastern and western areas designated by Vincent (1982). Section = the two regions broken into northern and southern groups. Replicate = individual field sites. Color = the coloration of models. Blotching = the presence or absence of blotching.

Source	DF	$\chi^2$	Prob > $\chi^2$
Region	1	1.3948	0.2376
Section [Region]	2	1.2506	0.5351
Replicate [Section, Region]	7	12.0121	0.1002
Color	1	0.9099	0.3401
Blotching	1	0.4779	0.4894
Color*Region	1	0.4927	0.4827
Blotching *Region	1	0.5105	0.4749
Color* Blotching	1	0.0910	0.7629

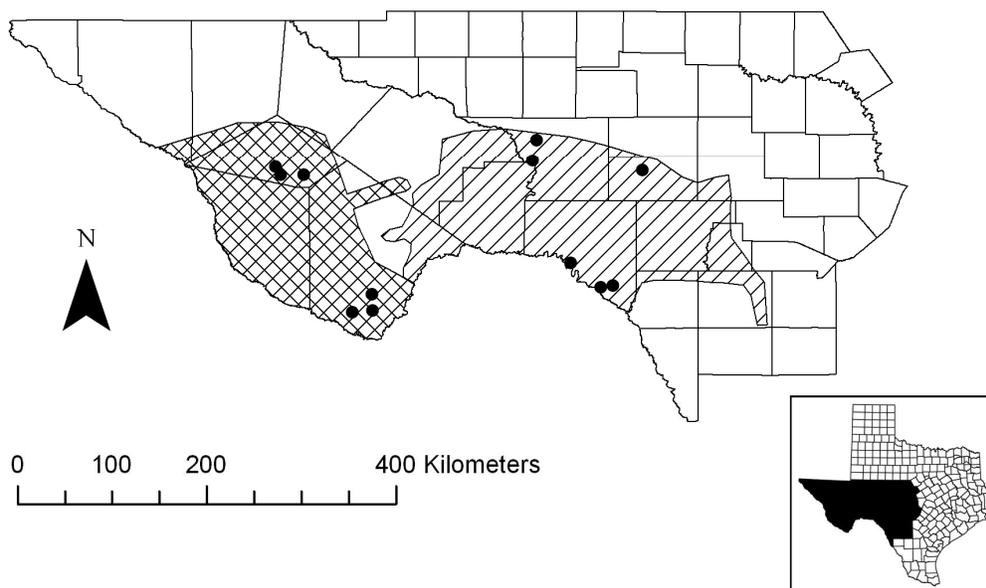


Figure 1. Map of southwestern Texas showing the ranges of the Stockton-Edward Plateau (Eastern) and Davis Mountains-Big Bend (Western) races described by Vincent (1982). The single hatched section represents the eastern races range in Texas and the double hatched section represents the western races range in Texas. Field sites for the predation experiment are indicated by black dots; refer to Table 1 for more detailed site information.



Figure 2. A side by side comparison of two live *Crotalus l. lepidus*. The light colored snake on the left is from Edwards County in the eastern portion of their range. The dark colored snake on the right is from Brewster County in the western portion of their range. Both specimens are part of the collection maintained by Michael Price at the San Angelo Nature Center, located in San Angelo, Texas.

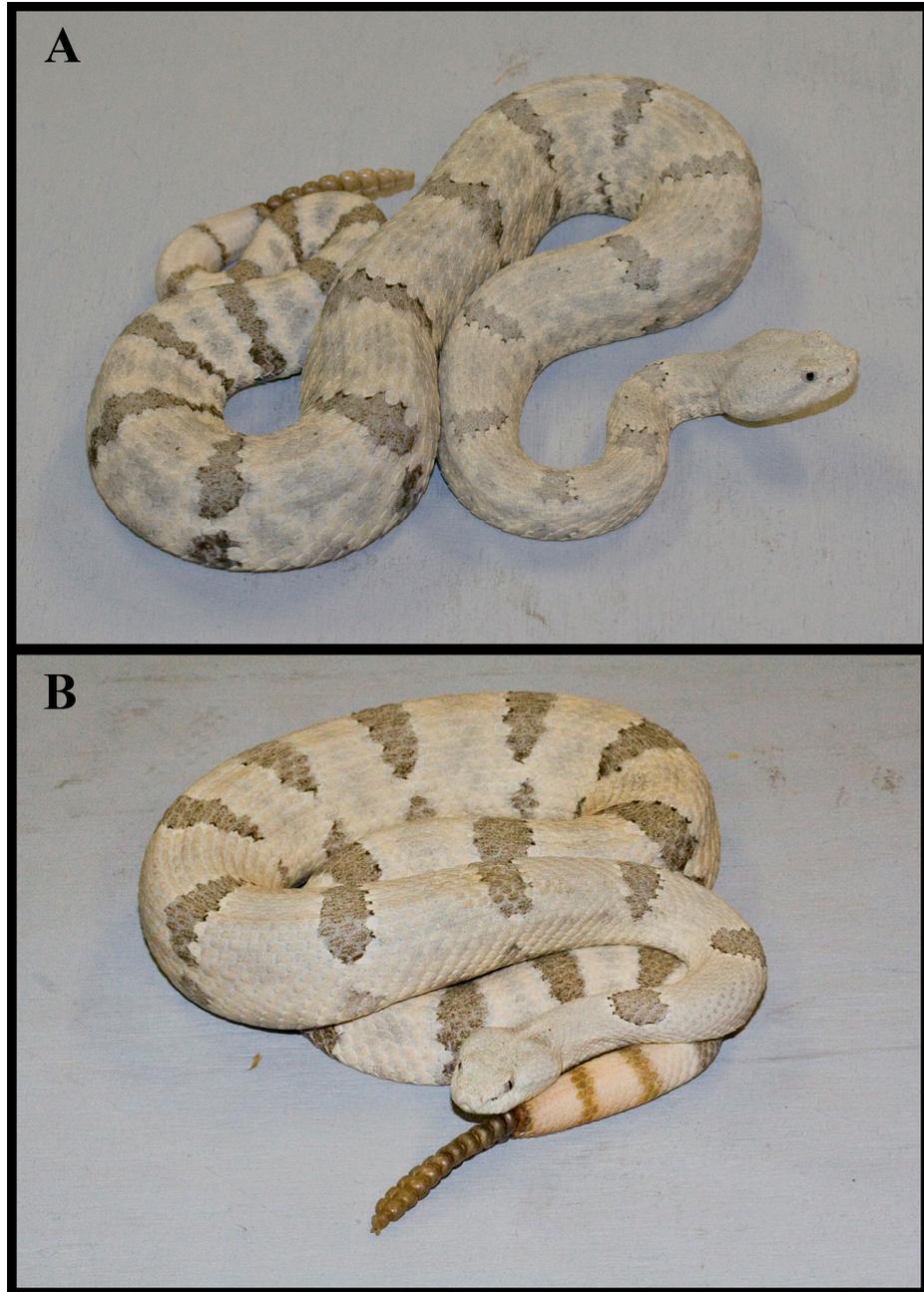


Figure 3. Two live specimens of *Crotalus l. lepidus* from the eastern portion of their range located on the Edwards-Stockton plateau in western Texas. A) Specimen from Sanderson City Park in Terrell County. B) Specimen from near Rocksprings in Edwards County. Both specimens are part of the collection maintained by Michael Price at the San Angelo Nature Center, located in San Angelo, Texas.

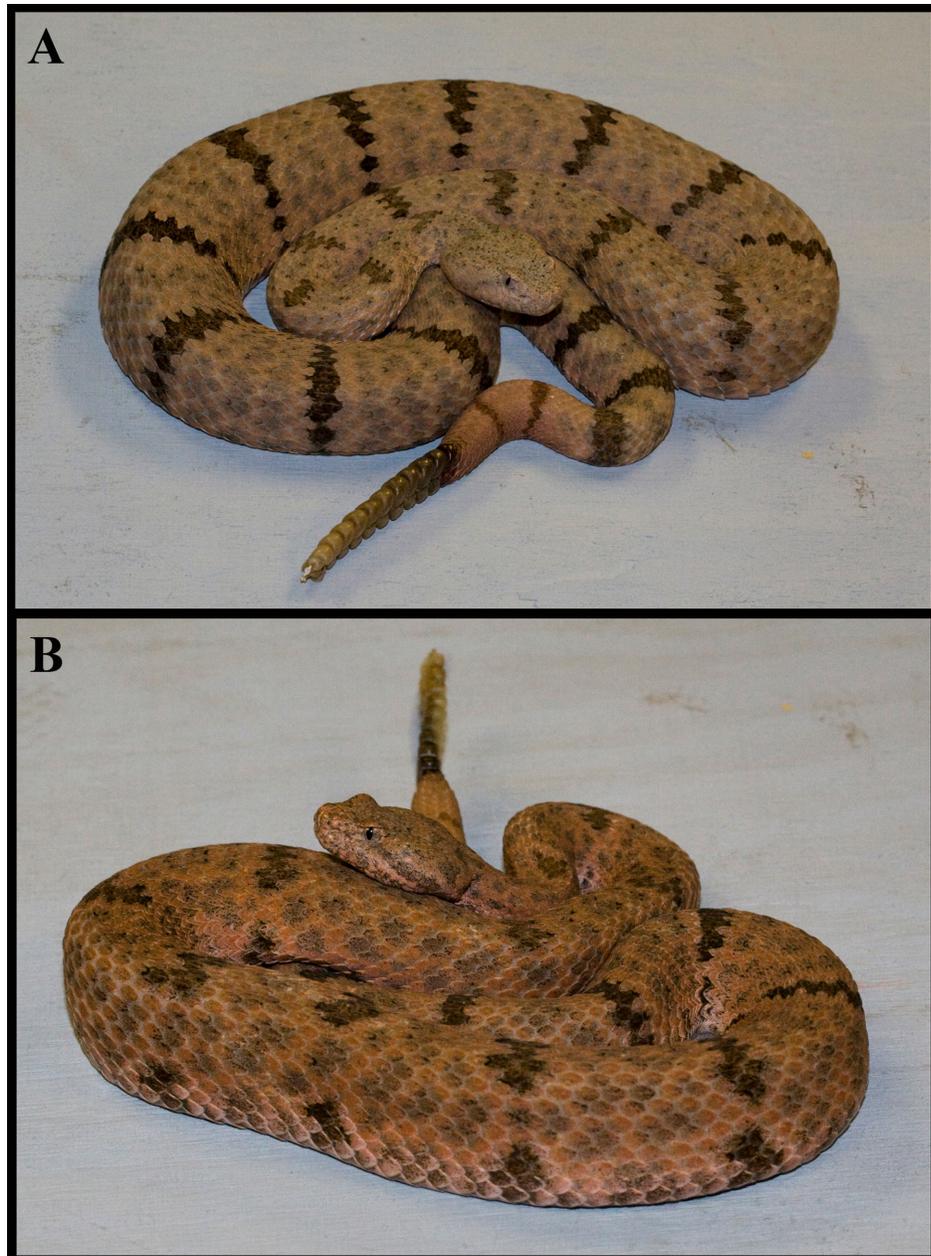


Figure 4. Two live specimens of *Crotalus l. lepidus* from the western portion of their range in the Big Bend region of Texas. A) Specimen from Quitman Pass south of Sierra Blanca in Hudspeth County. B) Specimen from west of Valentine in Presidio County. Both specimens are part of the collection maintained by Michael Price at the San Angelo Nature Center, located in San Angelo, Texas.



Figure 5. Photograph of the four treatments of model snakes representing the phenotypic extremes of *Crotalus l. lepidus* found in eastern and western regions of west Texas; refer to Fig. 1. The treatments are as follows from left to right, eastern unblotched, eastern blotched, western unblotched, and western blotched.

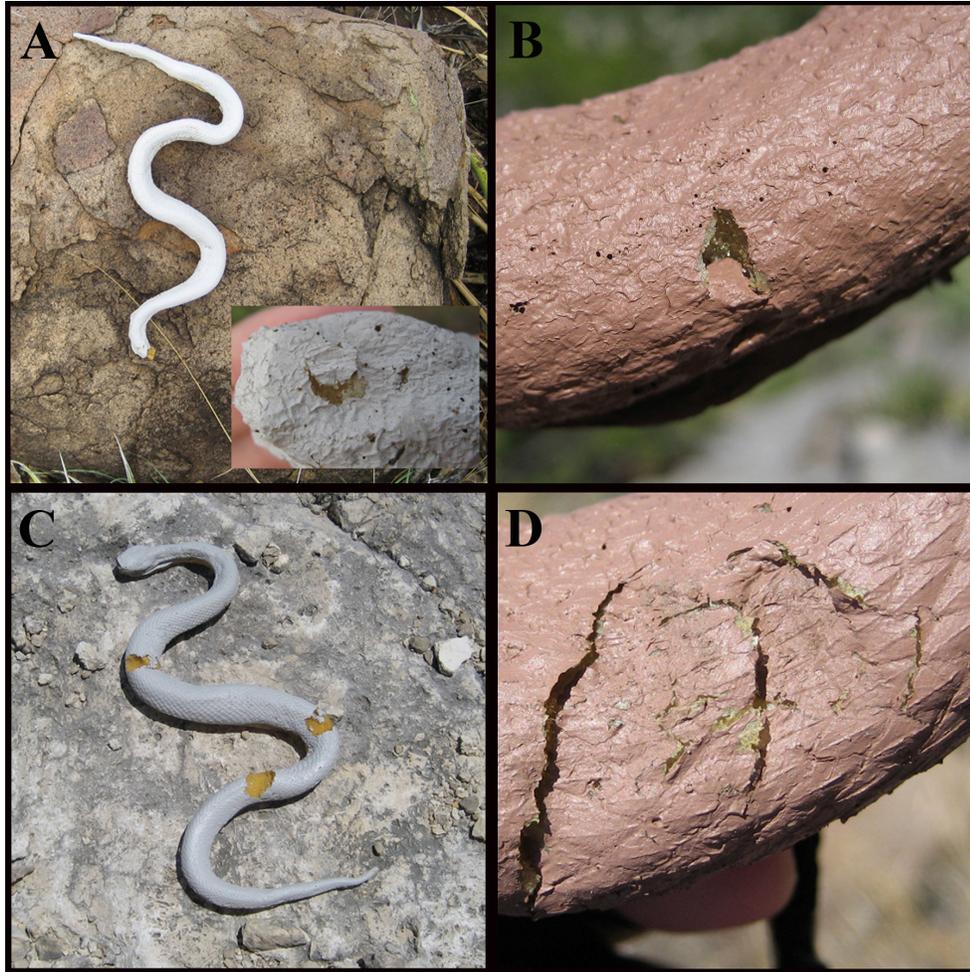


Figure 6. Examples of damage to model *Crotalus l. lepidus* during the course of the model predation study. All photos show damage on the dorsal surface of models. A) An example of a decapitated model, note the decapitated head in the bottom right hand corner which has a single peck mark in the center. Typically models found with breaks were either decapitated or broken in several locations. B) An example of a model showing a peck mark. Peck marks include single circular and triangular marks such as the one shown in this photo and also pairs of triangle shaped pecks indicating an open beak. C) An example of a model showing bite marks. Bites were either full round chunks removed from the model or the impression of teeth marks left in the model. D) An example of a model showing a questionable mark. In this case it is clear that a Barbary sheep (*Ammotragus lervia*) had stepped on the model. However, other questionable attacks include potential arthropod damage and incidences where it was unclear if an avian or non-predator attack occurred.



Figure 7. A comparison of a porcupine (*Erethizon dorsatum*) skull and bite marks on a foam model. The photo demonstrates the similarity of the teeth shape to the bite marks. This particular skull is slightly larger than the bite marks, but it is possible the marks were caused by a smaller porcupine or that a smaller rodent with a more compact set of incisors took two bites of the model. Additionally, not shown, are the corresponding marks made by the lower jaw on the opposite side of the model.

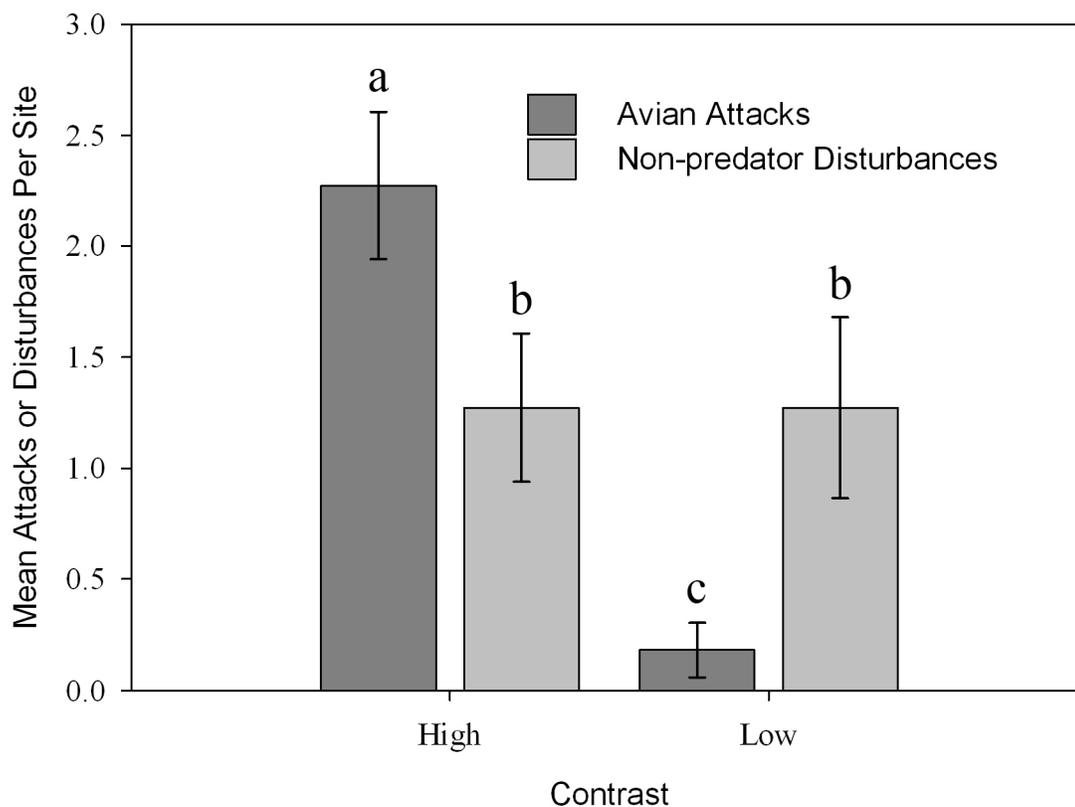


Figure 8. Mean avian attacks (dark bars) and non-predator disturbances (light bars) on artificial snake models per site during the course of the artificial predation study based on color treatment. High contrast indicates the model was painted to represent the dominant color of the opposite region of the site in which the model snakes were placed. Low contrast model were painted to represent the dominant color of the opposite region of the site in which the model snakes were placed. (e.g. light grey models which are representative of the eastern race are considered high contrast within sites of the western region and low contrast in the eastern region). Different letters above bars indicate significant differences.

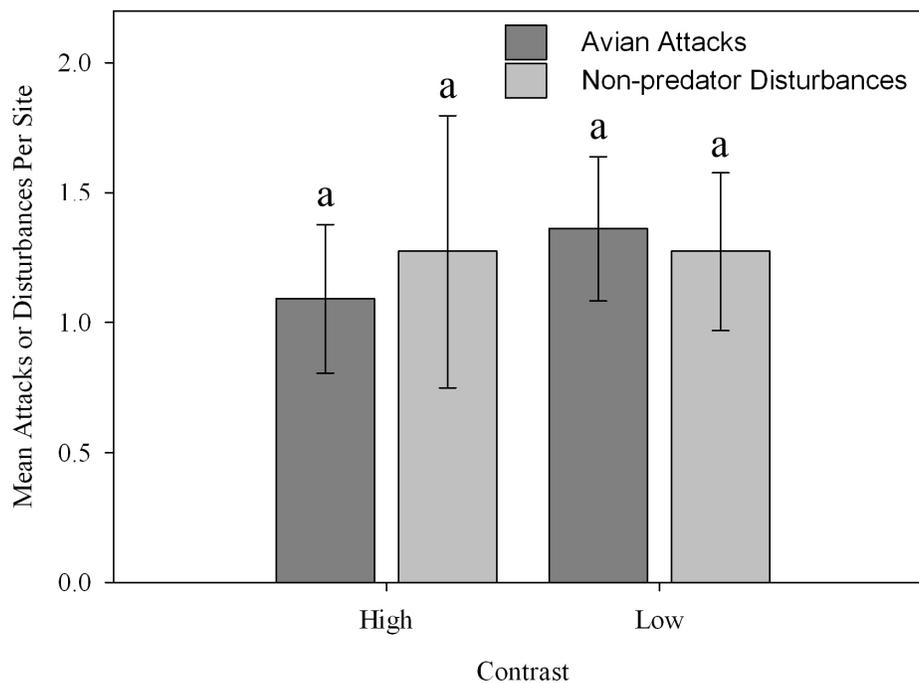


Figure 9. Mean avian attacks (dark bars) and non-predator disturbances (light bars) on artificial snake models per site during the course of the artificial predation study based on blotching treatment. High contrast indicates the model was painted to represent the blotching pattern associated with the opposite region of the field site in which snake models were placed. Low contrast models were painted to represent the blotching pattern associated with the region of the field site in which snake models were placed. (e.g. Blotched models which are representative of the western race are considered high contrast within the eastern region and low contrast in the western region). Different letters above bars indicate significant differences.

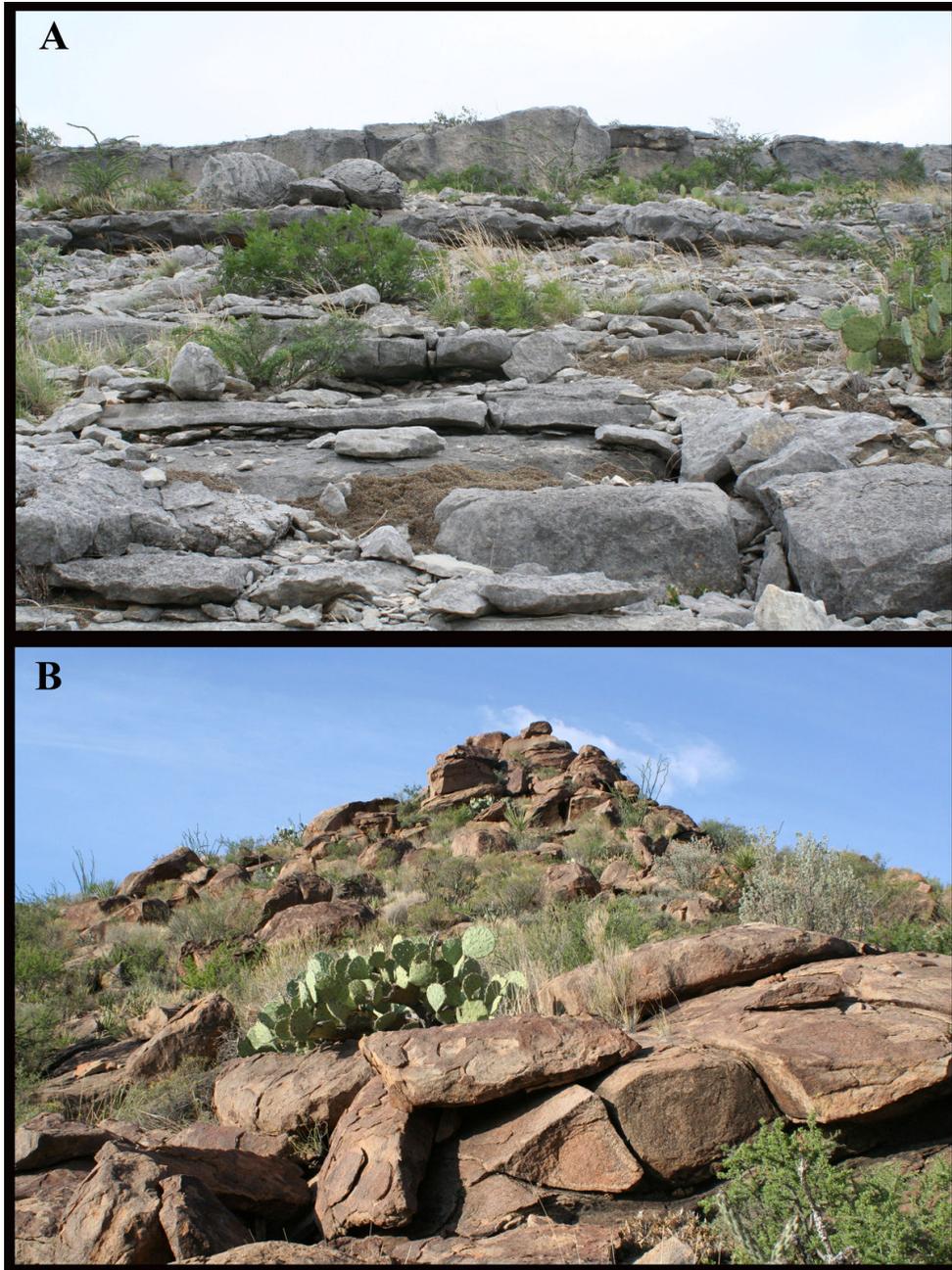


Figure 10. Photo examples of the habitat types present in the eastern and western regions of the *Crotalus l. lepidus* range proposed by Vincent (1982). Both photos were taken at field sites used in the artificial predation study. (A) Seminole canyon field site. (B) Grapevine hills field site. Further information about both field sites can be found in Table 1.

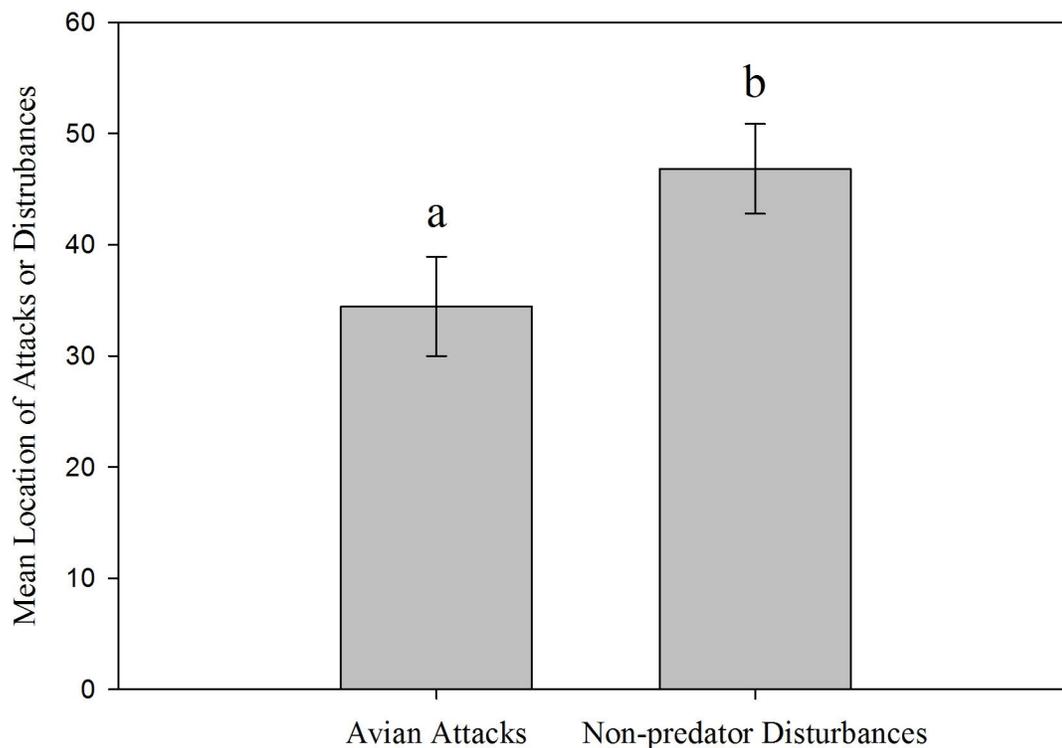


Figure 11. Representation of the location of damage caused by predators and non-predators the artificial predation experiment. The Y axis shows the percentage down the body in which an attack occurred. Therefore, the higher the number the closer to the posterior end of a model an attack occurred, while a lower number indicates an attack closer to the head of the model. Mean percentage down the body for predator damage was 34.43% and 46.81% for non-predator damage. Different letters above bars indicate significant differences.



Figure 12. Photograph of a *Crotalus l. lepidus* which was killed during a study conducted by Vincente Mata at the Indio Ranch Research Station in far west Texas. The predation was not witnessed but the snake was found still exhibiting muscle contractions indicating a recent death. Additionally, the snake is not in an area in which it was likely to encounter humans. Photo courtesy of Vincente Mata.

## APPENDIX A

### Preliminary Model Tests

Eighty models made out of Reoflex 30 urethane rubber were constructed using the same technique presented in the methods section used to construct the urethane foam models in order to determine if rubber was a potentially viable material for this experiment. Eighty rubber models were set out during July and August 2008 at the Sheffield field site (Table 1). These models were secured by tying fishing line to the models and to a tent stake that was hammered into the ground. The intent of this initial test was to a) determine if predators would attack models and, b) determine if marks would be captured by the rubber.

The preliminary tests with rubber models indicated that rubber was more difficult to paint and offered little possibility for predation marks such as teeth or beak imprints. The rubber was also not resistant to heat and UV exposure which resulted in models becoming discolored and cracked. The biggest drawback was only model displacement can be categorized as an attack which offers no way to verify if an attack occurred or if some other force caused the model disturbance. One beneficial result from the preliminary test of the rubber was that models did appear to be disturbed, which indicated that with the proper material attacks could be verified. Modeling clay, which has been used extensively in studies using artificial snakes, was determined to not be an ideal medium for this experiment because the extremely hot and dry habitat of *C. l. lepidus*

would have resulted in hardened clay that would have been useless in determining potential predators or if a predation attempt had occurred.

Foam models were not tested in the same manner as the rubber models in the field, but were exposed to varying weather conditions such as rain and intense heat to mimic meteorological extremes they may experience during the course of the study. Urethane foam was easily painted and stood up to extreme temperatures for extended periods of time. Most importantly the foam was strong enough to endure storage and transport to sites but brittle enough to leave defined marks and/or break when attacked. This allowed me to separate predation attempts from damage caused by non-predators. These tests indicated urethane foam was the most appropriate material for the purpose of my study.

Foam models were lightweight and therefore were secured to prevent accidental displacement by non-predators and abiotic factors. Two sets of male and female sided strips of industrial strength Velcro were attached to the models using the adhesive backing of the male side prior to visiting each site. The adhesive of the female side was then used to attach the models to rocks. To ensure that this method would secure the models I performed three tests. First, to ensure the attached models could withstand high wind speeds, I subjected the setup to various wind speeds by holding the rock with attached model out the window of a moving vehicle. To prevent the model from coming completely detached, a small string was tied around the model and the rock. I then tested for displacement at gradually increasing speeds ranging from 0-80 kph. Second, I placed attached models outside for two weeks in which they were exposed to the elements, including one rainstorm. Finally, I placed attached models under heat lamps which

caused the models to reach temperatures as high as 82°C for six hours every day for two weeks. The models, adhesive strips and Velcro all remained intact and secure during all tests, confirming the reliability of this method.

## APPENDIX B

### Spectrophotometry

Color values were obtained from a live *C. l. lepidus* kept in the collection of Michael R.J. Forstner originally obtained from nearby the Sheffield study site (Table 1). Color values were also obtained from a rock from this locality using similar methods to the spectrophotometer procedures discussed in the methods section. Five points, chosen haphazardly, were used to obtain the average color value for the rock. The values for the live specimen were taken in the same manner as the values for the banded models, with one exception. A point on the snake's neck was used in lieu of a point on the head to maintain safety of the experimenters. The average color value for the rock was 59.246 (R=21.071; G=20.997; B=17.178). The average color value for the live specimen's body was 89.9633 (R=29.970; G=30.623; B=29.370) and for the blotches was 88.732 (R=29.691; G=30.514; B=28.528).

Despite the difference in the combined color values, the calibrated substrate values from the photograph analysis indicate that there is considerable variation at this study site and many of the locations in which models were placed have color values that are more comparable to the color value of the live specimen than the particular rock used for this analysis. A more intensive spectrophotometry study was not performed due to the logistics of getting a representative sample of rocks back to the lab for

spectrophotometer analysis as well as an inability to capture *C. l. lepidus* during the course of the study.

## APPENDIX C

### Field Cameras

Game cameras were used to observe potential disturbances as well as determine potential predators and disturbers which encountered models. Three Cuddeback No Flash game cameras were placed with models at the Chihuahuan Desert Research Institute (CDRI) located six km south of Fort Davis, Texas. CDRI was chosen because it was relatively secure site which decreased the chance of camera theft or vandalism. The subsequent high rate of predation that occurred at the site during the predation experiment made this an ideal location for the cameras. Cameras were attached to 1.2 m “U” posts with plastic zip ties and an elastic band. Cameras were placed approximately 3 m from the model snakes and left for 3 intervals of 14 days, 18 days, and 60 days between checking.

Field cameras documented no predation attempts and one non-predator disturbance. The non-predator disturbance involved a Barbary sheep (*Ammotragus lervia*), biting a model multiple times. Additionally, many other species of animals such as gray fox (*Urocyon cinereoargenteus*), common ringtails (*Bassariscus astutus*), Barbary sheep (*Ammotragus lervia*), and porcupine (*Erethizon dorsatum*) were captured by the cameras in the presence of the models but there was no noticeable disturbance to the mode

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