SEXUAL DIMORPHISM IN THE *Sceloporus undulatus* SPECIES COMPLEX

A Thesis

by

DREW EDWIN DITTMER

Submitted to the Office of Graduate Studies of
Texas A&M University
in partial fulfillment of the requirements for the degree of

MASTER OF SCIENCE

August 2012

Major Subject: Wildlife and Fisheries Sciences

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Approved by:

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	Lee A. Fitzgerald
Committee Member,	James B. Woolley
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ABSTRACT

Sexual Dimorphism in the *Sceloporus undulatus* Species Complex.

(August 2012)

Drew Edwin Dittmer, B.S., University of Missouri-Columbia

Co-Chairs of Advisory Committee: Dr. Toby J. Hibbitts
Dr. Lee A. Fitzgerald

The Fence Lizard (*Sceloporus undulatus* complex) is a wide ranging North American species complex occurring from the eastern seaboard westward through the great plains and central Rocky Mountains and into the American Southwest. A recent phylogeny suggests four species lineages occur within *S. undulatus*. Traits within an interbreeding species that are influenced by sexual selection are under different selection pressures and may evolve independently from the selective forces of habitat. *Sceloporus* lizards have several characters that are influenced by sexual selection. I investigated sexual size dimorphism and allometric relationships of body size (snout vent length), torso length, rear leg length and three measurements of head size in 12 populations from the four species in the *S. undulatus* complex (N=352) specifically looking for variation among the 4 species. Additionally I investigated the size of signal patches between males and females in three species (N=339 specimens of *S. consobrinus, S. cowlesi, S. tristichus*) of the *S. undulatus* complex. Sexual confusion, was recently described in a population of the *Sceloporus undulatus* complex occurring in White Sands, New Mexico and the behavior is correlated with variation in badge size

between male and female lizards. To make inferences about sexual confusion at the species level I investigated the presence and absence of signal patches in female lizards, and compare the sizes of signal patches between males and females. My analyses suggest that torso length and head size are significant sources of sexual size dimorphism but the findings differ from earlier published investigations of sexually dimorphic characters in the species complex. I also find support for the *S. undulatus* complex being generally a female larger species complex. However two of the 12 populations I investigated displayed male biased sexual size dimorphism. Analysis of signal patches across three species of the *S. undulatus* complex suggests that sexual dimorphism in signal patch size for *S. cowlesi* and *S. tristichus* may not prevent sexual confusion. While the near total absence of signal patches in female *S. consobrinus* is evidence that sexual confusion is not possible with regards to signal patches.

DEDICATION

This thesis is dedicated to my grandfather Wilbur Edwin Meinershagen. He always supported my interest in reptiles and amphibians and when I was 11 years old he helped me capture my first *Sceloporus* lizard in New Mexico. He was also the best listener I've ever known.

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Finally I wish to thank Dr. Douglas A. Eifler and his wife Dr. Maria Eifler. Doug and Maria have included me on much of their field research sense 2003. Doug and Maria encouraged me pursue an advanced education studying reptiles and amphibians and are

two of the most genuine people I have ever known. I would not have made it in this far

without their mentorship, guidance, and support.

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CHAPTER I

INTRODUCTION

Phenotypic differences between males and females are known as sexual

dimorphisms. These differences in most cases cannot be explained by natural selection.

Darwin (1871) proposed the theory of sexual selection to explain sexual dimorphism.

Three patterns of sexual dimorphism are commonly observed. The first and often easiest

to observe is the asymmetry in size between sexes or sexual size dimorphism (SSD). The

second is the presence of weapons such as antlers or horns which are often referred to as

armaments. The third common dimorphism is the presence of conspicuously colored

scales, feathers, fins or hair, referred to as ornaments. All three of these dimorphisms can

occur simultaneously. Commonly these dimorphisms are described as signals, which

presumably communicate some aspect of individual fitness to (Hibbitts et al. 2007). An

important question surrounding these signals is what these signals are advertising and to

what audience are the signals being directed.

Signals that are considered armaments are generally used in male-male contests

(Andersson 1994). In regards to SSD in species where males are larger than females,

size in and of itself can be advantageous in contests for females (Darwin 1871; Ghiselin

1974) and may also function as an armament. The form of male-male competition

known as endurance rivalry can be explained in a SSD context as larger males are able

to defend larger territories, engage in more territorial disputes and

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This thesis follows the style of Journal of Herpetology.

therefore breed with more females (Andersson 1994). Armaments and SSD can also be signals that are subject to the selective forces of female choice. Females may choose to breed with larger males or males with the best armaments as males possessing superior traits may be signaling their physical condition, foraging ability, or they may be defending territories that have the best resources for the female's offspring (Andersson 1994)

Assuming females to be the discriminating sex, male-larger SSD is easily explained within the bounds of sexual selection, but female larger SSD is more complex and difficult to explain. Additionally there are no known cases among vertebrate species where females possess armaments that are larger than those of males, or where armaments are absent in males but present in females. Furthermore female larger SSD is the most common pattern of SSD among vertebrates and is rarely explained by sex role reversal, where large females compete for breeding access to males (Andersson 1994; Fairbairn 2007). Large female size is best explained as contributing to an increase in reproductive output. This is not necessarily a sexually selected trait (Andersson 1994) and is most commonly explained by the female fecundity advantage hypothesis, where larger females are able to produce either more or larger offspring (Darwin 1871; Ghiselin 1974; Andersson 1994). However in some cases males may actually select larger females (Côte and Hunte 1989), and in these instances both sexual selection and fecundity selection may be acting in concert. Additionally it has been shown that growing to a larger size takes time and energy and larger females may not have higher reproductive success over their lifetimes (Shine 1988). Further complicating female SSD

is the small male advantageous hypothesis. Small male size may be advantageous in scramble competitions, where small males mature earlier and find females faster. Small male size may also be beneficial in resource poor environments, where fewer resources are required to actively seek females (Andersson 1994).

Sexual Size Dimorphism and armaments are challenging to explain when considered from a female perspective. Armaments play a direct role in settling disputes, compared to ornaments which have been described as being uncostly to produce, and can be manipulated to deceive conspecifics (Whiting et al. 2003). The examples of signal based deception are numerous (Warner 1984; Gross 1991; Sinervo and Lively 1996). Much of the research on ornaments as signals has focused on their function in sexual selection contexts and has normally taken a decidedly male perspective. However, like SSD, signals can also be subject to selective forces other than sexual selection(Ryan et al. 1982), and signals are observed in females of many species. Lizards, in particular have been the focus of studies investigating the function of conspicuous color signals in females (Stuart-Fox and Whiting 2005; Chan et al. 2009). In many lizards conspicuous colors are sexually dichromatic, and females bear the strongest coloration while they are gravid (Vinegar 1972; Cooper 1984; Jones and Lovich 2009). Research has found support for the rejection hypothesis, where gravid females display these signals to courting males in an effort to avoid unnecessary copulation (Vinegar 1972; Cooper 1984; Chan et al. 2009).

While some female lizards have conspicuous colors strongly associated with the gravid condition, other lizards, including the genus *Sceloporus,* have similar conspicuous

signal patches in males and females. Specifically, in the four species of the *Sceloporus undulatus* complex, blue and black signal patches are present on the throat and belly. These signal patches are common in both males and females in at least two of the four species (*S. cowlesi* and *S. tristichus*). A field investigation by Robertson and Rosenblum (2010) investigated signal patches in *S. cowlesi* and described a behavior that is termed "sexual confusion", which is related to the overlap in signal patch size of males and females (2010). In *S. cowlesi* sexual confusion occurs when resident male confuses another male as a female. There are a couple of studies reporting male lizards interpreting conspecific males as females and courting or even breeding with them (Noble and Bradley 1933; Vinegar 1972), but Robertson and Rosenblum's 2010 work is the first to quantify and correlate the behavior to the variation in a sexually dichromatic signal.

Prior to 2002, the *Sceloporus undulatus* complex was considered to be one species with as many as ten subspecies occurring from the eastern and gulf coasts of the United States to the Rocky Mountains and the American southwest. Leaché and Reeder (2002) identified four species within the *S. undulatus* complex, (*S. undulatus, S. consobrinus, S. tristichus* and *S. cowlesi*) and no subspecies are presently recognized (Leaché 2009). Therefore the *S. undulatus* complex is an excellent group to explore SSD patterns at a large geographic scale and to explore the labile nature of sexual dimorphism (Cox et al. 2009). There are very few Broad scale investigations of SSD across geographically wide ranging species or genera (Roitberg 2009), and the *S. undulatus* species complex offers the opportunity to look for patterns of sexual dimorphism of

sexually selected traits that occur in a species with stereotyped territorial defense (Cooper Jr and Burns 1987). *Sceloporus undulatus* species complex has been a model organism for investigations of Sexual Size Dimorphism (SSD) as well as studies addressing evolution, ecology and morphology (Haenel et al. 2003; Pinch and Claussen 2003; Robertson and Rosenblum 2010). The recognition of four species within the *S. undulatus* species complex provides an opportunity to describe variation in SSD within each one of these species and to look for patterns that may have been obscured by considering *S. undulatus* as a single widespread species with multiple subspecies (Vinegar 1975; Fitch 1978).

Herein I describe my approach to investigate sexual dimorphism of body size, sexually selected morphological characters and conspicuously colored signal patches among the four species of the *Sceloporus undulatus* complex. My project has two major objectives that will be addressed in two chapters. First I will describe sexual size dimorphism (SSD) and the sexual dimorphism of selected traits in the *S. undulatus* species complex. Specifically, I will determine if patterns of SSD and the relationship of head size to body size are consistent within the newly described clades of the *S. undulatus* species complex. Also, I will determine if support for the female fecundity advantage and small male advantage hypotheses exists within the species complex. Second, I will quantify the size of signal badges in three species of the *S. undulatus* complex, *S. consobrinus*, *S. cowlesi*, and *S. tristichus*. I will compare my findings to those of Robertson and Rosenblum (2010) and determine if similar overlap in badge size among the three species and between males and females with in species provides

evidence of sexual confusion in populations other than that observed by Robertson and

Rosenblum (2010).

CHAPTER II

VARIATION IN SEXUAL SIZE DIMORPHISM AMONG 4 SPECIES IN THE

Sceloporus undulatus SPECIES COMPLEX

Introduction

Patterns of sexual dimorphism can evolve through natural selection, sexual selection, or fecundity selection. Most commonly SSD evolves due to sexual selection (Darwin 1871). This primarily occurs in two ways: by contest competition between members of the same sex or by mate choice where in most cases females select males based on secondary sexual characters (Andersson 1994). Another common source of SSD is through fecundity selection (Darwin 1871). This occurs when females have secondary sexual characters that develop to accommodate increased fecundity of females such as increased torso length or width enabling a female to carry more or larger eggs. Sexual size dimorphism can also develop through natural selection (Andersson 1994; Wikelski and Trillmich 1997; Székely et al. 2000). For example, males and females of file snakes have extreme differences in adult body size that is best explained by dietary differences between the sexes (Houston and Shine 1993).

In species where males are the larger sex (male-biased SSD) or where males have weapons (e.g. horns, claws, or increased muscle mass), contest competition favors the larger individual or the larger weapon (Darwin 1871; Ghiselin 1974). The winner of such contests contribute their genes for larger body size or larger weapons to the next generation resulting in male-biased SSD (Ghiselin 1974; Lindenfors et al. 2009). Females may also show a preference for males that are larger or that have larger

weaponry, which could lead to male-biased SSD, but this has received little attention due to the difficulty of determining a female's preference and the difficulty of disentangling selection for male-biased SSD via contest competition (Andersson 1994; Olsson et al. 2002; Hibbitts et al. 2007).

While male-biased SSD can generally be explained by sexual selection, across all animals females are usually the larger sex (Andersson 1994; Fairbairn 2007). The dominant explanation for female-biased SSD is the female fecundity-hypothesis, where larger females can produce more and or larger offspring (Darwin 1871). Female-biased SSD due to the female fecundity hypothesis occurs occasionally in a few mammals such as baleen whales, vespertilionid bats and hares (Ralls 1976). In birds like wading birds and some predatory birds, female-biased SSD is fairly common (Andersson 1994). Fish and amphibians are largely female-biased (Andersson 1994; Fairbairn 2007). In reptiles turtles are the group with the most consistent pattern of female-biased SSD (Andersson 1994; Cox et al. 2009). Female-biased SSD is also supported by the small male advantage hypothesis, where smaller males have a selective advantage because they require fewer food resources and are able to mature earlier and can therefore devote more resources towards acquiring mates. Examples of this hypothesis have been found most commonly in fish, butterflies and endoparasites (Ghiselin 1974; Andersson 1994).

Among the vertebrates, reptiles are popular organisms for studies of SSD, and provide a variety of opportunities to study the selective forces operating on male-biased and female-biased SSD. Lizards generally show male-biased SSD, but the alternative is not unusual (Cox et al. 2009) and except for studies of a few species (Pianka and Parker

1975; Zamudio 1998) reasons explaining female-biased SSD are understudied in lizards (Andersson 1994; Cox et al. 2009). Morphological characters associated with contest competition and fecundity selection are most commonly observed to exhibit SSD in lizards (Sugg et al. 1995; Herrel et al. 1999; Herrel et al. 2001; Olsson et al. 2002). A few studies have attempted to describe the variation in SSD across wide spread genera or species (Fitch 1978; Hibbitts et al. 2005; Roitberg 2009), but most studies of SSD in lizards have focused on the mechanisms and processes that influence SSD patterns within localized lizard populations (Shine et al. 1998; Cox 2005; Cox 2007; Kratochvíl and Frynta 2009). In particular, the lizard species *Sceloporus undulatus* has been a model organism for investigations of SSD as well as studies addressing evolution, ecology and morphology (Haenel et al. 2003; Pinch and Claussen 2003; Robertson and Rosenblum 2010). Prior to 2002 *Sceloporus undulatus* was considered one species occurring from the eastern and gulf coasts of the United States to the Rocky Mountains and the American southwest. The use of molecular systematics has helped to identify four species within the *S. undulatus* complex (*S. undulatus, S. consobrinus, S. tristichus* and *S. cowlesi*) (Leaché and Reeder 2002; Leaché 2009). An improved phylogenenetic hypothesis offers the opportunity to describe variation in SSD and to look for patterns that may have once been confounded by the historical taxonomy of the group (Fitch 1978).

My study targets the variation in snout-vent length (SVL), rear leg length, torso length and three measurements of head size to quantify patterns of SSD within the 4 species of the *S. undulatus* species complex. I aim to determine if these species display

female-biased or male-biased SSD, and if traits normally associated with contest competition (head size) show positive allometry in males. For support of the small-male advantage hypothesis I expect females to be the larger sex, and in males I expect isometry or negative allometry of traits associated with female fecundity and contest competition. For support of the female-fecundity advantage hypothesis I expect to see positive allometry of torso length and female-biased SSD in SVL . My analyses identify species-specific patterns of variation in SSD that are likely attributable to different selective forces acting on populations of the 4 species.

<div align="center">Materials and Methods</div>

Previous published information on size at sexual maturity of both males and females on the formerly wide ranging S. undulatus (Tinkle and Ballinger 1972; Cooper and Vitt 1989) is no longer accurate in light of the recent phylogenetic hypothesis that splits the *S. undulatus* species complex into four species (Leaché and Reeder 2002). . Therefore, I chose to use Q-Q plots to cull small lizards from my samples prior to conducting any additional analyses. A Q-Q- plot can be used for assessing one dimensional data sets to identify outliers and to assess the normality of a data set distribution (Wilk and Gnanadesikan 1968). I checked Q-Q plots with SVL paired against each morphological measure; individual outliers that represented small lizards were culled from our sample.

I measured 6 morphological characters on 179 female and 173 male museum specimens on the S. undulatus complex. The following measurements were taken on each lizard using digital calipers: snout-vent length (SVL), head length (HL), head depth

(HD), head width (HW), torso length (Torso), and right rear leg length (RRL). All measurements were natural log-transformed prior to analysis. For each of the four species I chose three populations (n=12 total populations). I chose populations based on maps in Leaché and Reeder (2002). To quantify SSD and to determine male-biased or female-biased SSD I used the size dimorphism index (SDI) described in Lovich and Gibbons (1992) ((larger sex/smaller sex)-1)). The SDI is preferable to other methods that quantify SSD because the results are symmetrical around 0 and directional (Roitberg 2009).

To determine the morphological characters that express the most variation I used Microsoft Excel® with the PopTools add-in (Hood 2010) to perform a principle components analysis (PCA) on the size measurements. The PCA has been used to describe patterns of sexual dimorphism in lizards (Zamudio 1998) and results from PCA informed my choice of which morphological characters to subject to reduced major axis (RMA) regression. It is advisable to use RMA when both the categorical and dependent variable are measured with error (Johnson et al. 2005; Fairbairn 2007). I used RMA to determine variation in allometry across the 4 species and 12 populations. RMA has been used to describe allometry in lizards and other taxa (Johnson et al. 2005; Schulte-Hostedde et al. 2011).

To perform RMA I used RMA v. 1.17 (Bohonak 2004) and entered SVL as the dependent variable and Torso, RLL, HL, HW and HD as the independent variables. The RMA was run for all lizards combined, each of the four species combined, and for each population of lizards.

Results

Sexual Dimorphism Index—Females were the larger sex when analyzing all lizards measured within the *S. undulatus* species complex (Figure 1). Females were also generally larger when analyzing SDI for each species separately. One population of *S. consobrinus* from east Texas showed no noticeable sexual size dimorphism in relation to SVL (SDI=-0.000306). *Sceloporus consobrinus* from Uvalde Co., Texas showed the highest degree of male-biased size dimorphism and *S. tristichus* from Coconino Co., Arizona was the only other population to show male-biased dimorphism. Among the four species, the greatest variation in SDI between populations was for *S. consobrinus* ($SDI_{max}-SDI_{min}=0.0523$) followed by *S. tristichus* ($SDI_{max}-SDI_{min}=0.0322$). *Sceloporus undulatus* and *S. cowlesi* showed little difference in degree of SDI ($SDI_{max}-SDI_{min}=0.0286$; and $SDI_{max}-SDI_{min}=0.0254$ respectively).
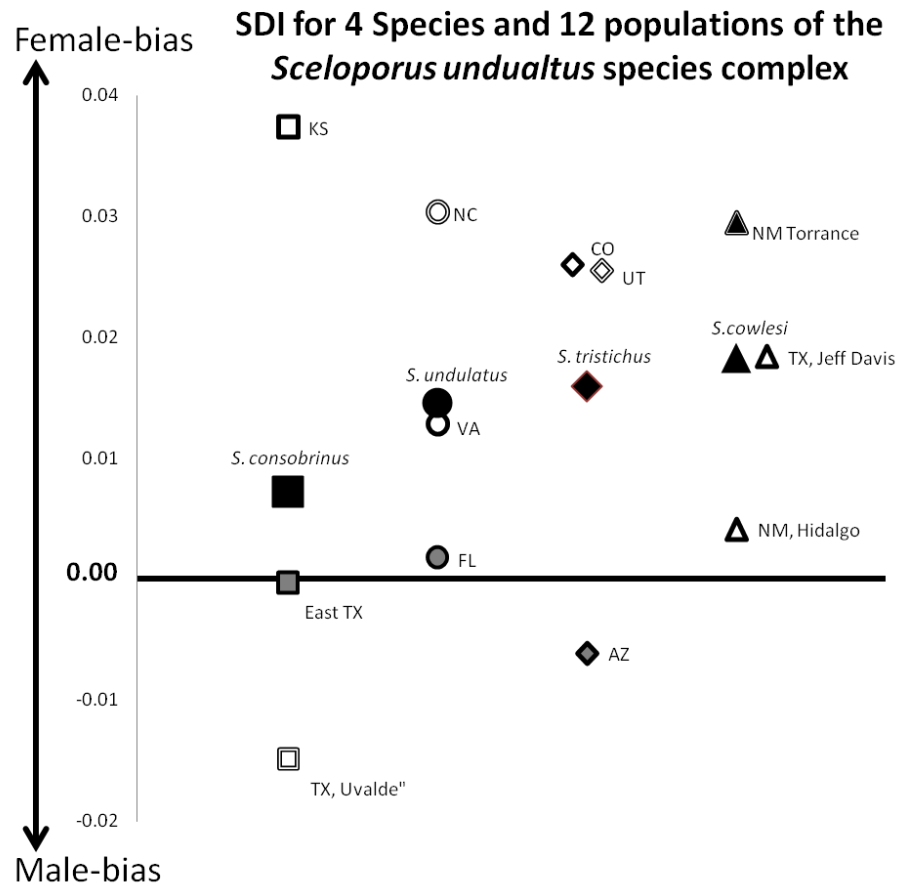
Figure 1. Sexual size dimorphism index (SDI) for all four species groups and all 12 populations of the *S. undulatus* complex. Points are jittered to more clearly show populations with equivalent SDI values. Black shapes are the results for all populations pooled into their respective species. Individually colored shapes show the results for each population analyzed independently.

Principle Component Analysis--The PCA for all lizards yielded 5 eigenvectors. The first eigenvector (PC1) explained 85.38% of the cumulative variation, and showed strong positive loadings of similar magnitude for all measured variables (Table 1). This can be interpreted as being a measure of overall size across all individuals. Because the SDI is preferable to PCA for interpreting the degree of SSD in regards to body size for

each species I did not use PC1 scores in my analyses. The second (PC2) and third (PC3)

eigenvectors explained an additional 12.89% of the variation and were strongly

influenced by the measures of Torso, RLL and HD, while PC4 and PC5 were influenced

entirely by measures of head size but only explained an additional 3.19% of the variation

Table 1. Results of PCA showing eigenvalues, cumulative variances and eigenvectors. Loadings in boldface are considered the most significant for this study

Eigenvectors for all Variables

PC Scores	% Var	Cum Var	Eigen Values	HL	HW	HD	TORSO	RLL
PC 1	0.8538	0.8538	0.0992	0.4128	0.4940	0.4551	0.4462	0.4236
PC 2	0.0661	0.9199	0.0077	-0.1342	-0.2755	-0.3957	**0.8651**	-0.0342
PC 3	0.0483	0.9681	0.0056	0.1379	-0.2294	**-0.4358**	-0.2181	**0.8312**
PC 4	0.0200	0.9881	0.0023	**-0.6717**	-0.3192	**0.5710**	0.0688	0.3408
PC 5	0.0120	1.0000	0.0014	**0.5843**	**-0.7250**	0.3470	0.0140	-0.1115

When PC2 scores were plotted against PC3 scores, a separation was observed in

quadrant IV of the cartesian plane (Figure 2). Most of the individuals in quadrant IV

were lizards from the Uvalde population and all of the males measured from Uvalde fall

into this quadrant. This quadrant can be explained as lizards with short RLL and long

Torso. It is interesting that *S. consobrinus* from Uvalde are one of only two populations

15

All species, both sexes

Legend:
- □ S. consobrinus
- △ S. undulatus
- • S. cowlesi
- ○ S. tristichus
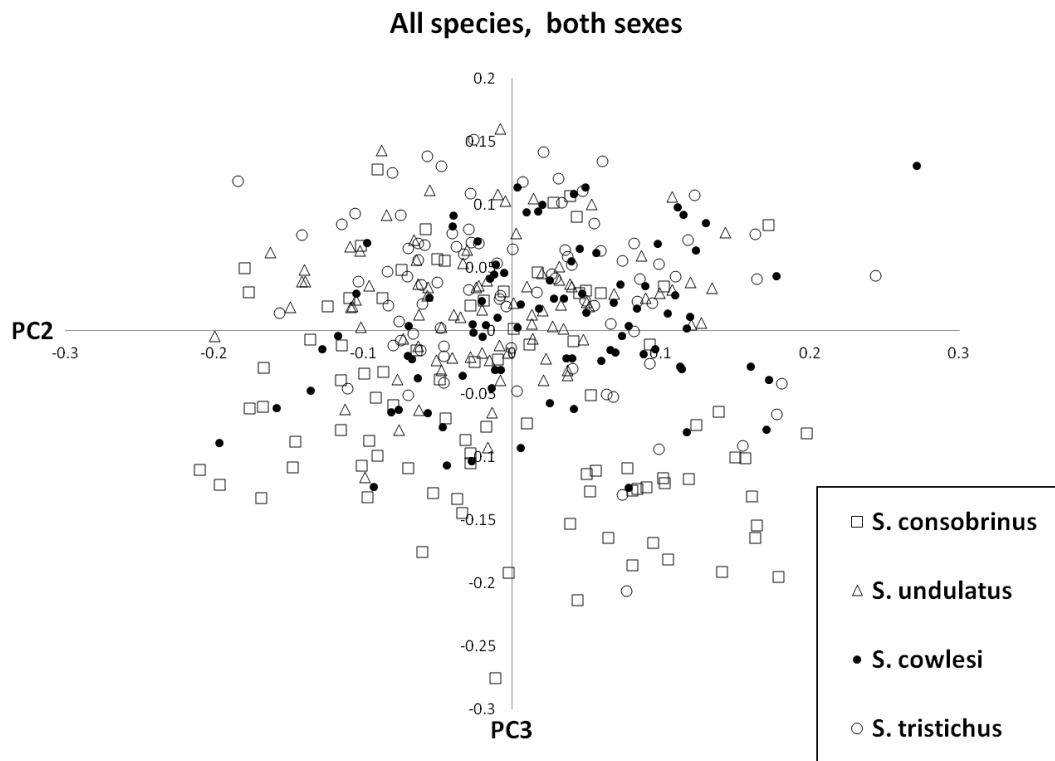
Figure 2. Scatter plot of PC2 and PC3 including both sexes and 4 species analyzed. PC2 is primarily a measure of Torso Length, and PC3 is primarily measure of increasing rear leg length and decreasing head depth.

measured to show male-biased SSD. Uvalde is relatively close to the Trans Pecos area of West TX which loosely defines part of the boundary between *S. cowlesi* and *S. consobrinus*. However the PCA showed almost no overlap with the individuals from Uvalde and individuals of *S. cowlesi*. Further, more *S. tristichus* from Coconino Co., AZ showed male-biased SSD but did not show any separation from the other lizards measured.

Reduced Major Axes Regression (RMA)--Male lizards showed no positive allometry for any of the 6 morphological measurements when regressed against SVL (Table 2 for summarized results, full RMA results are in Appendix 2). Male *S. consobrinus* had negative allometry for Torso, HD, HL and HW and isometric allometry for RLL. *Sceloporus undulatus* males demonstrated negative allometry only for HD and HW, all other measures were isometric. Male *S. tristichus* show negative allometry only for Torso, and all other measures were isometric. *Sceloporus cowlesi* males demonstrate negative allometry only for HD and HW and all other measures were isometric.

Table 2. Summary of reduced major axes regressions showing variation in allometric growth across the *S. undulatus* complex and sample sizes. Allometric growth is expressed as Negative (N), Positive (P), or Isometric (0). The rows corresponding to the species name are a composite value representing the pooled populations

	Torso		Rear Leg Length		Head Depth		Head Length		Head Width		Sample Size	Sample Size
	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female	Male	Females
S. consobrinus	N	0	0	0	N	0	N	P	N	0	44	46
Kansas	0	0	0	0	N	0	N	P	N	0	15	15
Uvalde, TX	0	N	0	0	0	0	0	P	N	0	15	15
East, TX	0	0	0	0	N	N	0	0	0	0	15	16
S. undulatus	0	0	0	P	N	0	0	P	N	0	42	45
Virginia	N	0	0	0	0	0	0	P	0	P	15	15
North Carolina	0	0	0	0	0	0	0	P	0	0	15	15
Florida	0	N	0	0	0	0	0	0	0	0	12	15
S. tristichus	N	0	0	0	0	0	0	0	0	0	43	46
Colorado	0	N	0	0	N	0	0	0	0	0	15	15
Utah	N	N	0	0	0	0	0	0	0	0	15	15
Arizona	0	0	0	0	0	0	0	0	0	0	13	16
S. cowlesi	0	0	0	P	N	0	0	P	N	0	43	42
Hidalgo, NM	0	0	0	0	0	0	0	P	0	0	13	12
Torrance, NM	0	N	0	0	N	0	0	0	0	0	15	15
Jeff Davis, Texas	0	0	0	0	N	0	0	P	0	0	15	15
All Individuals	0	0	N	P	N	0	0	0	N	0	173	179

At the population level males of the *S. undulatus* species complex were mostly isometric. Male *S. undulatus* from Virginia and *S. tristichus* from Utah yield negative allometry for Torso. In the following populations, males show a pattern of negative allometry: *S. undulatus* from Kansas and Uvalde Co., Texas, *S. tristichus* from Colorado, and *S. cowelsi* from Torrance Co., New Mexico and Jeff Davis Co., Texas. Head width was the only other body measurement where male *S. consobrinus* from Kansas and Uvalde Co., TX show negative allometry.

Female lizards yielded much broader variation in allometric relationships. Across all individuals females demonstrate isometry for Torso, HD, HL and HW and positive allometry for RLL. The RMA analysis showed no negative allometry when all females where included together. Female *S. consobrinus* showed positive allometry for HL and isometry for all other measured variables. *S. undulatus* and *S. cowlesi* females showed positive allometry for RLL and HL and otherwise demonstrated isometry. The female *S. tristichus* group is the only female group analyzed to display isometry for all morphological measures.

At the population level female lizards generally showed isometry for all traits. For measures of Torso females from the following populations showed negative allometry: *S. consobrinus* from Uvalde Co., TX, *S. undulatus* from Florida, *S. tristichus* from Colorado and Utah, and *S. cowlesi* from Torrance Co., New Mexico. Female *S. consobrinus* from East Texas showed negative allometry for HD and are the only other population to show negative allometry among all females. For the variable HL females from the following populations have positive allometry: *S. consobrinus* from Kansas and

Uvalde Co., Texas, *S. undulatus* from Virginia and North Carolina, *S cowlesi* from Hidalgo Co., New Mexico and Jeff Davis Co., Texas. Female *S. undulatus* from Virginia showed positive allometry for HW and were the only other population with a positive allometric relationship.

Discussion

Despite two populations showing male-biased SSD, the *S. undulatus* species complex in general can be described as having female-biased SSD. This pattern of SSD is explained by two hypotheses that are not mutually exclusive: the female fecundity hypothesis and the small male advantage hypothesis. Considering the latter hypothesis, in female-larger species, selection should favor small males because their small size requires fewer food resources, allowing more time for them to search out potential mates (Blanckenhorn 1999). I found that males were isometric or had negative allometry when comparing SVL to HD, HW, HL, Torso and RLL. I expected-this pattern to be present if the female-biased SSD was explained by the small male advantage hypothesis. However the known behavioral patterns of lizards in the *S. undulatus* species complex challenge parts of the small male advantage hypothesis, as these lizards are known to defend territories through the use of push-up displays, (Jones and Lovich 2009; Robertson and Rosenblum 2010) which would normally be associated with male-biased SSD. Female-biased SSD is usually only associated with rare cases of reversed sex roles where females select for males (Andersson 1994). Other signals are presumably used in contests between males in the *S. undulatus* species complex including their throat and belly patches as well as the aforementioned push-up displays. In the dwarf chameleon, also in which females are

larger, the fighting ability of males has been determined to have little to do with body size and more to do with specific traits (casque size and flank patch). These traits are associated with aggressiveness of individual males in male-male contests (Stuart-Fox et al. 2006). Interestingly, although none of the populations I studied showed positive allometry between SVL and head size, it has been found previously in the *S. undulatus* species complex (Cooper and Vitt 1989). This evidence would suggest the small male advantage hypothesis would not be an appropriate explanation for female-biased SSD in all populations, but the results do indicate that populations with morphological characteristics consistent with contest competition are rare. Future research aimed at describing aggressiveness between interacting males in the *S. undulatus* species complex could help elucidate what factors determine a successful male and provide further support to small male advantages and how male territoriality plays a role.

Although most populations had female-biased SSD I found inconclusive support for the female fecundity hypothesis. No populations showed positive allometry for Torso, a trait associated with increased fecundity, and five populations showed negative allometry. I observe two species (*S. consobrinus* and *S. tristichus*) where males show negative allometry for Torso. This could suggest that at least for some populations an increase in body size in females is adequate to increase fecundity and that males discontinue investment in Torso as they age, similar to the pattern found by Sugg et al (1995). It has been determined that in some horned lizard species body size does increase fecundity. However an increase in the degree of SSD does not yield a fecundity advantage in *P. hernandesi* (Zamudio 1998). I note however that body shape in the

genus Phrynosoma evolved largely due to adaptations for dietary specialization on ants (Pianka and Parker 1975).

It is clear that fecundity selection and sexual selection contribute to SSD in many organisms. However, Cox et al. (2003) suggested that sexual selection contributes to only 16% of the variation in evolutionary shifts of SSD in lizards (Cox et al. 2003). Cox's study only looked at instances of male-biased SSD in relation to sexual selection, therefore the contribution of lizards with female-biased SSD and the role of fecundity selection is unclear. Natural selection also contributes to mating success and SSD. Predation has been identified as a contributor or inhibitor to differences in SSD (Ryan et al. 1982; Magnhagen 1991). Research into the selective pressures on the *S. undulatus* species complex could identify other significant influences on body size and morphology (Blanckenhorn 2000) such as greater predation on larger males, or increased survival of females with longer legs. Further comparative field studies that identify both sexual selection forces on each sex and other selective pressures may shed light on the variations of SSD observed in the *S. undulatus* species complex.

In addition to predation hormones, especially testosterone, have been shown to have an effect on variety of SSD patterns in closely related species of *Sceloporus* lizards (Cox 2005). Testosterone has been shown to inhibit male growth in female larger species and promotes male growth in male larger species (Cox 2005). The variation in SDI and the variety of allometric relationships observed in the study re-enforce the description of the *Sceloporus* genus as having directionally labile SSD (Cox et al. 2009). Further

studies examining the effects of testosterone on the *S. undulatus* species complex could identify a hormonal mechanism to the observed variation.

A third explanation for the variation observed in the study is natural selection on ecomorphs. Ecomorphs are well known in the *S. undulatus* species complex and the variety of ecomorphs contributed to the abundant sub-species descriptions prior to the most recent phylogeny (Ferguson et al. 1980; Leaché and Reeder 2002). The PC2 axis described increasing torso lengths as other characters decrease, and on the PC3 axis a gradient of long legged to shallow headed lizards. More simply put I find a gradient of faster lizards to slower lizards across the PC3 axis (Miles et al. 1995; Bonine and Garland Jr 1999), thus the PCA is highlighting the existence of the ecomorphs within this group.

In conclusion *S. undualutus* complex is generally a female-biased species group, in relation to SSD. I find support for the small male advantage hypothesis in that males have negative allometry for measures of head size, and are generally smaller than females. I do not find strong support for the female fecundity advantage hypothesis as no measures of fecundity had positive allometry.

CHAPTER III

SEXUAL DIMORPHISM AND PATCH SIZE VARIATION IN THREE LIZARD

SPECIES SUGGESTS POTENTIAL FOR SEXUAL CONFUSION

Introduction

Many organisms possess traits that convey information about species recognition, fighting ability, or influence female choice of mates. For example the gray tree frog exists as two cryptic species (*Hyla chrysoscelis* and *Hyla versicolor*) that are genetically incompatible and males of each species have different calling rates that serve auditory signals directed toward potential mates (Littlejohn et al. 1960). Female *H. chrysoscelis* and *H. versicolor* are receptive only to the calls of their respective species (Gerhardt 1982; Gerhardt 1994). Fighting ability can be advertised with weapons or armaments, (i.e. teeth, antlers, horns etc.). Armaments can serve simultaneously to signal fitness to females (Clutton-Brock et al. 1982) and the fighting ability of a male to conspecific males. For instance in male caribou, violent fights between males of matched antler size is a rare occurrence, but light sparring and assessment of mismatched opponents is common (Barrette and Vandal 1990). Signals that generally influence female choice occur in the form of conspicuous colors and ornaments. *Anolis* lizards display a colorful dewlap to potential mates, and experiments that prevented males from extending the dewlap or altered the color of the dewlap reduced the likelihood that a male would be chosen as a mate (Crews 1975; Sigmund 1983).

Compared to armaments, ornaments can be subject to cheating or alternative mating strategies, as ornaments to do not require physical force to verify their

effectiveness (Whiting et al. 2003). In many cases cheating the expression of an ornament involves a male mimicking a female, these individuals are considered female mimics or sneaker males (Sinervo and Lively 1996; Wikelski et al. 1996). Female mimicry can be advantageous as it can enable sneaker males to exist in other male territories without engaging in territorial disputes. Thus these sneaker males can obtain mating opportunities that would otherwise be unavailable to them.

The use of ornaments as signal patches, and exploiting these signals in cheating behavior is well studied in male lizards (Hews et al. 1994; Sinervo and Lively 1996; Whiting et al. 2003; Whiting et al. 2009), but only a few studies have investigated the use of signal patches in females. These studies have supported sex role reversal, or the uncommon pattern of females competing with other females for breeding access to males (Andersson 1994; Eens and Pinxten 2000). Particularly in lizards, signal patches and conspicuous female colors are relatively common, and color patches commonly signal to males that the female has already bred and is gravid (Cooper 1984). However, many female lizards have color patches that are similar to those of males of the same species. For most of these patches it is not known what they are signaling or even if they function as a signal or are just ancestral characters without a current known function. In the family Phrynosomatidae, the genus *Sceloporus* has many species that display both male throat and belly patches (also known as badges), and female throat and belly patches. However, among members of the *Sceloporus undulatus* species complex, female lizards often have large ventral patches on the belly and throat. These patches can range from being small and faint to being very similar to the patches of males.

A population of *Sceloporus cowlesi* occurring in White Sands, New Mexico has been shown to overlap in the size of signal patches between males and females and inter and intrasexual interactions may result in sexual confusion (Robertson and Rosenblum 2010). Robertson and Rosenblum (2010) found that male *S. cowlesi* would often attempt to court conspecific males with smaller badges. This is the first time the term sexual confusion has been applied to any species in the *Sceloporus undulatus* species complex, but it is not the first description of courtship between two males. Vinegar (1972) observed several cases of male-male courtship and one case of a female using courtship behavior in an interaction with a con-specific female in *S. tristichus*. While Vinegar (1972) admitted that he was unable to correlate same sex courtship with signal patches or coloration, it is Robertson and Rosenblum who successfully showed that signal patch size is related to sexual confusion in at least one population of *S. cowlesi*.

I chose to investigate patch size in multiple populations across the range of *S. cowlesi* to determine if the observations of Robertson and Rosenblum (2010) were an isolated example of sexual confusion that was occurring in a unique habitat situation. I also chose to do the same analysis with the two closest relatives of *S. cowlesi*, *S. consobrinus* and *S. tristichus* to determine if sexual confusion could potentially be occurring in these taxa as well.

Materials and Methods

I used a total of 339 museum specimens to quantify sexual dimorphism of signal patches between males and females of the three species; *Sceloporus consobrinus(N)*, *S. cowlesi(N)*, and *S. tristichus(N)* (Table 3 see Appendix for locality information). No

known morphological characters exist to confidently identify the three species used in this study from one another. Presently the best way to identify museum specimens of these three species is by classifying them according to locality. I used range maps (Powell 2011) and HerpNET (Spencer 2010) to identify specimens from within the described range of each species. I used a SONY Digital Camera (Model Model DSC-H20) mounted on a photo table to photograph the venter all specimens. The camera was positioned 25 centimeters above the specimen and a metric ruler was placed adjacent to every specimen. To measure the variation in the sizes of signal patches between the sexes I used tpsDig2 to outline throat and belly patch size and to measure snout to vent length (SVL), all photos were calibrated to record measurements in millimeters before outlining any patches. The area of signal patches was calculated using the areapl function from the splancs package for R, this function calculates the area of non self-intersection polygons (Rowlingson 2012). To ensure only adult lizards were analyzed I used Q-Q plots to examine the distribution of SVL. Individual outliers that represented small lizards were culled from the sample. A Q-Q plot can be used for assessing one dimensional data sets to identify outliers and to assess the normality of a data set distribution (Wilk and Gnanadesikan 1968).

Table 3 The number of female and male specimens measured from each of the three species.

	Sceloporus consobrinus	*Sceloporus cowlesi*	*Sceloporus tristichus*
Female	42	63	64
Male	42	68	60
Total	84	131	124

Prior to analyzing the area of signal patches I categorized the type and frequency of patches occurring between males and females of the three species. Throat patches occurred in two forms, as a single colored patch covering the ventral surface of the head and neck, or as two separate patches on the right and left. When present, belly patches always occurred as a right and left patch. The combination of presence and absence of throat and belly patches resulted in 6 categories; (1) no throat or belly patches, (2) two throat patches and no belly patches, (3) one throat patch and no belly patches, (4) no throat patch and two belly patches, (5) two throat patches and two belly patches, (6) one throat patches and two belly patches (Figure 3). A histogram was used to show the number of males and females in each species that are represented in the 6 categories (Figure 4)
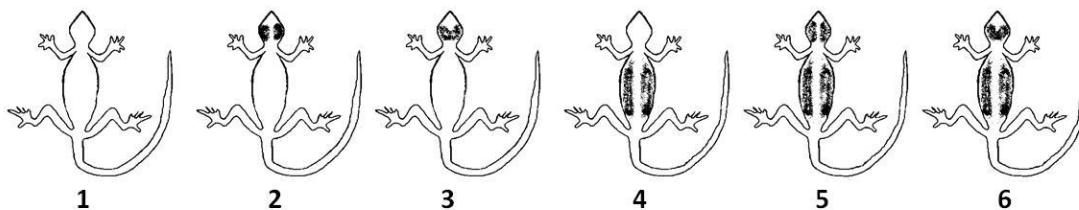
Figure 3 Individual specimens of *S. consobrinus, S. cowlesi* and *S. tristichus* were classified according to six categories; (1) no patches (2) two throat patches (3) one throat patch (4) two belly patches and no throat patches (5) two throat patches and two belly patches (6) one throat patch and two belly patches

All statistical analyses were performed using JMP™. The area of the signal patches were summed into a total badge area (TBA) and natural log transformed (LN) (the untransformed measures of TBA and SVL are reported in the Appendix C). To correct for body size in size corrected the LN TBA I divided each value by the corresponding LN SVL, this method has been used to standardize size measures in several studies of reptiles (Lee 1980; Brennan et al. 2008; Doan 2008; Santos and Llorente 2008). This method of size correction is preferable to using residuals from a regression, as the residuals would have produced negative values giving a false sense of variance for lizards that have no measurable TBA. I used a one-way ANOVA to test the null hypothesis that the mean TBA of males and females were equal within a species. I also used a Two One-Sided Tests (TOST) approach to test for a difference between the means of males and females from the ANOVA. The TOST tests that the difference between means is less than or equivalent to a pre-determined value, and is used as assurance that means do not differ by much or are practically equivalent (Ramírez and Ramírez 2009). I employ the TOST and use the minimum male TBA for each respective

species to test the null hypothesis that the difference in mean TBA between males and females is less than the minimum male TBA ($\mu_{Male\,TBA}$- $\mu_{Female\,TBA} \leq$ Male Minimum TBA). Rejecting the null hypothesis suggests that sexual dimorphism of badge size is sufficient to prevent sexual confusion in the species. Failure to reject the null hypothesis is evidence that the overlap in TBA of males and females could result in sexual confusion between males and females of a species. This test is intended to illustrate the potential for sexual confusion correlated with variations in badge size as reported by Robertson and Rosenblum (2010) in *Sceloporus cowlesi*

Results

Females occurred in all six categories of badge and throat patch combinations, while males never occurred in categories one, two or three (Figure 4). Because categories four, five and six have both the largest patches and/or the largest number of patches they have the highest TBA and are the most "male-like" categories. Female *S. tristichus* had more representatives in these male-like categories than female *S. cowlesi* while female *S. consobrinus* were never represented in "male-like" categories. Categories five and six are those that have belly patches and throat patches and *S. tristichus* and *S. cowlesi* males were predominately in these categories while *S. consobrinus* males were relatively evenly distributed across categories four, five, and six. Conversely, male *S. tristichus* had only two individuals in category four and *S. cowlesi* males were not represented in category four.

Sceloporus consobrinus males and females were significantly different in respect to TBA (p<0.0001, Table 4). Only five of the 42 females had measureable badges. Additionally male *S. consobrinus* always had two belly patches and most had belly patches and throat patches. The TOST also show that *S. consobrinus* are significantly different in relation to TBA (Table 4). The box plots visually illustrate that the difference in TBA for male and female *S. consobrinus* is the greatest for all three species (Figure 5).

Table 4. ANOVA and TOST of the difference between female and male TBA for *S. consobrinus*

ANOVA of *S. consobrinus* Male and Female TBA

Source	DF	Sum of Squares	Mean Square	F Ratio	Prob>F
Sex	1	32.9697	32.9697	835.7350	<.0001
Error	82	3.2349	0.0394		
Total	83	36.2046			

Means for Oneway ANOVA

Sex	Number	Mean	Std Error	Lower 95% CI	Upper 95% CI
Male	42	0.09549	0.03065	0.0147	0.1763
Female	42	1.34849	0.03065	1.2677	1.4293

TOST for *S. consobrinus* Male and Female Mean TBA

Values testing for Practical Equivalence		Test	t Ratio	p-Value
Minimum Male TBA	1.1709	**Upper Threshold**	1.8924	0.9690
Actual Mean Difference	1.2530	**Lower Threshold**	55.9258	<.0001
Std Error of Difference	0.0433	**Max Over Both**		0.9690

Sceloporus cowlesi males and female were significantly different in respect to TBA (p<0.0001, Table 5), while the results of the TOST show that that the difference between male and female TBA is not significantly different from minimum male *S. cowlesi* TBA. Most females measured 0 for TBA, but thirty-five females (greater than half) had positive measures for TBA. Thirteen female *S. cowlesi* had measures for TBA that included large belly patches. The box plots visually show that female *S. cowlesi* show a large range of values for TBA and that some overlap exists in TBA between males and females (Figure 5).

Table 5. ANOVA and TOST of the difference between female and male TBA for *S. cowlesi*

ANOVA of *S. cowlesi* Male and Female TBA

Source	DF	Sum of Squares	Mean Square	F Ratio	Prob>F
Sex	1	23.7340	23.7340	162.7925	<.0001
Error	129	18.8073	0.1458		
Total	130	42.5412			

Means for Oneway ANOVA

Sex	Number	Mean	Std Error	Lower 95% CI	Upper 95% CI
Male	63	0.5706	0.04811	0.4448	0.6964
Female	68	1.4225	0.04630	1.3014	1.5436

TOST for *S. cowlesi* Male and Female Mean TBA

Values testing for Practical Equivalence		Test	t Ratio	p-Value
Minimum Male TBA	1.316847	Upper Threshold	-6.9632	<.0001
Actual Mean Difference	0.8519	Lower Threshold	35.4813	<.0001
Std Error of Difference	0.0668	Max Over Both		<.0001

For *S. tristichus* there are significant differences between male and female TBA (p<0.0001, Table 6). But the results of the TOST show that the means do not differ by less than the male *S. tristichus* minimum TBA. For female *S. tristichus* only 4 females measured 0 for TBA. Most female *S. tristichus* had belly patches and throat patches and therefore had relatively large measures of TBA. The box plots visually show that the difference in TBA between male and female *S. tristichus* is the smallest of all three species (Figure 5).

Table 6. ANOVA and TOST of the difference between female and male TBA for *S. tristichus*

ANOVA of *S. tristichus* Male and Female TBA

Source	DF	Sum of Squares	Mean Square	F Ratio	Prob>F
Sex	1	1.547706	1.54771	20.9218	<.0001
Error	122	9.025032	0.07398		
Total	123	10.572737			

Means for Oneway ANOVA

Sex	Number	Mean	Std Error	Lower 95% CI	Upper 95% CI
Male	64	1.19159	0.03400	1.1243	1.2589
Female	60	1.41515	0.03511	1.3456	1.4847

TOST for *S. tristichus* Male and Female Mean TBA

Values testing for Practical Equivalence		Test	t Ratio	p-Value
Minimum Male TBA	1.315062	Upper Threshold	-22.3324	<.0001
Actual Mean Difference	0.223558	Lower Threshold	31.4805	<.0001
Std Error of Difference	0.048875	Max Over Both		<.0001
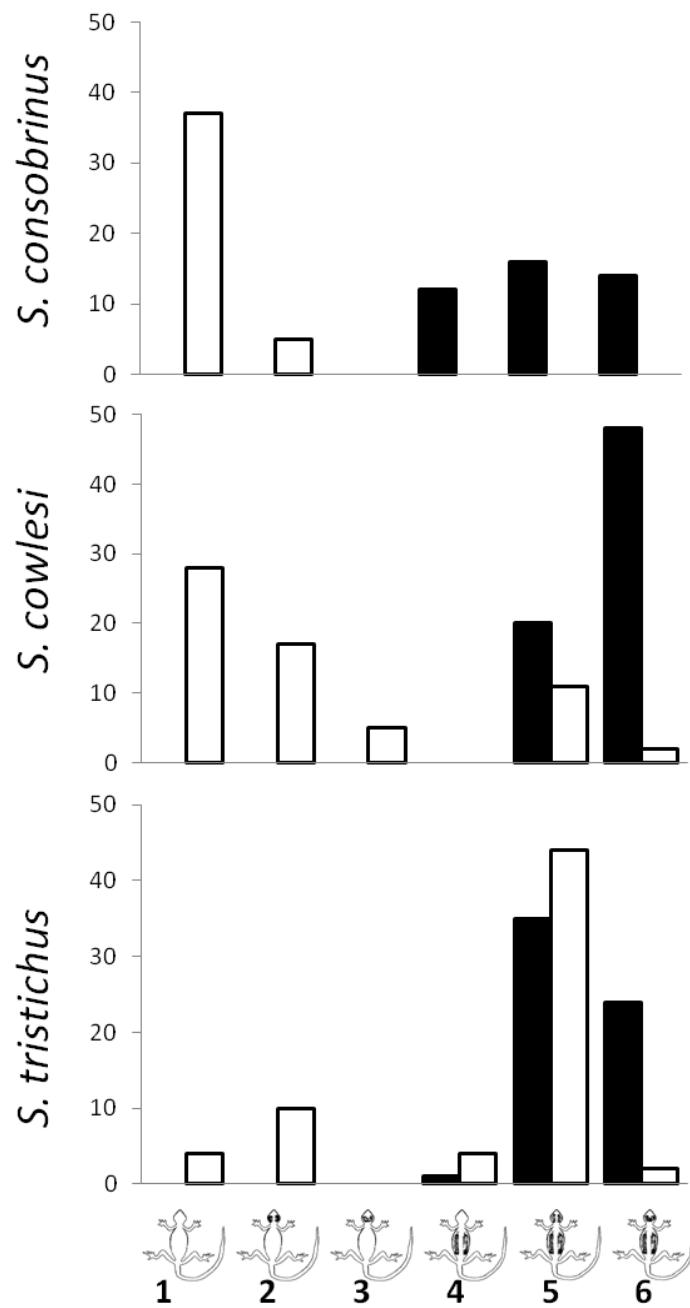
Size Corrected TBA vs. Species by Sex
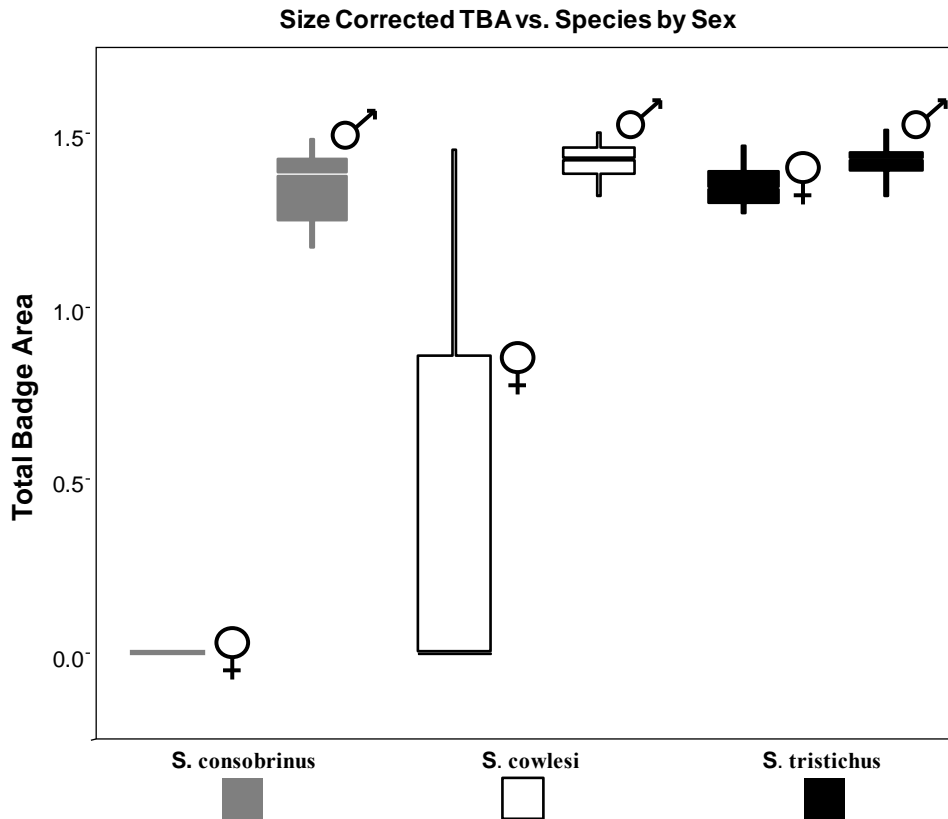
Figure 5. Boxplots showing the range of TBA for males and females by species. The boxplot for female *S. consobrinus* represents the only 4 females that have measures of TBA greater than 0.

Discussion

In *S. undulatus* species complex, sex recognition has been determined to be based on the extent of signal patch size (Cooper Jr and Burns 1987). But in lizards with significant overlap in signal patch size, males with smaller badge sizes are interpreted as females (Robertson and Rosenblum 2010). I found that sexual dimorphism in signal patches is significant enough to prevent sexual confusion in *S. consobrinus*. However, in *S. cowlesi* and *S. tristichus* enough overlap in TBA exists (Figure 5) to suggest that

sexual confusion may be occurring. I sampled specimens across a wide geographic distribution therefore the data suggest that sexual confusion in *S. tristichus* and *S. cowlesi* is possible at the species level. Female variation in TBA was the largest in *S cowlesi* and females in some populations did not have individuals in the "male-like" categories. It could be argued that *S. cowlesi* lives across the widest ranges of habitats, from the novel white and dark sands region into rocky outcrops and deserts. The variation observed in *S. cowlesi* in particular could be the result of many localized adaptations to the wide variety of habitats, this speculation agrees with explanations proposed by Robertson and Rosenblum (Robertson and Rosenblum 2009; Robertson and Rosenblum 2010).

The sexual confusion observed by Robertson and Rosenblum (2010), where a male attempts to court or breed with another male, is not specific only to sceloporine lizards. Males of the species *Ameiva chrysolaema* were observed attempting to breed with one another by Noble and Bradley (1933). Attempted male-male courting in other species of *Ameiva* and in *Aspedoscelis sexlineata* have also been observed (Noble and Bradley 1933). In *Ameiva chrysolaema* males are generally larger than females, and incidences of sexual confusion were thought to be associated with overlap in the size of males and females. Unlike *Ameiva chrysolaema*, *Aspedoscelis sexlineata* has sexually dichromatic green color patches on males, and these patches are reduced or absent in females. Noble and Bradley (1933) observed that these patches are displayed in aggressive male-male interactions, but male lizards courted and bred with females as well as males that failed to display aggressive behavior (Noble and Bradley 1933). These

instances of sexual confusion in *Ameiva* and *Aspedoscelis* are further complicated by the fact that female mimicry is not known in the family Teiidae. These few studies that have documented sexual confusion suggest that the behavior may not be rare. Only Robertson and Rosenblum (2010) offered an explanation for sexual confusion. They posit that sensory drive and ecological speciation in a novel habitat are responsible for sexual confusion in White Sands. It remains to be verified if sexual confusion occurs in other populations of *S. cowlesi* or if it occurs at all in *S. tristichus*. If the evidence from signal badges provided here is shown to result in sexual confusion in more populations and species, then alternative explanations for sexual confusion will be needed.

The investigations of Noble and Bradley (1933) are similar to those of Vinegar (1972) and Robertson and Rosenblum (2010), in that they focus on the interactions of males and the interpretation of sexual signals from the perspective of male lizards. Furthermore data on how signal patches function in *Sceloporus* lizards is biased towards male-male interaction and female-choice experiments. Very few experiments have looked at territoriality in female lizards (Mahrt 1998) or how signal badges function in female-female interactions or how males perceive females with badges larger than their own. Future work targeting interactions between sexes from the perspective of female lizards is necessary to further explain the existence of large female signal patches in *Sceloporus cowlesi* and *Sceloporus tristichus*. Furthermore, investigations focusing on female-female interactions will offer insight into the function of signaling and conspicuous colors in female lizards

CHAPTER IV

CONCLUSIONS

My results show that SSD in particular is highly variable at the population level, and some populations display male-larger dimorphism or no SSD which is inconsistent with descriptions of this species complex being female-larger. Furthermore, no measure of head size showed a positive allometric relationship for males of any species or any population. Perhaps more interesting is that head length did have a positive allometric relationship for females of all species except *S. tristichus*. It is difficult to speculate on the positive allometry of head size in females, but future studies could investigate the relationship of throat patches to head size in females. It may be possible that females have larger heads and use throat patch displays more than males in interactions with conspecifics.

Considering the female fecundity advantage hypothesis, when populations are pooled into their respective species, torso length shows isometric allometry with body size. This suggests that larger females do gain a fecundity advantage with an increase in body size. However, growing to a larger body size requires more time and resources, and this has been shown to counter the reproductive advantages of body size (Shine 1988). It should also be pointed out that females from five of the twelve populations I measured actually show negative allometry for torso length relative to body size. This might suggest that there is plasticity in torso length. Future studies that investigate life history and population dynamics with regard to the presence of different morphologies will be beneficial for understanding these variations.

Like the female fecundity advantage hypothesis, the small male advantage hypothesis seems to apply well to some populations of lizards, and poorly to others. Generally speaking females are larger than males in the *S. undulatus* complex, but there are two populations which show male-larger SSD and two more that show little or no SSD. While this clearly supports Cox et al's (2007) description of the labile nature of SSD in the *Sceloporus* genus, it does little to explain why there is a variety of SSD patterns within populations of the same species. It is possible that the small male advantage is supported for populations of the *S. undulatus* complex occurring in resource limited environments, but field studies will be needed to confirm this.

In consideration of the merits of the analyses I used to investigate SSD, my results highlight the value of using RMA regression for describing allometric relationships. RMA is preferable when both the predictor and the predicted variables are measured with error. Moreover, my use of RMA to analyze allometry of head size yielded results different from those previously published for *S. undulatus* that used ANCOVA (Cooper and Vitt 1989). This suggests that previously published results of allometric relationships of head to body size in lizards and allometric relationships of other taxa may benefit from being reanalyzed with RMA.

This investigation contributes to the importance of evaluating descriptive characteristics in species in concert with species trees generated from molecular phylogenetics. Certainly molecular phylogenetics is an excellent tool for elucidating evolutionary relationships of species. However, molecular phylogenetics leaves something to be desired when previously assumed morphological characters no longer

apply to many species. This is especially true for species that have a rich history of morphological descriptions and investigation, similar to the *S. undulatus* complex, as these previous descriptions can be confounded by new phylogenies. The results presented in this thesis illustrate the broad heuristic value of investigating sexual dimorphism and morphological patterns in the context of new molecular phylogenies.

In consideration of sexually dimorphic signals, the results presented in this thesis indicate that signal badges my not serve perfectly parallel functions in all species of the *S. undualtus* complex, particularly for *S. cowlesi* and *S. tristichus*. It has been shown empirically that sexual confusion results from overlap in signal patch size in males and females for a population of *S. cowlesi* occurring at White Sands, New Mexico (Robertson and Rosenblum 2010). However, my results suggest that sexual confusion may be common among *S. cowlesi*, and perhaps even more common among *S. tristichus*. I cannot disagree with Robertson and Rosenblum's (2010) observation of sexual confusion, but my data suggests that other explanations are possible. My data clearly shows that signal badges occur at a high frequency in female *S. cowlesi* and *S. tristichus*. Furthermore the variation in badge size between males and females of *S. cowlesi* and *S. tristichus* occurs in areas that are not novel habitats. Because signal patches occur on the belly and throat (i.e. inconspicuous areas) of *S. undulatus* complex, they are resistant to the forces of natural selection via predation. So the function of signal patches is best suited for investigations of how the signal patches are used in same sex and opposite sex interactions. Females that use similar signals as males may also be engaging in territorial disputes with conspecific females, perhaps to defend the best resources for their

offspring. The possibility that female signal badges function as a rejection signal to resist copulation with males while they are gravid is not supported as there is no evidence that female signal badges vary in size or color intensity with reproductive condition. It should be the priority of future field studies on *S. undulatus* complex to investigate female-female interactions and female-male interactions from the perspective of the female. In this way it will be possible to understand the function of signal patches in females.

LITERATURE CITED

Andersson, M. B. (1994). Sexual Selection. Princeton University Press, USA, Princeton, New Jersey

Barrette, C. and D. Vandal (1990). Sparring, relative antler size, and assessment in male caribou. Behavioral Ecology and Sociobiology 26:383-387.

Blanckenhorn, W. F. (1999). Foraging in yellow dung flies: testing for a small male time budget advantage. Ecological Entomology 24:1-6.

Blanckenhorn, W. U. (2000). The evolution of body size: what keeps organisms small? Quarterly Review of Biology 75:385-407.

Bohonak, A. J. (2004). Program RMA: software for reduced major axis regression. Version 1.17. software availble online at http://www.bio.sdsu.edu/pub/andy/RMA.html Archived by WebCite® at http://www.webcitation.org/68tAur1SW on 3 July 2012

Bonine, K. E. and T. Garland Jr (1999). Sprint performance of phrynosomatid lizards, measured on a high-speed treadmill, correlates with hindlimb length. Journal of Zoology 248:255-265.

Brennan, A. M., E. J. Censky and R. Powell (2008). Effects of chigger mite (Acari: Trombiculidae) infections on *Ameiva* (Squamata: Teiidae) from the Anguilla Bank. Contemporary Herpetology 1:1-3.

Chan, R., D. Stuart-Fox and T. S. Jessop (2009). Why are females ornamented? A test of the courtship stimulation and courtship rejection hypotheses. Behavioral Ecology 20:1334-1342.

Clutton-Brock, T. H., F. E. Guinness and S. D. Albon (1982). Red deer: behavior and ecology of two sexes. University of Chicago Press, USA, Chicago, Illinois

Cooper Jr, W. E. and N. Burns (1987). Social significance of ventrolateral coloration in the fence lizard, *Sceloporus undulatus*. Animal Behaviour 35:526-532.

Cooper, W. E. (1984). Female secondary sexual coloration and sex recognition in the keeled earless lizard, *Holbrookia propinqua*. Animal Behaviour 32:1142-1150.

Cooper, W. E. and L. J. Vitt (1989). Sexual dimorphism of head and body size in an iguanid lizard: paradoxical results. The American Naturalist 133:729-735.

Côte, I. and W. Hunte (1989). Male and female mate choice in the redlip blenny: why bigger is better. Animal Behaviour 38:78-88.

Cox, R. M. (2005). Testosterone has opposite effects on male growth in lizards (*Sceloporus* spp.) with opposite patterns of sexual size dimorphism. Journal of Experimental Biology 208:4679-4687.

Cox, R. M., M. A. Butler and H. B. John-Alder (2009). The evolution of sexual size dimorphism in reptiles. Pp. 38–49. D. J. Fairbairn, W. U. Blanckenhorn and T. Székely (Eds.) Sex, size, and gender roles: evolutionary studies of sexual size dimorphism. Oxford University Press, USA, Oxford, New York.

Cox, R. M., S. L. Skelly and H. B. John-Alder (2003). A comparative test of adaptive hypotheses for sexual size dimorphism in lizards. Evolution 57:1653-1669.

Cox, R. M. and H. B. John-Adler. (2007). Growing apart together; the development of contrasting sexual size dimorphisms in sympatric *Sceloporus* lizards. Herpetologica 63:245-257.

Crews, D. (1975). Effects of different components of male courtship behaviour on environmentally induced ovarian recrudescence and mating preferences in the lizard, *Anolis carolinensis*. Animal Behaviour 23:349-356.

Darwin, C. (1871). The Descent of Man in Relation to Sex. D. Appleton and Company, England, London

Doan, T. M. (2008). Dietary variation within the Andean lizard clade *Proctoporus* (Squamata: Gymnophthalmidae). Journal of Herpetology 42:16-21.

Eens, M. and R. Pinxten (2000). Sex-role reversal in vertebrates: behavioural and endocrinological accounts. Behavioural Processes 51:135-147.

Fairbairn, D. J., W. U. Blanckenhorn and T. Székely, Ed. (2007). Sex, Size, and Gender roles: Evolutionary Studies of Sexual Size Dimorphism. Oxford University Press, USA, Oxford, New York.

Ferguson, G. W., C. H. Bohlen and H. P. Woolley (1980). *Sceloporus undulatus*: comparative life history and regulation of a Kansas population. Ecology 61:313-322.

Fitch, H. S. (1978). Sexual size differences in the genus *Sceloporus* The University of Kansas Science Bulletin 51:441-461.

Gerhardt, H. C. (1982). Sound pattern recognition in some North American treefrogs (Anura: Hylidae): implications for mate choice. American Zoologist 22:581-595.

Gerhardt, H. C. (1994). Reproductive character displacement of female mate choice in the grey treefrog, *Hyla chrysoscelis*. Animal Behaviour 47:959-969.

Ghiselin, M. T. (1974). The Economy of Nature and the Evolution of Sex. University of California Press Berkeley, USA, Berkely, California

Gross, M. R. (1991). Evolution of alternative reproductive strategies: frequency-dependent sexual selection in male bluegill sunfish. Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences 332:59-66.

Haenel, G. J., L. C. Smith and H. B. John-Alder (2003). Home-range analysis in *Sceloporus undulatus* (eastern fence lizard). I. Spacing patterns and the context of territorial behavior. Copeia 2003:99-112.

Herrel, A., E. De Grauw and J. A. Lemos-Espinal (2001). Head shape and bite performance in xenosaurid lizards. Journal of Experimental Zoology 290:101-107.

Herrel, A., L. Spithoven, R. Van Damme and F. de Vree (1999). Sexual dimorphism of head size in *Gallotia galloti*: testing the niche divergence hypothesis by functional analyses. Functional Ecology 13:289-297.

Hews, D. K., R. Knapp and M. C. Moore (1994). Early exposure to androgens affects adult expression of alternative male types in tree lizards. Hormones and Behaviour 29:96-115.

Hibbitts, T. J., E. R. Pianka, R. B. Huey and M. J. Whiting (2005). Ecology of the common barking gecko (*Ptenopus garrulus*) in southern Africa. Journal of Herpetology 39:509-515.

Hibbitts, T. J., M. J. Whiting and D. M. Stuart-Fox (2007). Shouting the odds: vocalization signals status in a lizard. Behavioral Ecology and Sociobiology 61:1169-1176.

Hood, G. M. (2010). PopTools add-in for Microsoft Excel: analysis of matrix population models and simulation of stochastic processes. Version 3.2.5. software available online at http://www.poptools.org Archived by WebCite® at http://www.webcitation.org/68t8oMsfH on 3 July 2012.

Houston, D. and R. Shine (1993). Sexual dimorphism and niche divergence: feeding habits of the Arafura filesnake. Journal of Animal Ecology 62:737-748.

Johnson, J. B., L. D. McBrayer, D. Saenz and G. C. Carpenter (2005). Allometry, sexual size dimorphism, and niche partitioning in the Mediterranean gecko (*Hemidactylus turcicus*). The Southwestern Naturalist 50:435-439.

Jones, L. L. C. and R. E. Lovich (2009). Lizards of the American Southwest: A Photographic Field Guide. Rio Nuevo Publishers, USA, Tucson, Arizona

Kratochvíl, L. and D. Frynta (2009). Phylogenetic analysis of sexual dimorphism in eyelid geckos (Eublepharidae): the effects of male combat, courtship behaviour, egg size, and body size. Pp. 154–162. D. J. Fairbairn, W. U. Blanckenhorn and T. Székely (Eds.) Sex, size, and gender roles: evolutionary studies of sexual size dimorphism. Oxford University Press, USA Oxford, New York

Leaché, A. D. (2009). Species Tree Discordance Traces to Phylogeographic Clade Boundaries in North American Fence Lizards (*Sceloporus*). Systematic Biology 58:547-559.

Leaché, A. D. and T. W. Reeder (2002). Molecular systematics of the eastern fence

lizard (*Sceloporus undulatus*): a comparison of parsimony, likelihood, and

Bayesian approaches. Systematic Biology 51:44-68.

Lee, J. C. (1980). Variation and systematics of the *Anolis sericeus* complex (Sauria:

Iguanidae). Copeia 1980:310-320.

Lindenfors, P., J. L. Gittleman and K. E. Jones (2009). Sexual size dimorphism in

mammals. Pp. 16-26. D. J. Fairbairn, W. U. Blanckenhorn and T. Székely (Eds.)

Sex, size, and gender roles: evolutionary studies of sexual size dimorphism.

Oxford University Press, USA Oxford, New York

Littlejohn, M. J., M. Fouquette and C. Johnson (1960). Call discrimination by female

frogs of the *Hyla versicolor* complex. Copeia 1960:47-49.

Magnhagen, C. (1991). Predation risk as a cost of reproduction. Trends in Ecology &

Evolution 6:183-186.

Mahrt, L. A. (1998). Territorial establishment and maintenance by female tree lizards,

Urosaurus ornatus. Journal of Herpetology 32:176-182.

Miles, D. B., L. A. Fitzgerald and H. L. Snell (1995). Morphological correlates of

locomotor performance in hatchling *Amblyrhynchus cristatus*. Oecologia

103:261-264.

Noble, G. K. and H. T. Bradley (1933). The mating behavior of lizards; its bearing on

the theory of sexual selection. Annals of the New York Academy of Sciences

35:25-100.

Olsson, M., R. Shine, E. Wapstra, B. Ujvari and T. Madsen (2002). Sexual dimorphism in lizard body shape: the roles of sexual selection and fecundity selection. Evolution 56:1538-1542.

Pianka, E. R. and W. S. Parker (1975). Ecology of Horned Lizards: A Review with Special Reference to *Phrynosoma platyrhinos*. Copeia 1975:141-162.

Pinch, F. C. and D. L. Claussen (2003). Effects of Temperature and Slope on the Sprint Speed and Stamina of the Eastern Fence Lizard, *Sceloporus undulatus*. Journal of Herpetology 37:671-679.

Powell, R., J.T. Collins, and E.D. Hooper, Jr., Ed. (2011). A Key to the Herpetofauna of the Continental United States and Canada. University Press of Kansas, USA, Lawrence, Kansas

Ralls, K. (1976). Mammals in which females are larger than males. Quarterly Review of Biology 51:245-276.

Ramírez, J. G. and B. S. Ramírez (2009). Analyzing and interpreting continuous data using JMP: A step-by-step guide. SAS Publishing, USA, Cary, North Carolina

Robertson, J. and E. B. Rosenblum (2009). Rapid divergence of social signal coloration across the White Sands ecotone for three lizard species under strong natural selection. Biological Journal of the Linnean Society 98:243-255.

Robertson, J. M. and E. B. Rosenblum (2010). Male territoriality and 'sex confusion' in recently adapted lizards at White Sands. Journal of Evolutionary Biology 23:1928-1936.

Roitberg, E. S. (2009). Variation in sexual size dimorphism within a widespread lizard species. Pp. 143-153. D. J. Fairbairn, W. U. Blanckenhorn and T. Székely (Eds.) Sex, size, and gender roles: evolutionary studies of sexual size dimorphism. Oxford University Press, USA Oxford, New York

Rowlingson, B. (2012). Package 'splancs': Spatial and Space-Time Point Pattern Analysis Functions. Version 2.01-31. package available online at http://www.maths.lancs.ac.uk/~rowlings/Splancs Archived by WebCite at http://www.webcitation.org/68qFxueWx on 1 July 2012

Ryan, M. J., M. D. Tuttle and A. S. Rand (1982). Bat predation and sexual advertisement in a neotropical anuran. The American Naturalist 119:136-139.

Santos, X. and G. A. Llorente (2008). Gastrointestinal responses to feeding in a frequently feeding colubrid snake *Natrix maura*. Comparative Biochemistry and Physiology-Part A: Molecular & Integrative Physiology 150:75-79.

Schulte-Hostedde, A. I., J. Bowman and K. R. Middel (2011). Allometry of the baculum and sexual size dimorphism in American martens and fishers (Mammalia: Mustelidae). Biological Journal of the Linnean Society 104:955-963.

Shine, R. (1988). The evolution of large body size in females: a critique of Darwin's" fecundity advantage" model. The American Naturalist 131:124-131.

Shine, R., S. Keogh, P. Doughty and H. Giragossyan (1998). Costs of reproduction and the evolution of sexual dimorphism in a 'flying lizard' *Draco melanopogon* (Agamidae). Journal of Zoology 246:203-213.

Sigmund, W. R. (1983). Female preference for *Anolis carolinensis* males as a function of dewlap color and background coloration. Journal of Herpetology 17:137-143.

Sinervo, B. and C. M. Lively (1996). The rock-paper-scissors game and the evolution of alternative male strategies. Nature 380:240-243.

Spencer, C. (2010). HerpNET. available online at http://www.herpnet2.org/ Archived by WebCite® at http://www.webcitation.org/68tAbAtXD on 3 July 2012

Stuart-Fox, D. M., D. Firth, A. Moussalli and M. J. Whiting (2006). Multiple signals in chameleon contests: designing and analysing animal contests as a tournament. Animal Behaviour 71:1263-1271.

Stuart-Fox, D. M. and M. J. Whiting (2005). Male dwarf chameleons assess risk of courting large, aggressive females. Biology letters 1:231-234.

Sugg, D. W., L. A. Fitzgerald and H. L. Snell (1995). Growth rate, timing of reproduction, and size dimorphism in the southwestern earless lizard (*Cophosaurus texanus scitulus*). The Southwestern Naturalist 40:193-202.

Székely, T., J. D. Reynolds and J. Figuerola (2000). Sexual size dimorphism in shorebirds, gulls, and alcids: the influence of sexual and natural selection. Evolution 54:1404-1413.

Tinkle, D. W. and R. E. Ballinger (1972). *Sceloporus undulatus*: a study of the intraspecific comparative demography of a lizard. Ecology 53:570-584.

Vinegar, M. B. (1972). The function of breeding coloration in the lizard, *Sceloporus virgatus*. Copeia 1972:660-664.

Vinegar, M. B. (1975). Comparative aggression in *Sceloporus virgatus*, *S. undulatus consobrinus*, and *S. u. tristichus* (Sauria: Iguanidae). Animal Behaviour 23:279-286.

Warner, R. R. (1984). Deferred reproduction as a response to sexual selection in a coral reef fish: a test of the life historical consequences. Evolution 38:148-162.

Whiting, M. J., K. A. Nagy and P. W. Bateman (2003). Evolution and maintenance of social status-signaling badges. Pp. 47-81. J. K. M. S. F. Fox, T. A. Baird Lizard social behavior. Johns Hopkins University Press, USA, Baltimore, Maryland

Whiting, M. J., J. K. Webb and J. S. Keogh (2009). Flat lizard female mimics use sexual deception in visual but not chemical signals. Proceedings of the Royal Society B: Biological Sciences 276:1585-1591.

Wikelski, M., C. Carbone and F. Trillmich (1996). Lekking in marine iguanas: female grouping and male reproductive strategies. Animal Behaviour 52:581-596.

Wikelski, M. and F. Trillmich (1997). Body size and sexual size dimorphism in marine iguanas fluctuate as a result of opposing natural and sexual selection: an island comparison. Evolution 51:922-936.

Wilk, M. B. and R. Gnanadesikan (1968). Probability plotting methods for the analysis for the analysis of data. Biometrika 55:1-17.

Zamudio, K. R. (1998). The evolution of female-biased sexual size dimorphism: a population-level comparative study in horned lizards (*Phrynosoma*). Evolution 52:1821-1833.

APPENDIX A

Herein I have provided the locality data and voucher numbers for specimens used in the investigation described in chapter I. We used HerpNET (http://www.herpnet.org) to query and choose specimens. Specimens where obtained from the following institutions: University of Kansas Natural History Museum and Biodiversity Research Center (KUNHM), Smithsonian National Museum of Natural History, Washington, D.C. (USNM), Museum of Southwestern Biology, University of New Mexico (MSB), Florida Museum of Natural History, University of Florida (UF), Monte L. Bean Museum, Brigham Young University, Provo, UT (BYU). All specimens were sent to the Texas Cooperative Wildlife Collection, Texas A&M University (TCWC) where we complimented our project with specimens from the TCWC.

Sceloporus undulatus (complex)

(30) Kansas: Cherokee, Co.(KUNHM: 7817, 2321128771-72, 28775, 28776, 28781, 28784-85, 28788-89, 30084-85, 30093-95, 30097-103, 31092, 75150, 154017, 157817 159826 206700 289052)

(30) Virginia: Henrico, Co. (USNM: 324245, 325231,325233-44, 325247-48, 325251-52, 325254-56, 325258, 325260-67)

(30) North Carolina: Lenoir, Co. (USNM: 499937-67, 499972)

(30) Colorado: Garfield, Co. (MSB: 85934, 85936, 85938-39, 85941, 85946 ,85949, 85956, 85957, 85976, 85985-86, 85987-88, 85991, 85997-99, 86001, 86045, 86047-48, 86048, 86051, 86063, 86066-67, 86069, 86074, 86076, 86084)

(25) New Mexico: Hidalgo, Co. (MSB: 4427-28, 4449, 6168, 7292, 11129, 11153, 12141, 23248, 33813, 41197-98, 48822- 23, 48850, 51156, 51160 51161-63, 51165, 51168-69, 55903, 55915)

(30) New Mexico: Torrance Co. (MSB: 81-82, 7254, 10274, 11550, 18859, 18865-67, 21187-89, 21201-5, 23399, 23525, 26148-50, 26153-54, 26327, 31353, 31915, 42045, 52795, 87871)

(29) Arizona: Coconino, Co. (MSB: 17282-85, 17287-89, 17292-95, 17304-05, 17308-09, 23921-22, 23940, 23957, 23959, 23971, 23997, 35151, 35154-56, 35159-61)

(27) Florida: Alachua, Co. (UF: 461, 1144, 1978, 7790, 14589-90, 14592, 25191, 54449, 54452-53, 54459, 54461, 83731, 83734, 125193, 125258, 125291-92, 146034, 1389-4, 1389-5, 1389-6, 14593-1, 14593-2, 5942-2, 7553-2)

(30) Utah: Emery, Co. (BYU: 2392, 2806, 16296, 16300, 16407, 16464, 16539, 16765, 18032, 18034, 18355-61, 18363-64, 19026, 19054, 19056, 19057, 19096, 19107-08, 19121-22, 19124-25)

 (9) Texas: Anderson, Co. (TCWC: 5783, 5784, 5785, 14018, 29246-47, 39132, 54052, 82758)

(5) Texas: Jasper, Co. (TCWC: 18840, 65189, 67838, 79174, 79175)

(30) Texas: Jeff Davis, Co. (TCWC: 13059, 25290, 25918-20, 25922, 25924-27, 35343-47, 36871, 75770, 75810, 75815, 81549, 81556-57, 81584 81656-59, 83169, 83175, 84525)

 (4) Texas: Newton, Co. (TCWC: 8855, 8856, 48386, 48387)

(10) Texas: Polk, Co. (TCWC: 125, 5754, 5756-57, 5763-66, 5769, 46511)

(3) Texas: Tyler, Co. (TCWC: 5770, 8849, 14997)

(30) Texas: Uvalde, Co. (TCWC: 48920, 48935, 48951, 48966, 48974, 48979, 48981, 48986, 48988, 48992, 48995, 48999, 49002, 49008, 49010-11, 49013, 49015, 49017, 49020, 51202, 51208, 51210-13, 51216, 51218-20)

APPENDIX B

The full statistical output of reduced major axes (RMA) regression (mean±SD, slope, confidence intervals, R^2, and allomety).

Full results of the RMA conducted on SVL vs. Torso

Parameter	Mean±SD	Slope	CI	R^2	Allometry
All Males	3.36±0.14	0.9182	0.829-1.008	0.585	Isometric
Sceloporus consobrinus	3.30±0.15	0.5792	0.4296-0.7288	0.298	Negative
Kansas	3.22±0.15	0.9675	0.594-1.341	0.585	Isometric
Uvalde, TX	3.47±0.09	0.7889	0.502-1.076	0.63	Isometric
East Texas	3.21±0.08	1.086	0.617-1.555	0.481	Isometric
Sceloporus undulatus	3.37±0.13	0.9313	0.777-1.086	0.73	Isometric
Virginia	3.45±0.14	0.7887	0.5828-0.9946	0.81	Negative
North Carolina	3.33±0.10	1.266	0.783-1.749	0.595	Isometric
Florida	3.33±0.11	0.8441	0.544-1.144	0.745	Isometric
Sceloporus tristichus	3.45±0.14	0.7902	0.6505-0.9300	0.686	Negative
Colorado	3.37±0.08	1.06	0.597-1.523	0.469	Isometric
Utah	3.38±0.10	0.7773	0.5766-0.9780	0.814	Negative
Arizona	3.59±0.13	0.9463	0.505-1.387	0.506	Isometric
Sceloporus cowlesi	3.31±0.09	0.9966	0.794-1.199	0.584	Isometric
New Mexico, Hidalgo	3.33±0.09	0.9151	0.558-1.272	0.655	Isometric
New Mexico, Torrence	3.33±0.08	0.8052	0.422-1.188	0.37	Isometric
Jeff Davis, TX	3.28±0.10	1.001	0.659-1.514	0.675	Isometric
All Females	3.44±0.17	0.9563	0.886-1.026	0.758	Isometric
Sceloporus consobrinus	3.33±0.17	0.8765	0696-1.057	0.542	Isometric
Kansas	3.37±0.16	0.993	0.731-1.254	0.807	Isometric
Uvalde, TX	3.41±0.16	0.7554	0.5664-0.9443	0.826	Negative
East Texas	3.20±0.12	0.9009	0.684-1.118	0.823	Isometric
Sceloporus undulatus	3.45±0.17	0.9042	0.790-1.018	0.833	Isometric
Virginia	3.55±0.18	0.9677	0.799-1.136	0.916	Isometric
North Carolina	3.42±0.13	1.04	0.801-1.279	0.853	Isometric
Florida	3.39±0.15	0.729	0.5166-0.9415	0.763	Negative
Sceloporus tristichus	3.54±0.14	0.8667	0.727-1.006	0.72	Isometric
Colorado	3.52±0.11	0.5609	0.3749-0.7468	0.694	Negative
Utah	3.50±0.10	0.7379	0.4876-0.9882	0.679	Negative
Arizona	3.59±0.18	1.019	0.808-1.231	0.869	Isometric
Sceloporus cowlesi	3.45±0.14	0.8828	0.748-1.018	0.772	Isometric

New Mexico, Hidalgo	3.40±0.14	0.8239	0.617-1.031	0.873	Isometric
New Mexico, Torrence	3.51±0.15	0.6384	0.4431-0.8336	0.74	Negative
Jeff Davis, TX	3.43±0.10	0.9561	0.760-1.153	0.882	Isometric

Full results of the RMA run on SVL vs Head Depth

Parameter	Mean±SD	Slope	CI	R^2	Allometry
All Males	1.95±0.14	0.9052	0.8289-0.9815	0.689	Negative
Sceloporus consobrinus	1.88±0.14	0.6384	0.5266-0.7502	0.677	Negative
Kansas	1.91±0.15	0.747	0.6348-0.8593	0.937	Negative
Uvalde, TX	1.79±0.14	0.942	0.505-1.379	0.402	Isometric
East Texas	1.95±0.08	0.6056	0.4375-0.7736	0.785	Negative
Sceloporus undulatus	2.00±0.15	0.8061	0.6930-0.9192	0.807	Negative
Virginia	2.09±0.13	0.8536	0.668-1.040	0.868	Isometric
North Carolina	1.92±0.15	0.8566	0.614-1.099	0.776	Isometric
Florida	1.99±0.12	0.7509	0.420-1.082	0.608	Isometric
Sceloporus tristichus	2.01±0.12	0.9537	0.780-1.127	0.668	Isometric
Colorado	1.96±0.11	0.7894	0.5840-0.9948	0.811	Negative
Utah	2.01±0.09	0.801	0.502-1.100	0.613	Isometric
Arizona	2.08±0.12	0.9877	0.581-1.394	0.615	Isometric
Sceloporus cowlesi	1.92±0.13	0.6933	0.5914-0.7952	0.783	Negative
New Mexico, Hidalgo	1.95±0.10	0.8867	0.672-1.102	0.866	Isometric
New Mexico, Torrence	1.99±0.11	0.6149	0.3836-0.8462	0.606	Negative
Jeff Davis, TX	1.82±0.13	0.758	0.5480-0.9681	0.786	Negative
All Females	1.98±0.16	1.036	0.960-1.113	0.752	Isometric
Sceloporus consobrinus	1.91±0.16	0.9261	0.834-1.018	0.893	Isometric
Kansas	2.04±0.17	0.932	0.743-1.121	0.886	Isometric
Uvalde, TX	1.87±0.10	1.207	0.874-1.541	0.788	Isometric
East Texas	1.84±0.14	0.8189	0.6846-0.9532	0.918	Negative
Sceloporus undulatus	2.02±0.16	0.9159	0.779-1.053	0.765	Isometric
Virginia	2.12±0.16	1.076	0.892-1.260	0.919	Isometric
North Carolina	2.02±0.12	1.16	0.778-1.541	0.699	Isometric
Florida	1.90±0.13	0.8064	0.487-1.125	0.564	Isometric
Sceloporus tristichus	2.05±0.13	0.9327	0.768-1.097	0.664	Isometric
Colorado	2.06±0.08	0.7846	0.509-1.060	0.656	Isometric
Utah	2.09±0.06	1.13	0.567-1.692	0.308	Isometric
Arizona	2.01±0.19	0.9754	0.723-1.228	0.796	Isometric
Sceloporus cowlesi	1.95±0.14	0.8827	0.746-1.019	0.766	Isometric
New Mexico, Hidalgo	1.91±0.13	0.926	0.598-1.254	0.747	Isometric

New Mexico, Torrence	2.04±0.12	0.8359	0.614-1.058	0.804	Isometric
Jeff Davis, TX	1.86±0.11	0.8969	0.521-1.273	0.51	Isometric

Full results of the RMA run on SVL vs Rear Leg Length

Parameter	Mean±SD	Slope	CI	R^2	Allometry
All Males	3.61±0.15	0.9042	0.8372-0.9712	0.759	Negative
Sceloporus consobrinus	3.48±0.13	0.8473	0.659-1.035	0.481	Isometric
Kansas	3.55±0.14	0.9283	0.635-1.222	0.721	Isometric
Uvalde, TX	3.47±0.12	0.8377	0.408-1.267	0.267	Isometric
East Texas	3.41±0.11	0.8266	0.501-1.153	0.567	Isometric
Sceloporus undulatus	3.65±0.14	1.047	0.930-1.164	0.877	Isometric
Virginia	3.68±0.16	1.121	0.851-1.391	0.838	Isometric
North Carolina	3.68±0.13	1.138	0.977-1.300	0.944	Isometric
Florida	3.60±0.13	0.9429	0.601-1.285	0.735	Isometric
Sceloporus tristichus	3.72±0.13	0.9839	0.808-1.159	0.68	Isometric
Colorado	3.70±0.07	1.368	0.871-1.864	0.633	Isometric
Utah	3.75±0.12	0.8149	0.388-1.242	0.236	Isometric
Arizona	3.70±0.18	0.9004	0643-1.158	0.815	Isometric
Sceloporus cowlesi	3.60±0.09	1.184	0.916-1.453	0.483	Isometric
New Mexico, Hidalgo	3.56±0.10	1.026	0.557-1.495	0.526	Isometric
New Mexico, Torrence	3.64±0.06	0.967	0.474-1.460	0.276	Isometric
Jeff Davis, TX	3.58±0.09	1.366	0.951-1.781	0.743	Isometric
All Females	3.60±0.15	1.079	1.010-1.148	0.815	Positive
Sceloporus consobrinus	3.48±0.13	1.149	0.966-1.333	0.725	Isometric
Kansas	3.42±0.11	1.163	0.867-1.459	0.819	Isometric
Uvalde, TX	3.58±0.14	1.069	0.671-1.467	0.614	Isometric
East Texas	3.45±0.11	0.9715	0.638-1.305	0.641	Isometric
Sceloporus undulatus	3.66±0.13	1.108	1.010-1.206	0.918	Positive
Virginia	3.66±0.17	1.121	0.851-1.391	0.838	Isometric
North Carolina	3.67±0.12	1.062	0.886-1.237	0.924	Isometric
Florida	3.64±0.09	0.9898	0.733-1.246	0.813	Isometric
Sceloporus tristichus	3.72±0.11	0.9962	0.811-1.181	0.628	Isometric
Colorado	3.67±0.07	1.324	0.559-2.089	0.0701	Isometric
Utah	3.70±0.09	1.373	0.634-2.112	0.193	Isometric
Arizona	3.78±0.14	0.9812	0.754-1.209	0.836	Isometric
Sceloporus cowlesi	3.58±0.08	1.406	1.168-1.644	0.72	Positive
New Mexico, Hidalgo	3.59±0.10	1.247	0.789-1.705	0.728	Isometric
New Mexico, Torrence	3.58±0.07	1.205	0.858-1.553	0.769	Isometric

Jeff Davis, TX	3.56±0.08	1.275	0.856-1.694	0.699	Isometric

Full results of the RMA run on SVL vs. Head Length

Parameter	Mean±SD	Slope	CI	R^2	Allometry
All Males	2.69±0.13	1.028	0.968-1.088	0.851	Isometric
Sceloporus consobrinus	2.61±0.10	0.8601	0.7582-0.9626	0.79	Negative
Kansas	2.59±0.13	0.868	0.7557-0.9919	0.95	Negative
Uvalde, TX	2.58±0.10	0.8746	0.690-1.041	0.867	Isometric
East Texas	2.65±0.08	0.9671	0.673-1.828	0.45	Isometric
Sceloporus undulatus	2.72±0.12	1.035	0.910-1.161	0.856	Isometric
Virginia	2.77±0.10	1.072	0.872-1.195	0.922	Isometric
North Carolina	2.67±0.14	0.9232	0.665-1.313	0.783	Isometric
Florida	2.71±0.08	1.096	0.862-1.330	0.908	Isometric
Sceloporus tristichus	2.80±0.11	0.9599	0.852-1.082	0.875	Isometric
Colorado	2.76±0.09	0.9409	0.732-1.179	0.787	Isometric
Utah	2.75±0.09	0.8088	0.563-1.297	0.707	Isometric
Arizona	2.89±0.11	1.08	0.761-1.203	0.939	Isometric
Sceloporus cowlesi	2.64±0.09	1.028	0.848-1.182	0.666	Isometric
New Mexico, Hidalgo	2.61±0.09	0.9137	0.713-1.123	0.618	Isometric
New Mexico, Torrence	2.69±0.06	1.069	0.728-1.550	0.526	Isometric
Jeff Davis, TX	2.62±0.09	1.029	0.735-1.200	0.869	Isometric
All Females	2.72±0.14	1.035	0.930-1.153	0.751	Isometric
Sceloporus consobrinus	2.63±0.12	1.206	1.106-1.333	0.865	Positive
Kansas	2.70±0.12	1.194	1.014-1.464	0.834	Positive
Uvalde, TX	2.61±0.10	1.194	1.013-1.522	0.834	Positive
East Texas	2.58±0.11	0.9843	0.830-1.121	0.863	Isometric
Sceloporus undulatus	2.73±0.12	1.213	1.112-1.343	0.903	Positive
Virginia	2.77±0.15	1.186	1.049-1.424	0.924	Positive
North Carolina	2.75±0.11	1.223	1.086-1.494	0.934	Positive
Florida	2.69±0.10	1.08	0.899-1.317	0.822	Isometric
Sceloporus tristichus	2.84±0.12	0.9932	0.895-1.120	0.824	Isometric
Colorado	2.85±0.07	0.8901	0.506-1.269	0.444	Isometric
Utah	2.84±0.06	1.107	0.677-1.768	0.394	Isometric
Arizona	2.82±0.19	0.9961	0.860-1.069	0.946	Isometric
Sceloporus cowlesi	2.66±0.10	1.204	1.055-1.415	0.762	Positive
New Mexico, Hidalgo	2.59±0.07	1.679	1.166-2.452	0.805	Positive
New Mexico, Torrence	2.75±0.09	1.036	0.721-1.333	0.851	Isometric
Jeff Davis, TX	2.63±0.06	1.503	1.103-1.919	0.44	Positive

Full Results of the RMA run on SVL vs Head Width

Parameter	Mean±SD	Slope	CI	R^2	Allometry
All Males	2.25±0.15	0.8644	0.8046-0.9241	0.79	Negative
Sceloporus consobrinus	2.17±0.15	0.5923	0.4751-0.7096	0.588	Negative
Kansas	2.19±0.14	0.7993	0.6355-0.9632	0.883	Negative
Uvalde, TX	2.06±0.13	0.7433	0.390-1.097	0.37	Isometric
East Texas	2.30±0.10	0.6199	0.4637-0.7913	0.823	Negative
Sceloporus undulatus	2.29±0.13	0.8987	0.7976-0.9999	0.876	Negative
Virginia	2.38±0.12	0.901	0.750-1.052	0.922	Isometric
North Carolina	2.21±0.13	1.017	0.774-1.261	0.841	Isometric
Florida	2.28±0.10	0.9524	0.669-1.236	0.822	Isometric
Sceloporus tristichus	2.40±0.12	0.928	0.838-1.018	0.906	Isometric
Colorado	2.32±0.10	0.8765	0.682-1.071	0.862	Isometric
Utah	2.34±0.09	0.8244	0.602-1.047	0.797	Isometric
Arizona	2.46±0.13	0.9782	0.852-1.105	0.962	Isometric
Sceloporus cowlesi	2.21±0.12	0.7834	0.6665-0.9002	0.777	Negative
New Mexico, Hidalgo	2.21±0.11	0.7925	0.525-1.060	0.74	Isometric
New Mexico, Torrence	2.28±0.08	0.8302	0.502-1.158	0.565	Isometric
Jeff Davis, TX	2.12±0.10	0.9259	0.693-1.158	0.824	Isometric
All Females	2.28±0.17	1.015	0.943-1.086	0.773	Isometric
Sceloporus consobrinus	2.19±0.16	1.046	0.874-1.217	0.771	Isometric
Kansas	2.32±0.15	1.085	0.865-1.305	0.885	Isometric
Uvalde, TX	2.16±0.11	1.441	0.719-2.164	0.3	Isometric
East Texas	2.10±0.12	0.8988	0.716-1.082	0.874	Isometric
Sceloporus undulatus	2.31±0.16	0.9565	0.814-1.099	0.765	Isometric
Virginia	2.43±0.13	1.304	1.040-1.569	0.886	Positive
North Carolina	2.33±0.13	1.086	0.843-1.329	0.86	Isometric
Florida	2.19±0.11	0.9702	0.597-1.344	0.587	Isometric
Sceloporus tristichus	2.40±0.12	0.97	0.835-1.104	0.793	Isometric
Colorado	2.43±0.07	0.8482	0.481-1.215	0.479	Isometric
Utah	2.4±0.068	1.057	0.548-1.567	0.354	Isometric
Arizona	2.38±0.19	0.9962	0.849-1.143	0.934	Isometric
Sceloporus cowlesi	2.24±0.15	0.8964	0.785-1.008	0.849	Isometric
New Mexico, Hidalgo	2.17±0.13	0.9052	0.571-1.239	0.726	Isometric
New Mexico, Torrence	2.31±0.12	0.8063	0.6531-0.9595	0.899	Isometric
Jeff Davis, TX	2.14±0.10	0.9906	0.700-1.282	0.76	Isometric

APPENDIX C

Herein I provide locality data, voucher numbers and raw measurements for

specimens used in chapter III of this investigation. I used HerpNET

(http://www.herpnet.org) to query and choose specimens. Specimens were obtained from

the Museum of Southwestern Biology, University of New Mexico (MSB), and the Texas

Cooperative Wildlife Collection, Texas A&M University (TCWC). Herein I provide two

tables for each sex. Each table includes the state and county of collection, the collection

identification number, the raw untransformed Total Badge Area (TBA) and raw

untransformed snout to vent length (SVL).

Collections Data and Raw Measurements for all Female Specimens

Collection ID		State	County	Species	TBA	SVL
MSB	56565	NM	Lea	*S. consobrinus*	0	61.8271
MSB	56778	NM	Lea	*S. consobrinus*	0	62.3017
MSB	59874	NM	Lea	*S. consobrinus*	0	63.3444
MSB	60255	NM	Lea	*S. consobrinus*	0	56.1982
MSB	60417	NM	Lea	*S. consobrinus*	0	49.8486
MSB	60509	NM	Lea	*S. consobrinus*	0	49.8486
MSB	60531	NM	Lea	*S. consobrinus*	0	48.9275
MSB	60533	NM	Lea	*S. consobrinus*	0	58.8965
MSB	60929	NM	Lea	*S. consobrinus*	0	55.0320
MSB	57635	NM	Roosevelt	*S. consobrinus*	0	51.8152
MSB	59893	NM	Roosevelt	*S. consobrinus*	0	59.9459
MSB	59894	NM	Roosevelt	*S. consobrinus*	0	54.8725
MSB	59924	NM	Roosevelt	*S. consobrinus*	0	52.3520
MSB	59927	NM	Roosevelt	*S. consobrinus*	0	50.4669
MSB	59928	NM	Roosevelt	*S. consobrinus*	0	55.5981
MSB	59936	NM	Roosevelt	*S. consobrinus*	0	56.2699
MSB	59940	NM	Roosevelt	*S. consobrinus*	0	64.4547
TCWC	48966	TX	Uvalde	*S. consobrinus*	0	49.6148
TCWC	48969	TX	Uvalde	*S. consobrinus*	0	49.6107
TCWC	79167	TX	Bandera	*S. consobrinus*	0	70.0019

TCWC	80431	TX	Kerr	*S. consobrinus*	27.1741	72.2300
TCWC	48920	TX	Uvalde	*S. consobrinus*	18.4908	61.3404
TCWC	48937	TX	Uvalde	*S. consobrinus*	49.5254	64.6283
TCWC	48998	TX	Uvalde	*S. consobrinus*	21.5026	56.9294
MSB	22906	NM	Eddy	*S. consobrinus*	0	65.2921
MSB	22954	NM	Eddy	*S. consobrinus*	0	69.7794
MSB	26158	NM	Eddy	*S. consobrinus*	0	78.8293
MSB	31158	NM	Eddy	*S. consobrinus*	0	68.1793
MSB	31160	NM	Eddy	*S. consobrinus*	0	73.1154
MSB	33641	NM	Eddy	*S. consobrinus*	0	68.9705
MSB	38476	NM	Eddy	*S. consobrinus*	0	57.2676
MSB	38497	NM	Eddy	*S. consobrinus*	0	59.2604
MSB	38505	NM	Eddy	*S. consobrinus*	0	61.2265
MSB	43648	NM	Eddy	*S. consobrinus*	0	69.2264
MSB	46054	NM	Eddy	*S. consobrinus*	0	70.1751
MSB	48589	NM	Eddy	*S. consobrinus*	0	73.6866
MSB	48590	NM	Eddy	*S. consobrinus*	0	69.1457
MSB	61900	NM	Eddy	*S. consobrinus*	0	60.3801
MSB	71562	NM	Eddy	*S. consobrinus*	0	73.8084
TCWC	46514	TX	Kinney	*S. consobrinus*	0	64.2139
TCWC	46515	TX	Kinney	*S. consobrinus*	0	54.2078
TCWC	54071	TX	Kinney	*S. consobrinus*	26.1110	62.5240
MSB	60365	NM	Otero	*S. cowlesi*	0	61.9898
MSB	23399	NM	Torrance	*S. cowlesi*	0	65.4595
MSB	26046	NM	Valencia	*S. cowlesi*	0	69.3213
MSB	21113	NM	Torrance	*S. cowlesi*	56.3167	56.9441
MSB	11550	NM	Torrance	*S. cowlesi*	52.8420	69.7025
MSB	21105	NM	Torrance	*S. cowlesi*	69.1051	73.0519
MSB	21117	NM	Torrance	*S. cowlesi*	36.0364	69.4939
MSB	26148	NM	Torrance	*S. cowlesi*	35.5245	71.2026
MSB	6335	NM	Otero	*S. cowlesi*	37.8542	64.5813
MSB	16282	NM	Otero	*S. cowlesi*	26.0071	55.7215
MSB	48031	NM	Otero	*S. cowlesi*	35.6530	69.2035
MSB	60366	NM	Otero	*S. cowlesi*	30.9491	60.5681
MSB	60367	NM	Otero	*S. cowlesi*	30.6146	69.5198
MSB	60368	NM	Otero	*S. cowlesi*	23.5764	64.1262
MSB	60369	NM	Otero	*S. cowlesi*	26.0451	72.2332
MSB	26150	NM	Torrance	*S. cowlesi*	39.5927	78.1202
MSB	21114	NM	Torrance	*S. cowlesi*	56.7220	66.9330
MSB	21123	NM	Torrance	*S. cowlesi*	37.2090	59.7812

MSB	21203	NM	Torrance	*S. cowlesi*	37.8698	70.2739
MSB	7249	NM	Valencia	*S. cowlesi*	28.3683	65.9678
MSB	7251	NM	Valencia	*S. cowlesi*	13.6073	62.8052
MSB	21115	NM	Torrance	*S. cowlesi*	499.5412	72.4474
MSB	26149	NM	Torrance	*S. cowlesi*	297.2064	68.9566
MSB	6334	NM	Otero	*S. cowlesi*	227.3149	68.6022
MSB	18865	NM	Torrance	*S. cowlesi*	244.7470	61.0278
MSB	21108	NM	Torrance	*S. cowlesi*	160.9683	50.9515
MSB	26152	NM	Torrance	*S. cowlesi*	328.1760	65.7085
MSB	26327	NM	Torrance	*S. cowlesi*	311.8219	69.4237
MSB	26154	NM	Torrance	*S. cowlesi*	368.5055	70.2960
MSB	6814	NM	Valencia	*S. cowlesi*	207.6157	57.9157
MSB	7092	NM	Valencia	*S. cowlesi*	262.2492	65.7343
MSB	21199	NM	Valencia	*S. cowlesi*	282.4295	66.9102
MSB	21198	NM	Valencia	*S. cowlesi*	297.6377	64.4957
MSB	21191	NM	Valencia	*S. cowlesi*	181.5809	60.7111
TCWC	51988	TX	Terrell	*S. cowlesi*	0	69.3129
TCWC	72507	TX	Terrell	*S. cowlesi*	0	59.2620
TCWC	60553	TX	Val Verde	*S. cowlesi*	0	58.8965
TCWC	60554	TX	Val Verde	*S. cowlesi*	0	59.3544
TCWC	64702	TX	Val Verde	*S. cowlesi*	0	61.7394
TCWC	52205	TX	Edwards	*S. cowlesi*	0	64.9511
TCWC	67772	TX	Edwards	*S. cowlesi*	0	62.6272
TCWC	7197	TX	Edwards	*S. cowlesi*	0	61.6159
TCWC	16015	TX	Brewster	*S. cowlesi*	0	62.6417
TCWC	16017	TX	Brewster	*S. cowlesi*	0	61.3761
TCWC	16018	TX	Brewster	*S. cowlesi*	0	54.6724
TCWC	16020	TX	Brewster	*S. cowlesi*	0	61.7134
TCWC	16026	TX	Brewster	*S. cowlesi*	0	57.9907
TCWC	25918	TX	Jeff Davis	*S. cowlesi*	0	68.9094
TCWC	25922	TX	Jeff Davis	*S. cowlesi*	0	68.8879
TCWC	25924	TX	Jeff Davis	*S. cowlesi*	0	56.8099
TCWC	25925	TX	Jeff Davis	*S. cowlesi*	0	59.1401
TCWC	25926	TX	Jeff Davis	*S. cowlesi*	0	66.7151
TCWC	26125	TX	Jeff Davis	*S. cowlesi*	0	62.6508
TCWC	35347	TX	Jeff Davis	*S. cowlesi*	0	60.7689
TCWC	71586	TX	Jeff Davis	*S. cowlesi*	0	63.4584
TCWC	81556	TX	Jeff Davis	*S. cowlesi*	0	67.7033
TCWC	81584	TX	Jeff Davis	*S. cowlesi*	0	56.6808
TCWC	81656	TX	Jeff Davis	*S. cowlesi*	0	59.1131

TCWC	84525	TX	Jeff Davis	*S. cowlesi*	0	58.4365
TCWC	16021	TX	Brewster	*S. cowlesi*	16.3478	58.7332
TCWC	52209	TX	Edwards	*S. cowlesi*	22.4842	69.4231
TCWC	20719	TX	Val Verde	*S. cowlesi*	32.3264	63.6716
TCWC	54496	TX	Val Verde	*S. cowlesi*	27.1324	67.0899
MSB	82489	CO	Montezuma	*S. tristichus*	393.4121	78.3175
MSB	82490	CO	Montezuma	*S. tristichus*	281.2941	68.7824
MSB	82493	CO	Montezuma	*S. tristichus*	341.9425	75.7534
MSB	83014	CO	Montezuma	*S. tristichus*	272.5066	67.3408
MSB	83006	CO	Montezuma	*S. tristichus*	317.2331	77.6375
MSB	83007	CO	Montezuma	*S. tristichus*	421.5562	75.6908
MSB	83006	CO	Montezuma	*S. tristichus*	317.2331	77.6375
MSB	83011	CO	Montezuma	*S. tristichus*	347.0950	80.3956
MSB	87782	CO	Montezuma	*S. tristichus*	466.9852	78.5728
MSB	87882	CO	Montezuma	*S. tristichus*	268.2195	74.9558
MSB	14579	NM	Bernalillo	*S. tristichus*	0	63.1614
MSB	14675	NM	Bernalillo	*S. tristichus*	0	61.2351
MSB	16890	NM	Bernalillo	*S. tristichus*	0	64.2908
MSB	17264	NM	Sandoval	*S. tristichus*	0	54.3321
MSB	13163	NM	Bernalillo	*S. tristichus*	47.1971	77.0294
MSB	16574	NM	Bernalillo	*S. tristichus*	17.6055	55.9998
MSB	16576	NM	Bernalillo	*S. tristichus*	21.2051	66.2791
MSB	16995	NM	Bernalillo	*S. tristichus*	42.2754	70.3302
MSB	21190	NM	Bernalillo	*S. tristichus*	35.2024	72.6971
MSB	25974	NM	Bernalillo	*S. tristichus*	26.3806	73.6552
MSB	16888	NM	Sandoval	*S. tristichus*	21.4483	54.9722
MSB	17315	NM	Sandoval	*S. tristichus*	18.7502	60.7277
MSB	17316	NM	Sandoval	*S. tristichus*	20.5248	70.8660
MSB	76389	NM	Mickinley	*S. tristichus*	36.5211	67.8412
MSB	16477	NM	Bernalillo	*S. tristichus*	484.1792	74.1342
MSB	25837	NM	Bernalillo	*S. tristichus*	274.7938	69.1345
MSB	15972	NM	Bernalillo	*S. tristichus*	193.4820	57.1252
MSB	16612	NM	Bernalillo	*S. tristichus*	325.7322	70.5585
MSB	21208	NM	Bernalillo	*S. tristichus*	360.9930	66.2045
MSB	23522	NM	Bernalillo	*S. tristichus*	407.4995	69.3471
MSB	76285	NM	Cibola	*S. tristichus*	311.7578	71.7635
MSB	76385	NM	Cibola	*S. tristichus*	297.8101	72.4612
MSB	87840	NM	Cibola	*S. tristichus*	352.3958	70.5926
MSB	3212	NM	Mickinley	*S. tristichus*	756.4573	95.1929
MSB	3217	NM	Mickinley	*S. tristichus*	476.4050	85.8810

MSB	3218	NM	Mickinley	*S. tristichus*	306.5322	75.1365
MSB	11960	NM	Mickinley	*S. tristichus*	445.1829	72.1382
MSB	76376	NM	Mickinley	*S. tristichus*	163.3097	55.6301
MSB	76387	NM	Mickinley	*S. tristichus*	280.1656	68.3112
MSB	76410	NM	Mickinley	*S. tristichus*	243.8820	62.0186
MSB	77934	NM	Mickinley	*S. tristichus*	377.0175	73.0797
MSB	3181	NM	San Juan	*S. tristichus*	351.5229	77.4198
MSB	3183	NM	San Juan	*S. tristichus*	553.4925	90.2097
MSB	3193	NM	San Juan	*S. tristichus*	294.9486	71.3265
MSB	3194	NM	San Juan	*S. tristichus*	294.9486	71.3265
MSB	3220	NM	San Juan	*S. tristichus*	325.1569	76.3891
MSB	21782	NM	San Juan	*S. tristichus*	387.3275	69.9082
MSB	21785	NM	San Juan	*S. tristichus*	545.0869	74.3095
MSB	40658	NM	San Juan	*S. tristichus*	262.7891	71.8935
MSB	40659	NM	San Juan	*S. tristichus*	288.4467	67.9031
MSB	40668	NM	San Juan	*S. tristichus*	376.6657	79.3108
MSB	48915	NM	San Juan	*S. tristichus*	345.5227	72.7250
MSB	48917	NM	San Juan	*S. tristichus*	369.8052	80.5886
MSB	49987	NM	San Juan	*S. tristichus*	382.3376	72.8808
MSB	60304	NM	San Juan	*S. tristichus*	370.3662	73.0537
MSB	63176	NM	San Juan	*S. tristichus*	306.1003	77.3014
MSB	63177	NM	San Juan	*S. tristichus*	416.2134	77.8749
MSB	63178	NM	San Juan	*S. tristichus*	433.9067	79.7339
MSB	16476	NM	Sandoval	*S. tristichus*	556.0932	76.1882
MSB	17255	NM	Sandoval	*S. tristichus*	257.3591	58.5170
MSB	26147	NM	Sandoval	*S. tristichus*	513.6601	76.2503
MSB	73520	NM	Sandoval	*S. tristichus*	321.0734	68.1550
MSB	73521	NM	Sandoval	*S. tristichus*	432.6698	73.8875
MSB	73522	NM	Sandoval	*S. tristichus*	477.7920	80.9468

Collections Data and Raw Measurements for all Male Specimens

Collection ID		State	County	Species	TBA	SVL
MSB	55935	NM	Lea	*S. consobrinus*	181.2423	55.7758
MSB	56567	NM	Lea	*S. consobrinus*	88.1075	46.2609
MSB	60415	NM	Lea	*S. consobrinus*	93.1774	44.4544
MSB	60490	NM	Lea	*S. consobrinus*	182.5660	54.8789
MSB	60500	NM	Lea	*S. consobrinus*	103.6669	48.5572
MSB	60519	NM	Lea	*S. consobrinus*	108.5186	52.3983
MSB	60928	NM	Lea	*S. consobrinus*	135.1659	50.2885
MSB	74876	NM	Lea	*S. consobrinus*	98.3415	45.9313
MSB	56755	NM	Roosevelt	*S. consobrinus*	120.4711	47.2582

MSB	56757	NM	Roosevelt	*S. consobrinus*	106.0882	51.1712
MSB	59896	NM	Roosevelt	*S. consobrinus*	156.1133	54.7106
MSB	57622	NM	Roosevelt	*S. consobrinus*	148.0697	51.9604
MSB	16805	NM	Bernalillo	*S. consobrinus*	243.4671	52.8744
MSB	22948	NM	Eddy	*S. consobrinus*	454.0167	63.8612
MSB	38492	NM	Eddy	*S. consobrinus*	347.5925	62.1405
MSB	52122	NM	Eddy	*S. consobrinus*	361.0383	64.1824
MSB	22951	NM	Eddy	*S. consobrinus*	405.1210	67.4908
MSB	22953	NM	Eddy	*S. consobrinus*	276.6490	61.8638
MSB	38496	NM	Eddy	*S. consobrinus*	399.3252	66.0095
MSB	39040	NM	Eddy	*S. consobrinus*	348.8635	61.4382
MSB	39042	NM	Eddy	*S. consobrinus*	381.1943	62.1360
MSB	48543	NM	Eddy	*S. consobrinus*	403.0482	60.9830
MSB	48730	NM	Eddy	*S. consobrinus*	540.0926	70.0109
MSB	60574	NM	Eddy	*S. consobrinus*	261.7445	54.0011
MSB	66893	NM	Eddy	*S. consobrinus*	352.3885	65.8394
MSB	57617	NM	Roosevelt	*S. consobrinus*	122.9895	49.0768
MSB	57624	NM	Roosevelt	*S. consobrinus*	118.2200	48.9209
MSB	57634	NM	Roosevelt	*S. consobrinus*	119.6035	47.9229
MSB	12253	NM	Sandoval	*S. consobrinus*	284.2871	62.9511
MSB	25916	NM	Sandoval	*S. consobrinus*	368.8750	65.1447
TCWC	18839	TX	Kerr	*S. consobrinus*	408.2949	61.2253
TCWC	4464	TX	Kerr	*S. consobrinus*	227.6859	54.7788
TCWC	4465	TX	Kerr	*S. consobrinus*	249.1970	51.5361
TCWC	4466	TX	Kerr	*S. consobrinus*	340.9474	60.6942
TCWC	48910	TX	Uvalde	*S. consobrinus*	317.7559	55.8610
TCWC	48914	TX	Uvalde	*S. consobrinus*	298.6615	53.1151
TCWC	48927	TX	Uvalde	*S. consobrinus*	237.1561	53.0383
TCWC	51200	TX	Uvalde	*S. consobrinus*	224.1894	50.4316
TCWC	51211	TX	Uvalde	*S. consobrinus*	259.4330	58.8137
TCWC	51216	TX	Uvalde	*S. consobrinus*	325.9707	55.1616
TCWC	51986	TX	Kerr	*S. consobrinus*	307.6230	56.4987
TCWC	83925	TX	Kinney	*S. consobrinus*	231.3822	53.2575
MSB	66903	NM	Otero	*S. cowlesi*	295.2529	60.1226
MSB	7254	NM	Torrance	*S. cowlesi*	304.9273	58.5159
MSB	10273	NM	Torrance	*S. cowlesi*	281.5453	55.6281
MSB	10274	NM	Torrance	*S. cowlesi*	387.3349	60.0363
MSB	10275	NM	Torrance	*S. cowlesi*	433.9721	63.9081
MSB	18856	NM	Torrance	*S. cowlesi*	363.6948	56.5156
MSB	18866	NM	Torrance	*S. cowlesi*	306.2224	55.0405

MSB	18897	NM	Torrance	*S. cowlesi*	510.4993	66.3333
MSB	21104	NM	Torrance	*S. cowlesi*	428.0742	62.1130
MSB	21106	NM	Torrance	*S. cowlesi*	337.0792	60.6567
MSB	21111	NM	Torrance	*S. cowlesi*	234.8987	50.5936
MSB	21112	NM	Torrance	*S. cowlesi*	511.5112	69.2392
MSB	21116	NM	Torrance	*S. cowlesi*	243.5987	54.6450
MSB	21118	NM	Torrance	*S. cowlesi*	500.4126	70.6780
MSB	21120	NM	Torrance	*S. cowlesi*	327.4966	57.2691
MSB	21121	NM	Torrance	*S. cowlesi*	447.4290	64.1158
MSB	21124	NM	Torrance	*S. cowlesi*	369.3464	64.6491
MSB	21201	NM	Torrance	*S. cowlesi*	362.8763	61.4913
MSB	21202	NM	Torrance	*S. cowlesi*	494.5778	62.6123
MSB	21204	NM	Torrance	*S. cowlesi*	370.8063	55.3519
MSB	21205	NM	Torrance	*S. cowlesi*	500.6512	65.7948
MSB	26153	NM	Torrance	*S. cowlesi*	434.1302	65.1019
MSB	7256	NM	Valencia	*S. cowlesi*	274.4211	56.8248
MSB	21149	NM	Valencia	*S. cowlesi*	347.8514	65.4772
MSB	21150	NM	Valencia	*S. cowlesi*	284.8648	61.8063
MSB	25805	NM	Valencia	*S. cowlesi*	387.8761	65.8234
MSB	72549	NM	Valencia	*S. cowlesi*	318.8615	61.8655
MSB	72551	NM	Valencia	*S. cowlesi*	270.4430	59.5551
MSB	72553	NM	Valencia	*S. cowlesi*	359.3334	57.8202
MSB	60364	NM	Otero	*S. cowlesi*	390.9751	66.4605
MSB	21928	NM	Torrance	*S. cowlesi*	195.0064	46.0954
MSB	26317	NM	Torrance	*S. cowlesi*	158.6268	47.0995
MSB	7089	NM	Valencia	*S. cowlesi*	409.1367	65.1113
MSB	7091	NM	Valencia	*S. cowlesi*	309.0205	59.0148
MSB	21195	NM	Valencia	*S. cowlesi*	225.2664	52.1502
MSB	21193	NM	Valencia	*S. cowlesi*	415.1511	67.7589
MSB	25919	NM	Valencia	*S. cowlesi*	350.8069	70.4360
MSB	25920	NM	Valencia	*S. cowlesi*	350.8069	70.4360
MSB	21197	NM	Valencia	*S. cowlesi*	294.1080	58.9256
TCWC	16016	TX	Brewster	*S. cowlesi*	377.7102	58.9717
TCWC	16019	TX	Brewster	*S. cowlesi*	315.6495	53.9358
TCWC	16022	TX	Brewster	*S. cowlesi*	322.1553	58.2118
TCWC	16023	TX	Brewster	*S. cowlesi*	456.3237	58.9042
TCWC	52206	TX	Edwards	*S. cowlesi*	331.4372	53.6639
TCWC	52207	TX	Edwards	*S. cowlesi*	241.3049	52.4845
TCWC	52208	TX	Edwards	*S. cowlesi*	389.7406	58.1135
TCWC	52210	TX	Edwards	*S. cowlesi*	263.5506	51.3696

TCWC	52212	TX	Edwards	*S. cowlesi*	284.4878	55.9254
TCWC	35345	TX	Jeff Davis	*S. cowlesi*	415.1047	58.7171
TCWC	35346	TX	Jeff Davis	*S. cowlesi*	342.7814	54.3209
TCWC	39871	TX	Jeff Davis	*S. cowlesi*	176.6597	45.6918
TCWC	81657	TX	Jeff Davis	*S. cowlesi*	368.2654	58.0291
TCWC	81658	TX	Jeff Davis	*S. cowlesi*	327.2380	55.7157
TCWC	81659	TX	Jeff Davis	*S. cowlesi*	436.3496	63.5442
TCWC	39994	TX	Terrell	*S. cowlesi*	238.5597	53.8550
TCWC	80230	TX	Terrell	*S. cowlesi*	372.5834	58.8439
TCWC	38873	TX	Val Verde	*S. cowlesi*	434.7058	62.0791
TCWC	64701	TX	Val Verde	*S. cowlesi*	451.5070	59.1603
TCWC	16024	TX	Brewster	*S. cowlesi*	361.0415	59.2048
TCWC	16025	TX	Brewster	*S. cowlesi*	214.2101	58.6182
TCWC	52211	TX	Edwards	*S. cowlesi*	332.8390	56.6714
TCWC	25919	TX	Jeff Davis	*S. cowlesi*	456.5617	69.9480
TCWC	25920	TX	Jeff Davis	*S. cowlesi*	350.8069	70.4360
TCWC	35344	TX	Jeff Davis	*S. cowlesi*	175.9212	46.2102
TCWC	38729	TX	Jeff Davis	*S. cowlesi*	175.9856	47.8658
TCWC	71820	TX	Terrell	*S. cowlesi*	270.3330	57.7429
TCWC	64185	TX	Val Verde	*S. cowlesi*	248.3585	54.7962
TCWC	64700	TX	Val Verde	*S. cowlesi*	217.8578	50.8186
MSB	82491	CO	Montezuma	*S. tristichus*	470.5954	75.3390
MSB	82492	CO	Montezuma	*S. tristichus*	604.6043	80.0847
MSB	21946	NM	MicKinley	*S. tristichus*	181.7984	52.4868
MSB	13064	NM	Bernalillo	*S. tristichus*	476.1021	65.5888
MSB	13162	NM	Bernalillo	*S. tristichus*	633.1817	72.6647
MSB	13165	NM	Bernalillo	*S. tristichus*	406.4148	63.3191
MSB	13167	NM	Bernalillo	*S. tristichus*	490.9825	71.1721
MSB	14674	NM	Bernalillo	*S. tristichus*	377.9645	63.7296
MSB	14794	NM	Bernalillo	*S. tristichus*	291.0760	58.2575
MSB	15122	NM	Bernalillo	*S. tristichus*	408.6303	67.5817
MSB	16575	NM	Bernalillo	*S. tristichus*	230.7800	56.3099
MSB	16889	NM	Bernalillo	*S. tristichus*	388.7497	64.4724
MSB	21211	NM	Bernalillo	*S. tristichus*	353.9186	61.4328
MSB	25945	NM	Bernalillo	*S. tristichus*	382.2088	63.4877
MSB	25946	NM	Bernalillo	*S. tristichus*	396.8369	65.5932
MSB	52810	NM	Cibola	*S. tristichus*	425.6486	68.8039
MSB	73225	NM	Cibola	*S. tristichus*	355.5891	65.3661
MSB	11959	NM	MicKinley	*S. tristichus*	392.4387	62.5325
MSB	76407	NM	MicKinley	*S. tristichus*	417.7706	64.5815

MSB	12252	NM	Sandoval	*S. tristichus*	398.3997	62.0818
MSB	12399	NM	Sandoval	*S. tristichus*	442.7115	68.8376
MSB	14336	NM	Sandoval	*S. tristichus*	402.5499	69.5504
MSB	16805	NM	Sandoval	*S. tristichus*	243.4671	52.8744
MSB	17267	NM	Sandoval	*S. tristichus*	439.1107	69.5592
MSB	17312	NM	Sandoval	*S. tristichus*	234.2556	60.7991
MSB	17313	NM	Sandoval	*S. tristichus*	286.5366	58.8229
MSB	17314	NM	Sandoval	*S. tristichus*	277.8326	59.5461
MSB	14793	NM	Bernalillo	*S. tristichus*	411.9320	65.1778
MSB	47211	NM	Cibola	*S. tristichus*	372.3691	60.0517
MSB	54838	NM	Cibola	*S. tristichus*	395.2521	62.6585
MSB	61191	NM	Cibola	*S. tristichus*	257.5200	57.3948
MSB	61192	NM	Cibola	*S. tristichus*	260.3574	62.7159
MSB	76384	NM	Cibola	*S. tristichus*	313.1257	57.6857
MSB	76419	NM	Cibola	*S. tristichus*	290.0902	62.8790
MSB	3293	NM	MicKinley	*S. tristichus*	351.5956	64.2600
MSB	11951	NM	MicKinley	*S. tristichus*	293.5277	55.2260
MSB	11956	NM	MicKinley	*S. tristichus*	241.9808	54.4328
MSB	11957	NM	MicKinley	*S. tristichus*	270.9618	56.2316
MSB	11961	NM	MicKinley	*S. tristichus*	300.8999	57.1684
MSB	11962	NM	MicKinley	*S. tristichus*	376.9084	61.9648
MSB	11963	NM	MicKinley	*S. tristichus*	377.2648	60.1912
MSB	11964	NM	MicKinley	*S. tristichus*	367.6270	60.7053
MSB	33238	NM	MicKinley	*S. tristichus*	396.9748	60.5939
MSB	76386	NM	MicKinley	*S. tristichus*	290.4570	56.7679
MSB	76388	NM	MicKinley	*S. tristichus*	265.5109	58.4221
MSB	21762	NM	San Juan	*S. tristichus*	385.0005	71.0418
MSB	21771	NM	San Juan	*S. tristichus*	329.0188	66.1486
MSB	21776	NM	San Juan	*S. tristichus*	419.2225	72.4818
MSB	21779	NM	San Juan	*S. tristichus*	250.0572	57.0638
MSB	21780	NM	San Juan	*S. tristichus*	354.5142	64.6650
MSB	21781	NM	San Juan	*S. tristichus*	587.6860	78.1571
MSB	21791	NM	San Juan	*S. tristichus*	491.5514	74.4960
MSB	21831	NM	San Juan	*S. tristichus*	344.7640	66.7723
MSB	48037	NM	San Juan	*S. tristichus*	430.2068	78.3072
MSB	48038	NM	San Juan	*S. tristichus*	582.8336	81.5739
MSB	48039	NM	San Juan	*S. tristichus*	467.4871	76.1718
MSB	58276	NM	San Juan	*S. tristichus*	316.5791	67.7555
MSB	87791	NM	San Juan	*S. tristichus*	258.3965	62.4324
MSB	17047	NM	Sandoval	*S. tristichus*	358.3306	59.9697

| MSB | 73519 | NM | Sandoval | *S. tristichus* | 476.6398 | 65.0517 |

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Publications:

Dittmer, D., D. J. Leavitt, W.A. Ryberg, and L. A. Fitzgerald. 2012. ARIZONA ELEGANS

     ELEGANS (Kansas Glossy Snake). DIET AND FEEDING BEHAVIOR. Herpetological

     Review 43(1), 2012

Eifler, D. A., K. Baipidi, M.A. Eifler, **D. Dittmer,** L. Nguluka (2012). "Influence of prey

     encounter and prey identity on area-restricted searching in the lizard *Pedioplanis*

     namaquensis." Journal of Ethology 30(1): 197.