1-1-2010

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Recommended Citation
Messenger, Kevin Robert, "Growth and Age at Reproductive Maturity of the Carolina Pigmy Rattlesnake, Sistrurus m. miliarius (Reptilia: Serpentes)" (2010). *Theses, Dissertations and Capstones.* Paper 106.

Growth and Age at Reproductive Maturity of the Carolina Pigmy Rattlesnake, *Sistrurus m. miliarius* (Reptilia: Serpentes)

Thesis submitted to
the Graduate College of
Marshall University

In partial fulfillment of the
requirements for the degree of
Master of Science
Biological Sciences

by

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Marshall University

December 2010

ABSTRACT

Growth and Age at Reproductive Maturity of the Carolina Pigmy Rattlesnake, *Sistrurus m. miliarius* (Reptilia: Serpentes)

Kevin Robert Messenger

Growth and age at reproductive maturity are life history attributes that play an important role in the development of proper management strategies. The Carolina Pigmy Rattlesnake, *Sistrurus m. miliarius*, is one of two dwarf rattlesnake species. The subspecies ranges from eastern NC to nearly the southern tip of SC and into the northeastern portion of GA. In NC, where the species' status is of Special Concern, fragmentation and land development have destroyed most of its historic range. Its small size also makes it highly susceptible to predation. In some parts of the range, commercial collection is another pressure the species faces. Carolina Pigmy Rattlesnakes are difficult to study due to their elusive behavior; thus, little is known about their life history. I modeled growth and age at reproductive maturity for a stable population of pigmy rattlesnakes from a wildlife refuge in north-central SC. During a six-year mark-recapture study, I recorded growth intervals (snout to vent length, or SVL) from free-ranging Carolina Pigmy Rattlesnakes. I fit these data to both von Bertalanffy and logistic growth interval models and used residual error mean square for comparison. The von Bertalanffy model estimated age at reproductive maturity at 2.7 years (males) and 2.1 years (females), and asymptotic size at 46.7cm (42.3–51.5, males) and 45cm (36.4-53.7, females); the logistic model estimated maturity at 3.4 years (males) and 3 years (females), and a total length of 45.2cm (42.1–48.2, males) and 43.9cm (37.7–50, females). These results demonstrate an accelerated life history of Carolina Pigmy Rattlesnakes, especially when compared to other pit vipers. An understanding of these aspects of their life history is essential to a sound management plan.

ACKNOWLEDGMENTS

I have several people to thank over the years. The most obvious and direct individual would be my father, who took me snake hunting in the Sandhills of SC when I was 9 years old (and my mother for putting up with my love of these incredible animals). I fell in love with the Sandhills from that day on and spent countless days of my childhood there.

During my senior year of high school, my AP Biology teacher, Mr. Scott Moser, encouraged me to do a project on the Sandhills for my Senior Exit Essay Project. Without this push, none of this would have happened. Along the same lines, I owe a great amount of thanks to Scott Lanier, the refuge manager at that time. He was unsure of granting a Special Use Permit to a high school student and I am very glad he gave me the chance to prove myself. Over the years, the refuge staff was exceptionally kind to me (even providing me a house on site in which to stay for several years) and I owe a lot of my success to those in charge.

I owe a tremendous amount of thanks to Dr. Harold Heatwole. Upon my acceptance to North Carolina State University, he encouraged me to continue working on the Sandhills project throughout my undergraduate career and to turn it into a long-term study with the intention of using it as a master’s thesis.

Dr. Robert Reed at the University of Georgia’s Savannah River Ecology Laboratory contributed to this project in many ways, including instruction in marking techniques, funding, and future networking. All of these individuals were crucial in the completion of the project, and, if one of them were missing, the project simply would not have happened.

Through the course of this project, I met several significant friends and colleagues, including Mr. Wade Kalinowsky and Dr. Jayme Waldron. These two became incredibly

important later on in my life, with Jayme eventually becoming one of my many mentors and leading me to Marshall University. At Marshall University, I met Dr. Thomas Pauley, another significant figure in my life and current advisor over my master's degree. Jayme requires additional thanks for all her help with statistical knowledge. I thank Tyler Hern for assisting me with creating the GIS maps used in this thesis. I also thank Dr. Dan Evans for helping me with my manuscript and editorial contributions. All of my friends who helped me revise various drafts of this manuscript prior to submission are also much appreciated.

In the field I had some of my best friends help me on multiple occasions; I owe significant recognition to Joe Flowers, Mike Martin, Ross Maynard, Nathan Shepard, and Adrian Yirka. These five assisted me over countless hours and days throughout the years. If not for this project, I may not have even met some of them. Over 100 other individuals provided assistance during this study and I apologize for not naming everyone – they are all much appreciated!

Several sources provided funding during the course of this research: the North Carolina Herpetological Society, North Carolina State University, South Carolina Department of Natural Resources, the National Science Foundation (Grant # DBI-0139572), and the Savannah River Ecology Laboratory under Financial Assistance Award (DE-FC09-96SR18-546) between the University of Georgia and the U.S. Department of Energy.

The project was completed through IACUC #03-138-O.

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CHAPTER ONE

Study organism

Introduction and Species Account

The Carolina Pigmy Rattlesnake (*Sistrurus m. miliarius,* Linnaeus 1766) is one of two dwarf rattlesnake species in the genus *Sistrurus* (Garman 1883) (Family Viperidae; Subfamily Crotalinae). The generic name comes from the Latin word "*Sistrum,*" meaning a rattle and the Greek "*-oura*" meaning bearing. The specific name comes from the Latin word for millet, "*miliarum*," in reference to the diminutive or millet-like size of the rattle. The type locality is "Carolina," but Schmidt (1953) suggested that it should probably be restricted to "Charleston, South Carolina." The genus *Sistrurus* is known from fossils found during the Pleistocene Epoch (~2.5 million years ago [mya]) in Florida (Auffenberg 1963). More recently, an earlier fossil from the Late Miocene Epoch (~9 mya) was found in Nebraska (Parmley and Holman 2007). These results suggest that *Sistrurus* was a distinct lineage prior to the Late Miocene and has been present in the Great Plains of North America for at least the last 5 million years. Scientists estimate the date of origin for the two *Sistrurus* species to be between 9.58 mya and 10.23 mya (Douglas et al. 2006; Kubatko et al. 2010). Genetic work by Kubatko et al. (2010) suggests that currently described species within the genus originated over the late Pliocene with substantial diversification occurring in the middle to late Pleistocene.

Herpetologists currently recognize three subspecies of *Sistrurus miliarius*: *Sistrurus m. miliarius,* the Carolina Pigmy Rattlesnake; *Sistrurus m. barbouri*, the Dusky Pigmy Rattlesnake; and *Sistrurus m. streckeri*, the Western Pigmy Rattlesnake. These subspecies differ in color, pattern, scale counts and arrangements, and allopatric distributions (Gloyd 1935; 1940).

Description

Sistrurus differs from other rattlesnakes (genus *Crotalus*) by the presence of nine large cephalic scales and their diminutive size. *Sistrurus* has a proportionately smaller rattle when compared to *Crotalus*. Chamberlain (1935) noted that the fragile nature of the *S. miliarius* rattle does not allow for the retention of terminal segments. As a result, the rattles of *S. miliarius* seldom exceed five segments.

Typical adult size of *S. m. miliarius* is 38 to 51 cm. Sexual dimorphism is present in the species but not pronounced; males have thicker and slightly longer tails relative to their total length (12.2% ± 1.5%; n = 324) than females (10.8% ± 1.9%; n = 192). *Sistrurus m. miliarius* is the most temperate of the subspecies and, as such, is subjected to different environmental conditions.

Sistrurus m. miliarius has a gray to reddish background coloration with one to two rows of lateral spots. The dorsum typically has around 32 to 36 blotches with white borders (Palmer 1971). Most specimens have a red, orange, or yellow stripe down the dorsum (Figs. 01, 02). Anerythristic individuals have a white stripe (Fig. 03). Some individuals (more common in anerythristic specimens) have either a faint dorsal stripe or lack one altogether (Fig. 04). Like many pit vipers, pigmy rattlesnakes also have a band of dark pigment running through the eye and extending over the venom glands, which has been suggested to protect the venom glands from UV radiation (Pough et al. 1978).

Distribution

Sistrurus miliarius occurs from northeastern North Carolina, south to southern Florida, but does not extend into the Keys, despite persistent rumors (Lazell 1989), and west to eastern Oklahoma and Texas.

The Carolina Pigmy Rattlesnake (*S. m. miliarius*) is found on the Albemarle Peninsula of North Carolina, as far east as Hyde and Tyrrell counties (Beane and Corey 2010), and ranging south, just inland from the coast. A population, consisting of entirely erythristic (excessive production of red pigment; Fig. 05) individuals, is isolated to a few counties on the North Carolina coastline: Hyde, Beaufort, Onslow, Pamlico, Craven, and Carteret counties (Palmer 1971). Some individuals in northeastern GA can also be erythristic in color, but several color variations are present in this region. In NC, the species ranges southwestward through the Coastal Plain. There are isolated locality records in the interior southern Piedmont: one specimen from southeastern Cleveland County, two specimens from southwestern Gaston County, and one specimen from west-central Montgomery County (Palmer and Braswell 1995).

This patchy distribution in the North Carolina Piedmont continues into the South Carolina Piedmont, where the species remains sparse. Corrington (1929), while doing a survey of the herpetofauna near Richland County, South Carolina, reported the rarity of *S. m. miliarius* from this region, and the only specimen he found was from the Sandhills region. Martof et al. (1980) noted that *S. m. miliarius* occurred throughout South Carolina except for the mountainous region in the northwestern corner. Brown (1992) described pigmy rattlesnakes as being "rare and very limited in distribution" in reference to the Piedmont region of the Carolinas. He personally observed one specimen, from Cleveland County, just north of the South Carolina border. Palmer (1971) and Platt et al. (1999) recorded the presence of *S. m. miliarius* in York and Chester counties based on observations by Brown (1992), but, due to conflicting reports in these publications, these counties should probably be excluded from the known range of *S. m. miliarius*. Bruce (1965) failed to turn up the species in his assessment of the herpetofauna of the southeastern escarpment of the Blue Ridge Mountains and the adjacent Piedmont. Platt et al. (1999) reported only one voucher specimen from the South Carolina Piedmont in Pickens County (CUSC #81). However, several specimens have been photographed from Oconee County, South Carolina (Platt et al. 1999). In the South Carolina Coastal Plain, *S. m. miliarius* occurs throughout much of the region except for the extreme southern tip (Jasper and Hampton counties). These counties represent a zone of intergradation with the dusky subspecies, *S. m. barbouri*.

Sistrurus m. miliarius continues through the northern half of Georgia into northeastern Alabama. The three subspecies converge in Alabama: *S. m. miliarius* to the northeast, *S. m. streckeri* to the west, and *S. m. barbouri* in the southeast (Fig. 06). Though *S. m. miliarius* has a wide range, it is sparsely distributed and is typically thought of as rare to uncommon – partly due to its small size (making detection difficult) and elusive behavior.

The population of interest in this study is from the Carolina Sandhills National Wildlife Refuge in north-central South Carolina. The refuge is within the physiographic region commonly known as the Sandhills. This is in strong contrast to the North Carolina Sandhills, just 80 km to the northeast, where the species is of special concern (Beane et al. 2010), which means they are a protected species by law. The Sandhills physiographic region is a Sandhills belt of rolling hills consisting of loamy white sands that is approximately 64 km wide. It originates in south-central North Carolina and extends south and west through central South Carolina running along the fall line and into Georgia where it terminates along the western border (Fig 07).

Previous Work

The majority of previous work on *S. miliarius* was conducted on the subspecies *S. m. barbouri* in Florida (Farrell et al. 1995, 2009; Rabatsky and Farrell 1996; Glaudas et al. 2005). Save for the 1971 description by Palmer, there have been limited publications on the natural history of *S. m. miliarius*. Not only do most of the publications on *S. miliarius* come from the *barbouri* subspecies, but also the locality of the majority of the work comes from a population in central Florida (Farrell et al. 1995). Thus, published data are on *S. miliarius* in semi/ subtropical regions. For example, the coldest month (January) of the Florida study site where the majority of the work on *S. miliarius* has come from has a monthly average temperature (13.8°C), more than twice that of my study site in South Carolina for the same month (6.7°C). *Sistrurus m. barbouri* differs from *S. m. miliarius* in many ways. *Sistrurus m. barbouri* attains greater lengths, most likely due to the nearly year-round growing season (from the 32nd latitude, south to the 25th latitude). Recent genetic work by Kubatko et al. (2010) suggests that *S. m. barbouri* is more distantly related to the other two subspecies than previously thought. However, the sample size was small, and another genetic test yielded less clear results.

The information biologists know about the nominate subspecies is sparse. *Sistrurus m. miliarius* have a more temperate distribution (33rd latitude north to the 35th latitude), which may limit their size due to a hibernation period of four to five months and influences behavior and ecological adaptations that are absent in the semi-tropical subspecies. Work by

Ashton and Feldman (2003) showed that snakes reverse Bergmann's rule and that species increase in size as latitude decreases. This influence is less pronounced in *S. m. barbouri* and to a lesser extent, *S. m. streckeri*, which occurs both lower and higher in latitude than *S. m. miliarius*.

Description of Study Site

The Carolina Sandhills National Wildlife Refuge was established in Chesterfield County in north-central South Carolina in 1939 (Figs. 07, 08, 09). The refuge is 45,000-acres (18,210-hectares), contains a wide variety of habitats that range from marshy ponds to xeric shrub, and, as a result, yields an impressive herpetofaunal diversity of 81 species (Table 1). I selected the refuge as my study site because *S. m. miliarius* was the most common snake species encountered, providing a large sample size that would increase reliability and accuracy of the data. The ecotones of the refuge can be roughly broken into three categories characterized by distinct vegetation and soils. The refuge consists of several gentle to steep rolling hills of white sand (Fig. 10). With the exception of a few small outcrops, the entire area is devoid of rock (Garton and Sill 1977). The refuge borders two water systems. Black Creek, which forms the northern and eastern border, and the Lynches River, which forms the western and southern border. Numerous tributaries form a network through the refuge. These tributaries are small (3-m wide), shallow (1-m deep), and stained with dark tannins forming what is usually referred to as "black water." The refuge has dammed several of these tributaries by restricting output flow, forming large pools (Garton and Sill 1977).

Despite having an average precipitation of 114 - 124 cm per year (Fig. 11), the coarse sand covering the upland region results in xeric conditions and as such limits the vegetation that can successfully thrive there. Longleaf Pine (*P. palustris*) and Turkey Oak (*Quercus laevis*) dominate the upland region. Ground cover in these areas consists of wiregrass (*Aristida* sp.) and Bracken Fern (*Pteridium aquilinum*) (Garton and Sill 1977).

Ephemeral floodwaters inundate the lower elevations and layers of clay intersect the sand substrate. These lower slopes contain abundant soil moisture and, as a result, yield significantly different vegetation. Various evergreen shrubs occur here: Fetterbush (*Lyonia lucida*), Swamp Bay (*Persea palustris*), and Inkberry (*Ilex glabra*). The broader bottomlands are dominated by hardwoods -- Tupelo Gum (*Nyssa aquatica*), Red Maple (*Acer rubrum*), and White Cedar (*Chamaecyparis thyoides*) -- and are commonly bordered by Tulip Trees (*Liriodendron tulipifera*) and Sweetgums (*Liquidambar styraciflua*) (Garton and Sill 1977).

The Sandhills ecosystem is a fire-adapted community that traditionally burned at 5-year intervals via lightning strikes in the summer. Today, the refuge staff uses controlled burns to suppress the growth of hardwood trees. Though these burns take place in late winter and early spring, there is currently a movement to push for growing season (summer) burns (United States Fish and Wildlife Service 2010).

The average yearly temperature of the refuge is 17.1°C. The hottest month is July (average daily maximum temperature = 32.8°C) and the coldest month is January (average daily minimum temperature = 1.1°C) (Fig.12). The highest recorded temperature was 41°C in August 1983, and the lowest recorded temperature was -16°C in January 1982 (National Weather Service).

One of the most important reasons for the great success and diversity of the refuge is the limited number of public roads. Overall, only two main roads cut through the refuge (i.e., Wildlife Drive and Highway 145). Wildlife Drive is a paved road that is 13.5 km and bisects the Sandhills property (Fig. 13); the refuge closes this road to the public at night, thereby minimizing the number of animals killed by cars. Garton and Sill (1977) conducted the first herpetofaunal survey before Wildlife Drive was paved and not a single *S. m. miliarius* was found. In 1977, Wildlife Drive was paved and the beginning of a controlled burning regime by the refuge staff ensued. Eight man-made ponds are adjacent to the Wildlife Drive, which adds a significant amount of aquatic and semi-aquatic species to the diversity of the property (Fig. 14). The road also has significant changes in elevation (Fig. 15), dipping as low as 90 m and climbing as high as 167 m (higher than Sugarloaf Mountain, just outside the refuge property). These changes in elevation allow for a diversity of habitats. Habitat adjacent to the Wildlife Drive has been broken into three basic categories: xeric habitat accounts for 55.7% of Wildlife Drive; transitional habitat, accounts for 8.2%; and mesic habitat, for 36.2% (Fig. 16).

Description of Methods

I drove Wildlife Drive in the early evening and night to capture specimens. I surveyed for all snake species. I drove from approximately one hour before sunset until snake activity was over, which could sometimes last up to eight hours. I defined the end of activity as 90 minutes after I last encountered a snake. I attempted to sample on as many nights as possible and with the exception of the final year, I averaged 79 survey nights per year (range 65-94).

When I captured a snake, I recorded several variables. I recorded species, time of day, and GPS coordinates (spatial accuracy $\leq$ 4.5 m). I noted the direction the snake was moving so when I released the animal, I released it on the side of the road that corresponded to the direction in which the snake was moving. I recorded substrate temperatures (i.e., temperature of the substrate the snake was captured upon, which included pavement, soil, or road shoulder; to the closest 0.25°C), ambient temperature (to the closest 0.25°C), cloud cover, moon phase percentage, moon height in sky (below the horizon, at the horizon, overhead, etc.), and rainfall (via weather station) (Fig. 17). Substrate temperature was obtained by taking a temperature (Raytek infrared thermometer) of the road or substrate the snake was found on. Ambient temperatures were acquired by taking the surface temperature (Raytek infrared thermometer) of leaves from nearby trees at shoulder height. Multiple readings (≥ 5) were averaged for a final value. These thermometers register an instantaneous temperature so there is minimal delay from capturing the snake to recording data. I recorded these variables to examine the relationships between snake activity and environmental conditions. I scanned each captured snake for the presence of a microchip or examined for cauterized ventral scutes to note whether it was a recapture. Animals that had been recently captured (≤ 3 months) were not re-measured. I held all other captured snakes until surveys were completed for the night. I measured captured snakes for snout-to-vent (SVL; 0.5 cm) and total length (TL; 0.5 cm) via tubing and stretching along a tape measure, mass (1 g), and sex (via probing). I marked snakes with either a microchip (PIT tag – BioMark and A.V.I.D. [American Veterinary Identification Device]) or via ventral scale cauterization (Aaron Medical Change-A-Tip cautery units; Aaron Medical, St. Petersburg, Florida 33710, USA; www.aaronmed.com). Depending on the time of year and the environmental conditions, I released snakes the night in which they were captured, or they were kept for 24 hours and released the following night.

Reproduction

Like all North American pit vipers, *S. m. miliarius* are ovoviviparous. As a species (*S. miliarius*), young are born in the fall (August, September) after a long gestation period of 107 to 294 days (Fleet and Kroll 1978). The gestation periods lasts 219 days for *S. m. miliarius* (this study). Reproduction in free-ranging *S. m. miliarius* has not been documented, but Palmer and Braswell (1995) speculated courtship took place in the spring. Though this is possible with a short gestation period, a spring mating period would likely not allow for sufficient development time. Rather, female S. m. miliarius likely store sperm from fall matings to fertilize their eggs in the spring (Montgomery and Shuett 1989). During the course of this study, I held four gravid females in captivity until parturition, and 100% gave birth before 1 September. I have witnessed combat dancing and mating in captivity of wild-caught study animals (animals held for less than 24 hours) in the fall (Fig. 18). Carpenter (1979) reported the presence of combat rituals in *Sistrurus miliarius* between a male *S. m. streckeri* from Oklahoma and a male *S. m. barbouri* from Florida in captivity.

Copulation can last in excess of 11 hours (pers. obs.). Other eastern *Crotalus* species mate in the fall (Klauber 1972; Seigel and Ford 1987; Rubio 1998). There has been no evidence to suggest that *S. m. miliarius* are capable of mating each year, but most likely mate every other year as do many other crotalids (Siegel and Ford 1987). The most frequent reproduction witnessed within the study site was a female that reproduced two years apart. *Sistrurus m. barbouri*, by contrast, have both annual and biennial reproduction (Farrell et al. 1995; 2009).

Sistrurus m. miliarius have smaller litter sizes and smaller clutch masses than *S. m. barbouri*. In both subspecies, litter size and clutch mass are positively correlated with female body size (Bishop et al. 1996; Farrell et al. 1995), in contrast to other rattlesnakes such as *Crotalus horridus,* in which there is no correlation between litter size and either weight or length of mature females over 100 cm in snout-vent length (Gibbons 1972). The litter size of *S. m. miliarius* in North Carolina ranges from three to nine neonates ($\bar{x}$ = 5.30; n = 17) (Palmer and Braswell 1995). Fitch (1985) reported similar findings in his review of northern *S. miliarius,* in which he reported a mean litter size of 5.2 ± 0.3 (range 3-7; n = 16). Of seven litters observed from my study site, litter size ranged from four to seven individuals ($\bar{x}$ = 5.5). Pigmy rattlesnakes tend to have large litters in relation to body size. At the study site, four temporarily held gravid females had litter sizes that accounted for greater than 50% of their body mass (range 50% - 56.4%; n = 4). Rattlesnakes may have anywhere from 5-12% stillborn young or undeveloped eggs (Farrell et al. 2008). Farrell et al. (2008) noted that *S. m. barbouri* on average had 92.5% viable offspring.

Farrell et al. (1995) found a negative correlation in *S. m. barbouri* between the parturition date and clutch mass. Their study suggested that females might feed until they reach a critical mass, at which point they move from a foraging site to another location more conducive for thermoregulation to speed embryo development. Animals that fail to reach this critical mass must continue feeding in the foraging sites that might not be optimal for egg development, which can delay offspring development and birth date.

Aubret et al. (2002) compared sex hormones in male and female vipers (*Vipera aspis*). They measured sex hormone levels of male and female vipers in low and high body condition. Females with a low body condition showed low estradiol levels and did not show sexual receptivity. Males of all body conditions showed high levels of testosterone and displayed active courtship. Females with body reserves above a critical threshold had high levels of estradiol and sexual reception. This could likely be a relationship seen in many other vipers, including pit vipers such as *S. miliarius*.

Diet, caudal luring, and the rattle

Sistrurus m. miliarius prey on a number of items: rodents (*Microtus pinetorum, Peromyscus maniculatus),* small snakes (*Carphophis amoenus, Coluber constrictor, Diadophis punctatus, Nerodia sp., Sistrurus miliarius, Storeria dekayi*, *Thamnophis sauritus*), lizards (*Anolis* sp., *Cnemidophorus [Aspidoscelis] sexlineatus, Eumeces [Plestiodon] inexpectatus, Scincella lateralis*), anurans (*Acris* sp., *Bufo [Anaxyrus]* sp., *Gastrophryne carolinensis, Hyla* sp., *Rana [Lithobates] clamitans, R. [L.] sphenocephala*), beetles (*Copris minutus*), spiders, and centipedes (*Scolopendra heros, S. viridis*) (Chamberlain 1935; Clark 1949; Hamilton and Pollack 1955; Klauber 1972; Palmer and Braswell 1995; Palmer and Williamson 1971; Wright and Wright 1957). In addition, captive specimens have taken house mice (*Mus musculus*), lizards (*Eumeces [Plestiodon] fasciatus, Hemidactylus turcicus, Sceloporus undulatus*), salamanders (*Desmognathus fuscus, D. monticola, D. ochrophaeus*), crickets, and even chopped horsemeat (C. Ernst, pers. obs.; Kennedy 1964; May et al. 1997; K. Messenger, pers. obs.; Montgomery and Schuett 1989; Munro 1947; Verkerk 1987). Of 12 animals from Georgia, reptilian prey was in 50% of the stomachs, mammalian prey in 17%, and centipedes in 33% (Hamilton and Pollack 1955). Within the study site, I have witnessed (via regurgitation or fecal analysis) the predation of mammals, lizards, and invertebrates – particularly centipedes.

Sistrurus m. miliarius are ambush predators. They will coil along a game trail or next to a log and wait for unsuspecting rodents or lizards. Juveniles have a bright yellow tail that they use for caudal luring, though adults are also known to caudal lure but in far less frequency. Caudal luring is documented in *S. m. barbouri* by Jackson and Martin (1980) but has not been recorded in wild *S. m. miliarius* though it most certainly occurs. Rabatsky and Farrell (1996) noted an ontogenetic shift in foraging posture of *S. m. barbouri* in which juveniles were more often found with their tails exposed than older snakes. This observation suggests that adults lure less than juveniles and is consistent with the ontogenetic loss of the brightly color tail tip in *S. miliarius.* However, Farrell et al. (2010) experimented on the foraging success of tail color manipulation and caudal luring in *S. m. barbouri* and found no significant difference in the number of prey consumed, which suggests that snakes with cryptic tail color have as likely a chance of capturing prey as animals with brightly colored tails. Hagman et al. (2008) found similar results in Northern Death Adders (*Acanthophis praelongus*), in which tails that were painted brown were equally effective lures as tails that were yellow. Thus, the presence of conspicuous tail coloration in *S. miliarius* might be explained by phylogenetic inertia, selective benefits of small magnitude, or by habitat-related differences in prey composition or abundance (Farrell et al. 2010). At the study site where the work on *S. m. barbouri* was conducted, Southern Leopard Frogs (*Rana [Lithobates] utricularia*), Green Treefrogs (*Hyla cinerea*), and Green Anoles (*Anolis carolinensis*) were the most abundant prey source. One species not observed at this study site, but found drier more xeric habitats, were Six-lined Racerunners (*Cnemidophorus [Aspidoscelis] sexlineatus*). A congener of *C. sexlineatus*, *C. tigris*, both elicits and is strongly attracted to caudal luring by *Crotalus cerastes* (Reiserer and Schuett 2008).

Several studies have focused on the origin of the rattle in the subfamily Crotalinae and its purpose (Fenton and Licht 1990; Moon 2001). Very few examples of the family

Colubridae exhibit caudal luring; such examples include Black Ratsnakes (*Elaphe [Pantherophis] obsoleta*), Puerto Rican Racers (*Alsophis portoricensis*), and Jiboinhas (*Tropidodryas striaticeps*) (Tiebout 1997). Caudal luring is much more pronounced in the family Viperidae, especially in the New World and more specifically within the genus *Agkistrodon* (the moccasins), a sister taxon to the subfamily Crotalinae. One member of *Agkistrodon*, the Cantil (*A. bilineatus*), is well known for its ability to overtly caudal lure. The rattle present in *S. miliarius* is proportionally very small, even when scaled to *S. miliarius'* body size, and inefficient in producing an audible warning present in larger rattlesnakes (genus *Crotalus*). *Crotalus* is not known to employ caudal luring. Schuett (1984) suggests that the small or structurally simple rattles of early rattlesnakes may have evolved to augment the visual attractiveness of caudal luring, though Tiebout (1997) noted evidence to refute the caudal luring origin hypothesis. One of these hypotheses was that rattles larger than the button are not used in caudal luring. Chamberlain (1935) noted that he felt *S. m. miliarius* was incapable of retaining terminal segments due to the fragile nature of the rattle. Though data from this project supported this claim overall, rattles ranged from 1 to 9 segments with an average of 3.2 (SD = 2.0; n = 258). Work by Moon (2001) showed that the tail muscles in *Agkistrodon* displayed an intermediate respiratory capacity between *Crotalus* and non-crotaline pit vipers. The greater the respiratory capacity of the tail muscles, the better the species is at shaking its tail, e.g., a rattlesnake vibrating its rattle. *Sistrurus miliarius*, by comparison, showed an intermediate respiratory capacity between *Crotalus* and *Agkistrodon*.

Work by Rowe et al. (2002) indicated extremely high rates of rattle loss in *S. m. miliarius* (52.3%) and suggested that pigmy rattlesnakes be added to the so-called list of “rattleless” rattlesnakes, which includes *Crotalus catalinensis* (85-100% rattlelessness) and *Crotalus ruber lorenzoensis* (55% rattlelessness) (Shaw 1964, Klauber 1972). The same study documented that by their third year, *S. m. barbouri* typically are losing rattle segments as rapidly as they are adding them via shedding, and that by their fourth year the typical rates of rattle loss exceed the rate of segment addition (Rowe et al. 2002). They reached the conclusion that the rattle loss in *S. m. barbouri* is a result from segment slippage, not segment breakage. The bilobed tail tip in *S. miliarius* has poorly developed longitudinal grooves, and so with nothing for the older rattle segments to snag during ecdysis, the rattle chain just slips off the basal segment (Rowe et al. 2002).

One hypothesis of the purpose of the rattle in rattlesnakes has been to deflect attention of a predator away from the snake’s more vulnerable head (Greene 1988). Another hypothesis is that the rattle evolved to enhance feeding. Schuett et al. (1984) suggested that a proto-rattle might have not only enhanced the attractiveness of the lure but also protected or prevented damage to the tail when bitten by the prey. Tail injuries can be fatal in small snakes, as documented in three species of *Thamnophis* (Willis et al. 1982). Other species, such as Rubber Boas (*Charina bottae*) use their tails to absorb bites from attacking female rodents, particularly female rodents protecting their young from being eaten by the boas (Nussbaum and Hoyer 1974). *Charina* has fused caudal vertebrae that has been suggested to be an adaptation to better absorb such attacks (Greene 1973). Rattlesnakes also have fused caudal vertebrae (Klauber 1972). Results from Rowe et al. (2002) suggest support of the hypothesis that rattles evolved to enhance caudal luring or to protect vulnerable tails and that pigmy rattlesnakes are losing their rattles due to relaxed selection. The relaxed selection in this case would be the need to protect their tails from mammalian teeth (Rowe et al. 2002).

Longevity

In captivity, *S. m. miliarius* lives up to 19 years 9 months (J. Beane, pers. comm.), based on observations of a wild-caught individual that was a sub-adult at capture, and remained at the North Carolina Museum of Natural Sciences until its death. The second oldest documented record is from a *S. m. streckeri* at the Houston Zoo that lived 16 years, 1 month, and 4 days (Snider and Bowler 1992).

My study represents the first attempt at quantifying longevity in the wild of *S. m. miliarius*. The greatest time lapse observed was a pigmy rattlesnake that measured 33 cm (sub-adult) in September 2002, and measured 42.5 cm when recaptured in June 2006, a lapse of 3.7 years. The size at capture in 2002 is large enough to add at least one year in age to this value. May and Farrell (2010) documented longevity of wild *S. m. barbouri*; the oldest known-age female was 7.6 years of age, and the oldest known-age male was 8.4 years of age.

Habitat

Sistrurus miliarius is known to occupy a wide variety of habitats, including swamps, xeric Sandhills uplands, deciduous forests, mountains, and prairies (Conant and Collins 1998). *Sistrurus m. miliarius*, however, has a more narrow range. In North Carolina, this subspecies is in the Coastal Plain and Sandhills ecosystems. The Sandhills habitat is composed of xeric uplands, dominated largely by Longleaf Pines (*Pinus palustris*), scrub oaks (*Quercus* sp.), and wiregrass (*Aristida* spp.). The lowlands of this ecosystem are in stark contrast to the uplands. Native cane (*Arundinaria* sp.) is the dominant vegetation and the soils are usually saturated. In this ecosystem, *S. miliarius* occur in both the uplands and the lowlands, though personal experience has shown that they tend to occur more frequently in the uplands (53.6 snakes/ km of habitat) compared to the lowlands (20.8 snakes/ km of habitat) (this study).

Palmer (1971) wrote a formal description of the erythristic population found in northeastern North Carolina. This color phase is popular in the pet trade and has been illegally collected for a number of years. In Palmer's description, he proposed the idea that this population is distinct from the individuals of the Sandhills region; however, due to its limited range and large zone of intergradation, the species was not afforded taxonomic distinction. This erythristic population differs from mainland animals with subtle variations, as detailed by Palmer: "Among 88 specimens from the northeastern part of the range (Beaufort, Hyde, and Pamlico counties), the lower preocular scale was divided by a vertical suture in only 18%, whereas 36% of 50 snakes from various southern localities had the scale divided." The most obvious and notable difference of this population compared to the mainland population is coloration. The erythristic population is restricted to Hyde, Beaufort, Onslow, Pamlico, Craven, and Carteret counties. *Sistrurus m. miliarius* from this coastal population also tend to get larger than their inland counterparts. Lastly, they tend to populate more mesic habitats.

Sistrurus m. miliarius is far less common throughout the North Carolina Piedmont. In the 1980's there were two confirmed sightings of *S. m. miliarius* from Crowder's Mountain along the western edge of the North Carolina Piedmont. There have been no sightings since, and the habitat is very different from other known *S. m. miliarius* populations.

Predators and Defense

Due to its small size, *S. miliarius* is preyed upon by a wide variety of organisms, including mammals (domestic dog [*Canis lupus familiaris*], Virginia Opossum [*Didelphis virginianus*], domestic housecat [*Felis domesticus*], Bobcat [*Lynx rufus*], Striped Skunk [*Mephitis mephitis*], Northern Raccoon [*Procyon lotor*]), birds (Red-shouldered Hawk [*Buteo lineatus*], Barred Owl [*Strix varia*]), and snakes (Black Racer [*Coluber constrictor*], Eastern Indigo [*Drymarchon corais*], Common Kingsnake [*Lampropeltis getula*], Eastern Coral Snake [*Micrurus fulvius*], Pigmy Rattlesnake [*Sistrurus miliarius*]) (Allen and Neill 1950; Glaudas et al. 2005; Klauber 1972; Printiss 1994). When exposed to the odor of kingsnakes (*Lampropeltis*), which specialize in eating other snakes and are immune to the bite of venomous snakes, pigmy rattlesnakes will hide their head, body bridge, or thrash about (Gutzke et al. 1993).

When threatened, unlike larger rattlesnakes (*Crotalus*) which vibrate their tail in a blur, pigmy rattlesnakes erratically wiggle their tail. This flexibility and control over the tail lends credence to caudal luring in pigmy rattlesnakes, which is well documented in *S. m. barbouri*. *Crotalus*, by contrast, is incapable of this erratic wiggling. When threatened, *Crotalus* keeps its tail rigid. This erratic "rattling" or jerking of the tail in *S. m. miliarius* also results in a nearly inaudible rattle. Most people describe the sound of a pigmy rattlesnake akin to an insect buzzing in their ears. The sound is scarcely audible at a distance greater than one meter. Only 3% of *S. m. barbouri* rattled in response to provocation (Rowe et al. 2002). *Sistrurus m. barbouri* that were mute (rattleless) had an equal chance of yearly survival as individuals that were capable of “sounding off” when they rattled (50.0 vs 51.5%, respectively) (Rowe et al. 2002). In fact, the same study suggested that the rattling sounds could invite injury or death by indicating their small size to a fox (*Urocyon cinereoargenteus*) or bobcat (*Felis rufus*), and that perhaps this is why such as small percentage of pigmy rattlesnakes rattled when provoked by humans.

Rattlesnakes are among the few snakes to show evidence of maternal care. This fact is most commonly noted in Timber Rattlesnakes (*Crotalus horridus*), in which the female will remain with the young for several days following parturition (Martin et al. 2008). Although this maternal care is not overt, as the concept is typically perceived, it at least indirectly benefits the young. Verkerk (1987) witnessed anecdotal evidence of maternal defense in captive *S. m. barbouri*. When disturbed, the young hid behind the mother's back while she assumed a defensive posture. Greene et al. (2002) carried out a number of experiments with *Sistrurus m. barbouri* in regards to parental care. In one experiment, mothers were separated from their young by a crossable barrier. Of 16 females, 12 crossed the barrier, thereby significantly associating with their neonates. The proportion of females in association with their neonates increased with time, when 70% of females were in association with their neonates by the third morning after birth. Another experiment in the same study (Greene et al. 2002) showed that post-parturient females moved toward a predator (*Coluber constrictor*) significantly more often than non-reproductive females. In several cases, the mother would actively chase the *C. constrictor* out of the enclosure, after which returning to her young.

Sistrurus miliarius has small fangs, 5.2 - 6.3 mm (Klauber 1939). The venom of pigmy rattlesnakes is primarily hemotoxic and is hemorrhagic in nature. Venom yields are low. The typical adult yield is around 20 to 30 mg (Ernst 1992). The largest specimens yield no more than 35 mg (Tennant 1985). The subcutaneous LD50 (the lethal dose for 50% of the animals tested) of mice for *S. m. barbouri* is 24 mg/kg. To extrapolate this value for a lethal dose for a person weighing 60 - 80 kg would be around 1,500 to 2,000 mg, far beyond the physical capacity of any individual. Though not fatal, a bite can still be very painful and can still be dangerous to children. Guidry (1953) reported a bitten child that required several weeks of hospitalization. In Florida, where the species is far more common than elsewhere in its range, of 382 verified snakebites reported, 168 (44%) were by *S. m. barbouri* (Tu 1977).

Sistrurus miliarius is described as being exceptionally irritable. Many creative descriptions have been used over the years from several famous herpetologists to describe their defensive behavior. Ernst (1992) described pigmies as a "fiery tempered beast." Recent work by Glaudas et al. (2005), however, suggested that pigmy rattlesnakes are less defensive. Of 336 snakes tapped on the head by a gloved hand, only 27 (8%) bit the glove, indicating that this species is fairly nonaggressive and reluctant to bite (Glaudas et al. 2005). Their results are inconsistent with my observations, but this is likely due to differences in detection techniques. Glaudas et al. (2005) encountered pigmies during the day with the majority of the animals found coiled in ambush position. They noted that animals found stretched out were much more likely to elicit a striking response. In my study, nearly every animal found was stretched out, actively moving across a road at night. Glaudas et al. (2005) attributed an increase in defensive behavior because crypsis is less effective when a snake is stretched out and moving. The reputation of an aggressive and fiery temper is likely due the fact that the majority of public encounters with this species occur when individuals are active and on the move, as individuals are very difficult to see when they are at rest and in ambush positions.

CHAPTER TWO

Activity patterns

Introduction

Examining snake behavior and activity patterns can tell us a lot about the natural history of a species. They offer insight into what environmental conditions are favorable, such as temperature minimums, maximums, and the effect of rainfall on movement. A surge or influx in activity may be indicative of a breeding migration or some other significant event in the animals' life history. Perhaps a rain event brings out a particular prey item, causing a surge in activity of a predator species. Alternatively, perhaps it triggers a breeding response. Ambystomid salamanders move in mass breeding migrations during rain events at various times of the year. Knowing about movement patterns can be critical to understanding more about a species, as well as making steps to study and conserve the species more effectively. Translocation programs with snakes seldom end in success (Dodd and Siegel 1991; Reinert and Rupert 1999; Plummer and Mills 2000). This knowledge of movement patterns is especially helpful when trying to find rare or elusive species. If a specific environmental cue encourages activity, then surveying during that event will ideally yield large numbers of the target species, thus making surveys more efficient.

Snakes have surprisingly complex behaviors. Many factors influence their behavior, from abiotic and biotic conditions to predatory interactions (Zug et al. 2001). The most obvious environmental factor is temperature. Without optimal temperatures, snakes, and other ectotherms are limited in their abilities to forage and remain active. Other environmental factors include solar radiation, reflective radiation, precipitation, humidity, habitat, time of day, season, and food availability. Many of these factors directly affect temperature, such as solar radiation, rainfall, wind, and humidity. One way to eliminate several of these variables, and thus variance, is to concentrate on nocturnal species. The sun and the resulting solar radiation cause an immense amount of variables such as direct, indirect, reflective, and conductive radiation. Solar radiation creates thermal columns, which, in turn, can affect the wind. Evaporation from a local water body can create humid conditions and over several days culminate in rainfall. Solar radiation bounces off all objects, creating reflective and indirect radiation. Reptiles posture themselves accordingly depending on the needs of the individual. A sick animal may bask more openly and in warmer temperatures than a healthy animal (Dodd 1988; Zug et al. 2001); a gravid female may expose itself longer or at least the lower portion of its body in order to speed development of the embryos (Siegel et al. 1987, Van Damme et al. 1992). Snakes that have just eaten will usually expose themselves to higher temperatures than a snake without a meal in order to accelerate digestion (Zug et al. 2001). By examining nocturnal animals, one eliminates a great deal of variables, though not all, as solar radiation from the day affects the amount of heat stored in the substrate.

One influence on behavior that has received little attention is the moon. When examining snake literature, one finds little information about this topic. Clarke *et al*. (1996) looked at the pattern of movement of *Crotalus viridis* under a laboratory setting. They found a negative correlation between snake movement and simulated moonlight intensity. Campbell *et al.* (2008) also looked at the influence of simulated moonlight on a nocturnal species, *Boiga irregularis,* and also found a negative correlation with activity and increased illumination. These studies were done in enclosures and involved wild caught specimens kept in captive environments until time for the experiments. There are few field studies looking at the influence of moon phase (as opposed to illumination) on snake activity. Additionally, I am interested in examining the presence or absence of an endogenous lunar rhythm, not simply a response or avoidance to bright light. Duellman (1978) found that Amazonian snakes responded to the lunar cycle even under cloudy conditions, suggesting an endogenous rhythm; I have also personally witnessed this behavior at my study site. Andreadis (1997) examined the effect of moon phase on water snakes (*Nerodia sipedon*) in their natural habitat. The author of this study walked creeks and scanned for the presence of foraging snakes with spotlights. Andreadis (1997) found a negative correlation associated with the moon phase and activity. *Sistrurus m. miliarius*, like many other species present in the sandhills region, have a negative correlation between activity and large moon phases (Messenger, unpublished data). This correlation is relatively newly discovered and unexplored and has only been documented a few times in wild populations (Yamagishi 1974, Andreadis 1997, Brown and Shine 2002).

Lunar rhythms in animals are known in a few species, primarily marine organisms (e.g., Green Flatworms [*Convoluta roscoffensis*], Pacific Grunion [*Leuresthes tenuis*], Common Shore Crab [*Carcinus maenas*], sea turtles [Superfamily Chelonioidea]). Most animals that exhibit lunar rhythms are littoral organisms. The synchronizers of these animals may be tidal or lunar, or both. The only terrestrial animals to show lunar rhythms are invertebrates. Youthed and Moran (1969) illustrated that pit-building activity in the Antlion (*Myrmeleon obscurus*) reached a maximum at the time of the full moon. There was also a clear lunar-day (~24.8 hour) rhythm with a peak of activity about four hours after moonrise. There is no documentation of a terrestrial vertebrate exhibiting an endogenous lunar rhythm. The South American owl monkeys (*Aotus* spp) show a strong correlation with moon phase

(Fernandez-Duque 2003, Fernandez-Duque and Erkert 2006); however, this correlation may be masked by other behaviors such as predatory behavior. It is possible that the Colombian Night Monkey (*Aotus lemurinus*) is only active during these times because it can see its prey easier. This possibility would explain why a burst of activity is at dusk and dawn, due to the residual illumination from the sun (Fernandez-Duque and Erkert 2006). A few studies have investigated predator-prey interactions with respect to moon light and found a weak to no correlation (Bouskila 1995, Brown and Shine 2002). By comprehending the factors that influence snake behavior, we are better able to understand the underlying causes that dive such behaviors. Understanding snake behavior can have several ramifications. Perhaps the most foreseen advantage this information would provide is how to make surveys more effective.

Another technique to attempt to standardize activity and therefore limit variation is the concept of "relative high." In order to account for seasonality movement it was necessary to develop a new term called the "relative high," in reference to the temperature relative to the high temperature of the day. Examining snake activity as a relative high helps to standardize seasons. It allows us to consider conditions in which snakes are acclimated to in a given season. For example, in the early spring such as March, a night that averages 17°C, an above average temperature, usually yields a high amount of activity, however, 17°C in July, a below average temperature, usually yields no activity. The reason for this is because, in the early spring, snakes are "used to" colder temperatures and so 17°C may seem "warm," but in the summer when snakes are used to temperatures in the upper 20's and low 30's, 17°C is cold.

The objective of this study was to examine activity patterns with respect to moon phase and other environmental conditions, as well as note changes in seasonal behavior, and to assess population size. This information is important because this information will make it easier to sample for *S. m. miliarius*, which is rare and elusive throughout much of its range. The information obtained can be used to assess population strength and whether management practices need to be addressed in order to protect a local population if it is in danger of extirpation.

Methods

Study area: From 2002 to 2008, specimens were captured by driving the Wildlife Drive and waiting for individuals to actively cross the road. Wildlife Drive is an asphalt road within the Carolina Sandhills National Wildlife Refuge in Chesterfield Co., South Carolina, USA. I drove from approximately one hour before sunset until snake activity was over, which could sometimes last up to eight hours. I defined the end of activity as 90 minutes after I last encountered a snake. I attempted to sample on as many nights as possible and with the exception of the final year, I averaged 79 survey nights per year (range 65-94). Several searches on and off the road were made as well during the daytime.

Despite having an average precipitation of 114 - 124 cm per year (Fig. 11), the coarse sand covering the upland region results in xeric conditions and as such limits the vegetation that can successfully thrive there. Longleaf Pine (*P. palustris*) and Turkey Oak (*Quercus laevis*) dominate the upland region. Ground cover in these areas consists of wiregrass (*Aristida* sp.) and Bracken Fern (*Pteridium aquilinum*) (Garton and Sill 1977).

Ephemeral floodwaters inundate the lower elevations and layers of clay intersect the sand substrate. These lower slopes contain abundant soil moisture and as a result yield significantly different vegetation. Various evergreen shrubs occur here: Fetterbush (*Lyonia lucida*), Swamp Bay (*Persea palustris*), and Inkberry (*Ilex glabra*). The broader bottomlands are dominated by hardwoods -- Tupelo Gum (*Nyssa aquatica*), Red Maple (*Acer rubrum*), and White Cedar (*Chamaecyparis thyoides*) -- and are commonly bordered by Tulip Trees (*Liriodendron tulipifera*) and Sweetgums (*Liquidambar styraciflua*) (Garton and Sill 1977).

The average yearly temperature of the refuge is 17.1°C. The hottest month is July (average daily maximum temperature = 32.8°C) and the coldest month is January (average daily minimum temperature = 1.1°C) (Fig.12). The highest recorded temperature was 41°C in August 1983, and the lowest recorded temperature was -16°C in January 1982 (National Weather Service).

Snake capture and measurement: When snakes were captured, I recorded several variables. I recorded time of day, GPS coordinates (spatial accuracy $\leq$ 4.5 m), substrate and ambient temperatures (to the closest 0.25°C), cloud cover, moon phase percentage, moon height in the sky (below the horizon, at the horizon, overhead, etc.), and rainfall (via weather station). Substrate temperature was obtained by taking a temperature (Raytek infrared thermometer) of the road or substrate the snake was found on (sand, leaf litter, asphalt, etc.). Ambient temperatures were acquired by taking the surface temperature (Raytek infrared thermometer) of leaves from nearby trees at shoulder height. Multiple readings ($\geq$ 5) were averaged for a final value. These thermometers register an instantaneous temperature so there is minimal delay from capturing the snake to recording data. I scanned each captured snake for the presence of a microchip or examined for cauterized ventral scutes to note whether it was a recapture. Animals that had been recently captured (≤ 3 months) were not re-measured. I held all captured snakes until surveys were completed for the night. I measured captured snakes for snout-to-vent (SVL; 0.5 cm) and total length (TL; 0.5 cm) via tubing and stretching along a tape measure, mass (1 g), and sex (via probing). I marked snakes with either a microchip (PIT tag – BioMark and A.V.I.D. [American Veterinary Identification Device]) or via ventral scale cauterization (Aaron Medical Change-A-Tip cautery units; Aaron Medical, St. Petersburg, Florida 33710, USA; www.aaronmed.com). Depending on the time of year and the environmental conditions, I released snakes the night in which they were captured, or they were kept for 24 hours and released the following night.

In 2002, I began a mark-recapture program with *S. m. miliarius*. Initially, snakes were only marked with microchips, but in mid-2002 (June) I began cauterizing the ventral scales as well to individually mark animals. Using cautery as a method for marking is an extremely efficient method and in many ways superior to using microchips (Fig. 19) (Winne et al. 2006). The most obvious advantage is that it is cheaper and does not require equipment to read the identification of the animal. An additional advantage is that it allows snakes that are too small to be microchipped to still be permanently marked. Newborn *S. m. miliarius* are exceptionally small (approximately 12 to 15 cm, Fig. 20) and would be impossible to safely inject with microchips, but they can still be cauterized. There is documentation of an alarmingly high percentage (53%) of microchips being successfully passed via the gastrointestinal tract in Corn Snakes (*Elaphe [Pantherophis] guttata*) (Roark and Dorcas 2000). Willson noted a subadult Eastern Cottonmouth (*Agkistrodon p. piscivorus*) that had received both a PIT tag and a cautery mark in June 2004 that lost its PIT tag seven months later by the time it was recaptured in January 2005 (pers. comm.). For these reasons, I used cautery more often than microchipping, but I still microchipped from time to time to see if animals would pass the microchips. However, I never had any evidence of this.

Moon phase: To examine the influence the moon phase had on *S. m. miliarius* activity I first plotted the number of *S. m. miliarius* observed at night against the moon phase for that particular night (i.e., 8 snakes and 50% moon). All nights had the same amount of effort in that the road was surveyed until activity ceased.

There were three different levels of scrutiny I was interested in when examining the effect of moon phase on snake activity. The first level was examining snake activity (numbers of snakes) as it related to the moon phase for that night, regardless of what time the moon rose. This first level is not truly what is experienced when one examines the data more closely. There are some flaws at trying to correlate moon phase in this fashion. For example, if 8 animals were observed from sunset to one hour after sunset, but the moon did not rise until two hours after sunset, then the light levels under which the animals moved were minimal; for these reasons I decided to additionally plot activity between moonrise and moonset. I did this whether the sky was cloudy or clear. Snakes found outside of this range were not counted in this second level of examination. However, a third consideration needs to be taken into account when looking at moon phase interaction, and that is the issue of atmospheric attenuation. To account for atmospheric attenuation I took the halfway point between moonrise and moon transit (azimuth). This value was obtained by dividing the time between these two points by two (i.e., moonrise = 6:00 P.M., moon transit = 12:00 A.M. Six hours divided by two = 3 hours). This value varies depending on the moon phase and the day of the year. A corresponding value was calculated for the setting side of the moon cycle (i.e., a halfway point between moon transit and moonset was established as well). This time frame, the halfway point between moonrise and moon transit, and the halfway point between moon transit and moonset was termed the light spread (Fig. 21). The light spread represents the brightest half of the night, or at least of the moon cycle. My third level of examination consisted of analyzing snake activity during this light spread period. A regression was performed on all three levels of examination.

Activity by season: To measure *Sistrurus m. miliarius* by season, I tallied number of snakes found per night for a given month, divided by the number of nights searched in order to account for search efforts.

Activity by time and relative high: In order to get the relative high value I would take the air temperature at capture and divide it by the daily high temperature for that day (ambient). This value is then represented as a percentage of the daily high temperature for the day. For example, a snake that was captured when the air temperature was 17°C in March, when the daily high was 21°C equals a value of 80.1% (17/21 = 80.1). A snake that was captured when the air temperature was 17°C in July, when the daily high was 30°C equals a value of 56.7%..

Activity of translocated animals: Each year I would randomly assign individual *Sistrurus m. miliarius* to be translocated to a different part of the refuge. I was curious to know if the animals would attempt to return to their original site of capture or if they would re-establish residence and subsequent recaptures would take place at the translocation site. I expected the animals to return slowly to the original capture site. There was no formal protocol I followed; the decision to relocate a snake was made at random and often at the last minute. Nothing was planned. The distance of the translocation was also random (range 0.2 -

8.2 km). As such, this information should be viewed as anecdotal and hopefully future studies can decide whether there is a need to pursue this topic with this species.

Results

Five hundred and sixty-two *S. m. miliarius* were observed including recaptures. Eight of these (1.4%), were found dead on the road, hit by cars driving illegally on the road, which is closed to the public at night. Only one marked *S. m. miliarius* was dead. Four snakes were observed during the daytime (one on the road, two under logs, and one under tin). The individual that was active on the road during the daytime was a newborn with a fatal birth defect of the skull and head (Fig. 22) (Messenger 2008). Some specimens omitted from various analyses depending on the conditions that they were found or if information was missing (escapees, roadkill specimens, data not recorded, etc.). In summary, of 394 marked animals, 47 were recaptured within the same year marked, 33 were recaptured one year later, 20 were recaptured two years later, 2 were recaptured three years later, and 1 was recaptured four years (3.7 years) later (Fig. 23).

Activity patterns by moon phase

This first level of examination (snake activity correlated independent of time) revealed no relationship between a large moon phase and activity (Fig. 24; $r^2 = 0.0021$, p-value = 0.7359).

The second level of examination, I only noted animals that were active while the moon was above the horizon (including cloudy nights when the moon was not visible). This resulted in a slightly stronger correlation (Fig. 25; $r^2=0.1086$, p-value = 0.0026).

The third level of examination, I only noted snakes that were active during the light spread. This resulted in the strongest correlation (Fig. 26; $r^2 = 0.3831$, p-value < 0.0001).

Activity patterns by seasons

Sistrurus m. miliarius was active from March to November (Fig. 27, Fig. 28). During the summer (June – 11.5%; July – 12.4%) *S. m. miliarius* surface activity remains steady. Towards late July and into early August, the number of *S. m. miliarius* typically increases to about two per night. Gravid females are commonly found active on roads in mid to late July. This fact is in sharp contrast to many other viperids, which usually remain dormant or inactive late in their pregnancy.

By mid-August, it was not uncommon to find several *S. m. miliarius* in a single night. Encountering three to four *S. m. miliarius* in a single night is common, with observations of up to 11 *S. m. miliarius*. August accounts for 20.7% of all activity. This is the birthing and mating season for *S. m. miliarius* at this latitude and it coincides with rattlesnakes elsewhere in the country, but for different reasons, such as the onset of the monsoon season in the southwest. In North Carolina, 82% of activity occurs from July to October (Palmer and Braswell 1995); by comparison, only 59.2% of the activity I observed was during this time period.

This high surface activity remained until early September. In September, Timber Rattlesnakes (*Crotalus horridus*) were the most active. *Sistrurus m. miliarius* surface activity remained high but in lower numbers throughout September (14.6%) and typically into mid-October (11.6%) when it began to cool down and nighttime temperatures were no longer conducive for nocturnal activity. In one particularly warm year (2005), *S. m. miliarius* were found nocturnally active until 9 November. It is not documented in the study site if *S. m. miliarius* shifted to a more diurnal or crepuscular state because few have ever been found during the daytime. Several searches on and off roads were made, but very few yielded anything (4 snakes - 0.7% of observations).

Activity patterns by temperature

Within my study site, *S. m. miliarius* prefer an average road temperature of about 29.9°C (n = 524). The maximum road temperature a *S. m. miliarius* has been found on was 41.1°C and the minimum was 18.3°C (Fig. 29). The average air temperature preference is 24.2°C (n = 524). The maximum air temperature a *S. m. miliarius* has been found at was 32.2°C and the minimum was 12.5°C (Fig. 30).

Activity patterns by rainfall

During the survey period, if it rained and cooled the road surface to the point where it could not thermally recoup and evaporate before nightfall, it effectively ceased pigmy rattlesnake activity. Of 562 *S. m. miliarius* observations, only 28 (5%) were active after a rain event (i.e., a rain event that resulted in the road remaining wet after sunset). Only small rain events that occurred mid-day had little to no effect on movement that night. Very few individuals (2; <1%) were found while it was actively raining.

Activity patterns by time and relative high

This category is a combination of activity by season and temperature. Early in the year (i.e., March, average temperature = 12.8°C), after sunset, the average road temperature cools rapidly (approximately 1°C per 90 minutes). High air temperatures during the day do not sufficiently warm the basal ground temperature (the soil temperature beneath the surface). During this spring emergence period, snakes were usually found under cover. A few species, such as Black Racers (*Coluber constrictor*), were found actively basking by day. Animals retreated to underground burrows at nightfall. As the temperatures continued to warm later in the year, such as April with an average temperature of 16.9°C (Fig. 12), and the surface temperature penetrates deeper into the soil stratum, more snakes can be found actively foraging during the daytime. Some species can be found mating underground close to the surface (*Elaphe [Pantherophis] guttata*; pers. obs.). Nighttime temperatures were still generally cool during this time of year ($\bar{x}$ = 10.0°C) and as a result, surface temperatures did not retain heat for long (average decrease in surface temperature of 1°C per 120 minutes). Weather systems during this time of year are far from stable and cold fronts are common. These interruptions bring nocturnal snake activity to a standstill. Temperatures dipped below 7°C at night. It typically takes a minimum of three consecutive days of stable, increasingly warmer days to bring activity back to where it was prior to the cold front (pers. obs.). Usually by mid-May (average temperature = 21.4°C) weather systems have stabilized and the threat of a cold front is no longer present. This period is typically the onset of nocturnal activity for the year.

In May, most activity is around sunset and the end of civil twilight. Rapidly cooling road surfaces did not allow for optimal temperatures late into the night. As the basal temperature increases, surface activity extends later into the night when the majority of the species present at the study site are active (28 of the 32 known species). Basal temperatures increase until the soils become nearly isothermal in mid to late May. All of these observations are similar to observations made by Martin (1992) concerning the emergence of Timber Rattlesnakes (*C. horridus*) in the Appalachians.

By mid-summer, surface temperatures reached up to 58°C. Come nightfall, temperatures decreased to 43°C. These high temperatures seemingly cause a delay in activity (Fig. 31). The maximum temperature a pigmy was ever found active was 41.1°C (pers. obs.). Not only does this represent the highest temperature a pigmy was active, but this also represents the highest temperature any snake species has been found active at night within the study site.

In the fall, the thermal gradient reverses as soil temperatures at the surface cool below that of the subsurface layers (Martin 1992). This fact results in a delay of surface activity, an exact opposite of what is observed in the spring. In the fall when the sun goes down, the substrate temperatures are thermally charged from the previous months, permitting nocturnal activity despite cooler ambient temperatures. In the spring, ambient temperatures reach sufficient levels for activity, but the substrate acts as a heat sink due to the months of cold weather thus explaining why activity is not symmetrical about the summer solstice.

Another important aspect resulting in the interaction between season, time, and temperature is relative temperature. Relative temperature is the temperature at capture compared to what the highest possible value for the day reached (in other words, the daily high). For example, in the early spring when daily high air temperatures are relatively low (21ºC), come nightfall the greater the percentage the ambient temperature of the daily high, the more likely one will observe a high level of activity. For example, a day in March may have a high temperature of 21ºC. After the sun sets, the air temperature falls to 17ºC. Though this temperature is well below what most snakes at the study site will tolerate, relative to what snakes are acclimated to for this time of year it is “decent.” Comparatively, if one looks at a night during mid-summer when daily high temperatures reach 39ºC, and temperatures drop to 24ºC there will likely not be much surface activity, even though 24°C is well above 17°C. This is because the animals are acclimated to what is “normal” for that time of year. Early in the spring, snakes can be active when the air temperature is 17ºC because this temperature, relative to what the high for the day was, is relatively high (i.e., it is 81% of that daily high temperature). When one examines the summer example, even though 24ºC is warmer than 17ºC and one would expect more activity simply based on this fact but this is typically not the case. When one looks at what percentage 24ºC is to the daily high temperature of 39ºC there is a value of 62%. These values are significant in determining nocturnal snake movement in my study site. Granted there are minimum thresholds in the early spring. The daily high temperature has to be at least warm enough for snakes to be active. For a more specific example, on 16 July 2004 (mid-summer), I had a single snake active with air temperatures of 23°C and on 24 May 2003 (late spring), I had 11 snakes active with air temperatures averaging significantly cooler (18.3°C). In July, the nighttime temperature averaged 78% of the daily high value whereas in May the nighttime temperatures averaged 85% of the daily high value.

Activity patterns by sex

Sex ratios differed throughout the season with males being more active than females. This was especially true in August. One female was captured four times in proximity to the original capture site. The first recapture measured 0.54 km from the original capture site. The second recapture measured 0.36 km. The third recapture measured 0.2 km from the original capture site. A male that was captured seven times never traveled greater than 0.5 km from the original capture site.

Sex ratios varied year to year, from a low male to female ratio of 1.4:1 in 2006, to a high of 1.9:1 in 2007 (Fig. 32), 2008 was excluded due to a low sample size. In all years, males were encountered more often than females.

Combining years and looking at each month can tell a lot about the species' natural history (Fig. 33). In March, for all years combined, the male to female ratio is 2:1, however, March is typically too cold and it was only surveyed 3 times over the years. In April, females are more active than males and the ratio of males to females drops to 0.6:1. In May, females are twice as likely to be moving as males (0.5:1 male to female ratio). This is the biggest month of movement for females, compared to males. In June, the ratio is 1.56:1, and in July it is 1.76:1. Males reach their peak in August when the ratio is 2.57:1. In September, I found a slight decrease in proportions but males are still twice as likely to be moving as females (2:1). During the mating season males move to maximize their chances of encountering a receptive female. They often move in straight lines or toward specific habitats where females are concentrated (Duvall et al. 1985, 1990). In October, the sexes move equally (1:1). November was only successfully surveyed for two nights during 2005. In this instance, females were again slightly more likely to be found than males with a male to female ratio of 0.67:1 (Fig. 33).

Activity of translocated animals

Translocation programs with snakes seldom end in success (Dodd and Seigel 1991; Reinert and Rupert 1999; Plummer and Mills 2000). Over the first few years of the project, I noticed that recaptured pigmies were usually within a few meters of their original capture site on the road.

Each year I would randomly assign pigmies to be translocated to a different part of the refuge. I was curious to know if the animals would attempt to make their way back to the original site of capture or if they would stay put and subsequent recaptures would take place at the translocation site. I expected the animals to return slowly to the original capture site. There was no formal protocol I followed; the decision to relocate a snake was made at random and often at the last minute. Nothing was planned. The distance of the translocation was also random (range 0.2 - 8.2 km). As such, this information should be viewed as anecdotal and hopefully future studies can decide whether there is a need to pursue this topic with this species.

Of 19 pigmies translocated, only 6 (32%) were recaptured (one 13 days later, two one year later, two at two years later, and one up to three years later). Of those six recaptures, four remained at their exact translocation spots. One of these four was relocated a distance of 8.2 km from the original capture site. Of the remaining individuals that moved from their relocation spot, one moved 0.3 km two years later in the direction of the original capture site.

The other individual was only relocated a short distance (0.35 km) and two years later returned to its original capture site. Thirteen (68%) were never found again.

Discussion

One of the primary goals of this aspect of the study was to examine environmental conditions that *S. m. miliarius* found favorable for movement and to see if different times of the year showed an increase or decrease in activity. If a particular environmental cue had a significant impact on the species, then we could follow up on that trigger and examine the biological significance behind that behavior, i.e., was the behavior courtship based? Several species, such as Spadefoot Toads (*Scaphiopus*) and Ambystomid salamanders, are known to have explosive movement during specific environmental cues, in response to mating. Other species may become exceptionally active during a specific time of year due to the abundance of a particular prey type, such as 17-year Cicadas (*Magicicada*), which are commonly ingested by copperheads (*Agkistrodon contortrix*). Black Tiger Snakes (*Notechis ater*) become very active during the seagull-nesting season because their entire diet for the year will come from this one gorging event. If we identify these movement events, we can help make surveys more efficient. This is especially helpful with rare, threatened, or elusive species.

My results showed a number of interesting results. *Sistrurus m. miliarius* preferred an ambient temperature above 24°C with a range of 14° - 34°C and substrate temperatures above 28°C, with a range of 20° - 42°C. *Sistrurus m. miliarius* preferred a relative temperature that was 85.4% of the daily maximum temperature (Fig. 34).

August had a significant increase in activity. In North Carolina, 82% of activity occurs from July to October (Palmer and Braswell 1995); by comparison, only 59.2% of the activity I observed was during this same time period. August is the breeding season for *S. m. miliarius* at this latitude and the male to female ratio is 2.5:1, indicating that males are constantly on the move in search of receptive females. Females showed the greatest proportion of movement in May, when the male to female ratio was 0.6:1.

Little is known about their overwintering behavior. Small animal burrows, sawdust piles, and old logs have been used as hibernacula (Klauber 1972, Palmer and Williamson 1971). Beane (2008) has observed a *S. m. miliarius* basking outside a hibernaculum that was also known to house two Eastern Coachwhips (*Masticophis [Coluber] f. flagellum)* and likely housed a third Eastern Coachwhip and a Corn Snake (*Elaphe [Pantherophis] guttata*). Beane (2008) also observed a *S. m. miliarius* using a hibernaculum that was occupied by an Eastern Kingsnake (*Lampropeltis g. getula*) and a Northern Pine Snake (*Pituophis m. melanoleucus*) in previous years (pers. comm.).

Perhaps the most significant effect observed was that of the moon phase on *S. m. miliarius* activity. The moon phase is not going to be the strongest predictor of snake activity, but it still ended up accounting for a significant amount of variation. Several factors play a role in determining movement, most notably temperature, as well as rainfall, season, sex, condition (gravid/ not gravid), and time since last meal. The moon appears to account for approximately 40% of the movement observed at night. There are many reasons why the moon would have an impact on snake behavior. The brighter the moon, the easier it is for nocturnal predators, such as owls, to see. Price *et al.* (1984) noted a high correlation between rodent activity and predation from owls and lunar rhythms. Their study showed that mice avoided nights of bright moons. Several herpetologists have noted anecdotal evidence supporting the idea that bright nights are poor choices for finding snakes (Klauber 1939, Kauffeld 1957, 1969). On 31 July 2004, the night of a full moon, David Justice saw an owl pick up an adult *Sistrurus m. miliarius* in front of his vehicle in northeastern Georgia (pers. comm.). On another evening, I observed two active predations on snakes by owls in the Everglades National Park (pers. obs.). Mice and other prey species can also see predators easier on bright nights. By avoiding bright nights, snakes may decrease success of their predators and increase their own success in capturing prey. There is a positive relationship between snake activity and avoidance of large phases (i.e., large percent of the moon's disc is illuminated) of the moon. The avoidance could be caused by illumination from the moon, or it could be based on an endogenous lunar rhythm. There are several studies that demonstrate an avoidance of illumination or bright lights (Clarke et al. 1996, Campbell et al. 2008) but they do not answer whether or not the avoidance is based on an internal rhythm or just a natural instinct to avoid brightness. My study strongly suggests a lunar rhythm, as the presence of cloud cover had no effect on activity. For example, a night with a full moon and heavy cloud cover still had a low amount of activity. Andreadis (1997) also noted similar anecdotal evidence of low activity despite heavy cloud cover. This leads credence towards an endogenous rhythm, as if the snakes are aware of the presence of the moon and are not simply reacting to illumination.. While observing snake activity I noted cloud cover, but it did not seem to have any impact. There were several nights when there was a full moon with heavy cloud cover, and still hardly any snakes were seen. Had cloud cover showed a significant difference this would have led me to believe that the influence is light-based. However, if it is based on a lunar rhythm it would not be directly related to light. The influence the moon has over snake behavior is most easily observed a few days prior to a full moon, during a full moon, and a few days after a full moon. No other field studies have been performed on this subject and it would be interesting to see if the trend holds true for other snakes or other localities.

There were a few factors that may play a role that I did not take into account such as age. Juveniles may have a different prey base from adults (Heatwole and Davidson 1976, Rabatsky and Farrell 1996). Some prey may be independent of the moon phase effect, such as sleeping lizards. Alternatively, other prey items, such as centipedes may have a polar opposite reaction to the moon phase and may be more active on full moons, possibly increasing juvenile movement during large moon phases.

Temperature and other environmental factors should also be considered. Temperature is obviously the most important need to a snake. Once temperatures reach a relatively high mean (late spring, summer, and early fall), then moonlight may become the next most important parameter to influence snake movement.

There are different pressures on *S. m. miliarius* at different seasons of the year. In the spring, most snakes are acquiring their first meals of the year. Individuals that may be sick or injured from hibernation may be more inclined to expose themselves. In the summer, females are nearing the birthing season. In the early fall, females are giving birth and males are mating with receptive females. In late fall, snakes retreat to their hibernacula for the winter. Foraging activity is interspaced throughout the year. It would be interesting to look at how influential the moon phase is at these various seasons. Perhaps the drive to mate is more important than the risk of predation during a full moon, forcing male snakes to move in the fall on bright nights.

A light meter would give a better understanding of how, or if, light intensity influences snake behavior. The purpose of this study was to look at the moon phase and its role in snake activity and possibly to predict what nights will have favorable outcomes for activity.

CHAPTER THREE

Growth and Age at Reproductive Maturity

Introduction

Like all North American pit vipers, *Sistrurus m. miliarius* are ovoviviparous, meaning young are born live in a thin membrane sac. Neonate *S. miliarius* are born in the fall (August and September) after a long gestation period of 107 to 294 days (Fleet and Kroll 1978). Reproduction in free-ranging *S. m. miliarius* has not been documented (Palmer and Braswell 1995). There has been no evidence to suggest that *S. m. miliarius* are capable of mating each year but most likely mate every other year as do many other crotalids (Siegel and Ford 1987). *Sistrurus m. barbouri*, by contrast, have both annual and biennial reproduction (Farrell et al. 1995; 2009).

The knowledge of a species' life history is vital for conservation and management. Understanding growth patterns is especially important because it can offer insight into age, longevity, age-specific fecundity and behaviors attached to ontogenetic shifts such as diet, habitat preferences, or predator evasion techniques (Shine and Schwartzkopf 1992, Waldron and Pauley 2007). It is well known that species with "slow" life histories are especially susceptible to population declines, e.g. Tuatara (*Sphenodon*), which do not reach sexual maturity until 10 - 20 years and reproduces only once every three to four years (Cree et al. 2009). The slower the life style, the more vulnerable the species is to extinction, making knowledge of growth parameters an important component of conservation.

Many rattlesnakes (*Crotalus*) are long-lived, slow to mature, and reproduce biennially or in some cases triennially (Rubio 2010). Species with these characteristics are especially susceptible to the negative effects of habitat destruction, fragmentation, and human persecution because they require a long time to recover from the loss of adult females. Some species are less susceptible to such threats due to having small homes ranges that limit their interactions with human-made structures, such as roads. *Sistrurus m. miliarius*, by contrast, display traits that are suggestive of a shorter-lived species, such as a small adult size, rapid maturity, and high fecundity (May and Farrell 2010). *Sistrurus m. barbouri* is capable of increasing its body weight by more than 4-fold and 6-fold from birth to one and two years of age, respectively (May and Farrell 2010). Similar results have been reported in neonate Eastern Massasaugas (*Sistrurus catenatus*), a sibling species to pigmy rattlesnakes, in which they double in length by the end of their first year (Dreslik 2005).

Pigmy rattlesnakes, like most reptiles experience indeterminate growth, which means they continue to grow throughout their life time, but, once they reach a certain size or age, the extent of this growth slows dramatically (Fig.35, Fig. 36). May and Farrell (2010) noted that a small percentage of *S. m. barbouri* (<15%) experienced asymptotic growth, but that the majority of the population did not reach an asymptotic size and continued to grow throughout life. While the growth and age at reproductive maturity are important life history attributes, knowledge of the size and age at which an animal is capable of reproducing for the first time informs biologists about the life history those species most likely exhibit. In the case of *Sistrurus m. miliarius*, that life style is to mature quickly and to reproduce often, presumably due to a short life span.

The objectives of this study were to estimate the size and age at which *S. m. miliarius* reach sexual maturity. This documentation would provide land managers with valuable information about the life history of this species and offer insight into conservation impacts that the species may face, such as delayed maturity, slow growth, or low fecundity.

Methods

Study area: From 2002 to 2008, specimens were captured by driving the Wildlife Drive and waiting for individuals to actively cross the road. Wildlife Drive is an asphalt road within the Carolina Sandhills National Wildlife Refuge in Chesterfield Co., South Carolina, USA. I drove from approximately one hour before sunset until snake activity was over, which could sometimes last up to eight hours. I defined the end of activity as 90 minutes after I last encountered a snake. I attempted to sample on as many nights as possible and with the exception of the final year, I averaged 79 survey nights per year (range 65-94).

Despite having an average precipitation of 114 - 124 cm per year (Fig. 11), the coarse sand covering the upland region results in xeric conditions and as such limits the vegetation that can successfully thrive there. Longleaf Pine (*P. palustris*) and Turkey Oak (*Quercus laevis*) dominate the upland region. Ground cover in these areas consists of wiregrass (*Aristida* sp.) and Bracken Fern (*Pteridium aquilinum*) (Garton and Sill 1977).

Ephemeral floodwaters inundate the lower elevations and layers of clay intersect the sand substrate. These lower slopes contain abundant soil moisture and as a result yield significantly different vegetation. Various evergreen shrubs occur here: Fetterbush (*Lyonia lucida*), Swamp Bay (*Persea palustris*), and Inkberry (*Ilex glabra*). The broader bottomlands are dominated by hardwoods -- Tupelo Gum (*Nyssa aquatica*), Red Maple (*Acer rubrum*), and White Cedar (*Chamaecyparis thyoides*) -- and are commonly bordered by Tulip Trees (*Liriodendron tulipifera*) and Sweetgums (*Liquidambar styraciflua*) (Garton and Sill 1977).

The average yearly temperature of the refuge is 17.1°C. The hottest month is July (average daily maximum temperature = 32.8°C) and the coldest month is January (average daily minimum temperature = 1.1°C) (Fig.12). The highest recorded temperature was 41°C in

August 1983, and the lowest recorded temperature was -16°C in January 1982 (National Weather Service).

Snake capture and measurement: When snakes were captured, I recorded several variables. I recorded time of day, GPS coordinates (spatial accuracy $\leq$ 4.5 m), substrate and ambient temperatures (to the closest 0.25°C), cloud cover, moon phase percentage, moon height in the sky (below the horizon, at the horizon, overhead, etc.), and rainfall (via weather station). Substrate temperature was obtained by taking a temperature (Raytek infrared thermometer) of the road or substrate the snake was found on. Ambient temperatures were acquired by taking the surface temperature (Raytek infrared thermometer) of leaves from nearby trees at shoulder height. Multiple readings ($\geq$ 5) were averaged for a final value. These thermometers register an instantaneous temperature so there is minimal delay from capturing the snake to recording data. I scanned each captured snake for the presence of a microchip or examined for cauterized ventral scutes to note whether it was a recapture. Animals that had been recently captured ($\leq$ 3 months) were not re-measured. I held all captured snakes until surveys were completed for the night. I measured captured snakes for snout-to-vent (SVL; 0.5 cm) and total length (TL; 0.5 cm) via tubing and stretching along a tape measure, mass (1 g), and sex (via probing). I marked snakes with either a microchip (PIT tag – BioMark and A.V.I.D. [American Veterinary Identification Device]) or via ventral scale cauterization (Aaron Medical Change-A-Tip cautery units; Aaron Medical, St. Petersburg, Florida 33710, USA; www.aaronmed.com). Depending on the time of year and the environmental conditions, I released snakes the night in which they were captured, or they were kept for 24 hours and released the following night.

Growth: Methods followed those of Waldron and Pauley (2007). Growth rates were calculated as the percent change in total length (TL; cm), divided by the time interval between captures. I took the percent change and divided over the number of days between the two captures. I used the growing season (March to November) as the time interval because it was assumed that pigmy rattlesnakes do not grow during the winter. Because the models do not require knowledge of the age, I used the growth interval forms of the von Bertalanffy and logistic equations to model *S. m. miliarius* growth.

The von Bertalanffy growth interval equation,

$$L_2 = a - (a - L_1)e^{-rd}, \qquad (1)$$

and the logistic growth interval equation,

$$L_2 = a\,L_1 \big/ \left[L_1 + (a - L_1)e^{-rd}\right], \qquad (2)$$

were used, where L_1 was the length at first capture, L_2 was the length at recapture, d was the time between capture and recapture (i.e., number of growing seasons), e was the base of the natural logarithms, a was the asymptotic size, and r was the characteristic growth parameter (Fabens 1965, Schoener and Schoener 1978, Frazer and Ehrhart 1985, Aresco and Guyer 1999, Waldron and Pauley 2007). I used nonlinear least squares regression with the Marquardt algorithm (PROC NLIN; SAS vers. 9.1, SAS Institute, Inc., Cary, North Carolina, 2002) to fit recapture data to equations 1 and 2, and to estimate asymptotic TL (a) and the characteristic growth parameter (r).

I used the residual error mean square (REMS) to compare growth models, where the model with the lowest REMS and the most biologically appropriate estimate of a (Frazer et al. 1990) was considered the best fit to the recapture data. Specifically, an estimate of a is considered biologically appropriate when it is slightly larger than the average size of the largest individuals in the population. The average TL of the largest reproductively mature males (n = 248) in my study population was 38.7 (SE = 2.1; 95% CI = 42.38-51.1). The smallest reproductively mature male observed during the study was 32.4 cm. For females, the average TL of the largest reproductively mature female individuals (N = 124) was 33.7 (SE = 4.0; 95% CI = 36.4-53.7), which included females larger than 27.3 cm (obtained from the smallest reproductively active female observed). To obtain the average largest individuals used, TL measurements taken upon first capture of the largest 50% were used to determine the average size of the largest individuals.

When individuals were recaptured in subsequent years, I used the growth interval between the first and last capture in analyses. Measurements from 52 recaptures provided growth intervals for 13 females and 39 males.

Age at Maturity: I followed methods outlined by Waldron and Pauley (2007) to estimate age at maturation using the von Bertalanffy and logistic equation models. To estimate mean age and mean size at reproductive maturity I used the von Bertalanffy equation,

$$L = a\,(1 - be^{-rt}) \qquad (3)$$

where t = age, a = asymptotic size, r = characteristic growth parameter, and e is the base of the natural logarithms. The general logistic equation model used was:

$$L = a\,/\,(1 + be^{-rt}) \qquad (4)$$

with parameters defined in Equation 3. Since models 3 and 4 required knowledge of age, we solved for t by calculating parameter b using the estimates of a and r obtained from equations 1 and 2 (Frazer and Ehrhart 1985). Mean TL of newborn (h) *S. m. miliarius* (sex unknown) was 14 cm (SD = 1.27). Measurements came from neonates birthed from study animals held late in development until parturition. Neonates (n = 11) and their mothers were then released after they were measured. Thus, for the von Bertalanffy growth model (equation 3) , I solved for b using the following equation:

$b = 1 - (h / a)$

females: $b = 1 - (14 / 45.0983)$,

males: $b = 1 - (14 / 46.7691)$,

where h is the average TL for newborns. For the logistic model (equation 4), I solved for b using the following equation:

$b = (a / h) - 1$

females: $b = (43.9202 / 14) - 1$

males: $b = (45.2203 / 14) – 1$

Thus, the final von Bertalanffy models that were used included:

females: $L = 45.0983(1 - 0.689e^{-0.3465t})$

males: $L = 46.7691(1 - 0.700657e^{-0.387t})$

and the logistic models included:

females: $L = 43.9202 / (1 + 2.1371e^{-0.5097t})$

males: $L = 45.2203 / (1 + 2.230021e^{-0.6t})$

I solved for t at given values of $L = L_m$, i.e., an estimate of the mean size at reproductive maturity (Frazer and Ehrhart 1985), in which the average TL of the adult males and females in the population (i.e., females $\bar{x} = 33.7$, SE = 0.08; males $\bar{x} = 38.7$, SE = 0.03) was used as the upper limit for L_m, and the smallest recorded sizes of males and females observed mating were used as the lower limit for L_m.

Results

The von Bertalanffy fit best with observations in the field. It estimated age at reproductive maturity at 2.7 growing seasons for males and 2.1 growing seasons for females, and asymptotic size at 46.7 cm (42.3 – 51.5) for males and 45 cm (36.4 – 53.7) for females (Figs. 35, 36) (Table 3). The von Bertalanffy model had lower REMS than the logistic model (4.66 compared to 5.07) and had a more biologically relevant estimate of *a* (Table 4). By comparison, the logistic model estimated maturity at 3.4 growing seasons for males and 3 growing seasons for females, and asymptotic size of 45.2 cm (range: 42.1 – 48.2) for males and 43.9cm (range: 37.7 – 50) for females (Table 3). Because the logistic model had higher REMS than the von Bertalanffy model (5.07), it was considered to be a less biologically relevant estimate of *a*.

Growth rate indicated that smaller individuals (younger) have a more significant change in growth from year to year than larger individuals (older) (Fig. 37). The characteristic growth parameter *r* indicates that males grow more rapidly than females. Larger snakes increased in body mass at a greater rate than total length, resulting in a non-linear relationship between length and body mass; excluding gravid and post-partum females, males tended to be heavier than females of similar size (Fig. 38).

Discussion

My observations indicate that Carolina Pigmy Rattlesnakes reach sexual maturity much sooner than other crotalines, and even more interesting is that females reach sexual maturity at a younger age than males. Dreslik (2005) also reported that female *Sistrurus catenatus* increased their snout-vent length at a greater rate than males between shedding events. Few snake species exhibit females maturing faster than males (Parker and Plummer 1987). Growth data suggest that females could become reproductively capable the September 2 years after being born, assuming an average birth date in mid-August. Males, by contrast, will likely first reproduce in late June or early July of their 3rd year, again, assuming an August birth. Males typically reach maturity more quickly than females, which reflect the costs of ova development in females (Aubret et al. 2002). Females must store a sufficient amount of body fat to effectively allocate resources toward reproduction, whereas males require spermatogenesis and sufficient body fat to actively search for females. Some species (*Crotalus adamanteus* and the coastal plain variety of *C. horridus*) may take as long as 5 - 6 years to reach an adequate length and body mass (Fig. 39) to survive the pressures of pregnancy (Aldridge and Brown 1995; Waldron unpub. data, Gibbons 1972). Brown (1991) found that montane female *C. horridus* reached maturity at 7 - 11 years (mean = 9.3). Aldridge and Brown (1995) reported male maturity at 4 - 7 years (mean = 5.3) for the same population as Brown (1991). Brown (1993) reported male *C. horridus* maturity as young as four years in the southern and western extent of its range. Female *S. m. barbouri* varies in age at first reproduction, between 2-5 years, and a minimum SVL of 38 cm (Rowe et al. 2002, May and Farrell 2010).

For males, early maturation has few consequences; there is no threshold level of energy stores required to initiate reproduction (Bonnet and Naulleau 1996; Aubret et al. 2002). If males mate too early, they will be likely underweight compared to other males and thus outcompeted, or they will forego reproduction if they do not have sufficient body fat to find mates (Duvall and Beaupre 1998). If anything, an increase in size and mass aids in competition by allowing larger and heavier males to subdue smaller males, which is reflected by my estimate of 2.7 growing seasons to reach reproductive maturity. During this third year, prior to the fall mating season, individuals should gain mass and length to make them more competitive for accessing/acquiring mates. the mating season. If a young female, usually primiparous, reproduces too early, it can be detrimental to her health or even fatal. In the case of oviparous species (species that lay eggs instead of live birth), this cost usually presents itself in the form of dystocia (when the eggs are too large for the female to pass) (Barten 1985). In ovoviviparous species (live birth) dangers could come from not having enough fat storage to support the developing embryos, or an imbalance in minerals such as calcium, which are used in the development of the skeletons of the embryos. These larger species are also limited in their abilities to reproduce only once every other year and sometimes every third or fourth year (Brown 1991, Martin 1993). Like all K-selected organisms, larger crotalids compensate for these shortcomings in their life by having a greater longevity and a higher survivorship since they are less susceptible to predators simply due to physical size. *Sistrurus m. miliarius* are nearly the exact opposite in all aspects (closer to R-selected than K-selected), with the exception of the number of offspring. Due to their small size, they are extremely susceptible to predators compared to many other species of venomous snakes. Their venom yield is low, their fangs are short, and their rattle is not loud enough to scare away potential predators and in fact may actually invite unwanted attention. Their best defense is relying on crypsis to conceal their small body and to avoid detection.

In comparison to the larger rattlesnakes, pigmy rattlesnakes exhibit very rapid growth curves during their first few years of life. Accelerated growth patterns and younger maturation can arise from factors such as abundant resources and/or high adult mortality (Shine and Charnov 1992). May and Farrell (2010) documented growth rates of juvenile *S. m. barbouri* and noted an increase in length of 1.8-fold and 2.2-fold and an increase in weight by more than 4-fold and 6-fold from birth to one and two years of age, respectively. Most species reach sexual maturity size near the plateau of the von Bertalanffy and logistic growth curves. This fact means that, when they reach sexual maturity, they will continue to grow, but at the same rate or size. *Sistrurus m. miliarius* on the other hand reach sexual maturity a little over half way up their growth curve; i.e., once they hit sexual maturity they still have the potential to grow much larger. The potential benefit for this early maturation is that this allows the species to quickly reach sexual maturity and pass on its genetic material at least once before succumbing to predation.

The results of this study are important because they demonstrate that *S. m. miliarius* have an accelerated life history relative to other viperids. The species' fast maturation and reduced birthing intervals (May and Farrell 2010) suggests that pigmy rattlesnakes have the potential to recover quickly from population declines, provided proper habitat still exists. *Sistrurus m. miliarius* seems to have a relatively small home range, as individuals found on roads were captured close to their original capture site on subsequent recaptures, implying little movement (this study, Chap. 2). Unfortunately, many animals, not just snakes, fall victim to road mortality in areas where human densities are high, making it easy to decimate a location population, particularly in fragmented habitats. Understanding these aspects of pigmy rattlesnake life history is essential to a sound management plan for this disjunct and sparsely encountered species. Further, by identifying life-history attributes that might contribute to a species' sensitivity to regional decline is important in helping biologists and land managers recognize vulnerable populations and develop appropriate measures to circumvent potential threats. Farrell et al. (2008) noted that *S. m. barbouri* do not have high or consistent survival rates. My results suggest that with proper habitat, *Sistrurus m. miliarius* is likely to recover quickly. Both sexes are capable of growing to adulthood before their third year. Farrell et al. (2008) showed that neonate recruitment of *S. m. barbouri* is highly variable and that recruitment could vary up to six times in the most successful year when compared to the year with the lowest recruitment.

"A living dog is better than a dead lion. Shall a man go hang himself because he belongs to the race of pygmies, and not be the biggest pygmy that he can?"

- Henry David Thoreau, from Walden.

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Figure 01. Normal phase *Sistrurus m. miliarius*, showing characteristic red dorsal stripe and white rings around dorsal blotches.

Figure 02. Lavender phase *Sistrurus m. miliarius*.

Figure 03. Juvenile anerythristic *Sistrurus m. miliarius*. Anerythristic means a lack of red pigment, which is why the dorsal stripe is now white.

Figure 04. Anerythristic phase *Sistrurus m. miliarius*.

Figure 05. Erythristic phase *Sistrurus m. miliarius*. This coloration is restricted to northeastern North Carolina and northern Georgia.

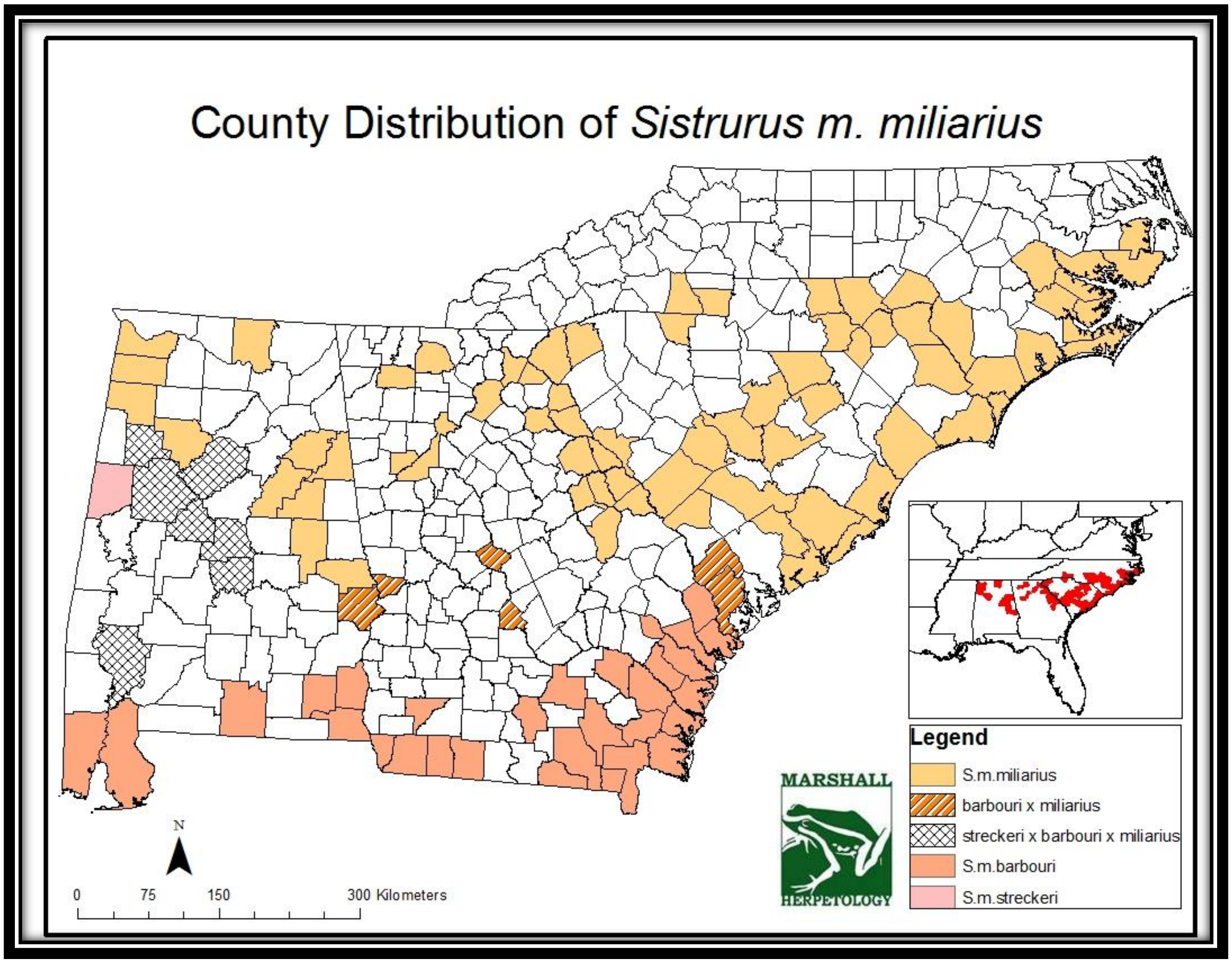

Figure 06. Distribution of *Sistrurus m. miliarius* in the Southeastern U.S. with intergrade zones and the peripheries of the other subspecies. The inset represents only *Sistrurus m. miliarius* distribution.

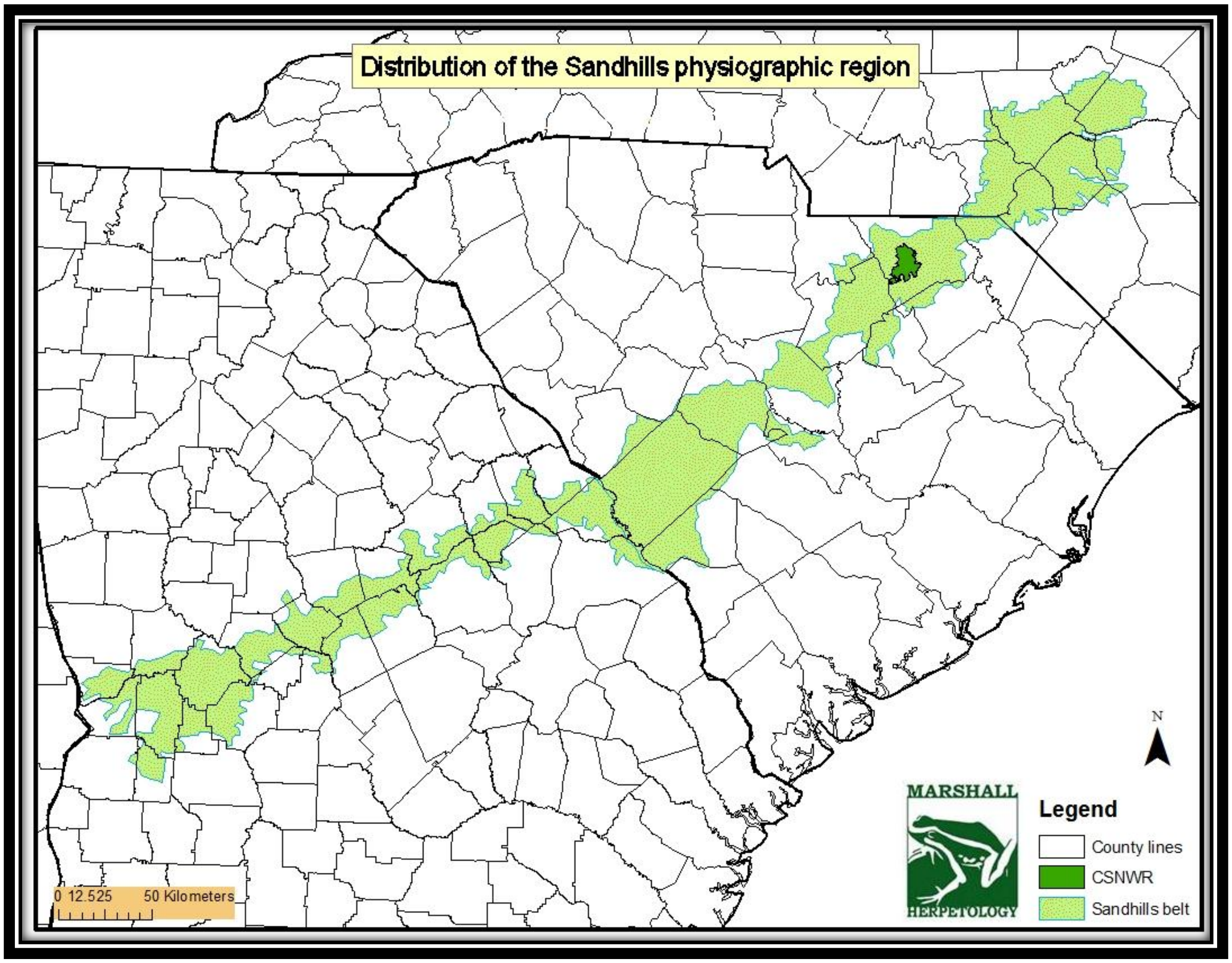

Figure 07. Distribution of the Sandhills physiographic region and placement of the Carolina Sandhills National Wildlife Refuge (CSNWR).

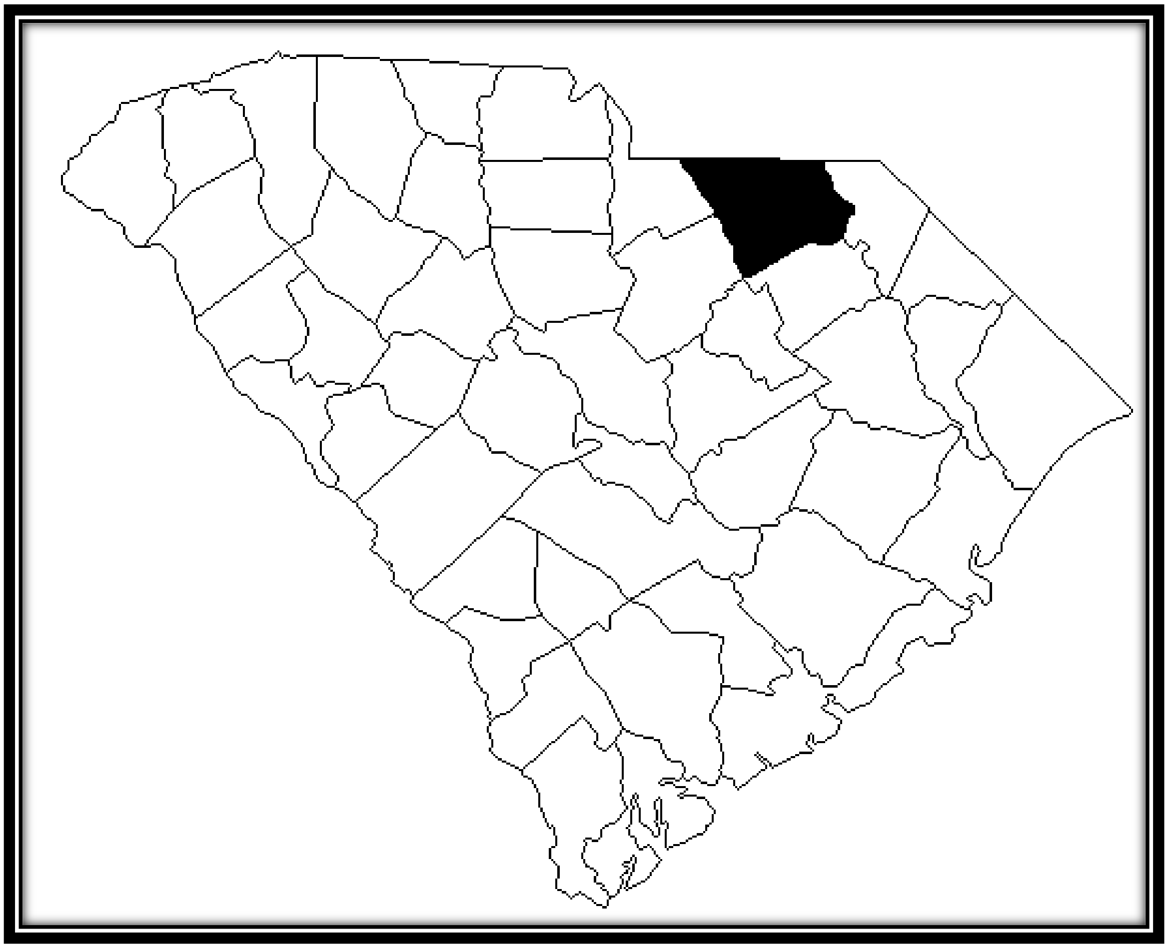

Figure 08. Location of Chesterfield County, SC

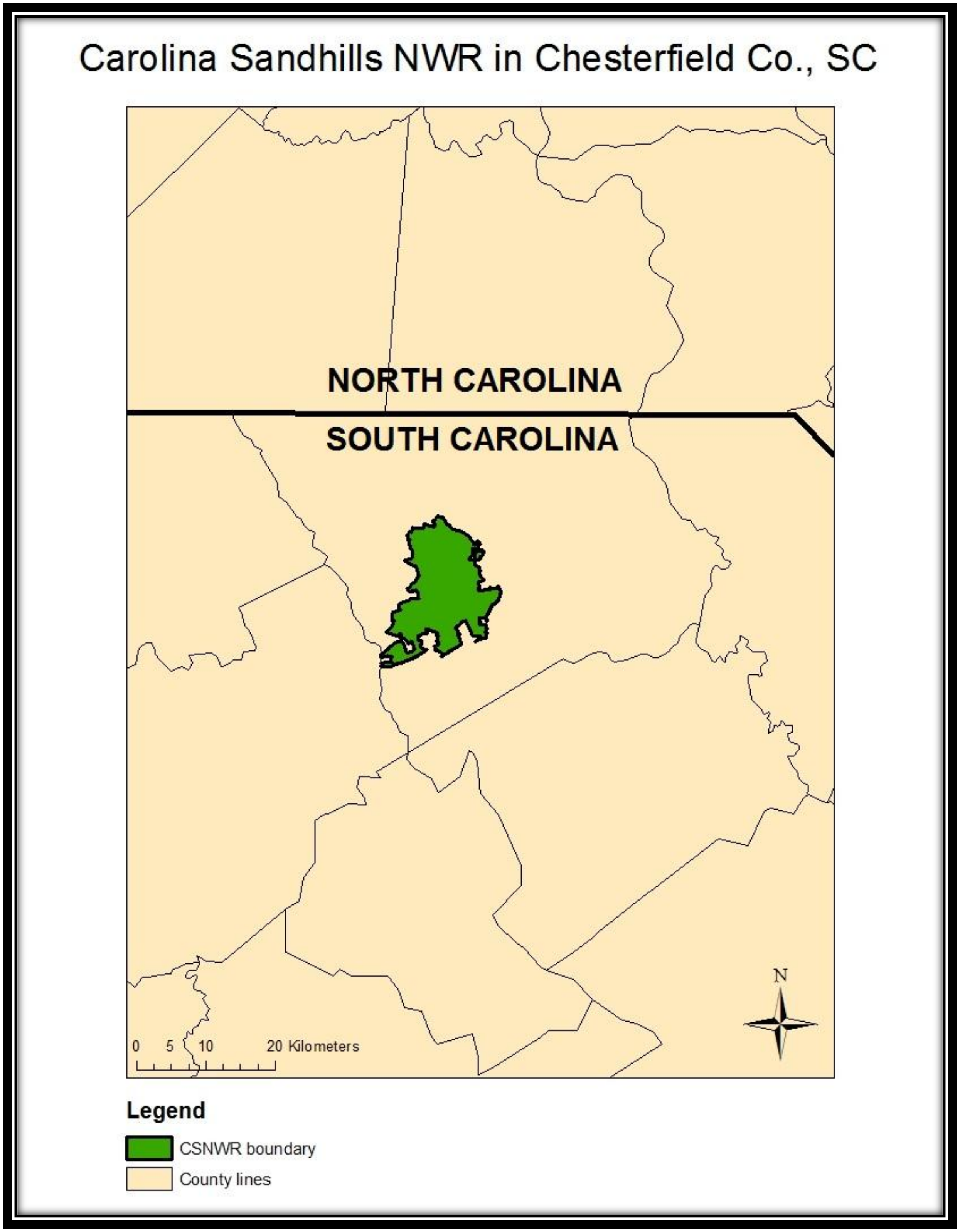

Figure 09. Location of the CSNWR within Chesterfield County

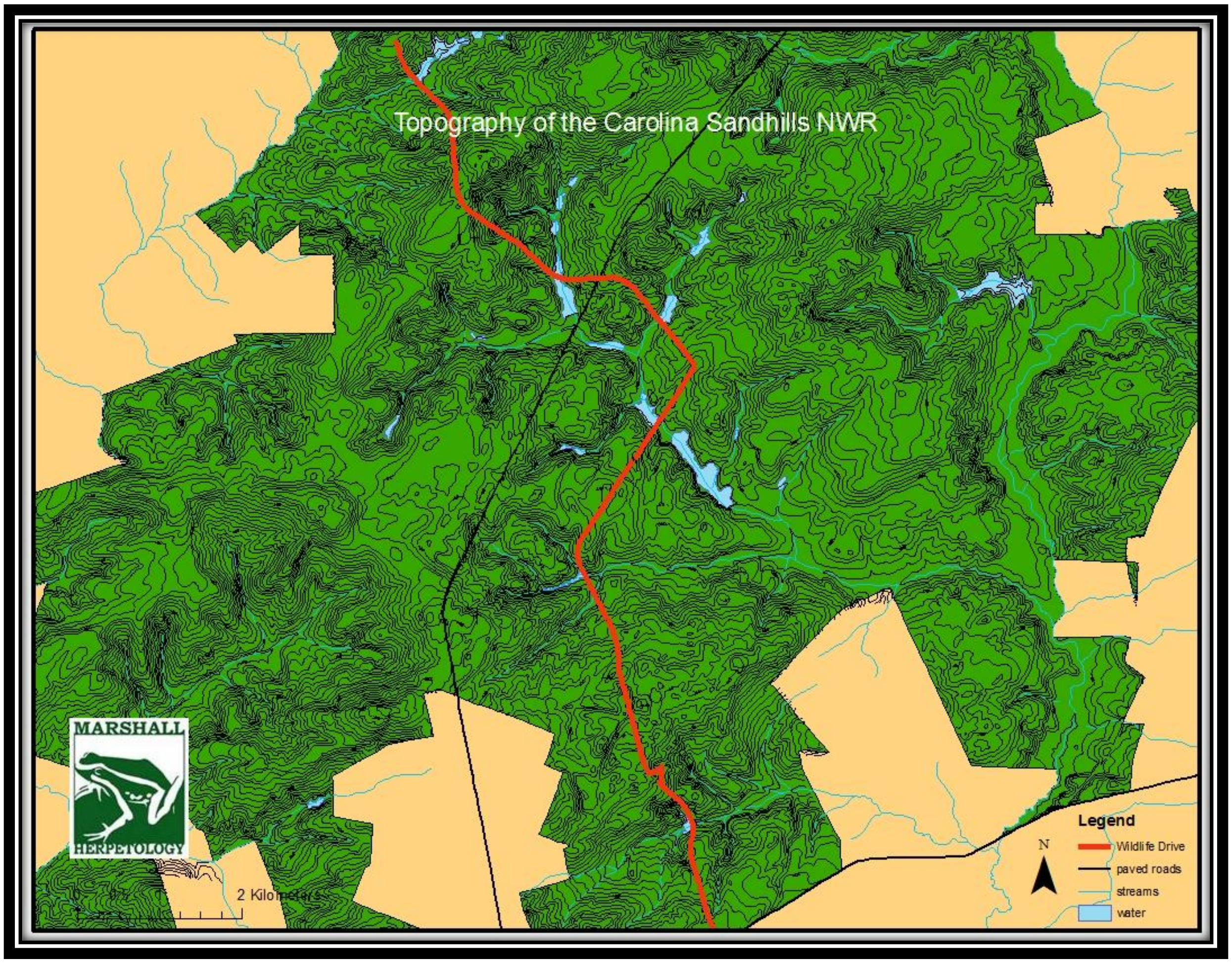

Figure 10. Topography of the CSNWR with emphasis on the area close to the Wildlife Drive.

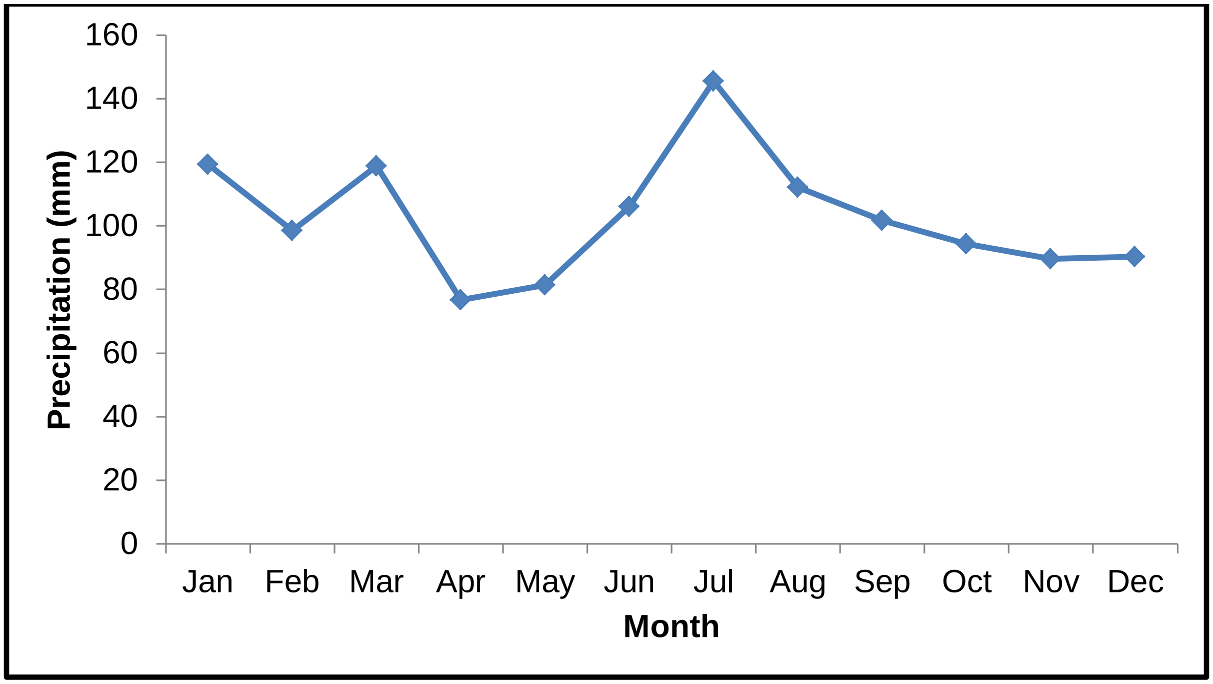

Figure 11. Average precipitation at the study site.

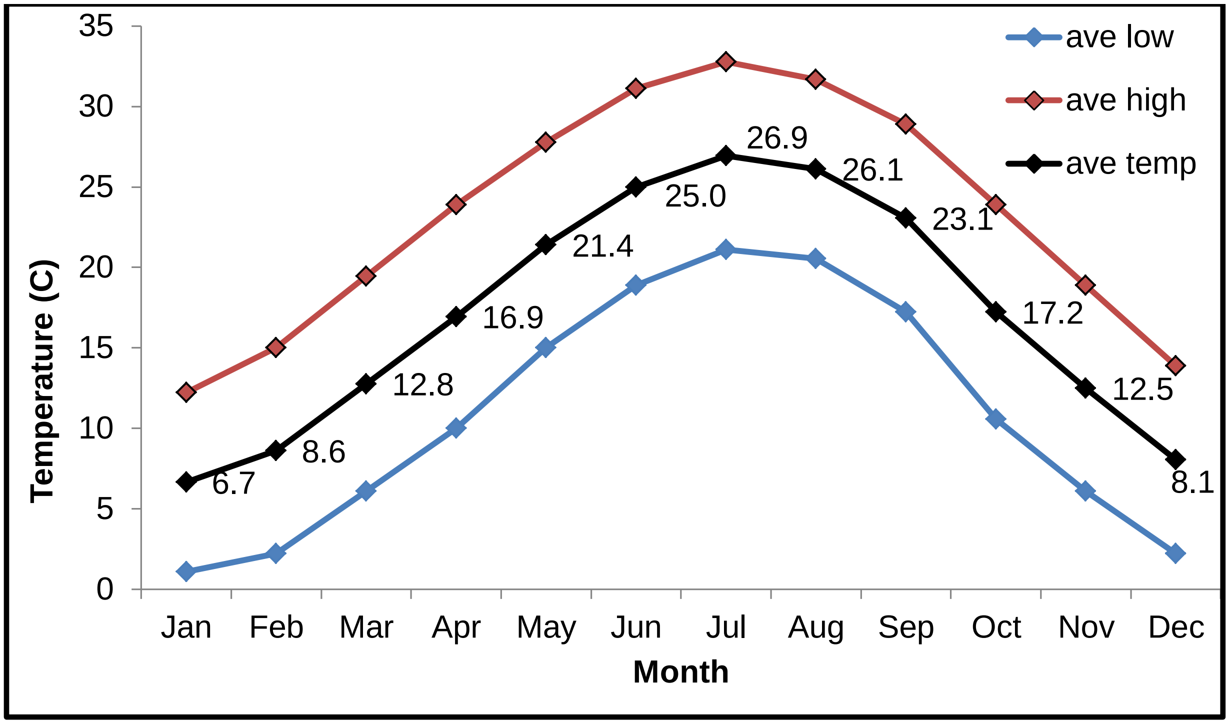

Figure 12. Average high and low ambient temperatures of CSNWR.

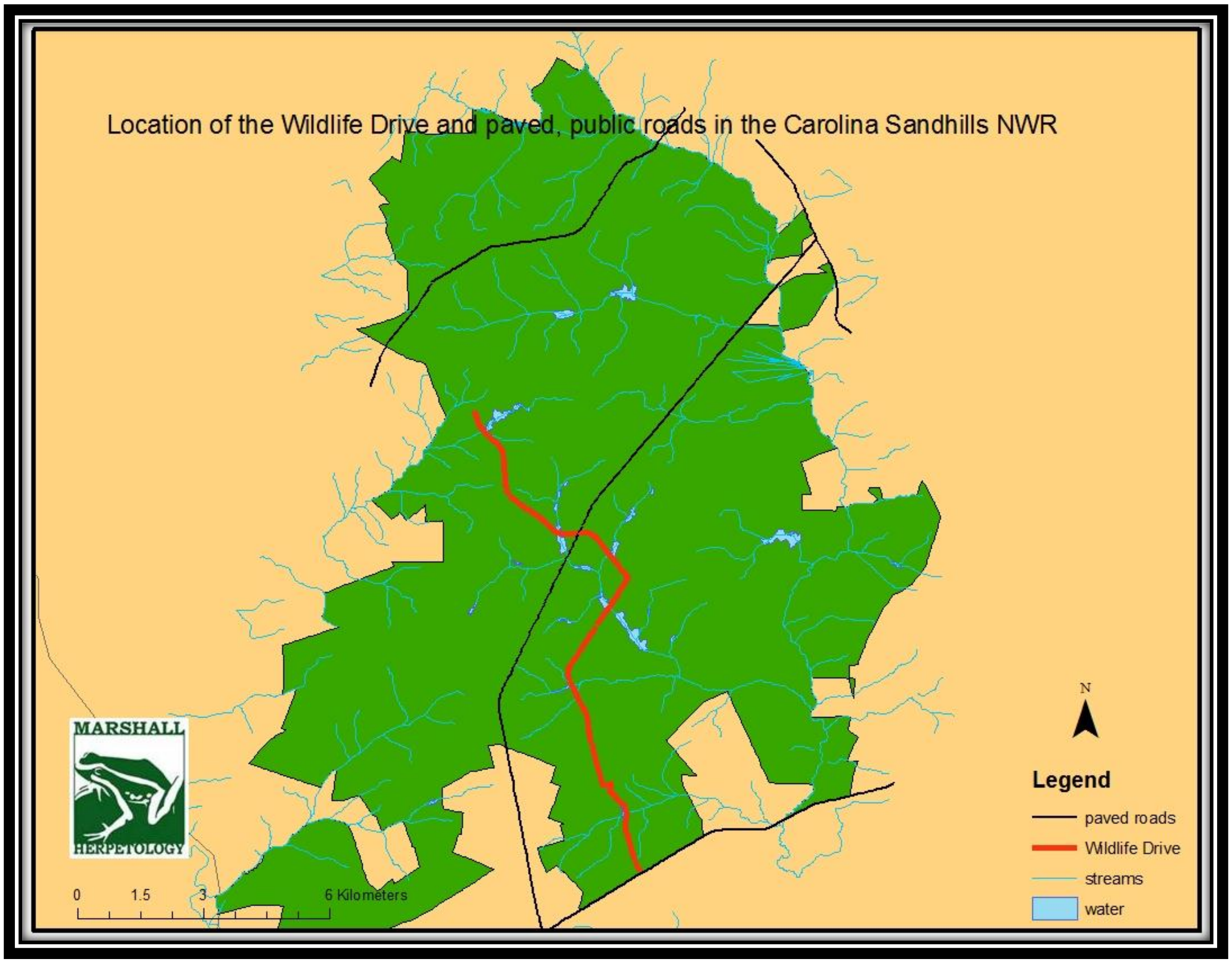

Figure 13. Location of the Wildlife Drive and paved, public roads in the Carolina Sandhills National Wildlife Refuge. US 1 borders the south of the map and Hwy 145 bisects the middle. Angelus road is in the upper left corner, and Hwy 109 is in the upper right corner. The Wildlife Drive is highlighted in red.

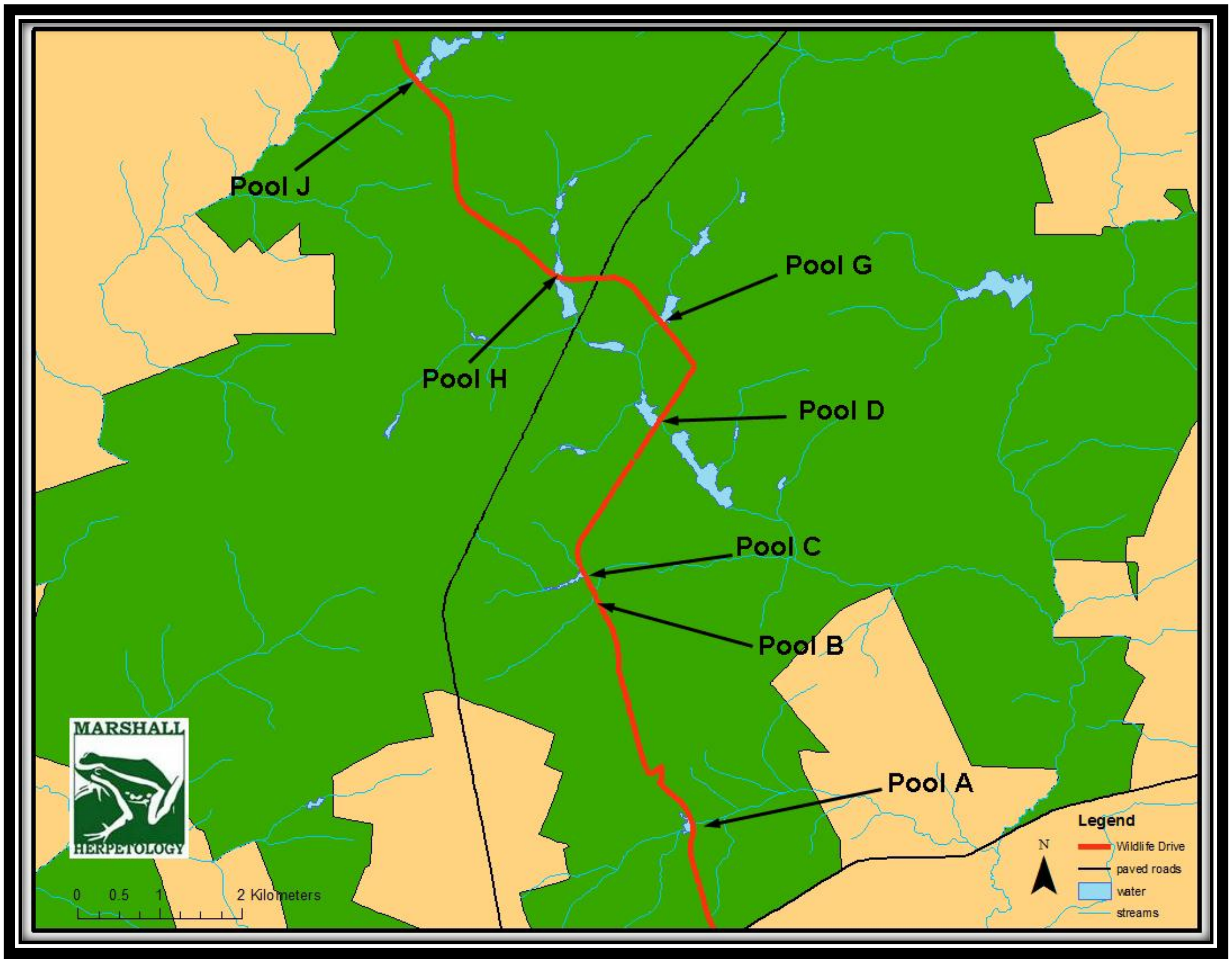

Figure 14. Location of man-made pools adjacent to Wildlife Drive.

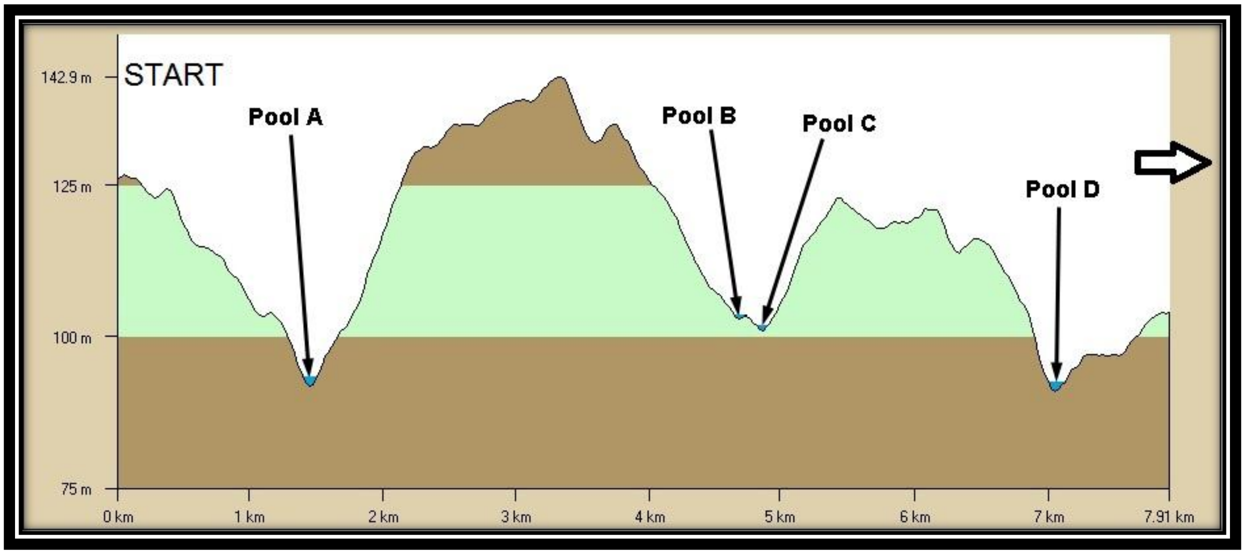

Figure 15a. Elevational Profile of the Wildlife Drive (south to north leg)

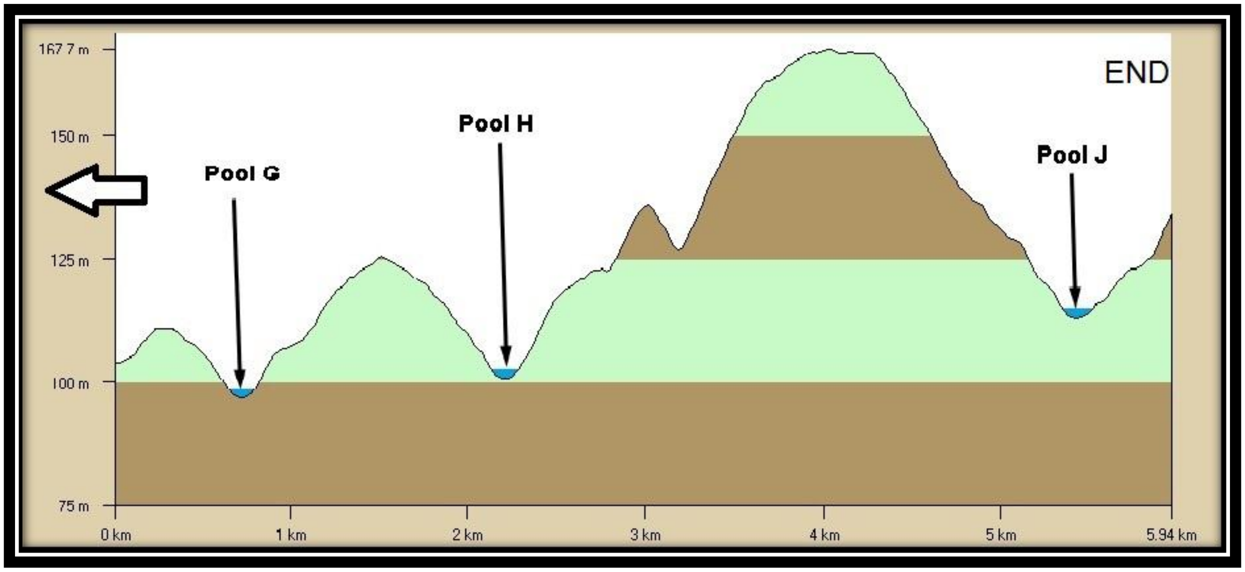

Figure 15b. Elevational Profile of the Wildlife Drive continued (east to west leg)

Figure 16. Satellite image via Google Earth of the Wildlife Drive and topography, illustrating changes in habitat (mesic, transitional, and xeric).

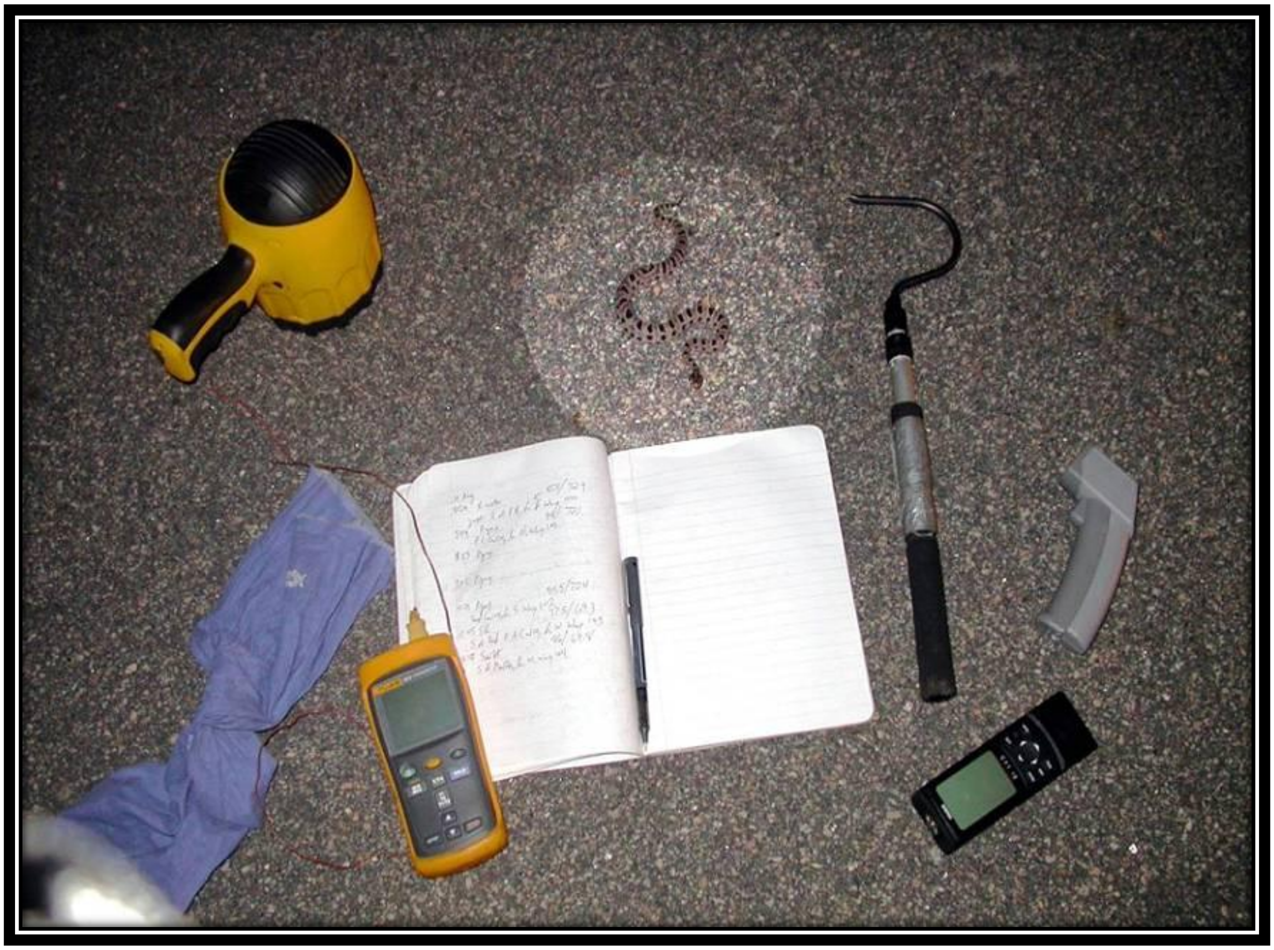

Figure 17. Equipment used while surveying.

Figure 18. Two wild caught males in combat. Placed in temporary cage (for additional measurements) and held in captivity for approximately three hours before being released.

Figure 19. A cauterized copperhead, specifically #115.

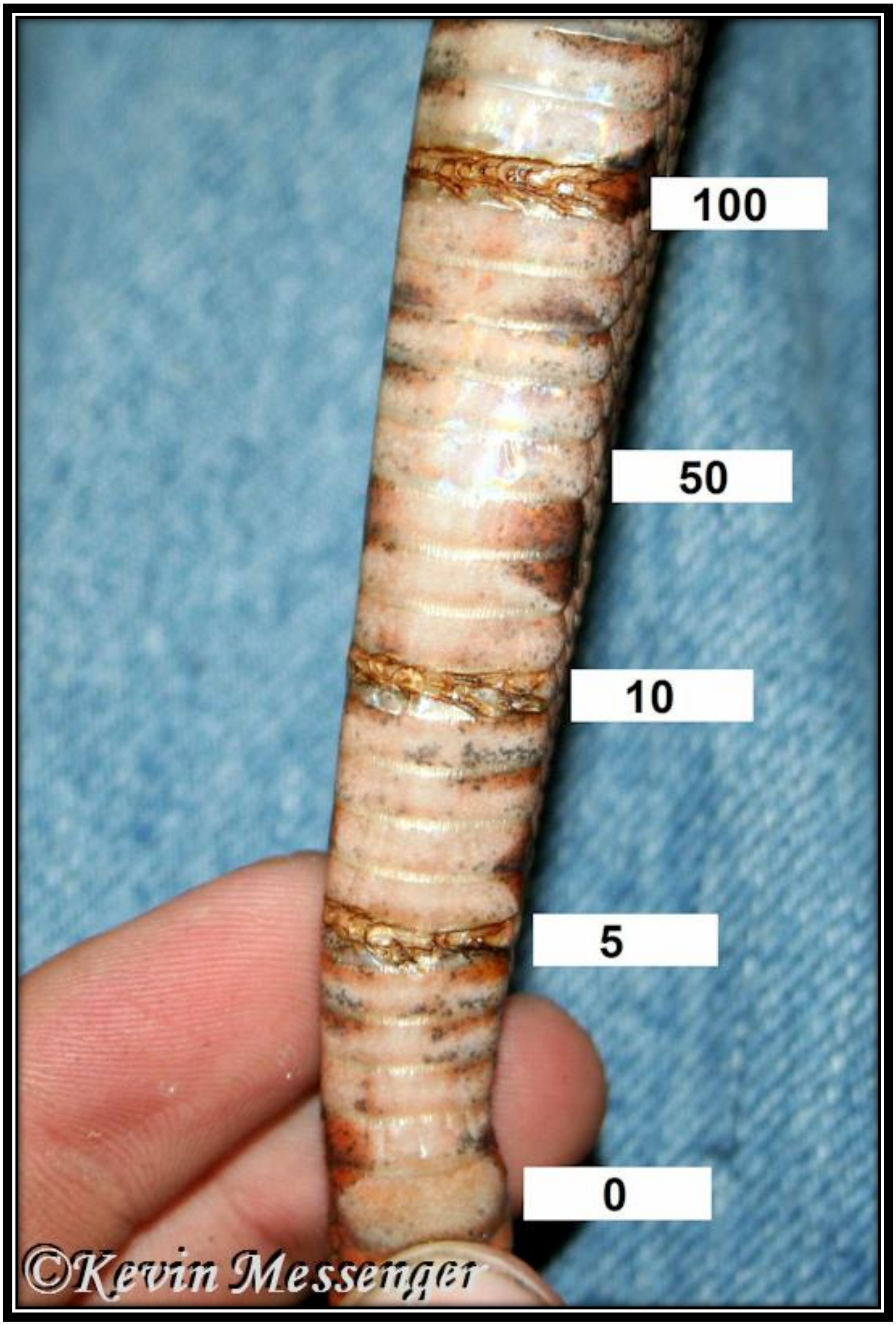

Figure 19. A cauterized copperhead, specifically #115.

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Figure 20. Size of newborn Carolina Pigmy Rattlesnake (*Sistrurus m. miliarius*)

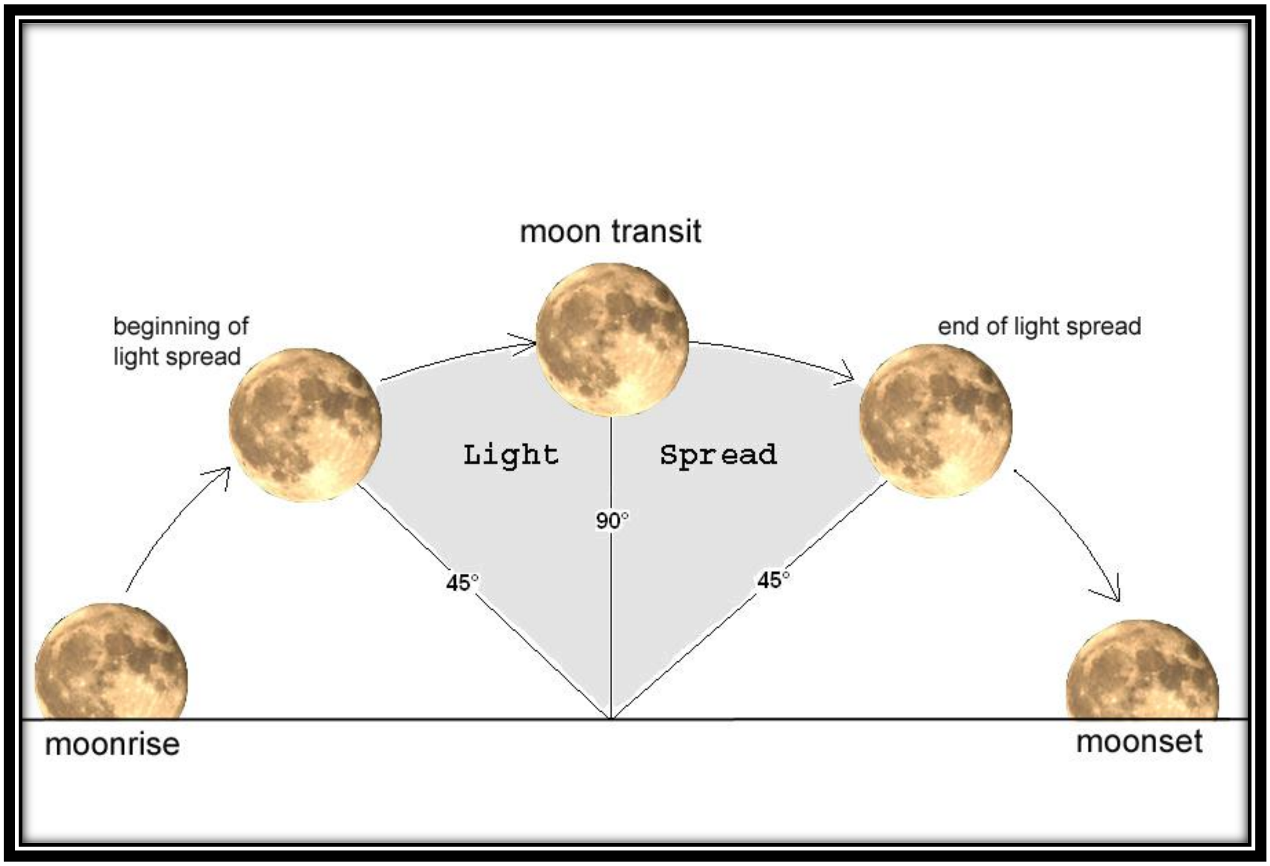

Figure 21. Diagram of the Light Spread

Figure 22. Newborn *Sistrurus m. miliarius* with birth defect of the skull and head.

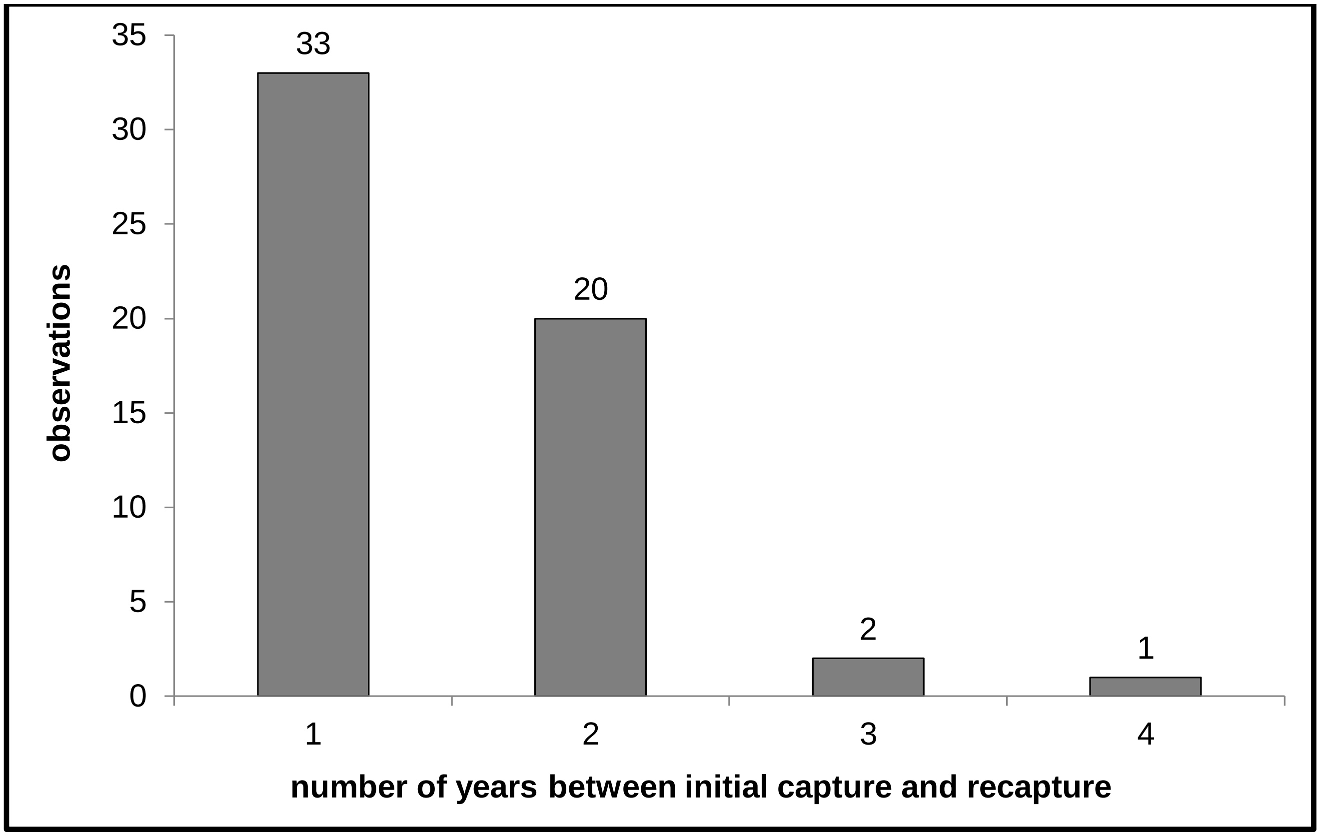

Figure 23. Frequency of interval recaptures.

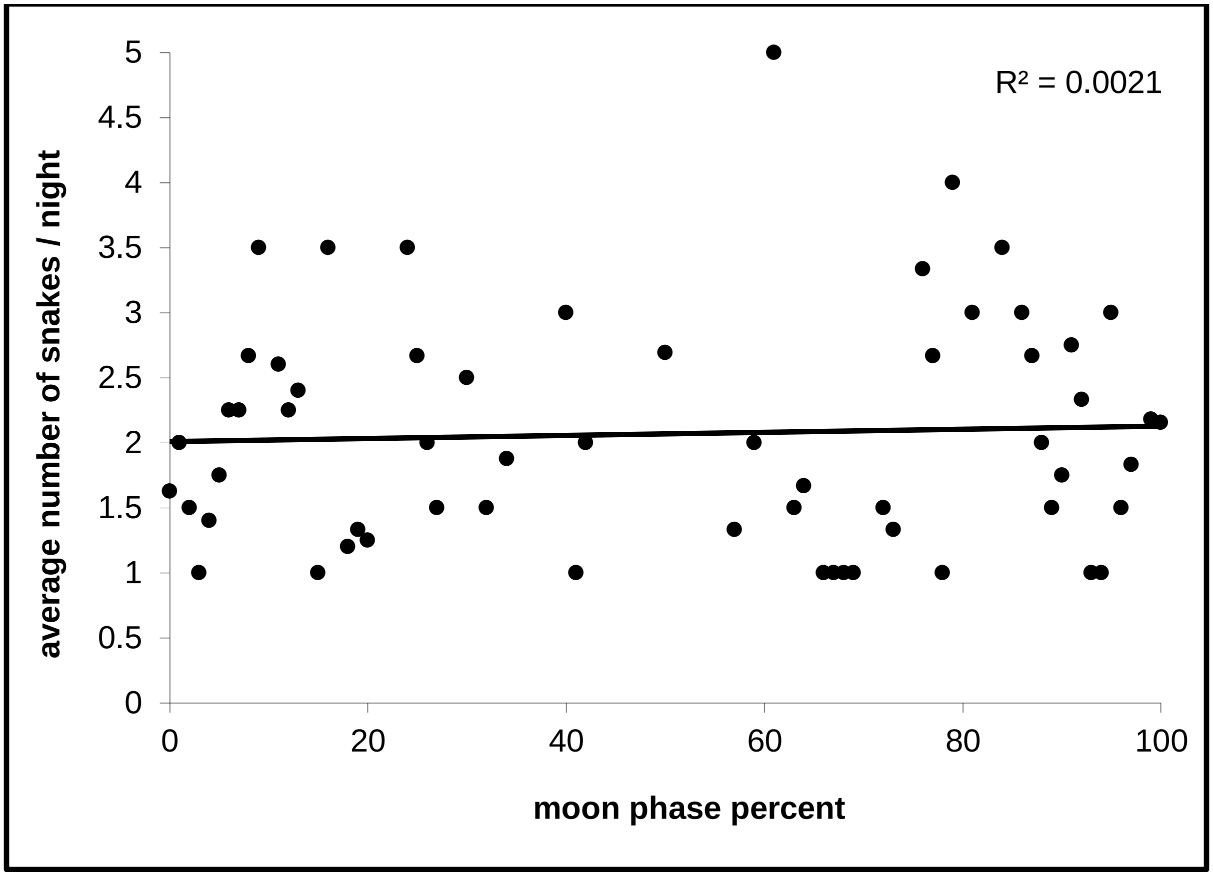

Figure 24. Activity of *Sistrurus m. miliarius* with respect to moon phase measured independent of time; n = 531, p-value = 0.7359.

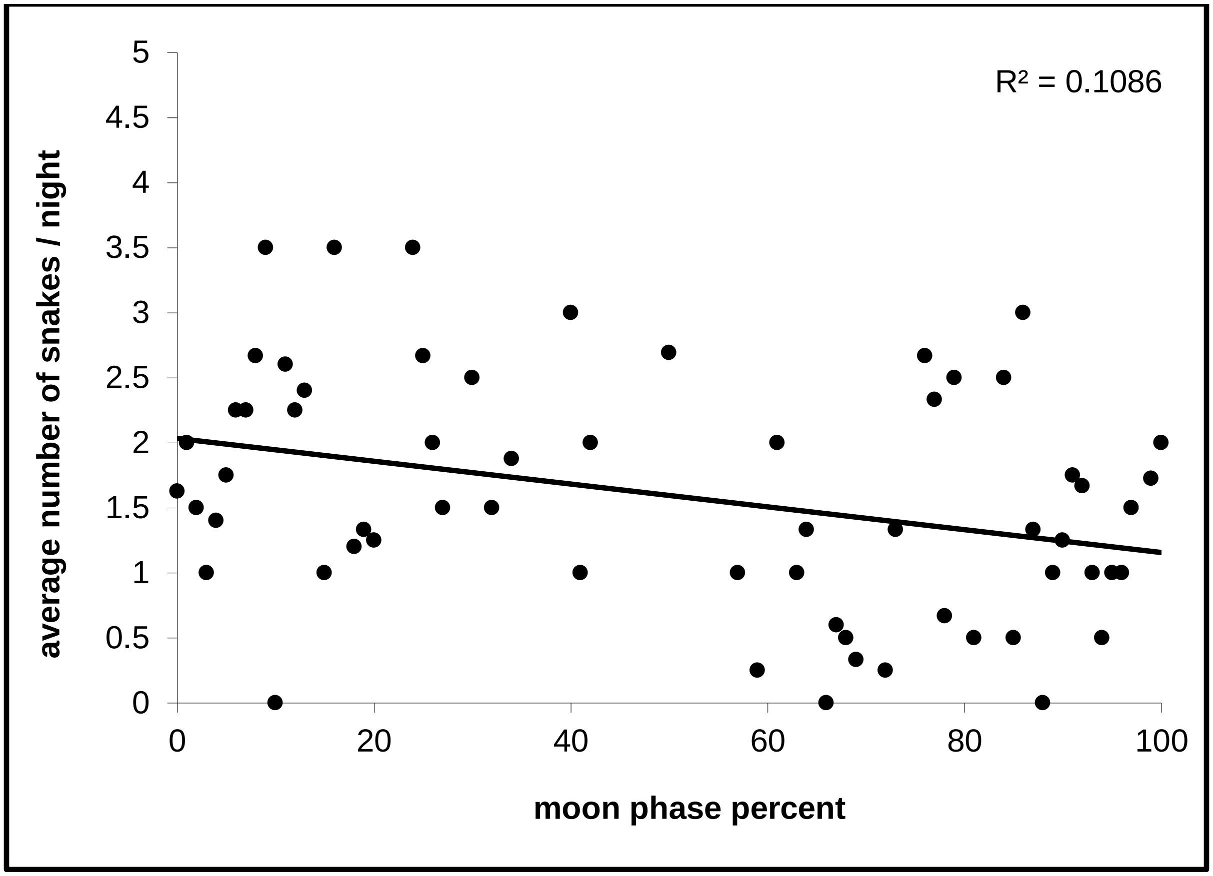

Figure 25. *Sistrurus m. miliarius* found between moonrise and moonset; n =396, p-value = 0.0026.

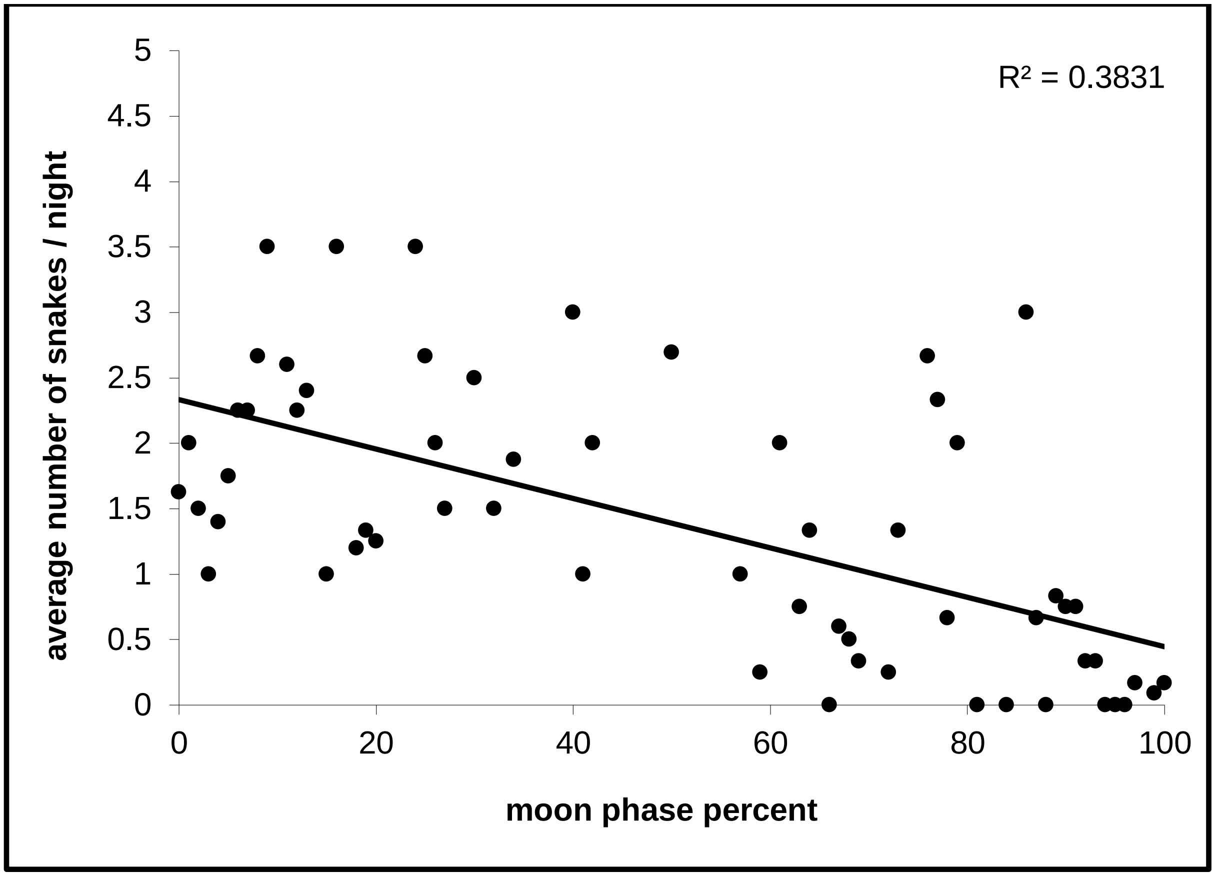

Figure 26. *Sistrurus m. miliarius* found during the light spread; n = 319, p-value < 0.0001.

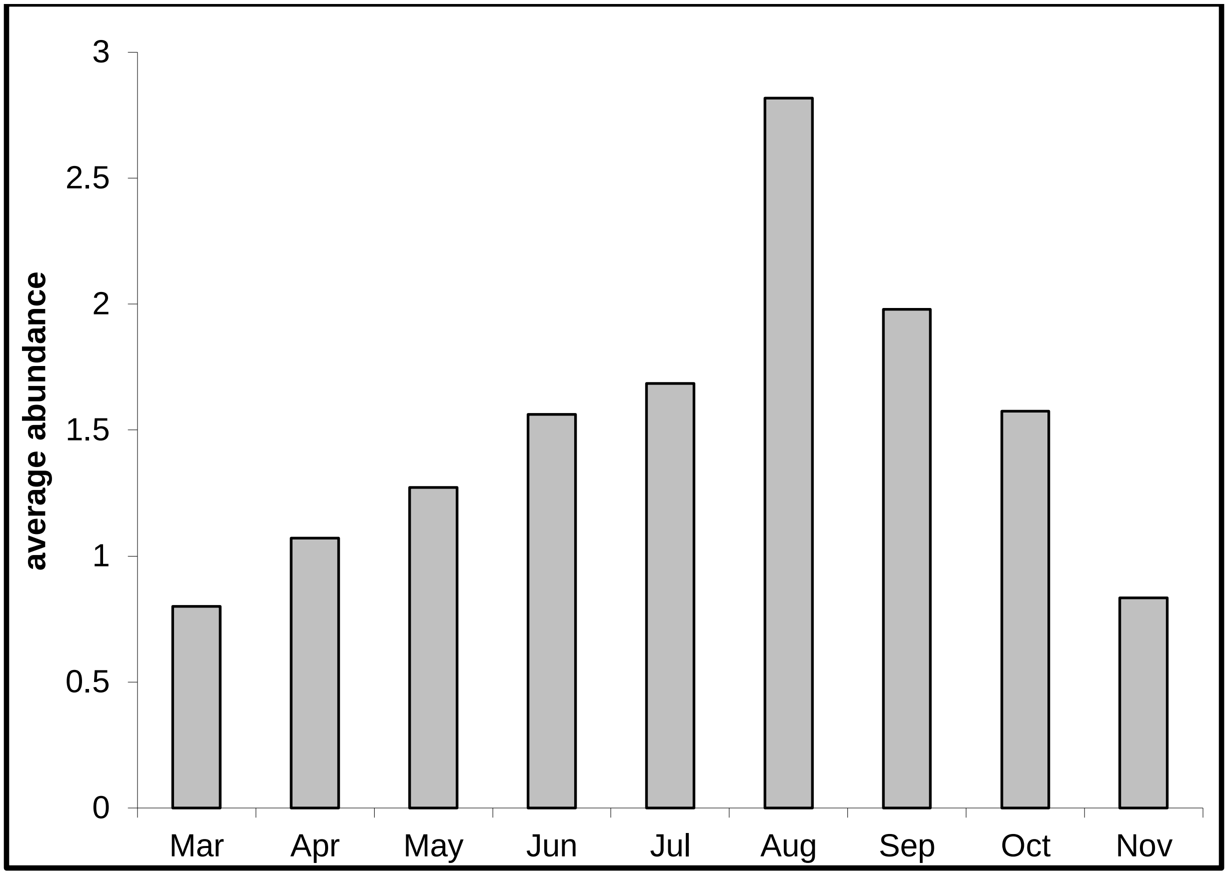

Figure 27. Monthly abundance (snakes/ night) of *Sistrurus m. miliarius* from 2000 to 2008.

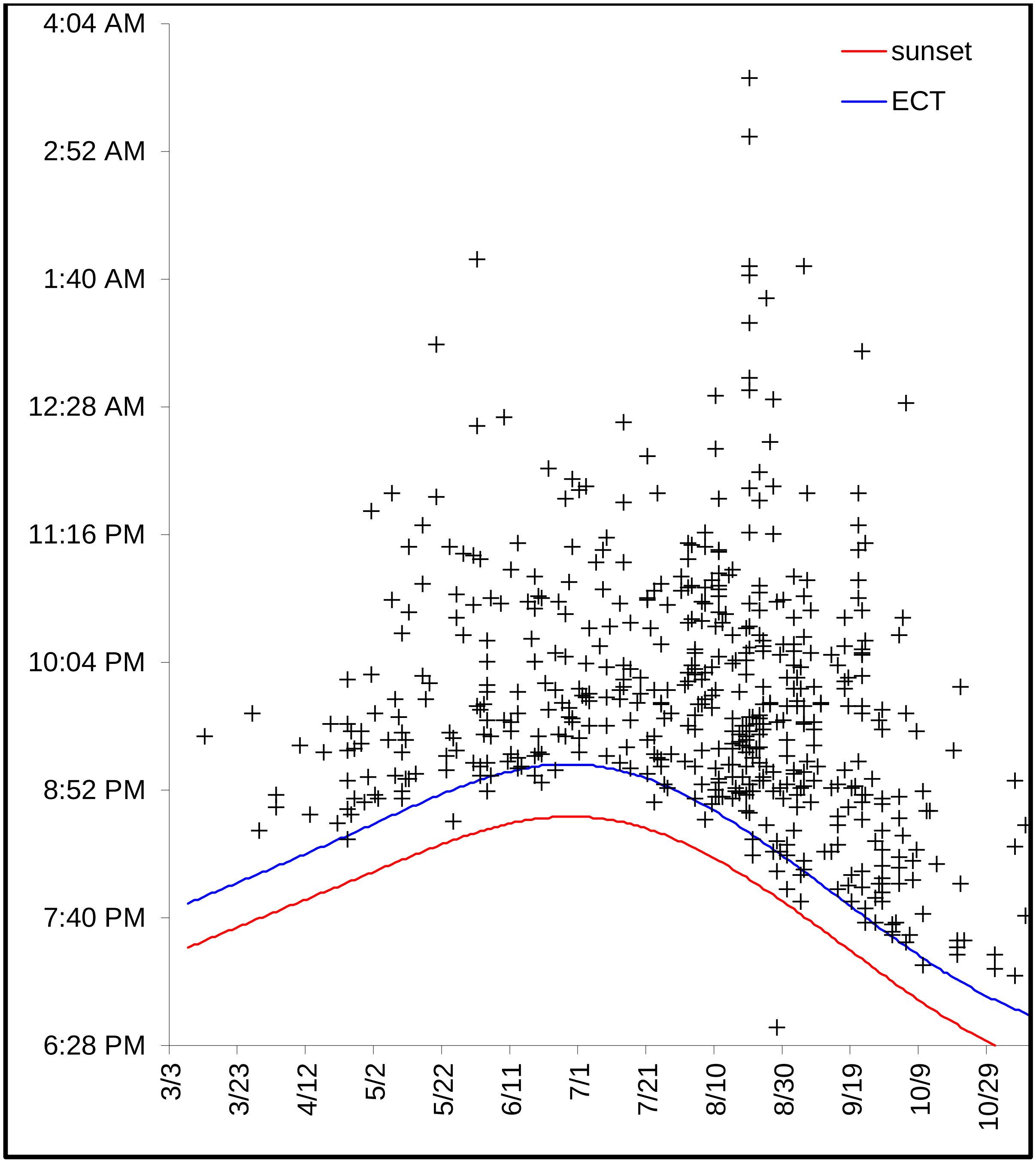

Figure 28. *Sistrurus m. miliarius* found on roads relative to sunset and end of civil twilight times (2000 to 2008; n = 550).

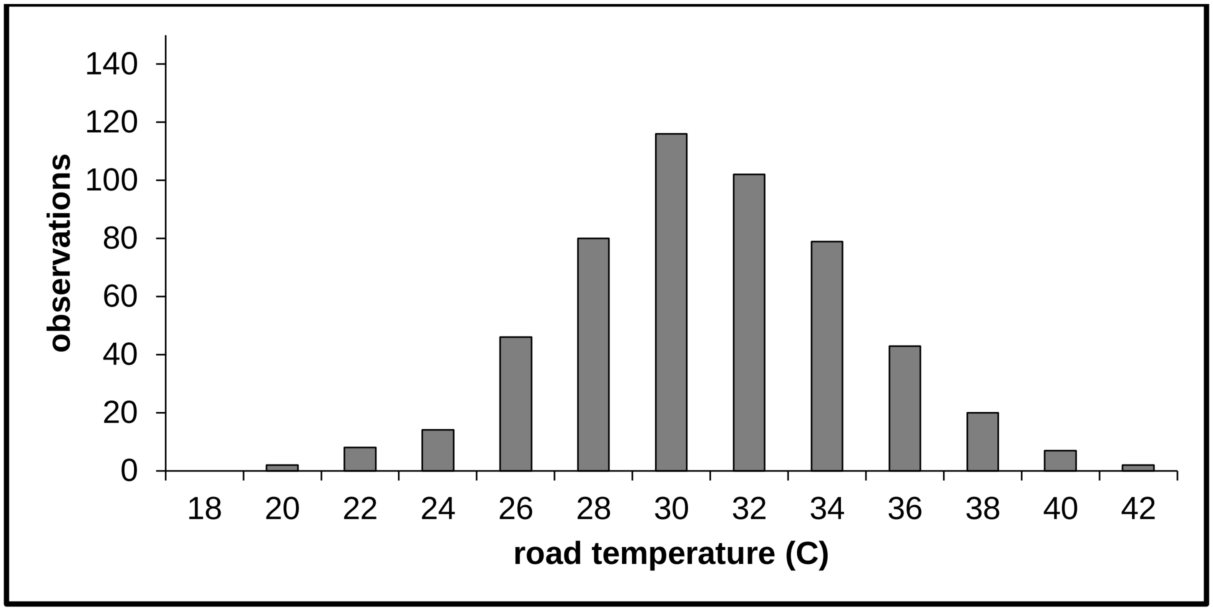

Figure 29. Road temperature observations of nocturnal *Sistrurus m. miliarius* during the sampling period (n = 519).

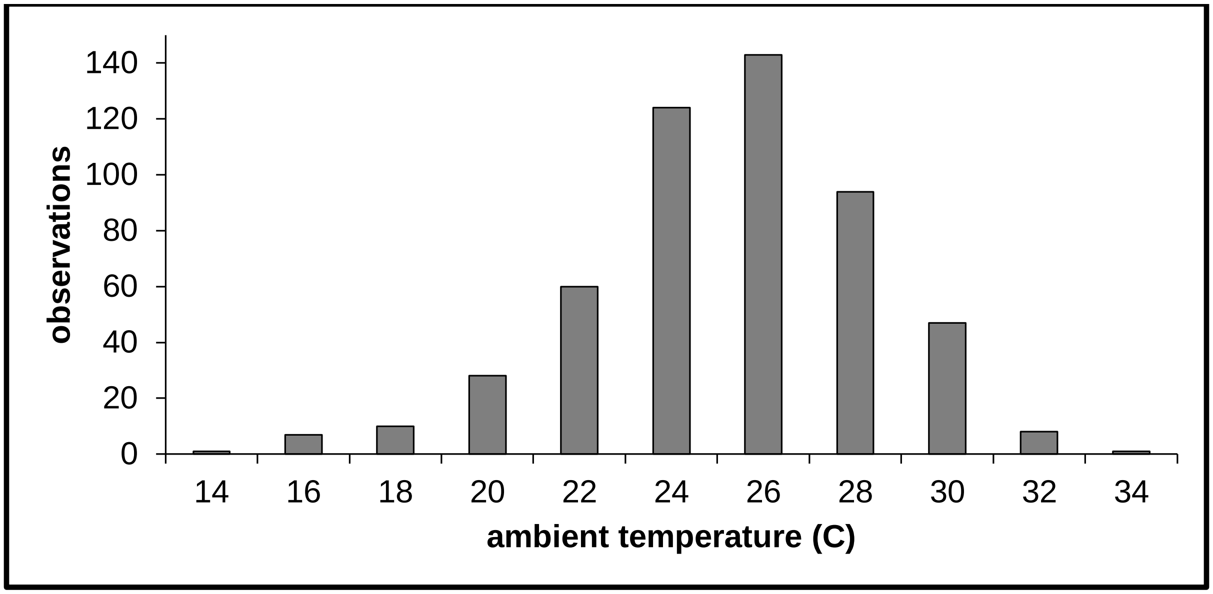

Figure 30. Ambient temperature observations of nocturnal *Sistrurus m. miliarius* during the sampling period (n = 523).

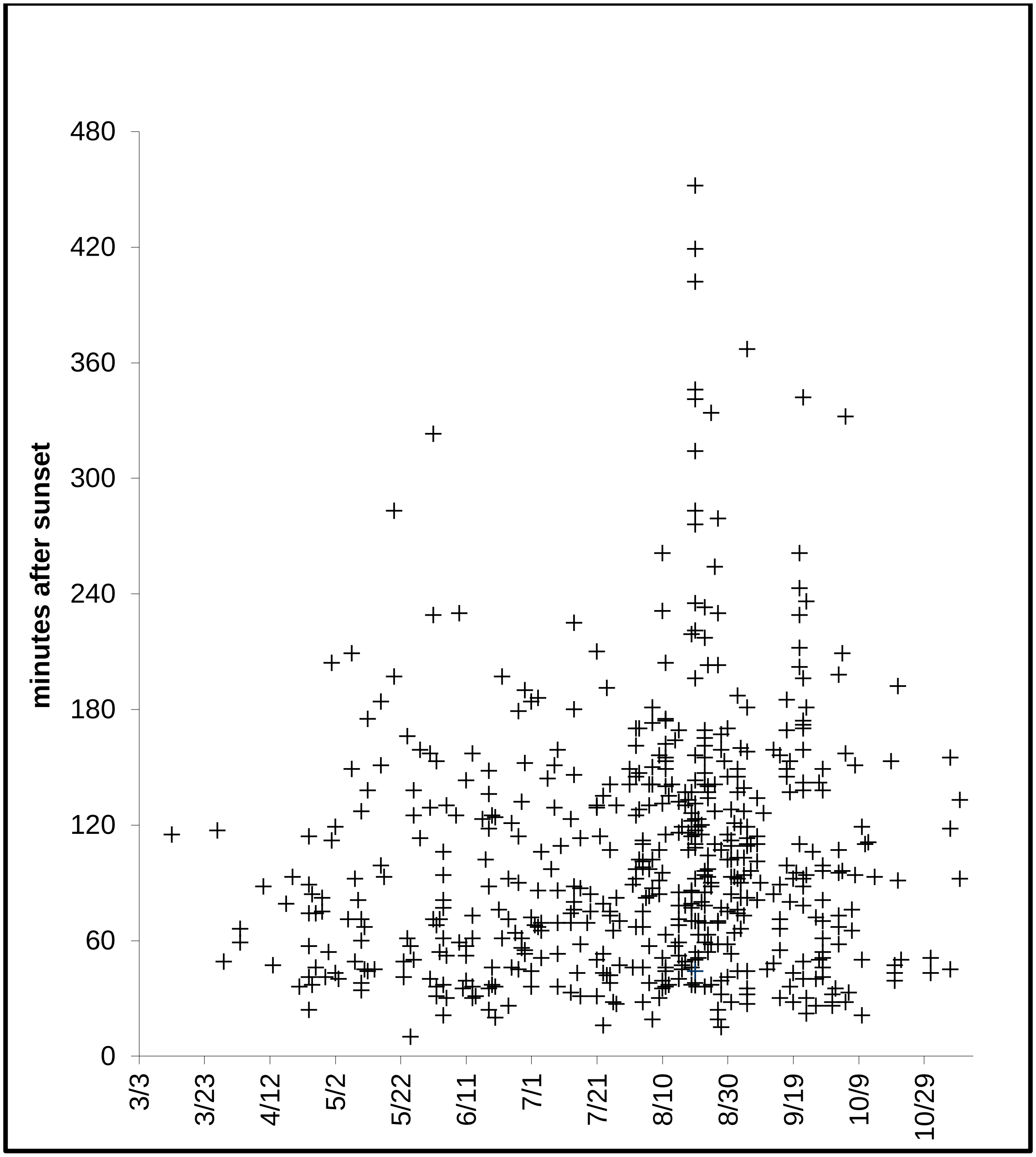

Figure 31. *Sistrurus m. miliarius* activity in relation to sunset (2000 - 2008; N = 550).

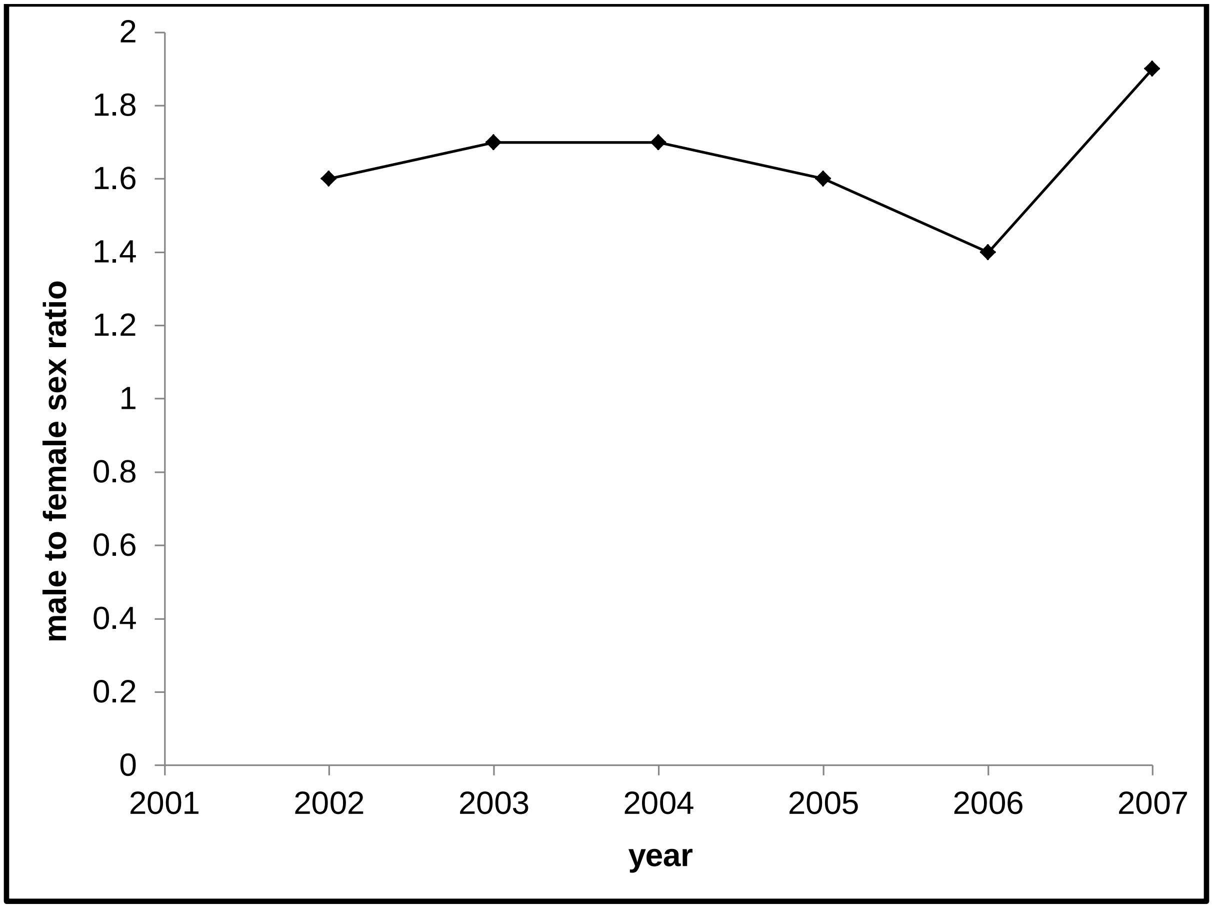

Figure 32. Male to female sex ratios from year to year (males, n = 309; females, n = 189). Excluding 2008 data.

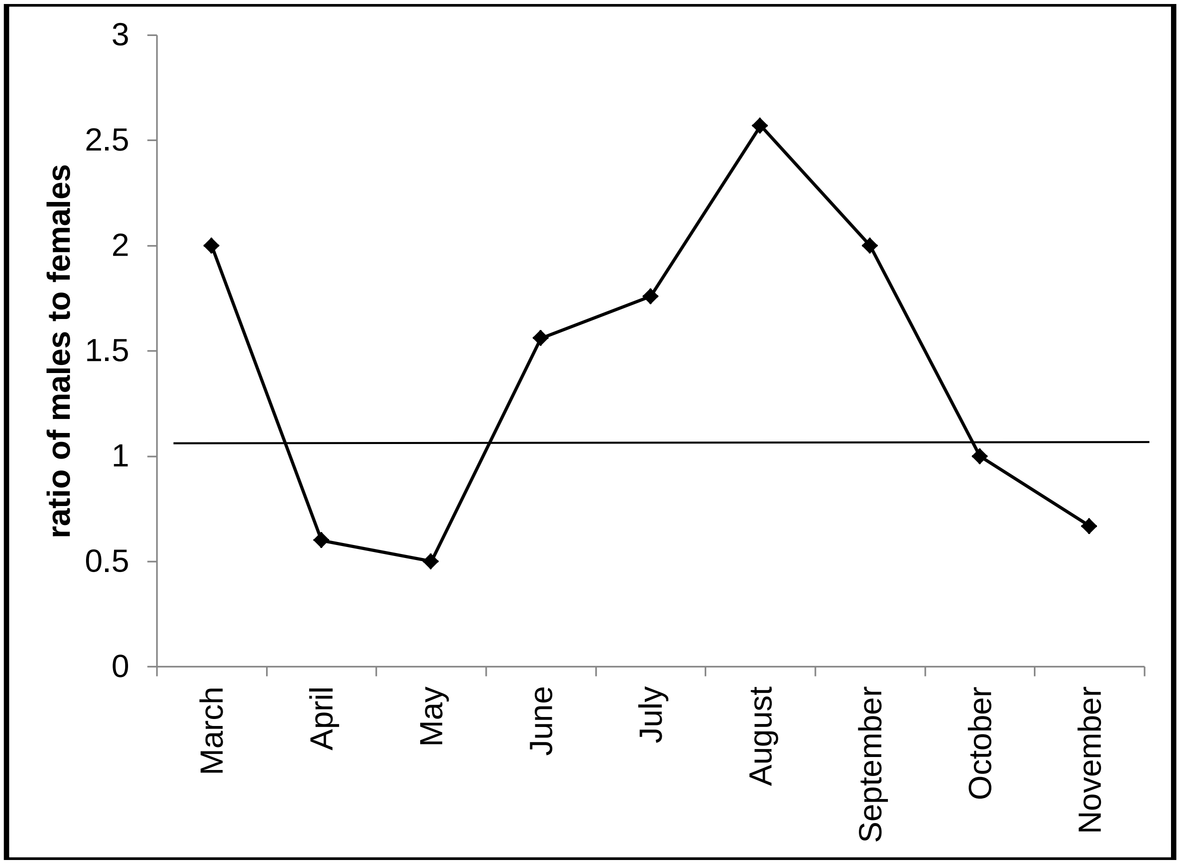

Figure 33. Male to female ratios by month from 2002 to 2008 (males, n = 327; females, n = 194). A ratio of 1:1 equates to equal distribution of the sexes. Above the value of 1 results in males being more common to females. A value below 1 equates to females being more active than males.

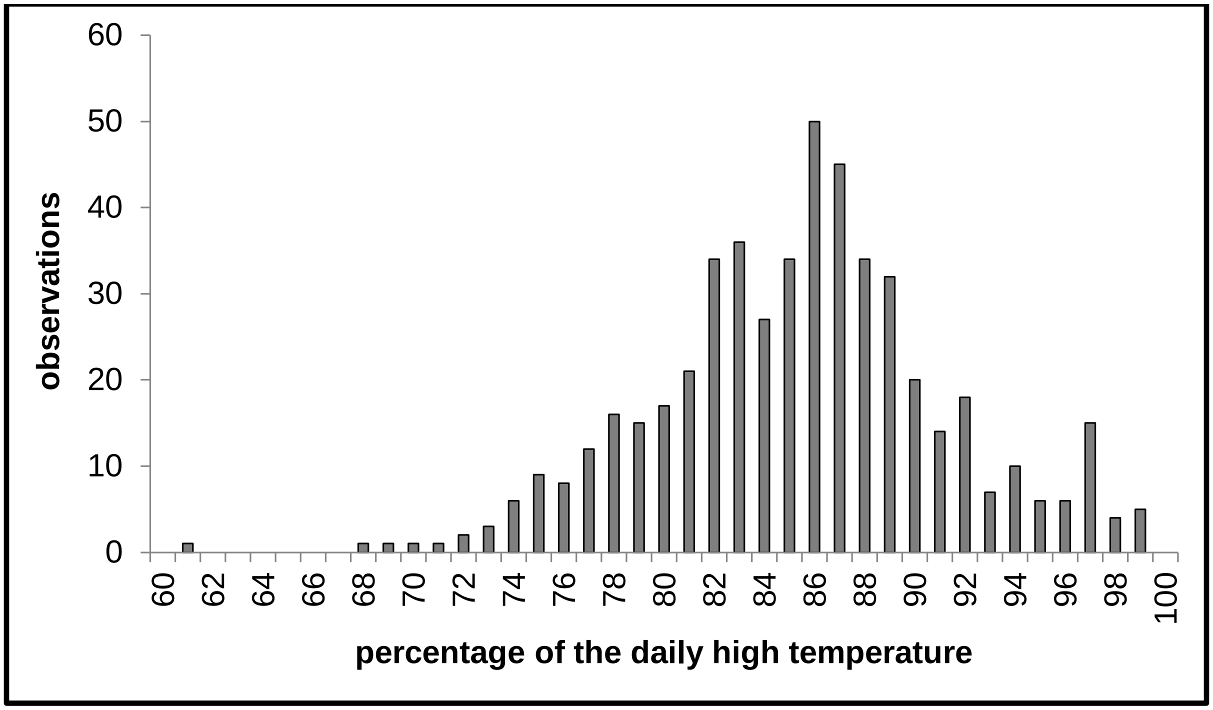

Figure 34. Relative high temperature observations of *Sistrurus m. miliarius* (n = 511). Values were obtained by dividing the ambient temperature at capture by the ambient high temperature of the day.

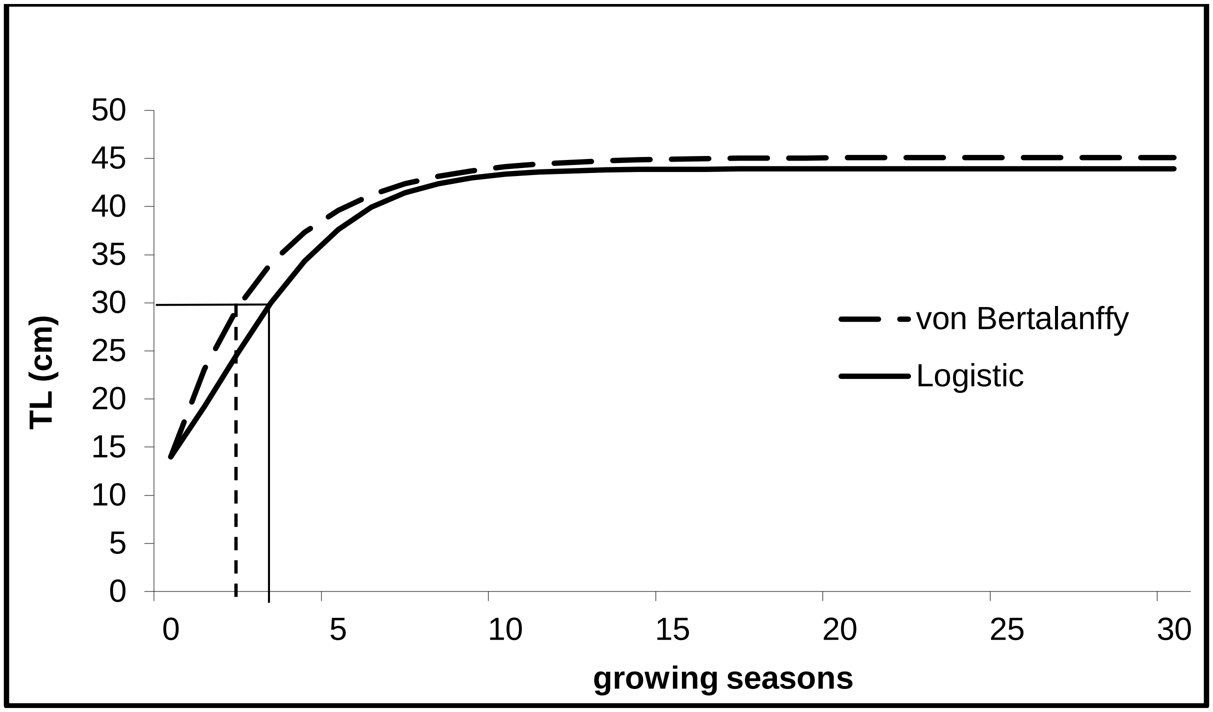

Figure 35. Size and age at maturity for female Carolina Pigmy Rattlesnakes (*Sistrurus m. miliarius*); n = 124.

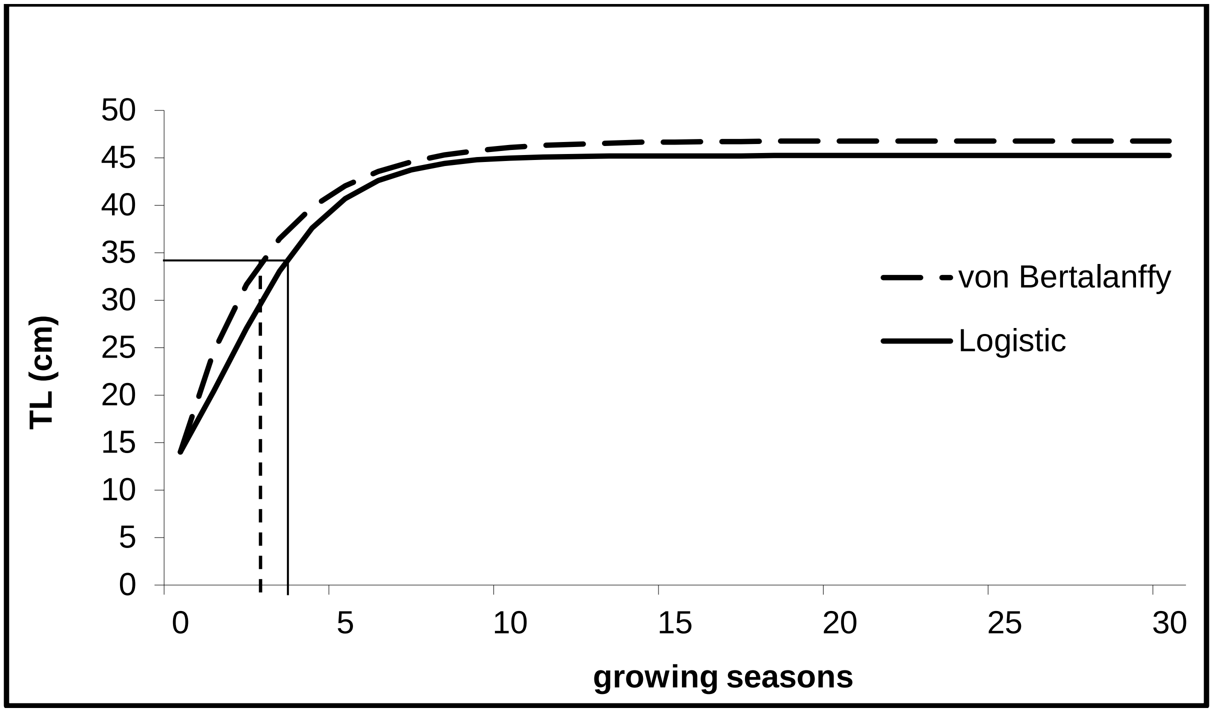

Figure 36. Size and age at maturity for male Carolina Pigmy Rattlesnakes (*Sistrurus m. miliarius*); n = 248.

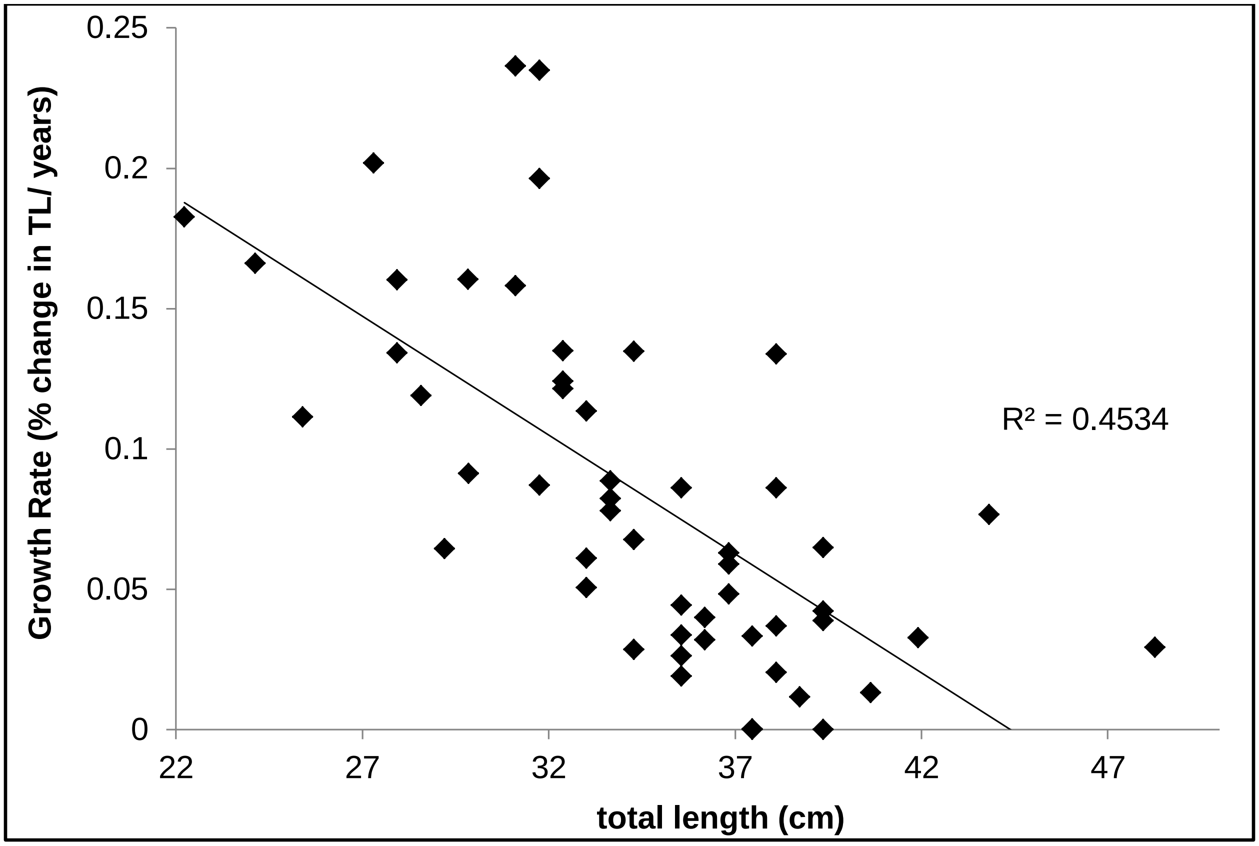

Figure 37. Growth rate plotted against initial Carolina Pigmy Rattlesnake (*Sistrurus m. miliarius*) snouth to vent length (SVL). Growth rates were calculated as the percent change in SVL (cm), divided by the time interval between captures. We used growing season (March-November) days as time intervals to control for inactivity during winter months when it was assumed the snakes did not grow.

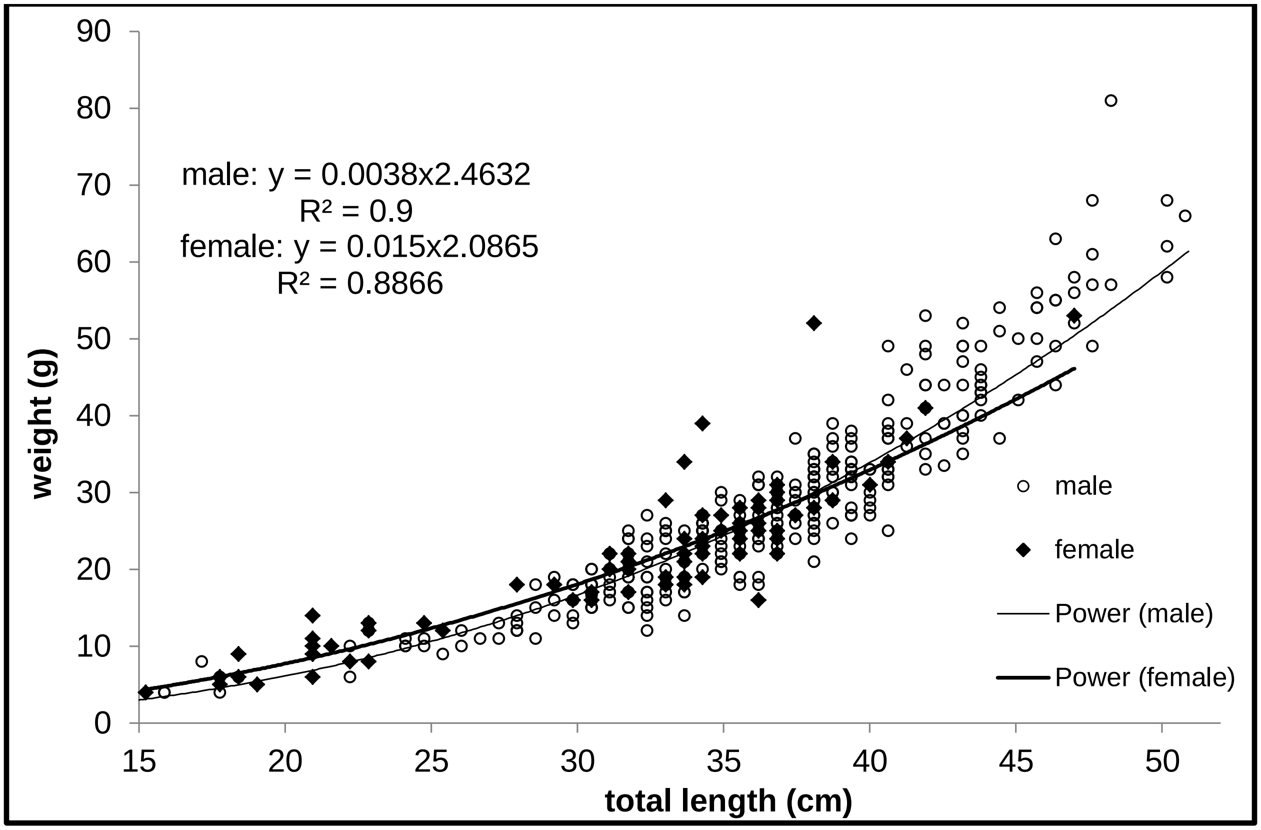

Figure 38. The relationship between total length and body mass in *Sistrurus m. miliarius.* Sample sizes are 378 for males and 78 for non-gravid females. No distinctions were made with regard to recaptured individuals.

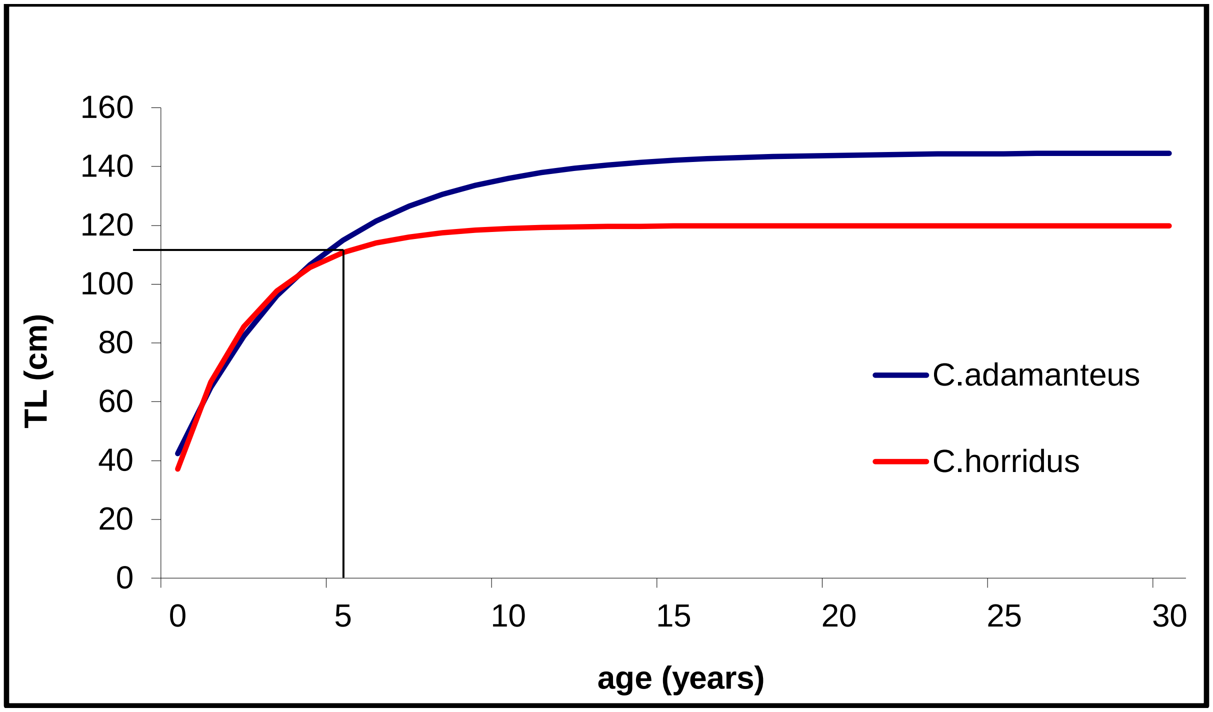

Figure 39. Size and age at maturity for other rattlesnakes using von Bertalanffy: *Crotalus adamanteus* and *C. horridus*. Adopted from Waldron unpublished.

Table 1. Summary of Animals Found

Year	**2000**	**2001**	**2002**	**2003**	**2004**	**2005**	**2006**	**2007**	**2008**
Found	8	11	100	78	104	111	49	76	25
DOR	1	0	1	1	1	0	1	3	0
AOR	7	11	99	77	103	111	48	73	24
Marked	0	0	70	63	76	80	36	59	19
Recaptured	0	0	14	14	26	29	9	14	3

Table 2. County records of *Sistrurus m. miliarius*

COUNTY	**STATE**	**SOURCE**	**NOTES**
Hyde	NC	Palmer et al. 1995	
Beaufort	NC	Palmer et al. 1995	
Craven	NC	Palmer et al. 1995	
Pamlico	NC	Palmer et al. 1995	
Cateret	NC	Palmer et al. 1995	
Onslow	NC	Palmer et al. 1995	
Pender	NC	Palmer et al. 1995	
Brunswick	NC	Palmer et al. 1995	
New Hanover	NC	Palmer et al. 1995	
Sampson	NC	Palmer et al. 1995	
Bladen	NC	Palmer et al. 1995	
Cumberland	NC	Palmer et al. 1995	
Harnett	NC	Palmer et al. 1995	
Hoke	NC	Palmer et al. 1995	
Scotland	NC	Palmer et al. 1995	
Richmond	NC	Palmer et al. 1995	
Pitt	NC	Beane et al. 2010	
Tyrell	NC	Beane et al. 2010	
Moore	NC	Palmer et al. 1995	
Montgomery	NC	Palmer et al. 1995	Last sighting: 1977
Gaston	NC	Palmer et al. 1995	Last sighting: 1984
Cleveland	NC	Palmer et al. 1995	Last sighting: 1967
Chesterfield	SC	Camper 1997	
Darlington	SC		
Kershaw	SC	Chamberlain 1935	
Dorchester	SC	Chamberlain 1935	
Horry	SC	Chamberlain 1935	
Georgetown	SC	Chamberlain 1935	
Charleston	SC	Chamberlain 1935	
Sumpter	SC	NCMS	
Berkeley	SC	Chamberlain 1935	
Orangeburg	SC	Chamberlain 1935	
Richland	SC	Chamberlain 1935	
Lexington	SC	Chamberlain 1935	
Aiken	SC	Hoy et al. 1953	
Cherokee	SC	Gloyd 1940	
Pickens	SC	Gloyd 1940;	Last sighting: 1981
York	SC	Palmer 1971; Brown 1992	
Barnwell	SC	Willson, pers. comm	
McCormick	SC	Putnam, pers. comm.	
Oconee	SC	Platt et al. 1999	
Jasper	SC	Rubio 2010	Intergrade zone
Hampton	SC	Rubio 2010	Intergrade zone

Table 2. County records of *Sistrurus m. miliarius* continued

COUNTY	**STATE**	**SOURCE**	**NOTES**
Stephens	GA	Jensen et al. 2008	
Hart	GA	Jensen et al. 2008	
Elbert	GA	Jensen et al. 2008	
Lincoln	GA	Jensen et al. 2008	
Columbia	GA	Jensen et al. 2008	
Richmond	GA	Jensen et al. 2008	
Jefferson	GA	Jensen et al. 2008	
McDuffie	GA	Jensen et al. 2008	
Warren	GA	Jensen et al. 2008	
Wilkes	GA	Jensen et al. 2008	
Madison	GA	Jensen et al. 2008	
Habersham	GA	Jensen et al. 2008	
Hall	GA	Jensen et al. 2008	
Gilmer	GA	Jensen et al. 2008	
Gordon	GA	Jensen et al. 2008	
Fulton	GA	Jensen et al. 2008	
Douglas	GA	Jensen et al. 2008	
Bibb	GA	Jensen et al. 2008	Intergrade zone
Pulaski	GA	Jensen et al. 2008	Intergrade zone
Muscogee	GA	Jensen et al. 2008	Intergrade zone
Russell	AL	Mount 1975	Intergrade zone
Madison	AL	Mount 1975	
Colbert	AL	Mount 1975	
Franklin	AL	Mount 1975	
Marion	AL	Mount 1975	
Walker	AL	Mount 1975	
Calhoun	AL	Mount 1975	
Cleburne	AL	Mount 1975	
Talladega	AL	Mount 1975	
Clay	AL	Mount 1975	
Tallapoosa	AL	Mount 1975	
Lee	AL	Mount 1975	
Jefferson	AL	Mount 1975	Tri-intergrade zone
Fayette	AL	Mount 1975	Tri-intergrade zone
Tuscaloosa	AL	Mount 1975	Tri-intergrade zone
Bibb	AL	Mount 1975	Tri-intergrade zone
Chilton	AL	Mount 1975	Tri-intergrade zone
Autauga	AL	Mount 1975	Tri-intergrade zone
Clarke	AL	Mount 1975	Tri-intergrade zone

Table 3. Comparison of von Bertalanffy and logistic growth interval models for Carolina Pigmy Rattlesnakes (*Sistrurus m. miliarius*). The models estimated asymptotic TL (*a*) and the growth parameter (*r*), and were compared using the residual error mean square (REMS), where the model that best fit the data had the lowest REMS value. Estimates on age at reproductive maturity were made for females and males based on general von Bertalanffy and logistic growth models of growth intervals (female n = 124, male n = 248). The models estimated age at reproductive maturity (*t*) in number of growing seasons. Ninety-five percent confidence intervals are shown in brackets, and standard errors are shown in parentheses.

Table 3a. Comparison of von Bertalanffy and logistic growth interval models for female Carolina Pigmy Rattlesnakes (*Sistrurus m. miliarius*).

Model	Asymptotic TL (*a*)	Growth parameter (*r*)	REMS	Age at maturity (*t*)
von Bert.	45.09 (4.02) [36.40-53.78]	0.34 (0.17) [-0.02-0.71]	8.28	2.07 (0.07) [1.92-2.22]
logistic	43.92 (2.83) [37.79-50.04]	0.50 (0.18) [0.11-0.90]	8.51	2.98 (0.08) [2.82-3.14]

Table 3b. Comparison of von Bertalanffy and logistic growth interval models for male Carolina Pigmy Rattlesnakes (*Sistrurus m. miliarius*).

Model	Asymptotic TL (*a*)	Growth parameter (*r*)	REMS	Age at maturity (*t*)
von Bert.	46.76 (2.15) [42.38-51.1]	0.38 (0.08) [0.21-0.56]	4.66	2.75 (0.03) [2.67-2.82]
logistic	45.22 (1.49) [42.17-48.26]	0.60 (0.09) [0.40-0.79]	5.07	3.49 (0.03) [3.41-3.56]

Table 4. Reptiles and Amphibians of the Carolina Sandhills National Wildlife Refuge

Species of Reptiles found in the Carolina Sandhills NWR: 49

Snakes

1.	*Agkistrodon c. contortrix*	Southern Copperhead	
2.	*Agkistrodon p. piscivorus*	Eastern Cottonmouth	
3.	*Cemophora coccinea copei*	Northern Scarlet Snake	
4.	*Coluber c. constrictor*	Black Racer	
5.	*Crotalus horridus atricaudatus*	Canebrake Rattlesnake	
6.	*Diadophis p. punctatus*	Southern Ringneck	
7.	*Elaphe [Pantherophis] g. guttata*	Corn Snake	
8.	*Elaphe [Pantherophis] o. obsoleta*	Black Rat Snake	
9.	*Farancia abacura*	Eastern Mud Snake	
10.	*Heterodon platyrhinos*	Eastern Hognose	
11.	*Heterodon simus*	Southern Hognose	*rediscovered in this study
12.	*Lampropeltis calligaster rhombomaculata*	Mole Kingsnake	
13.	*Lampropeltis elapsoides*	Scarlet Kingsnake	
14.	*Lampropeltis g. getula*	Eastern Kingsnake	
15.	*Masticophis [Coluber] f. flagellum*	Eastern Coachwhip	
16.	*Nerodia e. erythrogaster*	Redbelly Water Snake	
17.	*Nerodia f. fasciata*	Banded Water Snake	
18.	*Nerodia sipedon pleuralis*	Midland Water Snake	
19.	*Nerodia taxispilota*	Brown Water Snake	
20.	*Opheodrys aestivus*	Rough Green Snake	
21.	*Pituophis m. melanoleucus*	Northern Pine Snake	
22.	*Regina rigida*	Glossy Crayfish Snake	
23.	*Regina septemvittata*	Queen Snake	*discovered in this study
24.	*Seminatrix pygaea*	Black Swamp Snake	*rediscovered in this study
25.	*Sistrurus m. miliarius*	Carolina Pigmy Rattlesnake	
26.	*Storeria dekayi*	Brown Snake	
27.	*Storeria occipitomaculata*	Redbelly Snake	
28.	*Tantilla coronata*	Southeastern Crowned Snake	
29.	*Thamnophis sauritus*	Eastern Ribbon Snake	*discovered in this study
30.	*Thamnophis sirtalis*	Eastern Garter Snake	
31.	*Virginia striatula*	Rough Earth Snake	
32.	*Virginia valeriae*	Smooth Earth Snake	*discovered in this study

Lizards

1.	*Anolis carolinensis*	Green Anole
2.	*Cnemidophorus [Aspidoscelis] sexlineatus*	Six-lined Racerunner
3.	*Eumeces [Plestiodon] fasciatus*	Five-lined Skink
4.	*Eumeces[Plestiodon] inexpectatus*	Southeastern Five-lined Skink
5.	*Eumeces[Plestiodon] laticeps*	Broadhead Skink
6.	*Ophisaurus ventralis*	Eastern Glass Lizard
7.	*Sceloporus undulatus*	Eastern Fence Lizard
8.	*Scincella lateralis*	Ground Skink

Turtles

1.	*Chelydra serpentina*	Common Snapping Turtle	
2.	*Chrysemys p. picta*	Eastern Painted Turtle	*discovered in this study
3.	*Clemmys guttata*	Spotted Turtle	*rediscovered in this study
4.	*Kinosternon suburubrum*	Eastern Mud Turtle	
5.	*Pseudemys floridana*	Florida Cooter	
6.	*Sternotherus odoratus*	Striped Musk Turtle	
7.	*Terrapene carolina*	Eastern Box Turtle	
8.	*Trachemys scripta*	Yellow-bellied Slider	

Crocodilians

1.	*Alligator mississippiensis*	American Alligator	*likely a nomadic sighting

Species of Amphibians found in the Carolina Sandhills NWR: 32

Anura

1.	*Acris gryllus*	Southern Cricket Frog	
2.	*Bufo [Anaxyrus] quercicus*	Oak Toad *	(not seen since 1975)
3.	*Bufo [Anaxyrus] terrestris*	Southern Toad	
4.	*Bufo [Anaxyrus] fowleri*	Fowler’s Toad	
5.	*Gastrophryne carolinensis*	Eastern Narrowmouth Toad	
6.	*Hyla andersonii*	Pine Barrens Treefrog	*new breeding sites discovered
7.	*Hyla chrysoscelis/ versicolor*	Cope’s Gray/ Eastern Gray Treefrog	
8.	*Hyla cinerea*	Green Treefrog	
9.	*Hyla femoralis*	Pine Woods Treefrog	
10.	*Hyla gratiosa*	Barking Treefrog	
11.	*Hyla squirrela*	Squirrel Treefrog	
12.	*Pseudacris crucifer*	Spring Peeper	
13.	*Pseudacris ocularis*	Little Grass Frog	*discovered in this study
14.	*Pseudacris ornata*	Ornate Chorus Frog	*discovered in this study
15.	*Rana [Lithobates] catesbeiana*	Bullfrog	
16.	*Rana [Lithobates] clamitans*	Bronze Frog	
17.	*Rana [Lithobates] utricularia*	Southern Leopard Frog	
18.	*Rana [Lithobates] virgatipes*	Carpenter Frog	
19.	*Scaphiopus holbrookii*	Eastern Spadefoot	

Caudata

1.	*Amphiuma means*	Two-toed Amphiuma	
2.	*Siren intermedia*	Lesser Siren	
3.	*Ambystoma maculatum*	Spotted Salamander	
4.	*Ambystoma opacum*	Marbled Salamander	*discovered in this study
5.	*Ambystoma tigrinum*	Tiger Salamander	(only one sighting, 1995)
6.	*Desmognathus fuscus*	Northern Dusky Salamander	
7.	*Desmognathus auriculatus*	Southern Dusky Salamander	*discovered in this study
8.	*Eurycea cirrigera*	Southern Two-lined Salamander	
9.	*Necturus punctatus*	Dwarf Waterdog	
10.	*Notophthalmus viridescens*	Red-spotted Newt	
11.	*Plethodon chlorobryonis*	Atlantic Coast Slimy Salamander	
12.	*Pseudotriton montanus*	Eastern Mud Salamander	
13.	*Pseudotriton ruber*	Red Salamander	

Hypothetical Species

(species found very close to refuge boundary)

1.	*Ambystoma mabeei*	Mabee’s Salamander (found south of McBee in 1947)
2.	*Ambystoma talpoideum*	Mole salamander
3.	*Carphophis amoenus*	Eastern Worm Snake
4.	*Crotalus adamanteus*	Eastern Diamondback Rattlesnake
5.	*Deirochelys reticularia*	Chicken Turtle
6.	*Eurycea quadradigitata*	Dwarf salamander
7.	*Eurycea guttolineata*	Three-lined salamander
8.	*Farancia erytrogramma*	Rainbow Snake (sighting 16 mi from refuge)
9.	*Micrurus fulvius*	Coral Snake (within historical range)
10.	*Pseudacris feriarum*	Upland Chorus Frog (few hundred yards from refuge)
11.	*Rana capito*	Carolina Gopher Frog (sighting 11 mi from refuge)
12.	*Rhadinea flavilata*	Pine Woods Snake

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Education/ Degrees

- North Carolina State University, 2001 – 2006
  - Bachelor of Science, Zoology
- Marshall University, 2009 – 2010
  - Master of Science, Biological Sciences (December 2010)

Grants Received

Chicago Herpetological Society 2008:	$450
National Science Foundation 2003: (Grant # DBI-0139572)	$6,400
North Carolina Herpetological Society 2002:	$300
North Carolina Herpetological Society 2003:	$500
North Carolina Herpetological Society 2004:	$300
North Carolina State University, undergraduate award 2002:	$3,000
South Carolina Department of Natural Resources 2002:	$1,000
Marshall University Conference Presentation Grant 2010	$300

Publications

Beane, Jeff, Kevin Messenger, and David Stephan. 2010. A note of new prey ingested by *Heterodon simus*. *Herpetological Review*. (In press)

Messenger, K. 2005. Behaviour of *Lepidodactylus lugubris* on Heron Island, Great Barrier Reef, and a record of *Gehyra dubia* from that island. *Herpetofauna* 35(1): 37-39.

Messenger, Kevin. 2008. *Sistrurus miliarius miliarius* morphology. *Herpetological review*. 39 (4): 473.

Messenger, Kevin. 2010. Ophiophagy account in *Cemophora coccinea copei* from north central SC. *Herpetological review*. (In press)

Murphy, Katie, Kevin Messenger, Nathan Shepard, Jayme Waldron, and Thomas K. Pauley. 2010. Trail Avoidance and Habitat Fragmentation of Plethodontid Salamanders. (In review)

Shepard, Nathan and Kevin Messenger. 2010. *Crotalus adamanteus* from the Lower Keys. *Herpetological Review*. (In review)

YANG, Linsen, Kevin Messenger, and Ming-yao LIAO. 2009. Reptile and amphibian diversity of Shennongjia National Nature Preserve (in Chinese). *Sichuan Journal of Zoology* 2009 28(2).

Yirka, Adrian, Joe Flowers, Mike Martin, Kevin Messenger, and Nathan Shepard. 2008. New distribution of *Tantilla oolitica* in the Florida Keys. *Herpetological review*. (In review)

Research experience

2009 – 2010: Field biologist, field leader; Conducted research on the effects of habitat fragmentation on the federally protected Cheat Mountain Salamander (*Plethodon nettingi*). We used elastomer tags for mark-recapture surveys, fluorescent powder for tracking salamander movement patterns, and coverboard arrays for monitoring population densities and abundance – in cooperation with Dr. Jayme Waldron (University of South Carolina) and Dr. Thomas Pauley (Marshall University). Funded by USDA-Forest Service

2009 – 2010: Field biologist, assistant; obtained genetic samples of *Plethodon nettingi* and *P. cinereus* from various locations in the Monongahela National Forest – in cooperation with the WVDNR

2010: Field biologist, assistant; Captured specimens and obtained tail clippings for genetic work from an isolated population of threatened Smallmouth salamanders (*Ambystoma texanum*), suspected to be a new species – in cooperation with Dr. Zachary Loughman (West Liberty University)

2010: Field biologist, assistant; Captured and preserved 5 species of crayfish in western WV for morphological work – in cooperation with Dr. Zachary Loughman (WLU)

2010: Field biologist, lead; capture of specimens and tail clippings for genetic work from a disjunct population of threatened Streamside salamanders (*Ambystoma barbouri*) – in cooperation with Dr. Jessica Wooten (Findlay University)

2010: Field biologist, assistant; assisted in urban herpetology thesis project – Potential of Urban Habitats as Reptile and Amphibian Refuges in West Virginia – in cooperation with Scott Jones.

2010: Field biologist, assistant; assisted in thesis involving collection of specimens and excision of reproductively active salamander testes

2009: Field biologist, assistant; captured and measured southern black racers (*Coluber constrictor*) and eastern coachwhips (*Masticophis flagellum*) – in cooperation with David Steen (PhD candidate; Auburn University)

2009: Field biologist, assistant; capture of specimens of a suspected new species of *Desmognathus* – in cooperation with Dr. Jessica Wooten (Findlay University)

2009: Field researcher, assistant; mark-recapture thesis on the eastern hellbender Long term Growth and Monitoring of the Eastern Hellbender (*Cryptobranchus a. alleghenensis*) in Eastern West Virginia – in cooperation with Douglas Horcher.

2009: Field researcher, assistant; mark-recapture thesis involving snakes along fragmented corridors (ski slopes and roadways) – Effect of Snake Populations on Salamanders as a Result of Forest Fragmentation – in cooperation with Casey Bradshaw.

2009: Field researcher, assistant; thesis study involving fluorescent powder tracking of Green Salamanders – Movement Patterns and Artificial Arboreal Cover Use of Green Salamanders (*Aneides aeneus*) in Kanawha County, West Virginia – in cooperation with Sarah Miloski.

2000 – 2008: Field researcher, PI; long term mark-recapture study of snakes on a National Wildlife Refuge in SC. Employed coverboard arrays, road cruising, and active searching for mark-recapture study. Used PIT tags and cautery marking for individual identification. Developed growth models for Carolina Pigmy Rattlesnakes for my Master's Thesis, as well as population estimates, and activity patterns based on several different factors, both biotic and abiotic. Documented 3 new snake species (not including the re-discovery of 2 species not seen for 30+ years), 1 new turtle species, 2 new frog species, and 2 new salamander species (a transient alligator was also observed in 2004 but never since).

2007: Field biologist, assistant; capture and extraction of blood and venom from pigmy rattlesnakes (*Sistrurus miliarius*) – in cooperation with Dr. Lisle Gibbs (Ohio State University)

2007 – 2010: Field biologist, assistant; mark-recapture and abundance survey of eastern diamondback rattlesnakes (*Crotalus adamanteus*) on Marine Corps Recruit Depot, Parris Island, SC – in cooperation with Dr. Jayme Waldron (USC)

2006 – 2009: Field biologist, assistant; Project Simus – surveyed NC gamelands for the threatened southern hognose snake (*Heterodon simus*) – in cooperation with Jeff Beane and Alvin Braswell (North Carolina Museum of Natural Sciences)

2006 – 2008: Field biologist, PI; herpetofauna survey of Shennongjia Nature Reserve in Hubei Province, China. Catalog species within the reserve, several rare and several new species found to the province; 42 species found total. Job required learning Mandarin Chinese. In cooperation with Dr. Li Yiming and the Chinese Academy of Sciences, Beijing.

2005 – 2009: Field biologist, assistant; assisted in capture of invasive Burmese pythons (*Python molurus*) in the Everglades National Park – in cooperation with the National Park Service and the USGS

2005 – 2010: Field biologist, assistant; mark-recapture and radiotelemetry study of eastern diamondback rattlesnakes (*Crotalus adamanteus*) and canebrake rattlesnakes (*Crotalus horridus*) at the James W. Webb Center, SC – in cooperation with Dr. Jayme Waldron (USC) and SCDNR

2005: Field biologist, assistant; mark-recapture study, using photographs, of the threatened eastern tiger salamander (*Ambystoma tigrinum*) – in cooperation with Dr. Nick Haddad (North Carolina State University)

2003 – 2004: Field biologist, assistant; radiotelemetry study of northern pine snakes (*Pituophis m. melanoleucus*) in the NC gamelands – in cooperation with Dave Woodward (NCSU)

2003 – 2004: Field biologist, assistant; Savannah River Ecology Lab; assisted with herpetofauna survey of Kings Mountain National Military Park, SC. Photographic vouchers. Listened for frog calls at various times of the year – in cooperation with Dr. Robert Reed (University of Georgia)

2001: Field biologist, PI: mark-recapture study of the Mourning Gecko (*Lepidodactylus lugubris*) on Heron Island, Great Barrier Reef.

Present and Past Scientific Affiliations:

Association of Southeastern Biologists
Chicago Herpetological Society
Kansas Herpetological Society
North Carolina Herpetological Society
Society for the Study of Amphibians and Reptiles

Conference Presentations

First Annual South Carolina Herpetological Conference (2004)
- Biodiversity and Movement Patterns of Snakes from the Carolina Sandhills National Wildlife Refuge (oral presentation)

70th Association of Southeastern Biologists Conference (2009)
- Growth and Age at Reproductive Maturity of the Carolina Pigmy Rattlesnake (*Sistrurus m. miliarius*) (oral presentation)

71st Association of Southeastern Biologists Conference (2010)
- The Effects of Moon phase on Nocturnal Snake Activity (oral presentation)
- Growth and Age at Reproductive Maturity of the Carolina Pigmy Rattlesnake (poster presentation)

26th North Carolina Herpetological Society fall meeting (2004)
- Biodiversity and Movement Patterns of Snakes from the Carolina Sandhills National Wildlife Refuge (oral presentation)

42nd Chicago Herpetological Society spring meeting (2008)
- Herpetofauna of the Shennongjia National Nature Reserve, Hubei Province, China (oral presentation)

32nd North Carolina Herpetological Society fall meeting (2010)
- Snakes and Roads: Final report from a movement study in the Carolina Sandhills NWR (oral presentation)

Course work:

- Herpetology
- Ornithology
- Entomology
- Coral reef ecology (in Australia)
- Desert ecology
- Anatomy and histology
- Biological clocks and rhythms
- Amphibian conservation
- Geographical Information Systems
- Conservation Biology/ Policy
- Bio Statistics
- Organic chemistry
- Darwin and the Galapagos Islands (in Ecuador)
- Animal behavior
- Evolution and ecology
- Animal diversity
- Botany
- Organic Chemistry I & II
- Inorganic Chemistry I & II

Teaching Experience (teaching assistantships 2009 – 2010, Marshall University)

- Herpetology (lab and lecture)
- Human anatomy
- Human biology
- Introductory biology II

Jobs

Veterinary Specialty Hospital, emergency technician:	2007 to 2009
Carolina Veterinary Specialists, emergency technician:	2000 to 2007
Emergency Veterinary Clinic, technician assistant:	1997 to 2000
Instructor for Herpetology Merit Badge	1997 to 2002
Assistant Scout Master, Troop 144:	2000 to 2002
Reptile and Amphibian Day, Raleigh: Volunteer	2003
Reptile and Amphibian Day, Charlotte: Volunteer	2001 to 2002
BugFest: Volunteer	2007 – 2008

Other

Eagle Scout (Nov 2000; Eagle project involved constructing 10 sea turtle rescue/ transport boxes)

Founder, and first President of the Herpetology Club at North Carolina State University (2004 - 2006)

Conversant in Mandarin Chinese and Spanish

Published writer in three newsletter articles:

- North Carolina Herpetological Society, January 2004
- North Carolina Herpetological Society, April 2004
- North Carolina Herpetological Society, July 2004

Published photographer in 6 books and 4 magazines:

- A Guide to the Rattlesnakes of the United States. Hubbs, Brian and Brendan O'Conner. 2009. Tricolor Books. (3 images)
- The Encyclopedia of Snake Species: A Taxonomy of the Suborder *Ophidea*. Deben, Delhay. 2010. Herpetology Press. (19 images)
- Golden Monkeys in Shennongjia National Nature Preserve (in Chinese). Gu. 2008. (11 images)
- Snakes Alive: Copperheads. Colleen Sexton. 2010. Bellwether Media. (1 image)
- Snakes Alive: Cottonmouths. Colleen Sexton. 2010. Bellwether Media. (1 image)
- Snakes Alive: Rat Snakes. Colleen Sexton. 2010. Bellwether Media. (cover and 4 interior images).
- *North Carolina Wildlife* magazine, August 2008 (4 images)
- *Tactical Knives* magazine, Feb 2009 (1 image)
- *Tactical Knives* magazine, Sep 2009 (1 image)
- *Charleston* magazine, Dec 2009 (1 image)

References

Dr. Harold Heatwole, North Carolina State University	harold_heatwole@ncsu.edu
Dr. Thomas Pauley, Marshall University	pauley@marshall.edu
Dr. Jayme Waldron, University of South Carolina	ditmadden@hotmail.com
Dr. Robert Reed, United States Geological Survey	reedr@usgs.gov
Dr. Shane Welch, University of South Carolina	shanemwelch@gmail.com