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Ecology of the Rock Rattlesnake, Crotalus lepidus, in the Northern Chihuahuan Desert

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ECOLOGY OF THE ROCK RATTLESNAKE, *CROTALUS LEPIDUS*, IN THE NORTHERN CHIHUAHUAN DESERT

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Dedication

To my wife Sona and my son Amir.

ECOLOGY OF THE ROCK RATTLESNAKE, *CROTALUS LEPIDUS*, IN THE NORTHERN CHIHUAHUAN DESERT

By

VICENTE MATA-SILVA, M.S.

DISSERTATION

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Radiotracking rattlesnakes is not an easy task, primarily because it requires a relatively long time to acquire the information and therefore, cannot be easily undertaken exclusively by one individual. Because the process is composed of several stages, I gained the assistance of numerous people who kindly participated in some way to make this project come to fruition. I am extremely grateful to all of them.

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Abstract

The Rock Rattlesnake, *Crotalus lepidus* is a small species that is found from southern Arizona, southern New Mexico, and southern Texas, in the U.S., into northern Mexico. To date, little is known about the ecology of this species. Ecological information is becoming desperately needed for supporting the conservation and protection of species living in fragile environments such as the Chihuahuan Desert amid current local and global threats (e.g., habitat destruction and modification, urban development, and climate change). Although rattlesnakes spend a significant amount of time underground while overwintering, little is known about the physiology and behavior of these organisms during winter, and the same applies to the Rock Rattlesnake, *Crotalus lepidus*. The goal of this study was to investigate home range, movement patterns, habitats and microhabitats, and overwintering characteristics of the Rock Rattlesnake, *C. lepidus*, in an arid Chihuahuan Desert landscape on the Indio Mountains Research Station (IMRS), located in Hudspeth County, in far west Texas. From summers 2007-2010, 12 adult rattlesnakes were captured and monitored during the winter season (November-March), and from those, eight (two females and six males) were radiotracked during the active period (April-October). Average home range for all individuals was (13.69 ± 3.06 ha). Rattlesnakes leave their winter shelters primarily in early April and returned to shelters in early November. Average home range was 7.29 ± 0.89 ha (n = 2) for females and 15.82 ± 3.71 ha (n = 6) for males. The 50% kernel for all individuals averaged 2.83 ha, and varied from 1.6 to 6.1 ha. However, the average kernel area was smaller for females than for males (1.5 ± 0.10 ha and 3.26 ± 0.75 ha, respectively). Daily movement of all rattlesnakes averaged 8.46 ± 1.45 m/d, and individual daily mean movement ranged from 3.6 to 15.8 m/d. By month, rattlesnakes showed the highest average movement rates in September, followed by June, July and August. Conversely, snakes showed the average lowest

movement rates in April, followed by May, and October. Monthly movement rates were not statistically significant. Movement rate increased during the monsoon months, however; the relationship between movement and precipitation was not statistically significant.

Crotalus lepidus was observed in five habitats on IMRS, with arroyo habitat being the most frequented (407, 55%), followed by alluvial rocky slopes (128, 17%), rocky slopes (110, 15%), and alluvial slopes (77, 10%). Alluvial flats (18, 3%) had by far the lowest number of observations. Rattlesnakes were observed in 13 identified microhabitats, mostly from "under shrubs" (43%), followed by "under rocks" (19%). Most microhabitats utilized by *C. lepidus* recorded in a square meter at observation site were characterized by the regular presence of vegetation as the main ground cover component (% average = 54.8 ± 1.157 %), followed by rock, gravel and plant litter (19.9 ± 1.092, 12.0 ± 0.695, and 8.7 ± 0.568 %, respectively). A comparison of selected sites (n = 263) with random sites (n = 263) indicated that Rock Rattlesnakes in the study area preferred microhabitats with specific characteristics. Miscellaneous comments on rain harvesting, reproductive behavior, and predation are also discussed with respect to activities observed within the home ranges of *C. lepidus.*

Rattlesnakes overwintered at single sites from early November until late-March or early-April. Mean ingress date was 8 November during all winters. There was no significant difference between ingress dates for winters 2007-2008 and 2009-2010. Mean egress date was 31 March during all winters. There was no significant difference between egress date for winters 2007-2008 and 2009-2010. Overwintering period for all rattlesnakes had a mean of 143 days, ranging from 134 to 170 days. There was no significant difference in number of days spent overwintering between winter seasons 2007-2008 and 2009-2010. Average overwintering days for females (n = 2) was 140 days and 145 days for males (n = 10).

TABLE OF CONTENTS

LIST OF TABLES

CHAPTER I

CHAPTER II

List of Figures

Chapter I

CHAPTER II

General Introduction

... in wildness is the preservation of the world

Henry David Thoreau

Walking (1862)

As technology keeps advancing, it also produces a variety of methods that researchers can use for studying animals in the wild. These technologies have also been enthusiastically received by field herpetologists for studying secretive species, such as rattlesnakes. One such technological advance was using radiotelemetry to follow individual snakes within their home ranges and for deciphering ecological requirements and constraints. Initially, radiotelemetry had been applied on rattlesnakes with relatively large size (see review in Reinert, 1992); the primary reason for using only large snakes was due to technological limitations of transmitters being too big for many species of rattlesnakes. As time passed, radio receivers and transmitters became more efficient and especially smaller, enabling them to be inserted into smaller rattlesnakes, such as the Rock Rattlesnake (*Crotalus lepidus*).

Studies that have applied radiotelemetry on rattlesnakes have yielded a great amount of information revealing important insights on ecological requirements of rattlesnakes in their natural habitats (e.g., Cardwell, 2008; Goode et al., 2008; Degregorio et al., 2011; Wastell and Mackessy, 2011). Furthermore, this information has been critical in the developing programs aimed at protecting and conserving populations of rattlesnakes, along with their sometimes fragile environments already threatened by local pressures, like habitat reduction and total destruction driven by agriculture and urban development (Green, 1997; Sealy, 2002; Nowak et

al., 2002), which seems to be the case in the El Paso region. Additionally, changes and present ecological conditions may be exacerbated by global pressures, including global climate change.

The present dissertation focused on the ecology of the Rock Rattlesnake, *C. lepidus* occurring on Indio Mountains Research Station (IMRS), which is located in the northern Chihuahuan Desert of the Trans-Pecos region of far west Texas in Hudspeth County. IMRS is a 16,187 hectare facility controlled by The University of Texas at El Paso (Johnson, 2000; Worthington et al. 2004; available at www.utep.edu/indio/) that provides relatively pristine landscapes for observing and conducting experiments on wild species, like Rock Rattlesnakes. Even though this diminutive species has a significantly large distribution in the southwestern U.S. and Mexico, there is little information about its ecology. To date, no published studies on home ranges of this species have been reported, and movement dynamics have only been investigated in the Big Bend region of Texas (Beaupre, 1995a,b) and Peloncillo Mountains of New Mexico (Smith et al., 2001). The study presented herein used radiotelemetry as the principal technique for observing and gathering data on Rock Rattlesnakes on IMRS during the years 2007 through 2010, and discusses ecological aspects such as home range, movement rate, habitat and microhabitat, and overwintering characteristics of the Rock Rattlesnake. The primary advantages of radiotelemetry in ecological studies relates to the ability of having constant surveillance on the rattlesnakes involved, so there are few issues associated with locating samples at any time.

The present study is divided in two main chapters. Each chapter will contain an abstract, and sections on introduction, materials and methods, results, discussion, and, literature citations. All sections follow the style presented in the Journal of Herpetology. Chapter I discusses ecological aspects of the Rock Rattlesnake, such as home range, movement rate, and habitat and

microhabitat utilization during the warmer “summer” periods of April through October. Chapter II investigated ecological and behavioral aspects of this species during the colder “winter” periods of November through March, the time period that is normally thought of as a period of dormancy (hibernation). I found it interesting that relatively few in depth studies (Hirth, 1966; Jacob and Painter, 1980; Brown, 1982; Sexton et al., 1992; Klauber, 1997; Cobb and Peterson, 2008; Hamilton and Nowak, 2009) concerning winter ecology of rattlesnakes have been attempted. Possible explanations based on my experience include a combination of : 1) radiotracking rattlesnakes during winter period is not as exciting, because they are seldom observed during that time; 2) they only stay in one place, so the lack of movement can lead to disinterest; and 3) adverse weather conditions restricts or discourages investigators from visiting sites. However, as will be presented in Chapter II, overcoming those distractions lead to interesting and novel observations.

During the early stages of this project, the main goal was to focus on the home range and movement rate of *C. lepidus* on IMRS. Unfortunately, during the entire study period, I was able to capture and process only 12 adult rattlesnakes with the appropriate size for radiotracking. From those 12 rattlesnakes, I obtained only two females. Moreover, four males were lost to unknown predators at different stages of the radiotracking process, so consequently data from only eight individuals were used for home range analysis. Field studies of this sort are by their own predisposition determined by extrinsic factors that cannot be controlled by researchers (Reinert, 1992). Fluctuations in weather patterns on a seasonal and longer term can influence ecological dynamics of many if not most species (Green, 1997). Deviation in trophic level interactions brought on by drought, extreme precipitation, abnormal high and low temperatures, and even unexplained variances can affect population size, activity periods, reproductive timing,

among others (Beaupre, 1995a,b; Goode et al., 2008). Still, the 12 Rock Rattlesnakes tracked during this study produced a plethora of information related to their ecological and behavioral stricture. This is especially relevant because very little is known about the spatial dynamics of this species. The information conveys an important protocol and a baseline data set that can be used to help establish the designs of future studies for long-term monitoring on IMRS and other sites, and will also aid conservation-oriented individuals and organizations with determining ecological conditions needed to preserve settings needed for ecosystem viability.

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CHAPTER I

Home Range, Movement, and Habitat of *Crotalus lepidus* on Indio Mountains Research Station, Hudspeth County, Texas

ABSTRACT. - *Crotalus lepidus* is a small species of rattlesnake found in wide assortment of habitats in a geographical range that extends from southern Arizona, southern New Mexico, and southern Texas, in the U.S., into northern Mexico. Ironically, even though it has a significant geographic distribution, little is known about the ecology of this species. Ecological information is becoming desperately needed for supporting the conservation and protection of species living in fragile environments such as the Chihuahuan Desert amid current local and global threats (e.g., habitat destruction and modification, urban development, and climate change). The goal of this study was to investigate home range characteristics, movement patterns, and habitats and microhabitats of the Rock Rattlesnake, *C. lepidus*, in an arid Chihuahuan Desert landscape on the Indio Mountains Research Station (IMRS), located in Hudspeth County, in far west Texas. From summers 2007-2010, 12 adult rattlesnakes were captured and from those, eight (two females and four males) were radiotracked on IMRS nearly every weekend during the active period (April-October) in Chihuahuan Desert scrub habitats. Average home range for all individuals was (13.69 ± 3.06 ha). Rattlesnakes leave their winter shelters primarily in early April and returned to shelters in early November. Average home range was 7.29 ± 0.89 ha (n = 2) for females and 15.82 ± 3.71 ha (n = 6) for males. The 50% kernel for all individuals averaged 2.83 ha, and varied from 1.6 to 6.1 ha. However, the average kernel area was smaller for females than for

males (1.5 ± 0.10 ha and 3.26 ± 0.75 ha, respectively). Daily movement of all rattlesnakes averaged 8.46 ± 1.45 m/d, and individual daily mean movement ranged from 3.6 to 15.8 m/d. By month, rattlesnakes showed the highest average movement rates in September, followed by June, July and August. Conversely, snakes showed the average lowest movement rates in April, followed by May, and October. Monthly movement rates were not statistically significant (F = 1.507, P = 0.197).

Crotalus lepidus was observed in five habitats on IMRS, with arroyo habitat being the most frequented (n = 407, 55%), followed by alluvial rocky slopes (n = 128, 17%), rocky slopes (n = 110, 15%), and alluvial slopes (n = 77, 10%). Alluvial flats (n = 18, 3%) had by far the lowest number of observations. Rattlesnakes were observed in 13 identified microhabitats, mostly from “under shrubs” (43%), followed by “under rocks” (19%). Most microhabitats utilized by *C. lepidus* recorded in a square meter at a given observation site were characterized by the regular presence of vegetation as the main ground cover component (% average = 54.8 ± 1.157 %), followed by rock, gravel and plant litter (19.9 ± 1.092, 12.0 ± 0.695, and 8.7 ± 0.568 %, respectively). A comparison of selected sites with random sites indicated that Rock Rattlesnakes in the study area preferred microhabitats with specific characteristics (MANOVA, Wilk’s lambda = 0.019, F = 6679.5, P = <0.001). Miscellaneous comments on rain harvesting, reproductive behavior, and predation are also discussed with respect to activities observed within the home ranges of *C. lepidus.*

INTRODUCTION

According to Dodd (1993), if the goal of a conservation program is to protect a snake, then its habitat must be protected also. This implies that in order to properly protect habitats of a target species, we should have high-quality knowledge of its ecological requirements. Home range and movement patterns within home ranges of snakes are fundamental aspects of their ecology and important indicators of their resource requirements (Plummer and Congdon 1994; Charland and Gregory 1995; Johnson 2000). So, full comprehension of movement and spatial patterns of species should strengthen required program initiatives for developing reserves of appropriate size (Dodd 1987, Webb and Shine1997; Fitzgerald et al., 2002). However, despite the obvious importance of habitat selection in rattlesnakes (Reinert, 1992; Prival, 2008, Wastell and Mackessy, 2011), they have received limited scientific attention. The lack of such information severely downgrades understanding relationships between conspecific individuals and symbionts in natural habitats already experiencing deleterious biotic and abiotic pressures. The increasing human related modification of rattlesnake habitats, ranging from partial reduction to total elimination, is adding adverse pressures on their ability to survive and prosper, so the need for gaining accurate ecological information on them is becoming more relevant and urgent (Dodd, 1993). Moreover, the unpredictability and impact of future weather patterns, due to global climate changes, is especially alarming for those living in the relatively fragile habitats, like those found in the Chihuahuan Desert (Hoyt, 2002).

Information concerning home range and movement patterns of snakes has been largely unavailable, because their secretive behavior leads to the perception that they are intractable for ecological research (Reinert, 1992, Bonnet et al., 2002). The difficulty in observing free-ranging snakes has lead to inadequate and biased sampling, which in turn have resulted in general

confusion regarding patterns of snake movements and erroneous descriptions of habitat preference (Reinert, 1984; Gregory et al., 1987; Tiebout and Cary, 1987). Only within the last few decades have long-term, high resolution studies of snake ecology and related behavior been possible through the use of radiotelemetry technology (Brown and Parker, 1976; Reinert, 1984; Duvall et al., 1985; Tiebot and Cary, 1987, Green, 1997; Hardy and Greene, 1999, 2000, Prival, 2008, Wastell and Mackessy, 2011). With radiotelemetry, investigators have been able to observe snakes selecting different habitats at different times of the year and for more specific behaviors such as feeding, mating, selecting overwintering sites, and also movements related to environmental thermoregulation (Reinert, 1992; Beaupre, 1995a; Green, 1997).

The study presented herein provides a quantitative evaluation of variation in the home range, dispersion, and habitat use of the Rock Rattlesnake (*Crotalus lepidus*) on Indio Mountains Research Station (IMRS), located in the Chihuahuan Desert of Trans-Pecos, Texas. While *C. lepidus* populations have been the subject of a few ecological investigations (Beaupre, 1995a; 1995b, 1996; Prival, 2008), no systematic field research has been performed on most of its geographic distribution. As a result, our knowledge of the ecology and behavior of *C. lepidus* in the Trans-Pecos region is limited. Only very general information is known about areas where it does well, not to mention the paucity of recognized features identifying important microenvironments where daily and seasonal activities take place, such as basking, foraging, mating, and overwintering sites.

Crotalus lepidus, is a relatively small rattlesnake (maximum 600-700 mm total body length, [Campbell and Lamar, 2004; Klauber, 1997]). Fig. 1 depicts an adult male *C. lepidus* from IMRS. This species ranges from southeastern Arizona, southern New Mexico, and southwestern Texas through central Mexico (Campbell and Lamar, 2004). As mentioned before,

few studies have focused on the biology of this species, and it is still under taxonomic evaluation on a range-wide scale.

FIG. 1. An adult male *Crotalus lepidus* (TL = 620 mm) from Indio Mountains Research Station, Hudspeth County, Texas.

Currently, *C. lepidus* is tentatively classified into four subspecies (*C. l. klauberi, C. l. lepidus, C. l. maculosus,* and *C. l. morulus*), based mainly on scale counts and body length criteria (Dorcas, 1992) that poorly substantiate this classification, especially for those populations in the northern portion of its range where there is a sizable degree of intrapopulational variation (Vincent, 1982; Dominguez, 2000; Campbell and Lamar, 2004). In addition, subspecies as a formal taxonomic category in modern phylogenetic systematics is questionable at best (Johnson et al., 2010) under the general lineage concept of species (de Queiroz, 2005, 2007), which suggests that formal categories, at any level of the modern taxonomic hierarchy, should include only taxa belonging to separate evolutionary lineages.

Recognizable populations (pattern classes; Grismer, 2002) within a species exhibiting intergradation along geographic clines, or locally fashioned adaptive characters, are not separate evolutionary lineages. Therefore no subspecific distinction is used for the population of *C. lepidus* at IMRS.

Given the overall lack of ecological information on *C. lepidus*, in this study I determined movement patterns and home range parameters by selected *C. lepidus* during the active seasons on IMRS using radiotelemetry. Consequently, I was also able to identify the general habitats and microhabitats used by those snakes during those seasons.

MATERIALS AND METHODS

All methods described in this study were approved by the UTEP IACUC (#A-200704-2, for the period of 1 July 2007 through 30 August 2010).

Description of Study Area.- This study took place within the 16, 187 hectare IMRS (Fig. 2) centered on coordinates 30.75°N, 105.00°W, which is located in the southeastern corner of Hudspeth County, Texas, about 40 km southwest of Van Horn. The facility is controlled by The University of Texas at El Paso (UTEP). The following description of IMRS is based on Johnson (2000), Schmidt (1979), and Worthington et al. (2004; http://www. utep.edu/indio/).

FIG. 2. Indio Mountains Research Station Headquarters, located in southeastern Hudspeth County, Texas.

IMRS is delineated by the Indio Mountains that generally run from north to south with primarily slopes facing east and west. In general, most of the mountainous portions of peaks, ridges, rugged slopes and steep arroyos are composed of intermittent conglomerate, sandstone, limestone, and igneous substrates, or a mixture of them where they adjoin. Radiating off the steeper slopes in the flats are alluvial fans transected by local small arroyos and by larger arroyos draining primary watersheds originating in the mountainous portions. Major arroyos either drain into the Rio Grande to the south and southwest or eastward into the Green River.

The vegetation is typical of the Chihuahuan Desert scrubland consisting of dominant species, such as Creosotebush (*Larrea tridentata*), White-thorn Acacia (*Acacia constricta*), Catclaw (Acacia greggii), Honey Mesquite (*Prosopis glandulosa*), and clumps of Prickly Pear (*Opuntia* spp.), mostly on alluvial flats and along arroyos, and Lechuguilla (*Agave lechuguilla*), Pitaya (*Echinocereus enneacanthus*), Ocotillo (*Fouquieria splendens*), Sotol (*Dasylirion leiophyllum*), Torrey's Yucca (*Yucca treculiana*), Eve's Needle (*Yucca faxoniana*), and clumps of Prickly Pear (*Opuntia* spp.) on rocky slopes, interspaced with grasses such as Black Grama (*Bouteloua eriopoda*), Arizona cottontop (*Digitaria californica*), and Tanglehead (*Heteropogon contortus*). The combinations of these and other plant species provide a great variety of microhabitats for organisms living in the area. Much of the flora is similar to that of the Big Bend area which ascends the Rio Grande Valley. Remnants of widespread desert grasslands occur throughout IMRS that are more typical of Chihuahuan Desert grasslands that occur on the northern and eastern sides of the Indio Mountains. The average annual precipitation in IMRS is typically 235 mm, with most rainfall (70%) occurring during the summer monsoon season (from June to September). Frontal systems producing rainfall coming from the east and northeast tend to release more rain on the eastern slopes of the mountain range (De la Cerda-Camargo,

2011).The annual average temperature for the areas near IMRS Headquarters is about 18º C (de la Cerda-Camargo, 2011).

Snake Procurement.- This project was carried out on IMRS from July 2007 through August 2010. Active searches for rattlesnakes were based on a weekly schedule from April to October (warm months) from three to four days a week, in early morning and late afternoon during daylight hours and at night (mostly from 21:00 to 24:00 h). In total, 12 adult *C. lepidus* (two females and ten males) were found opportunistically by walking transects of ca. 2 km in areas containing habitats that were previously known to be used by them. Areas searched included different kinds of plant associations, different facing slopes, different substrates, along arroyos, on alluvial flats, and on different types of rocky outcrops. In addition, snakes were located by driving unpaved roads at night in the study area. Once a rattlesnake was found, it was captured with a Pilstrom Tong (Midwest tongs.com), placed in a five-gallon bucket with a screw-type lid (Gamma Seal Inc.) and then transported to IMRS Headquarters for processing. From all rattlesnakes captured (n = 19), twelve adult rattlesnakes (ten males and two females) with appropriate size (> 100 g) were selected for transmitter implantation and then monitored continually for mostly a year. Snakes that did not fit the size criterion mentioned above were marked with a PIT-tag (Avid, Inc.) (Fig. 3) and released at the site of capture for possible future identification. PIT-tagging (Camper and Dixon, 1988) is an efficient and non-evasive way to quickly identify snakes in the field.

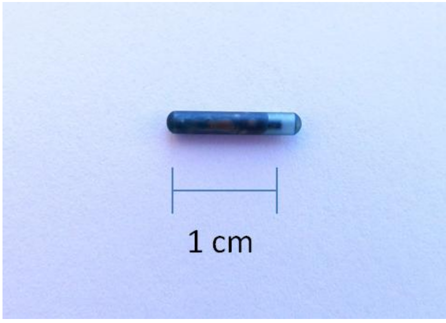

FIG. 3.- A PIT-tag (Avid, Inc) like those used for identifying rattlesnakes.

Transmitter Implantation Surgery.- The method proposed by Reinert and Cundall (1982) and modified by Hardy and Greene (1999, 2000) was followed; the latter was specifically developed for used under field conditions. Before and after the surgical procedures, rattlesnakes were always handled using Pilstrom Tongs to avoid accidental envenomation.

The following is a short description of the PIT-tagging and surgical procedures used on each rattlesnake. Immediately before the rattlesnake was processed, it was weighed and then coaxed to crawl from its storage container into a transparent plastic tube to a depth of about one-third its body length. This made accidental envenomation impossible because the head is completely secured inside the tube. The posterior two-thirds portion of the rattlesnake's body was grabbed and held by hand for direct manipulation during PIT-tagging and transmitter implantation surgery. Once in the tube, measurements of snout-vent length (SVL) and tail length (TL) were taken using a 1 m ruler and the sex was also determined using a clean herpetological metal probe. Next, a PIT-tag was inserted subdermally into the right dorsolateral area, previously disinfected with 70 % ethanol, approximately 20 cm from the cloaca using a sterile PIT-tagging syringe. After implanting the PIT-tag, antiseptic liquid bandage (New Skin) was applied to the small needle puncture to induce healing and to prevent infection.

The tubed rattlesnake was then placed on a sterilized table and positioned anteriorly into an anesthesia chamber for general inhalation anesthesia using liquid isoflurane (.25 to 1 ml). Cotton was placed between the tubed rattlesnake and walls of the chamber to minimize release of excess gas into the laboratory room. At the same time, a fan was positioned to vent off, toward an open window and away from surgery personnel, any anesthesia that escaped the surgery chamber. Anesthesia was carefully dispensed from a syringe into cotton mass located in the chamber directly in front of the tubed rattlesnake's head. Response to the anesthetic was monitored using tail withdrawal reflex, by observing the rate and depth of respiration, and the rate of the cardiac impulse. Prior to surgery, the transmitter (SB2, 5g; Holohil Systems Ltd.) (Fig. 4), along with clean surgical instruments were placed in sterilizing solution (benzalkonium chloride) for a minimum of 1 hour.

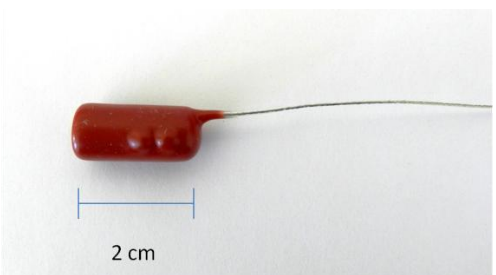

FIG. 4.- 5g SB2 transmitter (Holohil Systems Ltd) used to radiotrack *C. lepidus* on IMRS.

The surgery process lasted from 10 to 15 minutes. After the rattlesnake was anesthetized, a wide area of skin was prepared around the incision site using Betadine solution. A 1 cm longitudinal incision was made into the peritoneal cavity on the right side (ventrolateral) of the body around the end of the second third of the rattlesnake's body and the transmitter implanted into the cavity. The antenna was then inserted subcutaneously along the body, between scale

rows 2 and 3 anterior to the transmitter, using a fine bore brass tube that was removed through a small incision placed a distance slightly greater than antenna's length from the transmitter. Finally, incision was closed in a single layer using an "interrupted, horizontal mattress" stitch. After surgery, the rattlesnake, while still inside the plastic tube, was removed from the anesthesia chamber. The chamber was taken outside the laboratory into the open air for complete ventilation of residual anesthesia. During the awakening period, the rattlesnake remained in the plastic tube while it was observed for adequacy of respiration and circulation. When normal breathing and strong muscle tone was detected and regular coordinated movements and tongue flicking were observed, the snake was returned gently to the storage container and kept warm (between 25º and 30º C). Over the next several hours, the snake was frequently checked visually and gently prodded to be sure recovery was uneventful. The rattlesnake was returned to the wild at its original site of capture within 24 hours.

Home Range and Movement Patterns.- Radiotracking rattlesnakes began one week after transmitter implantation to allow for transmitter acclimation. The 12 rattlesnakes were located and radiotracked during the day using R-1000 telemetry receivers and RA-150 Yagi type directional antenna (Communication Specialists Inc.) (Fig. 5). However, four male rattlesnakes were killed and eaten by unknown predators (possibly foxes, badgers, or birds of prey) within the first months of the tracking; therefore the field data covers eight individuals, two females and six males. Because most individuals were originally found late during the activity season, they were radiotracked for at least five months beginning in late summer of the first year, continuing after winter dormancy, through summer of the second year. Every time a rattlesnake was located during the tracking process, the following data were recorded: date, time, coordinates, elevation, and body position. Slope and aspect of rattlesnake's microhabitat were determined using a

Brunton compass (Brunton Inc.). Also, the angle to the horizon in the eight cardinal directions for each location was determined with a protractor. Geographic locations obtained with a GPS were displaced on an aerial photograph of the study site in a geographic information system (GIS) (ArcMap 9.3, ESRI, Redlands, CA).

FIG. 5.- R-1000 telemetry receivers and RA-150 Yagi type directional antenna (Communication Specialists Inc.) used during the radiotracking period.

Home ranges were determined using minimum convex polygons (MCP, ha) (Hayne, 1949). Core areas were the areas containing an animal during 50% of locations, ha, and determined based on 50% kernels using Hawth's Analysis Tools for ArcGIS (Beyer, 2004. http://www.spatialecology.com/htools). Core kernel areas were estimated by matching the 95% kernel area to the MCP area by adjusting the smoothing factor (Row and Blouin-Demers, 2006). Although several techniques are available for estimating home range (reviewed by Powell, 2000, Kernohan et al., 2001), Row and Blouin-Demers (2006) suggest that when attempting to

determine maximum home range, minimum convex polygons (MCPs) are preferred for reptiles, and when the goal is to examine habitat preference, kernel estimators are more appropriate. Even though many radiotelemetry studies used the recommended least-square cross validation (LSCV) method (Worton, 1989) for choosing the smoothing parameter, it may still present a great amount of variation that might not reflect the exact area used by an individual and therefore it also makes comparisons difficult between other snake studies (Row and Blouin-Demers, 2006).

Because only a small sample (eight) of rattlesnakes were radiotracked, parametric (t test, ANOVA, MANOVA) and non parametric (Chi square) tests were employed, depending on whether parametric assumptions were met, with $p < 0.05$ to assess statistical significance. Statistical analyses were performed using Systat Version 10.2 (Systat software Inc., 2002). Average daily movement rate (m/day = total distance moved by and individual divided by the total number of days tracked) (Beaupre, 1995a) was calculated for each month of the active season from straight line movement distances of the rattlesnakes. Monthly movement means were compared with repeated measures ANOVA.

Habitat and Microhabitat.- Although there has been no completed study of the habitat types in the study area on IMRS, those selected by the rattlesnakes were identified using the following topographic characteristics of the terrain: rocky slopes, alluvial rocky slopes, alluvial slopes, alluvial flats, and arroyos; classification of plant associations follow those of Henrickson and Johnston (1983) and Texas Natural Heritage Program (1993).

Every time a rattlesnake was located, the microhabitat type was determined. For each microhabitat, ground cover composition (%) was recorded in a square meter taking the rattlesnake as the center of it (Reinert, 1984). Ground cover composition included elements such

as vegetation, rocks (> 50 mm), gravel (< 50 mm), sand, alluvium, and vegetation litter; actual microhabitats are identified in results section. However, sand and alluvium elements were not included in the analysis because they accounted only for <1% when they were present. A photograph of the microhabitat was taken every time a rattlesnake moved to a new location. Habitats and microhabitats frequencies were analyzed with Chi square tests (X^2).

Selected sites vs Random sites.- In total, 263 sites selected by rattlesnakes were compared to 263 random sites to determine if there is a preference for specific sites in home ranges. Random sites were obtained by determining a UTM coordinate from a random distance (10-200 m) at a random bearing from the original location of the snake (Sperry and Taylor, 2008) using the software Random.org (http//www.random.org). Locations used more than once by a snake were only included one time in microhabitat analysis and sites where snakes were actively crossing were not included (Reinert, 1984; Blouin-Demers and Weatherhead, 2001). Sites were compared using MANOVA with repeated measures and Wilk's lambda to test for significant differences.

Finally, geographic locations of the rattlesnakes were plotted on a digital vegetation map to determine if there was a pattern between the snake movements and the distribution of the different vegetation classes identified in the study area. The GIS map containing a total of 11 vegetation classes and physical features was developed by Rebecca Marin in UTEP's System Ecology Laboratory. The vegetation classes and features are as follow: 1 = Shadow, 2 = Bare ground, 3 = River, 4 = River riparian, 5 =*Yucca*/Grassland/Mixed scrub, 6 = *Bouteloua* scrub, 7 = *Agave*/*Bouteloua*/*Viguiera*, 8 = *Larrea*/*Acacia*, 9 = *Larrea*/Shrubland, 10 = Tanks, 11 = Arroyo bottom.

Results

Home Range and Movement.-From July 2007 to August 2010, eight rattlesnakes were radiotracked during the active seasons for durations ranging from 138 to 488 days (Table 1). The number of snake relocations per individual ranged from 39 to 184 (mean = 95.1 ± 21.4). On IMRS most rattlesnakes emerged from their winter refuges in early April and returned to their winter refuges in late October or early November. Most of the snakes used winter refuges within their normal movement area, although two male individuals overwintered ca. 200 m away from that area. Home ranges for all individuals averaged 13.69 ± 3.06 ha and ranged in size from 6.4 to 29.1 ha. By sex, average MCP home range was 7.29 ± 0.89 ha (n = 2) for females and 15.82 ± 3.71 ha (n = 6) for males (See Table 1 and Appendix I). The 50% kernel for all individuals averaged 2.83 ha, and it varied from 1.6 to 6.1 ha. However, the average kernel area was smaller for females than for males (1.5 ± 0.10 ha and 3.26 ± 0.75 ha, respectively).

Daily movement averaged 8.46 ± 1.45 m/d (Table 1). Individual daily mean movement ranged from 3.6 to 15.8 m/d. Due to small sample size, statistical comparisons were not made. By month, snakes showed the highest average movement rates in September, followed by June, July and August. On the other hand, snakes showed the average lowest movement rates in April, followed by May, and October (Fig. 6). There were no significant differences between average monthly movement rates (F = 1.507, p = 0.197), and there was no significant relationship between mean monthly snake movement and mean monthly rain (r = 0.489, R^2 = 0.239, n = 7, p = 0.266).

TABLE 1. Home range (MCP), kernel size, and movement (dispersion) data of *C. lepidus* radiotracked on IMRS. * = Individual killed by unknown predator.

ID	Sex	TBL (mm)	Body mass (g)	MCP (ha)	Kernel (50%)	Tracked days	Total meters	Meters per day
003	♀	540	99.5	6.4	1.4	324	2571	7.9
004	♀	529	118.0	8.18	1.6	248	912	3.6
001	♂	700	176.8	25.0	5.1	488	3185	6.5
002	♂	625	175.0	12.1	2.5	406	2406	5.9
021	♂	625	140.1	13.2	2.3	159	2445	11.5
022	♂	645	128.2	8.6	1.8	138	1579	11.4
023	♂	550	105.3	6.9	1.8	149	765	5.1
024	♂	620	175.9	29.1	6.1	147	2663	15.8
005*	♂	595	108.2	-	-	-	-	-
006*	♂	678	173.2	-	-	-	-	-
007*	♂	575	143.0	-	-	-	-	-
008*	♂	635	150.2	-	-	-	-	-
Average	-	-	-	13.69	2.83	-	-	8.46

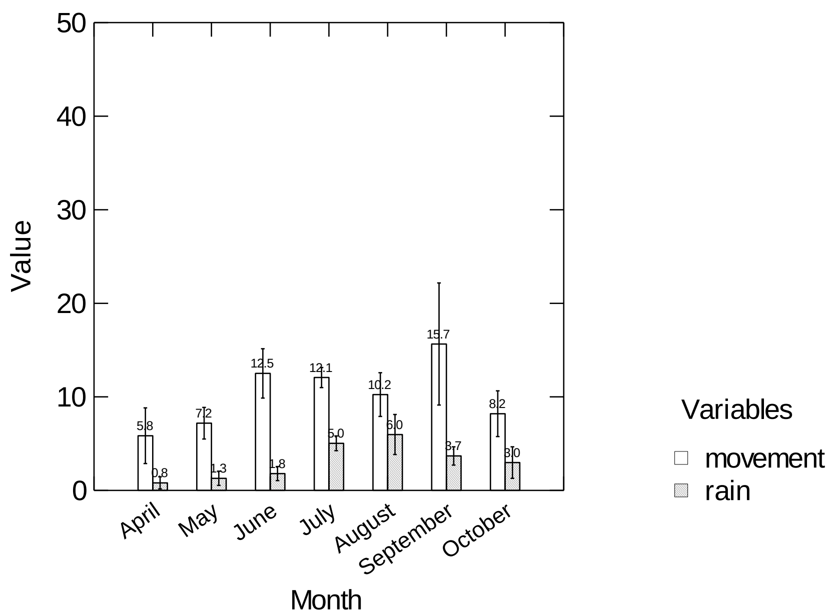

FIG. 6. Mean daily movement (m/d) traveled by *C. lepidus* (n = 8 individuals), and mean of total rain (mm) by month. Bars denote standard error.

Habitat and Microhabitat.- Of the five main habitats utilized by *C. lepidus* on IMRS, the habitat "arroyo" was the most frequented with 407 (55%) observations recorded (Fig. 7), followed by alluvial rocky slopes (128, 17%), rocky slopes (110, 15%), and alluvial slopes (77, 10%). Alluvial flats (18, 3%) had by far the lowest number of observations. The distribution of these observations was highly significant ($X^2 = 613.959$, df = 4, $p < 0.001$).

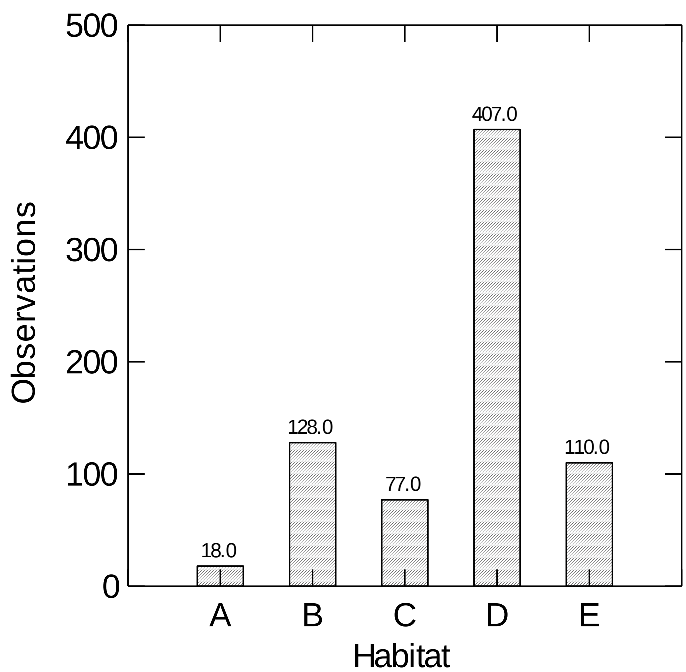

FIG. 7. Number of observations of *C. lepidus* among habitats: A = Alluvial flats, B = Alluvial rocky slopes, C = Alluvial slopes, D = Arroyo bottom, and E = Rocky slopes.

Rattlesnakes were observed in 13 identified microhabitats, mostly from under shrubs (43%), followed by under rocks (19%) (Table 2). The distribution of these observations was highly significant, as well (X^2 = 1625.892, df = 12, p < 0.001).

TABLE 2. Number of times and percentages of rattlesnakes observed in different microhabitats on IMRS.

Microhabitat	Observations	%
in crevice	36	5
on alluvium	4	1
on grass	1	0
on gravel	38	5
on rock	38	5
on sand	8	1
under grass	72	9
under ground	34	5
under herbs	1	0
under plant litter	24	3
under log	34	4
under rock	143	19
under shrub	327	43
Total	**760**	**100**

Ground cover composition (%) from a square meter showed that microhabitats contained mostly vegetation (average = 54.8 ± 1.157 %), followed by rock, gravel and plant litter (19.9 ± 1.092, 12.0 ± 0.695, and 8.7 ± 0.568 %, respectively) (Fig. 8). The Manova for comparison between 263 snakes sites and 263 random sites showed a significant difference (Wilk's Λ = 0.019, F = 6679.5, P = <0.001) (Table 3).

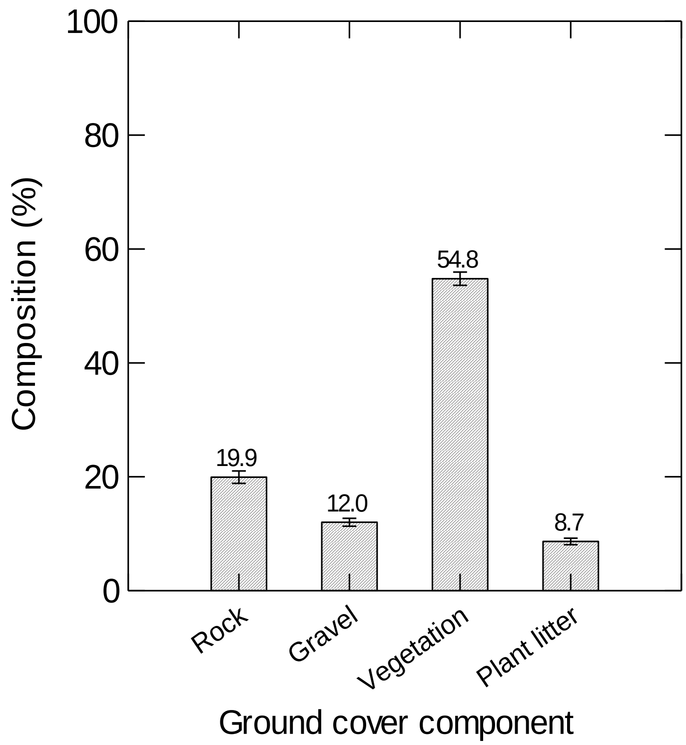

FIG. 8. Overall mean percentage of ground cover components in a square meter of microhabitats used by *C. lepidus* (n = 761 observations). Error bars denote standard error.

TABLE 3. Ground cover of microhabitats selected by *C. lepidus* and random sites on IMRS. Test statistic and p values from MANOVA are included.

	Selected by snakes		Random			
Variable	Mean	SE	Mean	SE	F	P
Rocks (% ground cover)	20.19	1.834	14.677	1.834	180.756	< 0.001
Gravel (% ground cover)	14.848	1.747	40.989	1.747	510.542	< 0.001
Vegetation (% ground cover)	53.878	1.798	38.289	1.798	1313.684	< 0.001
Plant litter (% ground cover)	7.243	0.847	3.042	0.847	73.783	< 0.001

By month, vegetation was the main ground cover component of microhabitats for May to October (Fig. 9). However, in April the average ground cover of microhabitats was dominated by rocks. Although gravel and plant litter were present during the seven months, they were in proportions lower than 20 %. Rocks were in low proportions as well, but only from May to October.

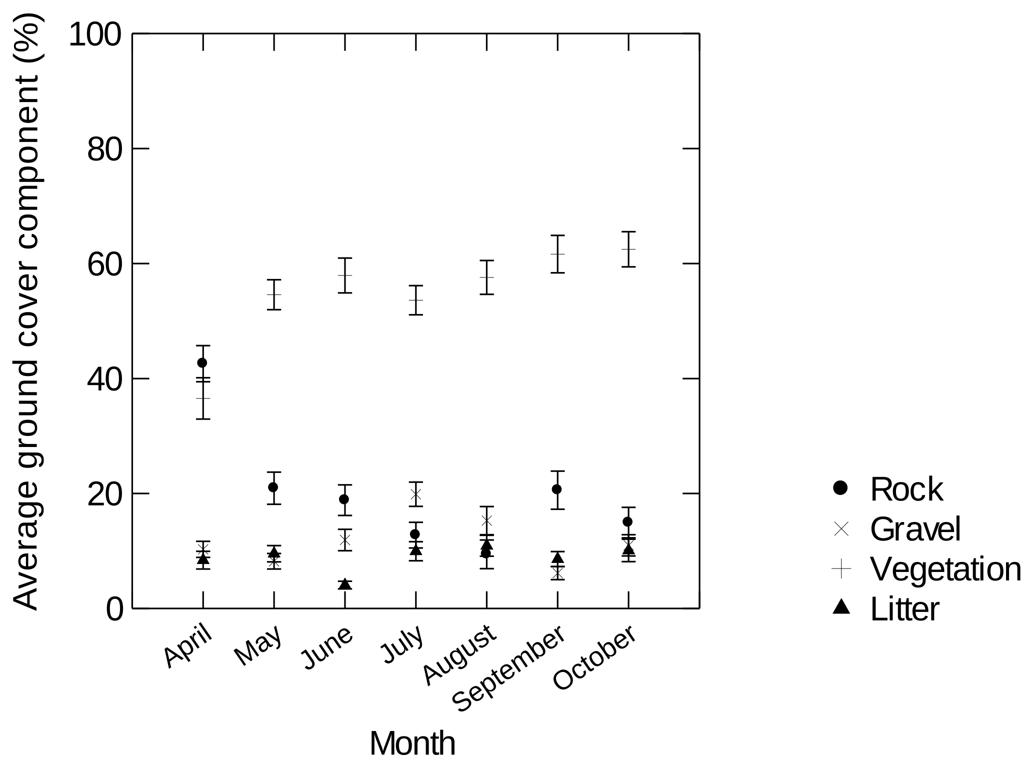

FIG. 9. Monthly mean percentage of ground cover of microhabitats used by *C. lepidus* (n = 761 observations) during the active period. Error bars denote standard error.

The overlap of the snakes' geographic locations with the GIS map analysis containing the 11 vegetation classes and physical features showed that snakes were observed primarily in

vegetation classes *Yucca/* Grassland/Mixed scrub, *Agave*/*Boutoloua*/*Viguiera,* and *Larrea*/*Acacia* shrubland (30%, 26% and 24 %, respectively) (Table 4), while the rest of the vegetation classes contained very low observations (less than 5%). Observed frequencies were highly significant ($X^2 = 46.8$, df = 10, $p < 0.001$).

TABLE 4. Vegetation classes, physical features, and number of times and percentage of rattlesnakes observed in each class on IMRS (N = 760 observations).

Vegetation class	**Observations**	**%**
Shadow	32	4
Bare ground	26	3
River	0	0
River riparian	0	0
Yucca/Grassland/Mixed scrub	224	30
Bouteloua scrub	19	3
Agave/Bouteloua/Viguiera	183	24
Larrea/Acacia shrubland	195	26
Larrea Shrubland	25	3
Tanks	24	3
Arroyo	32	4
TOTAL	**760**	**100**

Discussion

Home range and Movement.-All individuals spent most of the time moving back and forth along arroyos or washes and spent the winter on slopes next to their active home ranges. All the rattlesnakes monitored in this study overwintered alone in relatively small crevices. However, two individuals of *C. molossus* and one of *C. atrox* were found overwintering in crevices 1-2 m away from three male *C. lepidus*. In general average home range size (MCP) of *C. lepidus* was larger for males than for females. The same pattern was observed with the 50% kernel, as well. Although the 50% kernel area fell within the arroyos with sandy and gravely substrate for most of the snakes, that kernel area for female 004 fell mostly in an arroyo with mostly rocky substrate. Although male average home ranges have been found to be larger than female home ranges (Prival, et al., 2002; Cardwell, 2008; Goode et al., 2008), it is not unusual to find individual females with larger home ranges than some males, as was the case for the home range of female 003. Snakes were located either at the bottom of arroyos containing interspersed vegetation or on the bordering slopes of arroyos where microhabitats were formed mainly by vegetation and rocks (Fig. 10). Prival (2008) found that *C. lepidus* on the Chiricahua Mountains of Arizona is found mostly in talus and the gravid females tend to use open spaces more frequently.

FIG. 10. Typical arroyo habitat utilized by *C. lepidus* on IMRS; snakes normally occupied the vegetated areas.

Seasonal shift in habitat use often associated with movements to and from winter hibernacula, have been documented for other rattlesnake species (Brown et al., 1982; Reinert and Kodrich 1982; Duvall et al., 1985; Reinert 1993; Secor, 1994; Wastell and Mackessy, 2011). However; Beck (1995) found that seasonal changes in habitat and shelter site selection of individuals of *C. atrox*, *C. molossus*, and *C. tigris*, in southeastern Arizona, were associated mostly with movements out of rocky sites and onto foraging areas in the flats and arroyos during the summer. Similarly, *C. lepidus* on IMRS seemed to spend most of the active season inside and along arroyos, and on adjacent slopes and flats. Individual 002 was observed preying on a snake,

Hypsiglena jani, within an arroyo containing interspersed vegetation (Mata-Silva et al., 2010) and individual 021 was found eating a lizard, *Cophosaurus texanus*, on an alluvial rocky slope bordering an arroyo (Mata-Silva et al., 2011). Although alluvial flats are frequently found between arroyos, they seemed to be the least exploited habitat by Rock Rattlesnakes on IMRS. They seem to contain less plant diversity and less vegetation cover than arroyos, which probably make them less attractive to *C. lepidus*.

Areas exploited by rattlesnakes are assumed to contain higher prey densities, so capture success rates should be greater there, and thus making them more attractive to rattlesnakes as foraging sites (Beck, 1995). In addition to the presence of prey, environmental factors must also play an important part influencing site selection by rattlesnakes (Reinert, 1993). Individuals of *C. lepidus* probably move along arroyos during summer months because rocky outcrops in the study area get exceptionally hot during daytime hours, which could compromise rattlesnake survival. For example, Beck (1995) found that volcanic rocky slopes can be extremely hot during summer, and they may retain heat longer than shelter sites within the *Larrea* flats and arroyos. At midnight during most of the summer, surface temperatures along the rocky slopes were warmer than surface temperatures on sandy or gravelly areas in the flats.

Comparisons of home range and movement parameters of *C. lepidus* with other species of rattlesnakes are only on the broad-spectrum level, because of variation in tracking protocols, such as tracking periods, relocation frequency, sample size, and geographic location (Gregory et al., 1987). When home range size is compared to other rattlesnake species living in the southwestern United States, *C. lepidus* from IMRS had a larger average home range than *C. pricei*, a small species inhabiting Arizona's Chiricahua Mountains (Prival et al., 2002). Besides living in conifer and other woodland habitats there, the home range of *C. pricei* was calculated

from July to September, the monsoon season; while *C. lepidus*' home range on IMRS was calculated from April to October. *Crotalus lepidus* had a larger home range than populations of *C. atrox*, *C. molossus*, and *C. tigris* in the Sonoran Desert of southeastern Arizona (Beck, 1995), as did a population of *C. tigris* (Goode et al., 2008) in the Sonoran Desert, near Tucson, Arizona. Results of those comparisons are very interesting because the three species are relatively larger than *C. lepidus*. On the other hand, *C. lepidus* had a smaller home range than a population of *C. cerates* in the Kelso Dunes system in the eastern Mojave Desert in California (Secor, 1992, 1994), a population of *C. abyssus* from the Little Colorado River Canyon in Arizona (Reed and Douglas, 2002), a population of *C. scutulatus* in the Mohave Desert (Cardwell, 2008), and *Sistrurus catenatus* in southeastern Colorado (Wastell and Mackessy, 2011).

Like other populations of rattlesnakes (*C. atrox, C. molossus, C. tigris, and C. abyssus*) studied in the southern regions of the southwest (Beck, 1995; Reed and Douglas, 2002), *C. lepidus* on IMRS did not show separate summer and winter home ranges. However, this was not the case for *C. cerastes* in the Mojave Desert of California (Secor, 1994), and for *S. catenatus* in southeastern Colorado (Wastell and Mackessy, 2011).

With respect to movement, *C. lepidus* had two specific patterns on IMRS that were dependent on the time of the year. Individuals were observed basking or active during late morning and early afternoon in late March and early April when they abandoned their winter refuges and in late October and early November when returning to their winter refuges. These observations were very likely due to the availability of favorable temperatures during those times of the day in spring and fall. Conversely, by late May Rock Rattlesnakes on IMRS shifted to nocturnal activity, leaving their shelters at dusk and going back to their shelters by 0930 hrs in the morning, very likely to avoid lethal temperatures. Beaupre (1995a) also reported highest

capture success in the Big Bend area during those hours during summer months. Rattlesnakes on IMRS usually retreated into shelters when ground temperatures would reach 36-38 °C. In general, movement of *C. lepidus* on IMRS seemed to increase once the monsoon rains began. Similar results were found for *C. atrox*, *C. molossus*, *C. tigris* (Beck, 1995), *C. pricei* (Prival et al., 2002), and *C. tigris* (Goode et al., 2008) in the Sonoran Desert. Although *C. lepidus* in the study herein showed a positive relationship between movement and precipitation, only 23.9% of the variation of this movement was explained by rain. Increase movement by *C. lepidus* on IMRS also coincided with feeding activity (Mata-Silva et al., 2010; 2011) and with most individuals (eight) displaying mating behavior along arroyos. All males moved more often than females, which was partially due to males searching for receptive females. Observations of courtship activity during August and September suggest that *C. lepidus* on IMRS mates only in late summer and early fall (unimodal pattern). Similar reproductive pattern was reported for *C. lepidus* in the Chiricahua Mountains of Arizona (Prival, 2008). Unimodal reproductive pattern in the southwest has been also reported on species such as *C. mitchellii* (Glaudas and Rodriguez-Robles, 2011; Brattstrom, 1965; Klauber, 1997; Goldberg, 2000; Gartner and Reiserer, 2003), *C. molossus* (Schuett et al., 2005; Greene et al., 2002), *C. pricei* (Prival et al., 2002), *C. ruber* (Dugan et al., 2008), *C. oreganus* (Fitch and Gladding, 1947), and *C. willardi* (Holycross and Goldberg, 2001), as well. However, mating activity in spring and late summer/fall, or summer (bimodal pattern) has been also reported for populations living in the southwest such as *C. atrox* (Taylor et al., 2004; Taylor and DeNardo, 2005; Schuett et al., 2005); *C. cerastes* (Secor, 1994); *C. oreganus* (Dugan et al., 2008); *C. scutulatus* (Schuett et al., 2002; Cardwell, 2008); *C. tigris* (Goode et al., 2008); and *C. oreganus* (Hersek et al., 1992). Mating patterns of rattlesnakes in

temperate zones are considered to be the result of phylogenetic inertia (Aldridge and Duvall (2002).

Beside this study, the movement rate of *C. lepidus* has been studied only by Smith et al. (2001) and Beaupre (1995a,b, 1996) in two populations (males only). One at Boquillas and the other at Grapevine Hills, with both localities being found in Big Bend National Park, located about 265 and 230 kilometers respectively, to the southeast of IMRS. Both localities differed in elevation, vegetation cover, with Boquillas being hotter and drier with less vegetation cover; both sites are located at lower elevation than IMRS. Rattlesnakes included in the study reported herein moved significantly less than populations of male *C. lepidus* studied by Beaupre (1995a,b, 1996) at both Boquillas and Grapevine Hills, in Big Bend (average 20.4 ± 3.0 m/d). Beside these differences being explained by biotic and abiotic factors characteristic of each site; they may also be partially explained by disparity in sample size and period of time the rattlesnakes were radiotracked. Populations studied by Beaupre were monitored from May to August, while rattlesnakes on IMRS were radiotracked from April to October. When rattlesnakes from this study were compared to those from Beaupre (1995a,b, 1996) for the same radiotracking period (May-August), *C. lepidus* from IMRS still showed a lower movement rate (average = 10.5 m/d). On the other hand, another study by Smith et al. (2001) found that *C. lepidus* (five males) tracked from May to July on the Peloncillo mountains of New Mexico showed a movement rate (average = 9.9 m/d) similar to the study herein (average = 10.6 m/d) for those three months.

When compared to other rattlesnake species of the southwestern deserts, *C. lepidus* showed a higher daily movement rate than sympatric *C. willardi obscurus* (three individuals) in Peloncillo Mountains of Southern New Mexico and Arizona (Smith et al., 2001). On the contrary, *C. lepidus* showed a lower daily movement rate than a population of *C. pricei* in the

Chiricahua Mountains (Prival et al., 2002), populations of *C. atrox, C. molossus* and *C. tigris* studied by Beck (1995) in the Sonoran Desert, and a population of *C. scutulatus* (especially males) from the Mohave Desert (Cardwell, 2008). Also, *C. lepidus* moved less than *C. abyssus* in the Little Colorado River Canyon, Arizona (Reed and Douglas, 2002). These differences may be due in part because the latter species are larger than *C. lepidus*. However, even though *C. lepidus, C. cerastes, and S. catenatus* are relatively similar in size, the former moved less than a population of *C. cerastes* studied in the eastern Mojave Desert (Secor, 1992, 1994) and *S. catenatus* in southeastern Colorado (Wastell and Mackessy, 2011). These differences may be due in part to the population of *C. cerastes* living in a unique habitat such as sand dunes where individuals have to cross relatively large sandy areas to go from one patch of microhabitat to another and *S. catenatus* living in patches of favorable grassland habitats, which would require more movement to maintain optimal conditions.

The fact that rattlesnakes were located mostly under the "shrub" microhabitat (43%) may be due to the fact that shrubs seem to be abundant in the arroyos where rattlesnakes spent most of the time, especially during the hottest months. It is very likely that the high density of shrubs found in arroyos provide a greater range of microclimatic conditions than shrubs located on flats or rocky slopes. These microhabitats not only increase the presence of Rock Rattlesnakes, but they may also increase the presence of lizards (*pers. obs.*), and possibly provide better microhabitats for predator avoidance. "Under rocks" was the second most frequented microhabitat (19%), especially in April and October when rattlesnakes were on slopes either approaching or leaving their winter shelters. It is very likely that rattlesnakes achieved more comfortable body temperatures under rocks located on slopes during cold nights, instead of being in arroyos that typically reach lower temperatures earlier in the evening. As seen in Figs. 8 and 9,

vegetation seemed the most important ground cover component in a square meter of microhabitats used by *C. lepidus* on IMRS during most of the active season. Although rocks, gravel and leaf litter were used in lower proportions in the microhabitat, they were constant elements for many observations that very likely provided the necessary conditions for the presence of rattlesnakes and prey.

Results of MANOVA indicated that Rock Rattlesnakes seem to use microhabitats non-randomly. Rattlesnakes selected microhabitats that contained a significant amount of vegetation and they were almost always inside or near arroyos, demonstrating that the arrangement of the structure of the vegetation and the other ground cover components may play an important distributional role of Rock Rattlesnakes within the study site. From the 11 vegetation classes and physical features identified on the GIS map, rattlesnake location matched mostly with three of them (80%). These classes contained primarily plant associations such as *Larrea-Acacia*, *Yucca* Grassland/Mixed Scrub, and *Agave, Boutoloua-Viguiera*. These plant associations are very well represented along arroyos. However, rattlesnake locations minimally matched with "arroyo" class; only 4%. This was probably due to a geo-rectification error of the map, because the rms error of the icon image could have been up to 12 m. Furthermore, most arroyos lack vegetation at the bottom. These observations suggest that *C. lepidus* on IMRS exploits certain microhabitats over others. The results are also more detailed than previous reports on the habitat and microhabitat of *C. lepidus* elsewhere (reviewed in Ernst and Ernst, 2003; Campbell and Lamar, 2004). Although individuals of *C. lepidus* have been previously reported in different kinds of habitats, they have been mostly associated with rocky areas such as talus slopes, rock strewn hillsides, rocky outcrops with crevices, dry rocky arroyos, and rocky canyons in brushland (Werler and Dixon, 2000; Ernst and Ernst, 2003; Campbell and Lamar, 2004). Eastern

populations of *C. lepidus* have been reported in mesquite grassland and deserts (reviewed in Werler and Dixon, 2000; Ernst and Ernst, 2003, Campbell and Lamar, 2004). Results from radiotracking reported herein demonstrated that *C. lepidus* spent more time along arroyos and adjacent slopes containing a substantial amount of shrubs. Individuals were observed in rocky slopes or outcrops on some occasions, but mostly when they were leaving or returning to their overwintering shelters. Although habitat differentiations have been found in other species of rattlesnakes (Reinert, 1984; Beck, 1995), it remains to be seen if those utilized by *C. lepidus* differ from the other larger rattlesnakes (*C. atrox* and *C. molossus*) on IMRS that inhabit the same area.

Until now, a substantial amount of research on rattlesnakes has enhanced our understanding of their ecology and snakes in general (Beaupre and Duvall, 1998). However, because of the nature of the projects and rattlesnake behavior, most knowledge has been obtained from studies of single populations over relatively short periods of time. Because of the relatively small sample considered in this study and because of the wide geographic distribution of *C. lepidus* (Campbell and Lamar, 2004) it is important to do a more in-depth study using a larger sample size, especially one including more females and juveniles. Also, results of movement and habitat selection found in this study might reflect only local patterns and not a generalization of the behavior and habitat selection of *C. lepidus* range-wide.

Compared to larger populations of *C. lepidus* in the Bing Bend region (Beaupre, 1995a,b) and to other relatively abundant species known for using communal hibernacula (e.g., Klauber, 1997; Hamilton and Nowak, 2009; Wastell and Mackessy, 2011), only a relatively small number of adult individuals were found in the study area, even though a great amount of searching effort was invested. Failing to locate a greater number of individuals was also likely exacerbated by the

small size and the cryptic coloration of *C. lepidus* on IMRS. The combination of background matching with the microhabitat, showing little propensity to rattle, and nocturnal activity during the summer made them more difficult to find.

In addition, rattlesnakes radiotracked in this study were located in the central portion on the western and southwestern facing slopes of the Indio Mountains, which may fall under a rain shadow. Frontal systems producing rainfall coming from the east and northeast tend to release more rain on the eastern slopes of the mountain range (De la Cerda-Camargo, 2011). It would be interesting to radiotrack rattlesnakes living on eastern slopes to see if amount of precipitation affects home range, movement patterns, and habitat preference.

It is important that the information gleaned in this study be used by U.S. conservation agencies to determine the ecological parameters necessary for the continued existence of *C. lepidus*, especially in regard to the environmental conditions needed for defining limitations to its natural history in the northern Chihuahuan Desert. IMRS is relatively pristine and its natural focus can be used to identify conditions vital for designing refuges elsewhere allowing *C. lepidus* to thrive under optimal circumstances. This is especially true today when major portions of the Chihuahuan Desert are being altered by humans, chiefly by livestock grazing and mining interests. Much of the distribution of *C. lepidus* is in Mexico where it is considered a species under special protection by Mexican laws (Lavin-Murcio and Lazcano, 2010), even though it is relatively unstudied there. The study presented here can be an important aid to Mexican conservation authorities for determining the proper protecting status, at least for populations in the Chihuahuan Desert of that country.

MISCELLANEOUS OBSERVATIONS

The radiotracking technique applied on IMRS also increased the chances of finding rattlesnakes in the wild performing activities that otherwise would be almost impossible to witness. Herein I describe two events of rain water harvesting by *C. lepidus*, comment on the predation of four individuals along with their possible predators, and identify reproduction related events rarely witnessed by field investigators.

Rain Harvesting.-The unpredictable availability of water in arid environments and its acquisition represents quite a challenge for most if not all animals. This has driven organisms living in deserts to develop different strategies (physiological, morphological, and ethological) to survive in such harsh and unstable conditions (Costa, 1995; Bradshaw, 1997). Among these strategies, rain-harvesting seems to be used widely by reptiles in North American deserts. Animals collect water on the surface of their bodies or on other physical objects during precipitation events, and subsequently drink it (Sherbrooke, 1990). Episodes of rattlesnakes acquiring water from rain, sleet, or snow in arid habitats during the active or inactive (overwintering) seasons have been reported for *C. molossus* (Greene, 1990), *C. oreganus* (Aird and Aird, 1990; Ashton and Johnson, 1998), *C. scutulatus* (Cardwell, 2006), *C. atrox* (Repp and Schuett 2008), and *C. mitchellii* (2009). Although the Rock Rattlesnake has a wide geographic distribution, including the southwestern United States and Northern Mexico (Campbell and Lamar, 2004), information related to rain-harvesting behavior has not been reported. Through the use of radiotelemetry I was able to observe individual 008 harvesting rainwater during mid-winter, and individual 001 in summer during the monsoon rains.

Male Rock Rattlesnake 008 was observed harvesting rainwater on 16 February 2008, at 1120 h. The weather that morning was highly unstable, being sunny and windy early and later on light rain, sleet, and winds dominated. At the time of the observation the rattlesnake's body temperature was 14.5 °C; air and substrate temperatures were 5 °C and 7 °C, respectively. This rattlesnake was located outside its hibernaculum on a rocky conglomerate-sandstone slope facing southeast near an arroyo that also functions as an unpaved road. The rattlesnake was observed in a loose coil position with its body flattened. It proceeded to lick water drops with its tongue for about two minutes from the dorsal section of his body. Unfortunately, the rattlesnake detected our presence and slowly returned to its hibernaculum. After that observation we visited all other hibernacula sites, but none of the rattlesnakes were outside their dens. Although it was cloudy and windy at all other sites no evidence of rain or sleet was observed.

The second male rattlesnake (001) was observed harvesting raindrops during the monsoon season on 11 July 2008 at 1810 h, after a hot afternoon turned windy with sporadic episodes of light rain. The rattlesnake was found at the edge of an arroyo on an alluvial north-facing slope. The rattlesnake was in an elongated position licking water drops from a rock surface during a light rain. After ten minutes the rattlesnake turned and started licking water from the anterior dorsal section of its body. The rattlesnake's body temperature was 30 °C; air and substrate temperatures were 29.5 °C and 27.5 °C, respectively. Unfortunately, because of darkness, I was not able to observe the other rattlesnakes to verify if they were also harvesting rainwater.

In general, just like other rattlesnakes living in arid environments, *C. lepidus* seems to apply similar water harvesting behaviors when situations arise regardless of season or time of day. Cardwell (2006) found that *C. scutulatus* only collected rainwater from their own bodies

and not from surrounding substrates. However, Ashton and Johnson (1998) Greene (1990), Repp and Schuett (2008), and Glaudas (2009) observed rattlesnakes (*C. oreganus*, *C. molossus*, *C. atrox* and *C. mitchellii*, respectively) collecting rainwater from their bodies or from other structural features, like rocks. Those differences were attributed to the availability of structural features in their environments that would hold water. With respect to *C. lepidus*, most of the landscape within the study area is represented by alluvial rocky slopes, so my observations demonstrate that *C. lepidus* will harvest raindrops from either their bodies or from rock surfaces.

Reproduction and Parental Care. Female 004 was found with four neonates on 20 July 2008 (Fig. 11). She had retreated onto a rocky slope at the edge of her home range and had her offspring in a crevice, ca. 60 cm deep. Average total body length of the neonates was 21.5 cm, ranging from 20.6 to 22.7 cm; the average body mass was 10.1 g, ranging from 9.4 to 10.6 g. This is the first report of clutch size for *C. lepidus* on IMRS. The clutch size is similar to those reported for *C. lepidus* from the Chiricahua Mountains in Arizona (Prival, 2008) and for other geographic locations (Kauffeld, 1943; Werler, 1951; Minton, 1959; Klauber, 1993; Armstrong and Murphy, 1979; Tenant, 1984; Beaupre, 1995a). In general, a low clutch size and the fact that many *C. lepidus* usually do not reproduce every year (Beaupre, 1995a; Prival, 2008) supports the hypothesis that they may become exposed to local extinction if the species experiences significant mortality rates.

When the female and her offspring were found in the crevice, the mother was observed loosely coiled at the entrance of the crevice with the neonates resting on top of her (Fig. 11). After my arrival, the neonates started withdrawing deeper into the crevice, but the mother remained at the entrance in the same position without displaying any defensive behavior. Shortly thereafter, I proceeded to collect the mother and the neonates to determine body measurements

and weights. After capturing all the individuals, I proceeded to examine the crevice for more neonates but only found two neonate shed skins, which suggested the young were born a few days previously and that the mother stayed with them during that time period. Parental care, or parental assistance (any act from a parent after parturition that increases chances of offspring survival) (Shine, 1988) has been documented for all species of rattlesnakes living it temperate regions (Greene et al., 2002). However, only a few instances of parental care have been reported for *C. lepidus* (Armstrong and Murphy, 1979; Greene et al., 2002), and the record presented herein is the first report from a Texas population.

FIG. 11. Female 004 with four neonates on IMRS.

Courtship/Mating Activity. Courtship and mating behavior of *C. lepidus* was observed on IMRS (six times) in August and September when high environmental temperatures started decreasing. Mating activity of *C. lepidus* has been reported elsewhere from late July through early October (Ernst and Ernst, 2003). The individuals observed on IMRS underwent mating activities normally under vegetation found on the edge of arroyos. The time periods for the

observations were usually in the early hours of the morning or later in the afternoon when air temperature was around 30 °C. Most mating pairs copulated while hidden under vegetation where they were mostly inconspicuous (Fig. 12), although in one instance a couple was observed after sunset mating in the open next to bunch of Black Grama (*Bouteloua eriopoda*) (Fig.13). Males displayed typical behavior as described by Armstrong and Murphy (1979) such as frequent head bobs and tongue flicks on the female's back. In most cases, once females became aware of my presence, they moved deeper into the vegetation to avoid exposure to a potential predator. On the other hand, males never seemed to notice my presence and continued focusing on courtship or copulation activity. This seemingly indifferent behavior supports the idea that males are more susceptible to predators during the mating season, which incidentally was the time period when four rattlesnakes were killed by unknown predators (see below).

FIG. 12. Male and female *C. lepidus* copulating under vegetation on IMRS.

FIG. 13. Male and female *C. lepidus* during courtship behavior right after sunset on IMRS.

Predation.- Unfortunately, four male adult *C. lepidus* (005, 006, 007, 008) were lost to unknown predators during early stages of the radiotracking process that coincided with the time period of mating activity. Rattlesnake fatalities in two happened once in the early morning and another late in the afternoon when rattlesnakes typically abandon their shelters. Individual 006 was found in the morning of 21 October 2007 at 0700 h on an alluvial rocky slope, with his head and rattle completely missing from his body. However, his body was still contorting, which suggested that he had been attacked a few minutes prior to his discovery. Individual 008 was found dead during late (1800 h) afternoon on19 July 2008 at the edge of an arroyo. Examination of his body indicated that his head had been crushed, very likely a few hours before it was found. With respect to the other two rattlesnakes (005, 007), only the transmitters were located. Most likely those two rattlesnakes were killed several days before transmitters were found, indicating that predators either ate the entire rattlesnake or they spread the body parts in a way that widely disseminated the remains. Klauber (1997) and Greene et al. (2002) reported several vertebrates as enemies of rattlesnakes, including deer, antelope, sheep, goats, horses, cattle, peccaries, hogs, badgers, coyotes, foxes, dogs, skunks, weasels, opossums, bobcats, domestic cats, rodents,

raccoons, ring-tailed cats, eagles, hawks, owls, roadrunners, wild turkeys, king snakes, racer snakes, bull snakes, Gila monsters, alligators, turtles, amphibians, fishes, and human beings. They either kill rattlesnakes because they perceive them as a threat or because they are potential food items. From those predators, deer, Barbary sheep, horses, cattle, peccaries, badgers, coyotes, foxes, skunks, bobcats, ring-tailed cats, hawks, owls, roadrunners, racers, and bull snakes are present in the study area. However, personal observations plus the use of video cameras with rattlesnake models painted with colors similar to Rock Rattlesnakes and placed in sites where individuals were killed, indicated that deer, peccaries, foxes, badgers, skunks, and bobcats seem to be the most common there; so one or more of those may be the primary suspects for killing the four Rock Rattlesnakes. Deer are known to kill rattlesnakes by stomping them repeatedly with their front feet; which could have been the fate of individual 008. Peccaries kill rattlesnakes by jumping on them several times with their hoofs and eat the remains and Badgers are well known for even digging rattlesnakes out from their shelters and then kill them (Klauber, 1997).

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Appendix

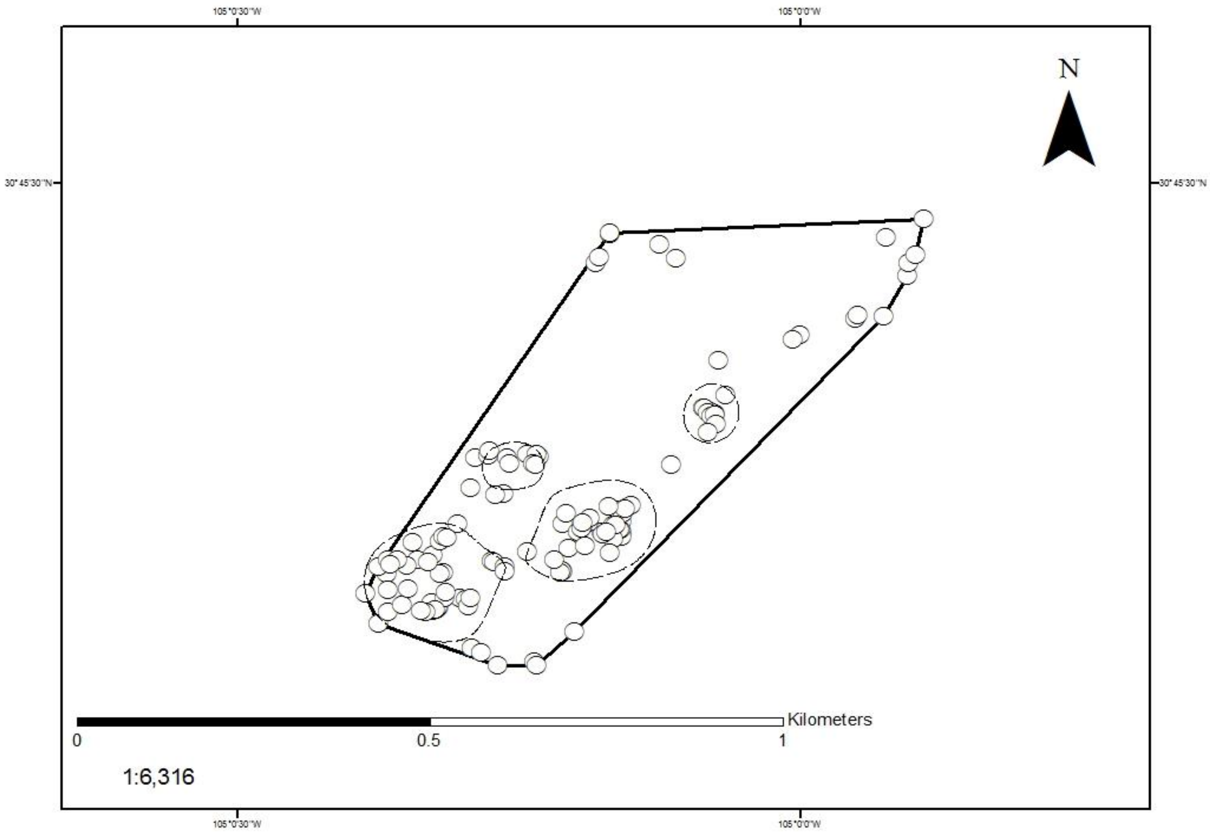

Figure A-1.- Geographic locations (circles), MCP (continuous line) and 50% kernel area (dashed lines) of male *C. lepidus* ID: 001, radiotracked at IMRS from September, 2007 to August, 2009.

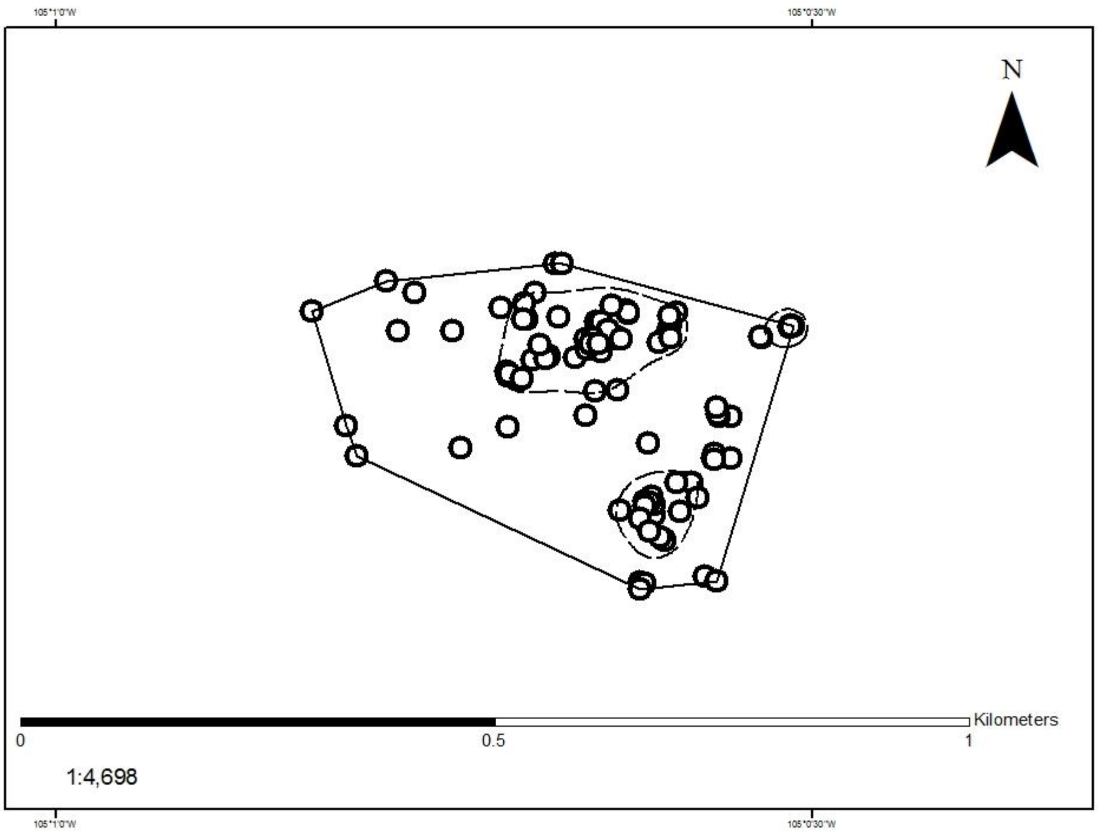

Figure A-2.- Geographic locations (circles), MCP (continuous line) and 50% kernel area (dashed lines) of male *C. lepidus* ID: 002, radiotracked at IMRS from July, 2007 to June, 2008, and from July, 2009 to June, 2010.

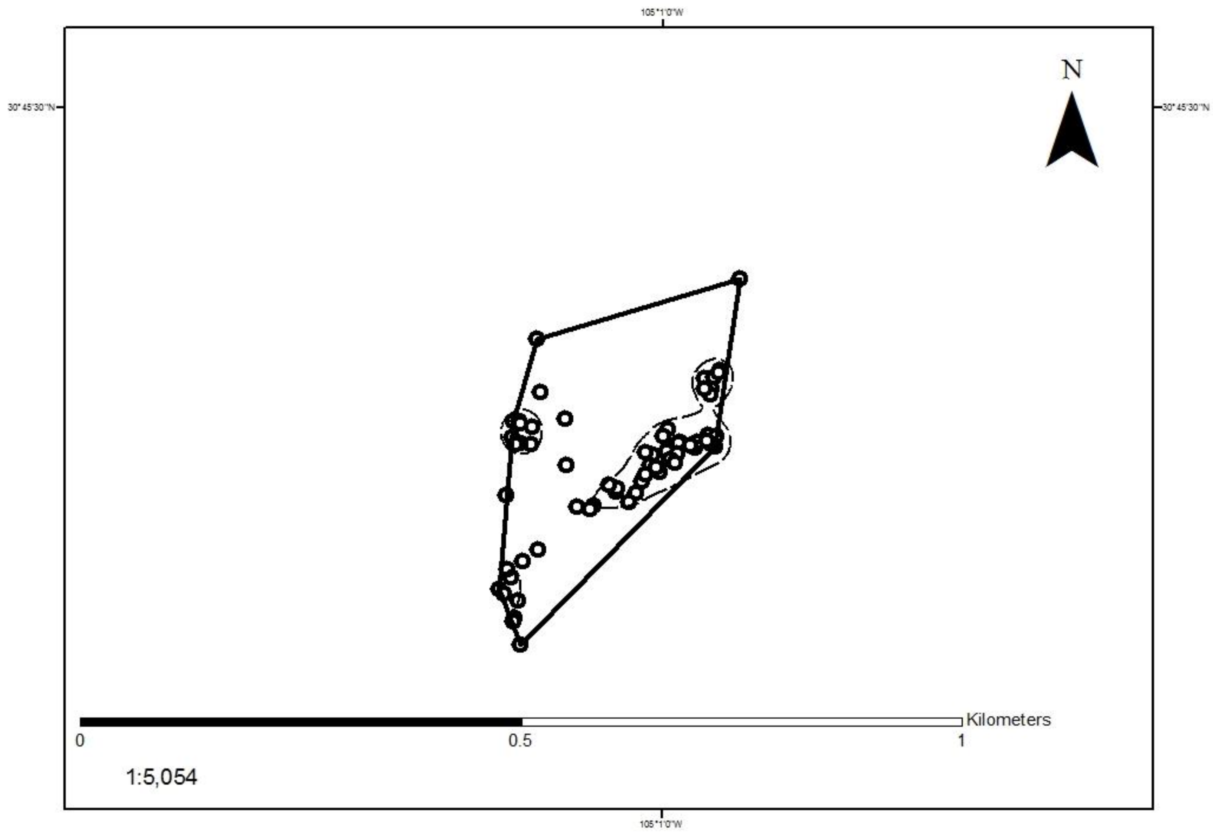

Figure A-3.- Geographic locations (circles), MCP (continuous line) and 50% kernel area (dashed lines) of female *C. lepidus* ID: 003, radiotracked at IMRS from October, 2008 to June, 2010.

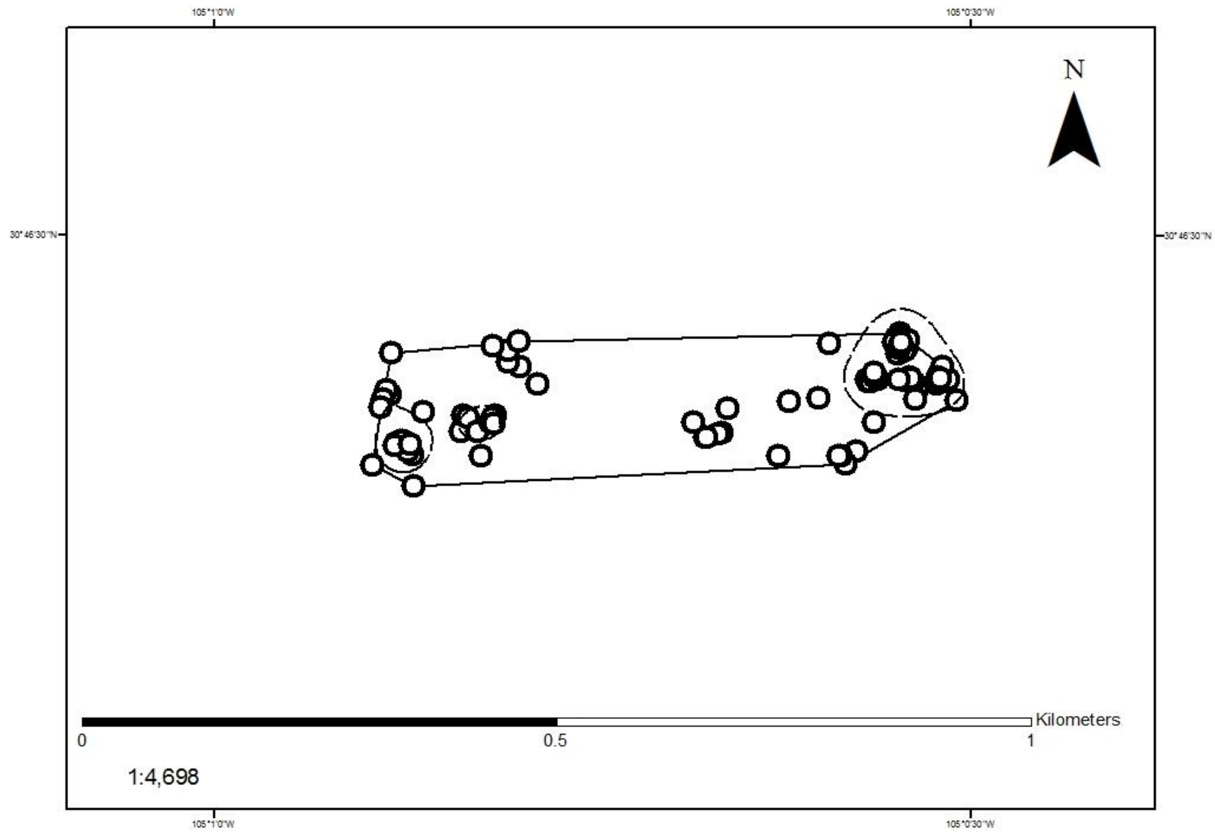

Figure A-4.- Geographic locations (circles), MCP (continuous line) and 50% kernel area (dashed lines) of female *C. lepidus* ID: 004, radiotracked at IMRS from July, 2007 to July, 2008.

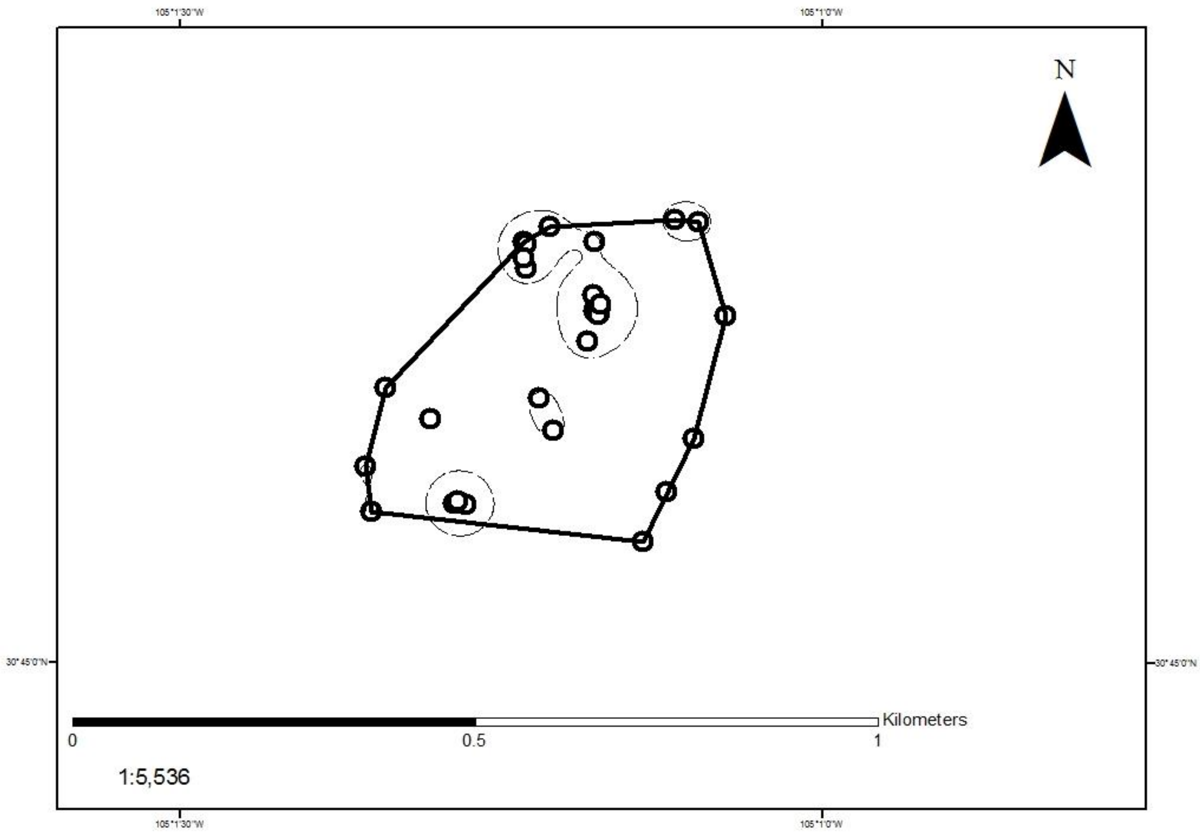

Figure A-5.- Geographic locations (circles), MCP (continuous line) and 50% kernel area (dashed lines) of male *C. lepidus* ID: 021, radiotracked at IMRS from August, 2009 to July, 2010.

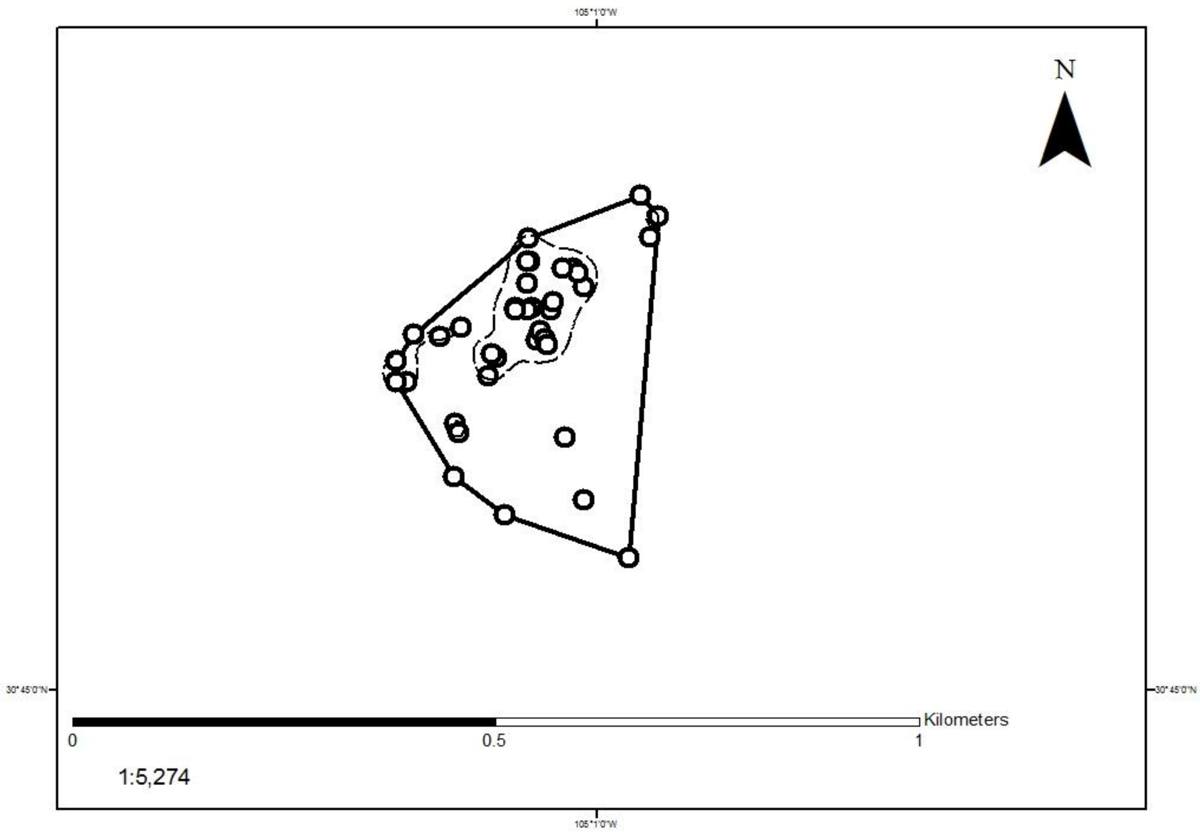

Figure A-6.- Geographic locations (circles), MCP (continuous line) and 50% kernel area (dashed lines) of male *C. lepidus* ID: 022, radiotracked at IMRS from September, 2009 to August, 2010.

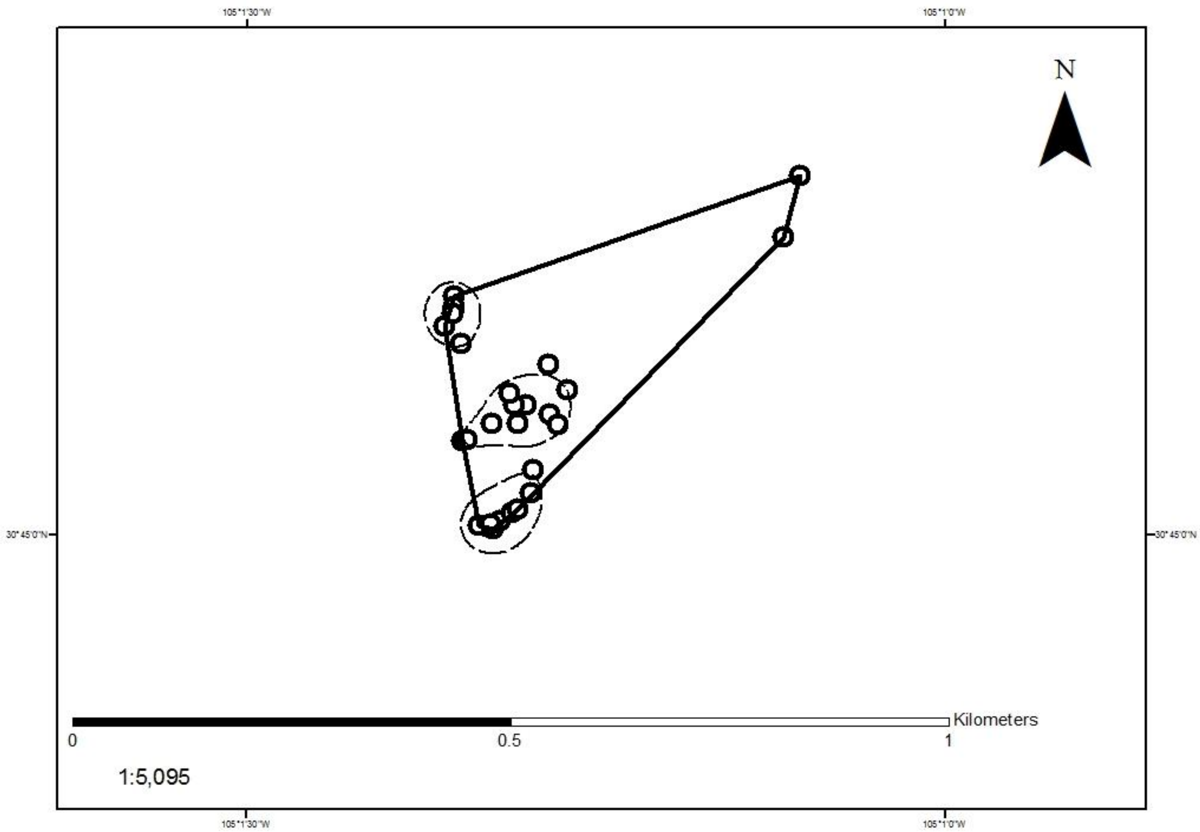

Figure A-7.- Geographic locations (circles), MCP (continuous line) and 50% kernel area (dashed lines) of male *C. lepidus* ID: 023, radiotracked at IMRS from September, 2009 to August, 2010.

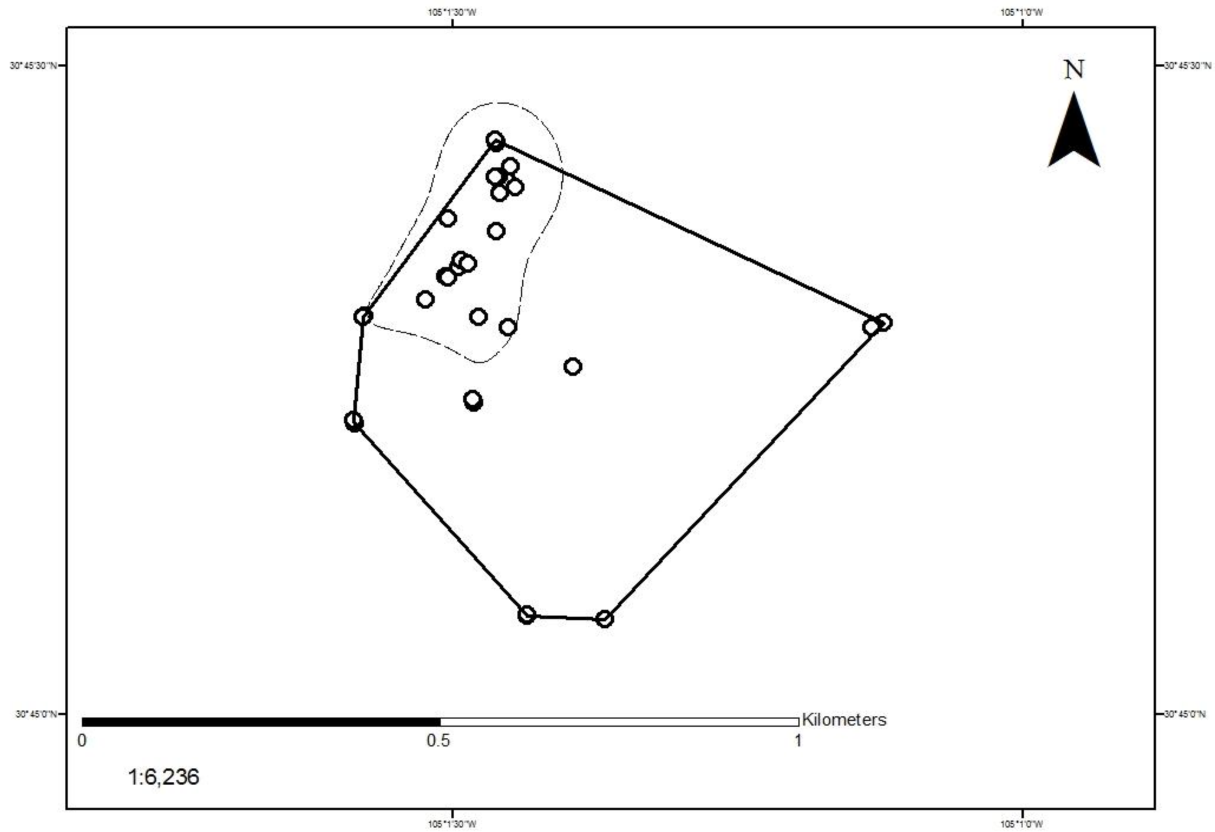

Figure A-7.- Geographic locations (circles), MCP (continuous line) and 50% kernel area (dashed lines) of male *C. lepidus* ID: 024, radiotracked at IMRS from September, 2009 to August, 2010.

CHAPTER II

Overwintering Characteristics of the Rock Rattlesnake, *Crotalus lepidus*, On Indio Mountains Research Station, Hudspeth County, Texas

ABSTRACT. - Due to their ectothermic nature, most rattlesnakes in North America spend winters below the surface in order to avoid lethal temperatures and predators. Although rattlesnakes spend a significant amount of time underground while overwintering, little is known about the physiology and behavior of these organisms during winter, and the same applies to the Rock Rattlesnake, *Crotalus lepidus*. The main goal on this study was to investigate through radiotelemetry, body temperature, ingress and egress dates from winter shelters, slopes selection, and time period that Rock Rattlesnakes spend during winter months on Indio Mountains Research Station (IMRS), located in the northern Chihuahuan Desert of west Texas in Hudspeth County.

Four rattlesnakes were monitored during winter 2007-2008, two in 2008-2009, and six in 2009-2010. Rattlesnakes overwintered at single sites from early November until late-March or early-April. Mean ingress date was 8 November during all winters. There was no significant difference between ingress dates for winters 2007-2008 and 2009-2010 (Mann-Whitney $U = 15.000$, $p = 0.211$, $n = 9$). Mean egress date was 31 March during all winters. There was no significant difference between egress date for winters 2007-2008 and 2009-2010 (Mann-Whitney $U = 17.50$, $p = 0.053$, $n = 9$). Overwintering period for all rattlesnakes had a mean of 143 days, ranging from 134 to 170 days. There was no significant difference in number of days spent

overwintering between winter seasons 2007-2008 and 2009-2010 (Mann-Whitney U = 17.00, $p = 0.082$, $n = 9$). Average overwintering days for females ($n = 2$) was 140 days and 145 days for males ($n = 10$).

Average body temperature recorded from six individuals during winter 2009-2010 averaged 19.2 ± 0.055°C ($n = 4471$). Average diurnal body temperature was 19.7 ± 0.095°C ($n = 1911$) and nocturnal temperature was 18.8 ± 0.063°C ($n = 2560$); the comparison was statistically significant ($t = 7848$, $df = 4469$, $p < 0.001$).

Rattlesnakes during the winter period of 2009-2010 (November through March) had the highest body temperatures in November (21.6 ± 0.119°C, $n = 754$), followed by March (20.1 ± 0.104°C, $n = 927$) and December (19.3 ± 0.104°C, $n = 1005$). On the other hand, rattlesnakes experienced the coldest average body temperatures in January (16.4 ± 0.110°C, $n = 936$) and February (18.8 ± 0.106°C, $n = 846$). All average monthly temperatures were statistically significant ($p < 0.001$).

Hourly average body temperature profiles for all the rattlesnakes during the entire winter period of 2009-2010 indicated that in general individuals maintained comparatively stable conditions. Rattlesnakes attained somewhat higher average temperatures (20.4-21.2 °C) between 1400 and 1700 hrs and lower temperatures (17.8-18.0 °C) between 0700 and 0900 hrs.

Average body mass lost from nine rattlesnakes during winters 2007-2008, 2008-2009 and 2009-2010 was 13.9 ± 4.40 g (10.9% of body weights) and ranged from 1.0 to 44.6 g. Comparison of body mass before and after winter was statistically significant ($t = 2.841$, $df = 7$, $p = 0.025$, $n = 8$).

Eight rattlesnakes overwintered on southeast facing slopes, two overwintered on west facing slopes, one spent the winter on a southwest facing slope, and another individual selected a northwest facing slope. Although southwest facing slopes are the most abundant in the study area they were not the preferred slopes by *C. lepidus*. However, ground temperature readings from the eight cardinal slopes directions during winter of 2010-2011 indicated that in general, southern facing slopes were warmer than slopes facing other directions, with the highest ground temperatures being recorded on the southeast facing slope. Overwintering sites were not frequently used during activity periods during warmer months, but it is important that all sites be included in protection and conservation plans aimed at addressing survivability of *C. lepidus* in Chihuahuan Desert scrub habitats. Because *C. lepidus* has a large geographic range, including a wide latitudinal variance and significant variation in elevation ranging from desert flats to high mountains, an analysis of *C. lepidus* range-wide is needed to fully understand all overwintering features for the species.

INTRODUCTION

As ectothermic organisms, rattlesnakes depend on surrounding heat sources to accomplish behavioral and physiological processes (Huey, 1982; Lillywhite, 1987). Although ectothermy could be perceived as a limitation, rattlesnakes thrive in a variety of habitats located at different latitudes and elevations in the northern hemisphere (Shine and Madsen, 1996; Daltry et al., 1998). This success relies partly on the ability of rattlesnakes to adapt to the seasonal changes habitats experience, although they are more active during warmer periods of the year (Gibbons and Semlitsch, 1987). On the other hand rattlesnakes utilize different strategies to avoid cold periods that otherwise would expose them to low temperatures that could lead directly to death from temperature alone, or by exposing them to predators. The most common strategy to avoid deleterious cold periods is hibernation (Spelleberg, 1976; Gregory, 1982), a phenomenon characterized by a decrease of body temperature leading to a decrease in surface activity. Hibernation is more relevant at higher latitudes and higher elevations where snakes may remain inactive for several months (Gregory, 1982; Zuffi et al., 1999; McNab, 2002). Populations of rattlesnakes living at higher latitudes and elevations typically hibernate in large groups (hundreds or even thousands) in dens located away from their summer ranges, while individuals of populations at lower latitudes and elevations spend the winter singly in hibernacula normally located within their summer ranges (Klauber, 1997). With respect to latitude, 38°N has been suggested to be separation point for these wintering behaviors (Sexton et al., 1992). Dates of movement to (ingress) and away (egress) from the hibernacula have been also investigated (Macartney, 1985; Cobb and Peterson, 2008), but no clear patterns have been identified. One major question that herpetologists want to answer about rattlesnake overwintering characteristics is what body temperatures are maintained inside their winter shelters. Because southern facing

slopes receive more solar radiation during winter months in the northern hemisphere (Sexton and Hunt, 1980; Hamilton and Nowak, 2009), rattlesnakes selecting those slopes have higher probabilities of experiencing more favorable temperatures. While remaining relatively inactive during cold periods, they have been shown to lose a significant amount of weight (Hirth, 1966; Klauber, 1997; Cobb and Peterson, 2008). Although many rattlesnakes spend a significant amount of time hibernating (up to nine months in more northern latitudes; Brown, 1982), so far aspects of thermal regulation during cold period have been reported only for populations belonging to the following six species out of the 18 distributed within North America north of Mexico (Beaman and Hayes, 2008): *C. viridis* (Jacob and Painter, 1980); *C. horridus* (Brown, 1982); *C. molossus, C. atrox, C. tigris* (Beck, 1995); *C. pricei* (Prival et al., 2003); and *C. oreganus* (Cobb and Peterson, 2008).

Although *Crotalus lepidus* (Fig. 1) is a relatively small rattlesnake (600-700 mm maximum total length; Campbell and Lamar, 2004; Klauber, 1997), it has a relatively wide geographic distribution, ranging from southeastern Arizona, southern New Mexico, and southwestern Texas southward to central Mexico (Campbell and Lamar, 2004). Until now, little information concerning the overwintering characteristics of *C. lepidus* has been reported.

The study presented herein contributes to the knowledge of behavioral and physiological aspects (e.g., body temperature, ingress and egress dates, movement, and body mass loss) of *C. lepidus* during winter periods in a population located in the northern portion of the Chihuahuan Desert, which positions it into an ecological regime that includes warm winter periods along with cold spells when the temperature falls well below activity levels for snakes.

FIG. 1. An adult male *Crotalus lepidus* (TL = 620 mm) from Indio Mountains Research Station, Hudspeth County, Texas.

MATERIALS AND METHODS

All protocols followed in this study were approved by the UTEP IACUC (#A-200704-2) for the period of 1 July 2007 through 30 June 2010.

Study Area.- This study was performed on Indio Mountains Research Station (IMRS), (30.75°N, 105.00°W), which is located within the northern Chihuahuan Desert in southeastern Hudspeth County, Texas, about 40 km southwest of Van Horn (Fig. 2). A detailed description of the area can be found in Worthington et al. (2004; available at www.utep.edu/indio/).

FIG. 2. Indio Mountains Research Station Headquarters, located in the Chihuahuan Desert, Hudspeth County, Texas.

The study site is located on the Indio Mountains range, which in general runs from north to south with slopes primarily facing east and west. In general, most of the mountainous portions of peaks, ridges, rugged slopes and steep arroyos are composed of intermittent conglomerate, sandstone, limestone, and igneous substrates, or a mixture of them where they adjoin. Radiating off the steeper slopes in the flats are alluvial fans transected by local small arroyos and by larger arroyos draining primary watersheds originating in the mountainous portions. Major arroyos either drain into the Rio Grande to the south and southwest or eastward into the Green River.

Average annual precipitation in IMRS is typically 235 mm, with most rainfall (70%) occurring during the summer monsoon season (from June to September). Annual average temperature for areas near IMRS headquarters is about 18º C.

The vegetation is typical of the Chihuahuan Desert scrubland consisting of dominant species, such as Creosotebush (*Larrea tridentata*), White-thorn Acacia (*Acacia constricta*), Catclaw (*Acacia greggii*), Honey Mesquite (*Prosopis glandulosa*), and clumps of Prickly Pear (*Opuntia* spp.), mostly on alluvial flats and along arroyos, and Lechuguilla (*Agave lechuguilla*), Pitaya (*Echinocereus enneacanthus*), Ocotillo (*Fouquieria splendens*), Sotol (*Dasylirion leiophyllum*), Torrey's Yucca (*Yucca treculiana*), Eve's Needle (*Yucca faxoniana*), and clumps of Prickly Pear (*Opuntia* spp.) on rocky slopes, interspaced with grasses such as Black Grama (*Bouteloua eriopoda*), Arizona cottontop (*Digitaria californica*), and Tanglehead (*Heteropogon contortus*).

Transmitter Implantation.- The project reported herein was carried out on IMRS from the winter 2007-2008 through the winter 2009-2010. Rattlesnakes studied during those winter periods were the same individuals that were collected opportunistically and radiotracked during

the corresponding warmer months of those years. Individuals were implanted with 5g transmitters using the method proposed by Reinert and Cundall (1982) and modified by Hardy and Greene (1999, 2000). In brief, every time a rattlesnake was found, it was brought to the headquarters to be processed. The rattlesnake was coaxed to crawl into a transparent plastic tube to a depth of about one-third its body length. The posterior two-thirds portion of the rattlesnake's body was held by hand for insertion of a PIT-tag and transmitter implantation surgery. First, a PIT-tag was inserted subdermally into the right dorsolateral area, previously disinfected with 70 % ethanol, approximately 20 cm from the cloaca using a sterile PIT-tagging syringe. After implanting the PIT-tag, antiseptic liquid bandage (New Skin) was applied to the small needle puncture to induce healing and to prevent infection. Snout-vent length, sex, and weight were recorded, as well. The tubed rattlesnake was then placed on a sterilized table and positioned anteriorly into an anesthesia chamber for general inhalation anesthesia using liquid isoflurane (.25 to 1 ml). Cotton was placed between the tubed snake and walls of the chamber to minimize release of excess gas into the laboratory room. Anesthesia was dispensed from a syringe into cotton mass located in the chamber directly in front of the tubed snake's head. Response to the anesthetic was monitored using tail withdrawal reflex, by observing the rate and depth of respiration, and the rate of the cardiac impulse. After the snake was anesthetized, a wide area of skin was prepared around the incision site using Betadine solution. A 1 cm longitudinal incision was made into the peritoneal cavity on the right side (ventrolateral) of the body near the end of the second third of the snake's body, and a transmitter (SB2, 5g; Holohil Systems Ltd.) previously sterilized with benzalkonium chloride for a minimum of one hour was implanted into the cavity. Next, the antenna was then inserted subcutaneously along the body, between scale rows 2 and 3 anterior to the transmitter, using a fine bore brass tube that was removed through a

small incision placed a distance slightly greater than antenna's length from the transmitter. Incision was closed in a single layer using an "interrupted, horizontal mattress" stitch. After surgery, the rattlesnake, while still inside the plastic tube, was removed from the anesthesia chamber that was taken outside the laboratory into the open air for complete ventilation of residual anesthesia. While the rattlesnake remained in the plastic tube, respiration and circulation was monitored. Once normal breathing and strong muscle tone was detected and regular coordinated movements and tongue flicking were observed, the snake was returned gently to the storage container and kept warm (between 25º and 30º C). The snake was frequently checked visually and gently prodded to be sure recovery was uneventful during the following several hours and finally returned to the wild at its original site of capture within 24 hours. Transmitter implantation lasted from 10 to 15 minutes.

Ecogeographic Monitoring.- In total, 12 adult rattlesnakes were monitored during the winter months (November through March), four in winter 2007-2008 (one female and three males), two in winter 2008-2009 (one female and one male), and six in winter 2009-2010 (one female and five males). One female was monitored twice (female 003: 2008-2009, and 2009-2010), as were two males (male 001: 2007-2008, 2008-2009; male 002: 2007-2008, 2009-2010). All statistical analyses were performed using Systat Version 10.2 (Systat software Inc., 2002). Parametric (t test) and non parametric (Mann-Whitney U test, Chi square) tests were employed, depending on whether parametric assumptions were met, with $p < 0.05$ to assess statistical significance.

Winter shelters were located when a rattlesnake was first detected at a site during the first cold days and remained there throughout the entire winter season. Those observations determined the start and the end dates of the overwintering period for each individual. Ingress

and egress dates, and total overwintering days between winters 2007-2008 and winter 2009-2010 were compared with Mann-Whitney U tests. Winter 2008-2009 was not included in the latter comparison because only two individuals were radiotracked during that period. Once the winter period started, rattlesnakes were monitored every other weekend (Friday-Sunday) until the rattlesnake left the site and began its warm season activities. Geographic location, elevation, slope direction, substrate type, and vegetation of shelter locality were recorded to determine if particular environmental conditions were selected by the rattlesnakes. Slope direction was determined using a Brunton compass (Brunton Inc.) using true north as a reference. Each time individuals were monitored, their body temperatures were obtained by determining time intervals between eleven continuous signals emitted by the temperature sensitive transmitters calibrated by their suppliers (Holohil Systems Ltd.), with shorter intervals indicating warmer temperatures; corresponding temperatures were obtained from plotted curves for each transmitter. During the winter of 2009-2010 body temperature was recorded for six snakes every ten minutes for 24 hours using an MP3 digital voice recorder (Olympus Inc.). From those, hourly, monthly, and seasonal body temperature profiles were plotted to determine temperature variation. When individuals were observed outside their shelters, date and time, body and substrate temperature, physical position, and behavior were recorded. Calibrated temperature HOBO data-loggers (Onset Computer Corporation Inc.) were used for recording environmental temperatures (Te) at ground level near the overwinter shelters. A two-sample t test with Bonferroni adjusted probabilities was used to compare diurnal versus nocturnal average body temperatures. Average body temperatures per month as well as per individual were analyzed with paired sample t tests with Bonferroni adjusted probabilities.

Nine individuals were weighed in grams before and after the winter period to determine if they lost body mass and if they did, what was the average percentage lost at the end of the cold period. Body mass loss before and after winters, was analyzed with a one sample t test.

The percentage of eight cardinal slope directions within the study area (N, NE, E, SE, S, SW, W, NW) was determined to see if rattlesnakes preferred certain slopes during the winter period and if the preference was due to site availability or to other factors. Percentage of slope directions was estimated on a map from a contiguous area containing approximately 16, 187 hectare units using GIS ArcMap 9.3 (ESRI, 2004) tools; frequencies of pixels and their corresponding slopes were analyzed with a Chi square test (X^2). Overwintering shelters were then documented for placement onto its proper slope direction for analysis. After the radio-tracking stage of the project, during winter of 2010-2011, ground temperatures were taken 15 cm below the surface at each of the eight slope directions on a hill within the study area to gather thermodynamic characteristics of each slope. The data was then used to see if rattlesnakes select shelters based on temperature differentials on different slopes during winter months. Ground temperatures were recorded every two hours from November to March using calibrated temperature HOBO data-loggers (Onset Computer Corporation Inc.).

RESULTS

A total of 12 Rock Rattlesnakes were radiotracked during the winters 2007-2008, 2008-2009, and 2009-2010. In general rattlesnakes overwintered at single sites from early November until late-March or early-April. The earliest individual (008, male) reached its shelter on 2 November 2007 and the latest (001, male) arrived on 17 November 2007 (Table 1). Mean ingress date was 8 November for all winters. There was no significant difference between ingress dates of winters 2007-2008 and 2009-2010 (Mann-Whitney $U = 15.000$, $p = 0.211$, $n = 9$). On the other hand, the first individuals (003, 021, 023, 024; one female and three males, respectively) abandoned their shelters on 21 March 2010, and the last individual (008, male) left on 20 April 2008. Mean egress date was 31 March for all winters. There was no significant difference between egress date of winters 2007-2008 and 2009-2010 (Mann-Whitney $U = 17.50$, $p = 0.053$, $n = 9$). Overwinter period for all rattlesnakes had a mean of 143 days, ranging from 134 to 170 days. There was no significant difference in number of days spent overwintering between winter seasons 2007-2008 and 2009-2010 (Mann-Whitney $U = 17.00$, $p = 0.082$, $n = 9$). Average overwintering days for females was 140 days and 145 days for males.

In total, 4471 body temperature measurements were recorded from six individuals during winter 2009-2010. Average body temperature for the entire winter period was 19.2 ± 0.055°C, ranging from 11.5°C to 33°C (Fig. 3). Average diurnal body temperature was 19.7 ± 0.095°C ($n = 1911$) and nocturnal was 18.8 ± 0.063°C ($n = 2560$) (Fig. 4). Although average nocturnal and diurnal body temperatures appeared close to being similar, they were statistically significant ($t = 7848$, $df = 4469$, $p < 0.001$).

TABLE 1. Overwintering periods of *C. lepidus* on IMRS during winters 2007-2008, 2008-2009, and 2009-2010.* = rattlesnake monitored for a second overwintering period. ** = rattlesnake killed by predator before the overwintering period.

Snake ID	Sex	TBL (mm)	Ingress date	Egress date	Total days	Winter
003	♀	540	8-Nov	27-Mar	139	2008-2009
004	♀	529	11-Nov	6-Apr	147	2007-2008
001	♂	700	17-Nov	5-Apr	140	2007-2008
002	♂	625	10-Nov	5-Apr	147	2007-2008
008	♂	635	2-Nov	20-Apr	170	2007-2008
021	♂	625	7-Nov	21-Mar	134	2009-2010
022	♂	645	7-Nov	7-Apr	151	2009-2010
023	♂	550	6-Nov	21-Mar	135	2009-2010
024	♂	620	6-Nov	21-Mar	135	2009-2010
003*	♀	540	7-Nov	21-Mar	134	2009-2010
001*	♂	700	9-Nov	31-Mar	142	2008-2009
002*	♂	625	8-Nov	8-Apr	151	2009-2010
005**	♂	595	-	-	-	-
006**	♂	678	-	-	-	-
007**	♂	575	-	-	-	-
Average	-	612.1	-	-	143	-

Rattlesnakes during the winter period of 2009-2010 (November through March) had the highest body temperatures in November (21.6 ± 0.119°C, n = 754), followed by March (20.1 ± 0.104°C, n = 927) and December (19.3 ± 0.104°C, n = 1005) (Fig. 5). On the other hand, rattlesnakes experienced the coldest body temperatures in January (16.4 ± 0.110°C, n = 936) and February (18.8 ± 0.106°C, n = 846). All average monthly temperatures were statistically significant ($p < 0.001$) (Table 2). In general, average body temperatures patterns followed environmental temperatures, with the average Te being lower during all months except March (Fig. 6). Average Te for all five months was 14.8 ± 0.005°C (n = 25702). With respect to

individual body temperatures, rattlesnake 002 had the highest average body temperature (22.3 ± 0.068°C) and rattlesnake 003 had the lowest (17.1 ± 0.145°C) (Table 3). Average body temperatures for each rattlesnake were statistically significant ($p < 0.001$) (Table 4).

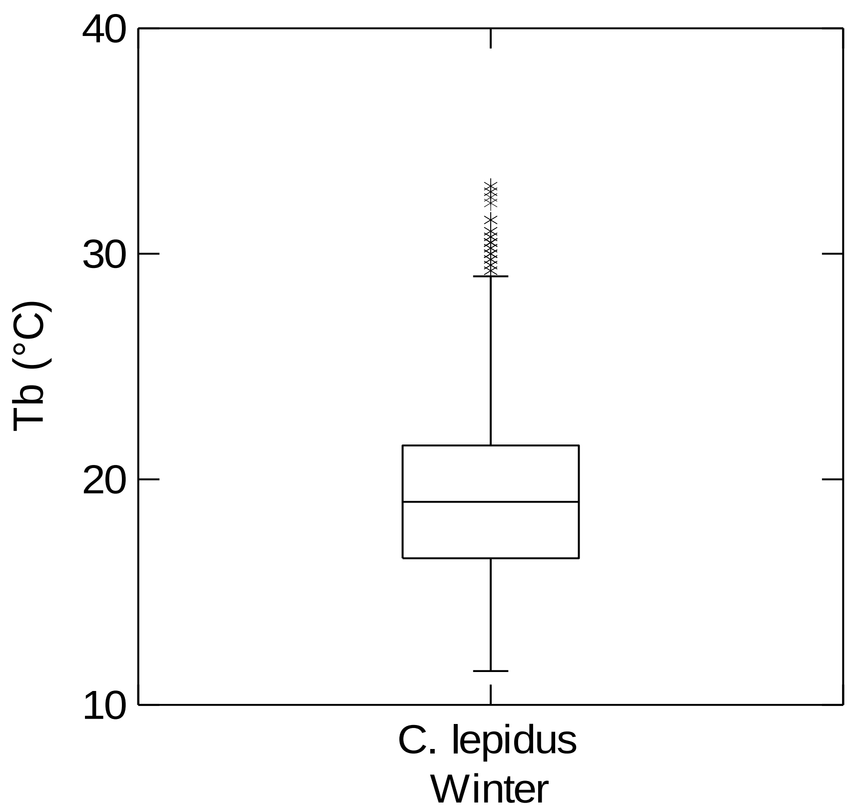

FIG. 3. Box plot of body temperature of six individual *C. lepidus* for winter 2009-2010 on IMRS.

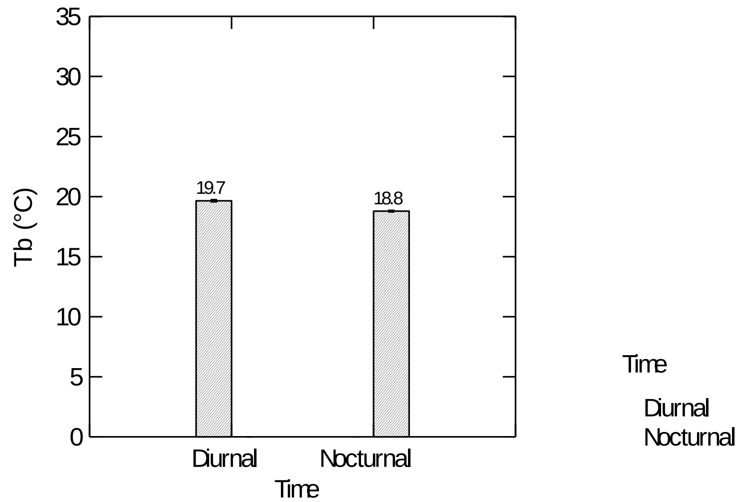

FIG. 4. Average diurnal and nocturnal body temperatures of six individual *C. lepidus* during the winter 2009-2010.

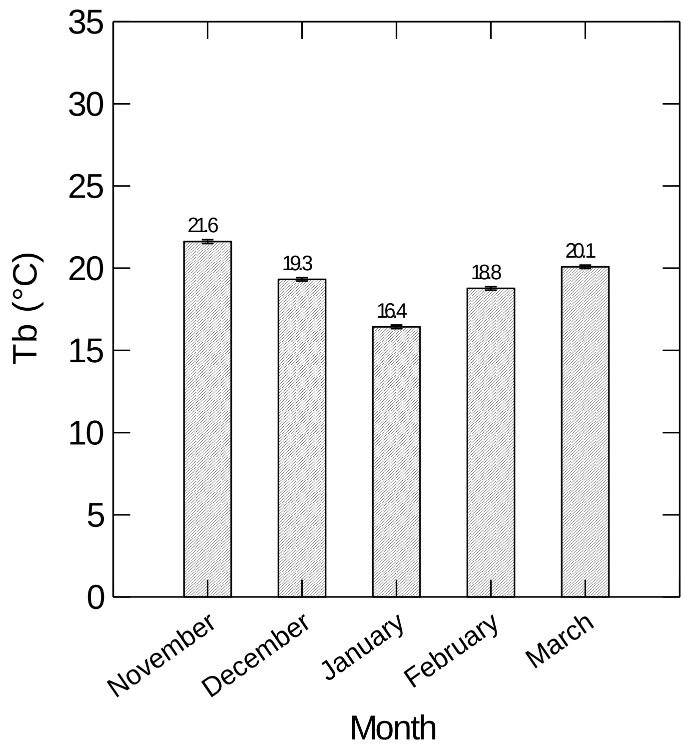

FIG. 5. Monthly mean body temperatures of six individual *C. lepidus* on IMRS (n = 4471) during the winter of 2009-2010. Error bars denote standard error.

TABLE 2. Matrix of pair-wise mean differences and comparison probabilities (in parenthesis) of body temperatures (Tb) of *C. lepidus* between months from winter 2009-2010.

Month	Nov	Dec	Jan	Feb	Mar
Nov	0				
Dec	2.527 (<0.001)	0			
Jan	6.070 (<0.001)	3.030 (<0.001)	0		
Feb	2.751 (<0.001)	0.691 (<0.001)	-2.653 (<0.001)	0	
Mar	1.245 (<0.001)	-0.602 (<0.001)	-3.677 (<0.001)	-1.464 (<0.001)	0

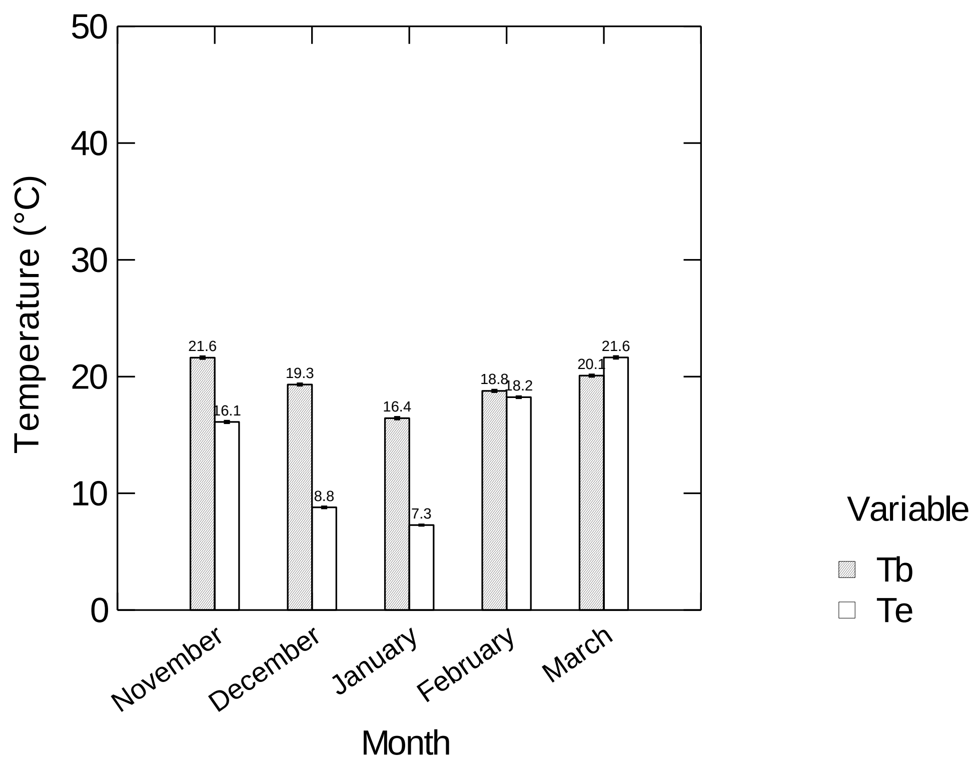

FIG. 6. Monthly average body temperatures (Tb) of six *C. lepidus* and environmental temperatures (Te) from winter 2009-2010. Error bars denote standard error.

TABLE 3. Body temperatures (°C) of six individual *C. lepidus* from winter 2009-2010.

Snake ID	Sex	Average Tb	Minimum Tb	Maximum Tb	N	Slope
003	♀	17.1 ± 0.145	11.5	33.0	1106	SE
002	♂	22.3 ± 0.068	18.5	26.0	721	SE
021	♂	21.8 ± 0.087	16.5	27.8	640	SE
022	♂	19.0 ± 0.072	16.3	29.8	628	SE
023	♂	17.9 ± 0.110	12.0	25.0	758	NW
024	♂	18.2 ± 0.060	16.0	21.5	618	W

TABLE 4. Matrix of pair-wise mean differences and comparison probabilities (in parenthesis) of body temperatures (Tb) between six individual *C. lepidus* from winter 2009-2010.

Snake ID	002	003	021	022	023	024
002	0					
003	6.3 (<0.001)	0				
021	0.813 (<0.001)	-5.685 (<0.001)	0			
022	3.615 (<0.001)	-2.911 (<0.001)	2.868 (<0.001)	0		
023	4.403 (<0.001)	-1.941 (<0.001)	4.11 (<0.001)	1.358 (<0.001)	0	
024	4.431 (<0.001)	-2.119 (<0.001)	3.73 (<0.001)	0.835 (<0.001)	-0561 (<0.001)	0

Hourly average body temperature profiles for all the rattlesnakes during the entire winter period of 2009-2010 (Fig. 7) showed that in general individuals maintained comparatively stable conditions. Rattlesnakes attained somewhat higher average temperatures (20.4-21.2 °C) between 1400 and 1700 hrs and lower temperatures (17.8-18.0 °C) between 0700 and 0900 hrs. By

month, hourly average body temperatures indicated that rattlesnakes attained higher average body temperatures at specific time periods during the day. During November rattlesnakes remained the warmest (23.7-27.7°C) between 1300 and 1600 hrs (Fig. 8). During December rattlesnakes had the highest body temperatures (20.0-21.0 °C) between 1200 and 1600 hrs (Fig. 9).

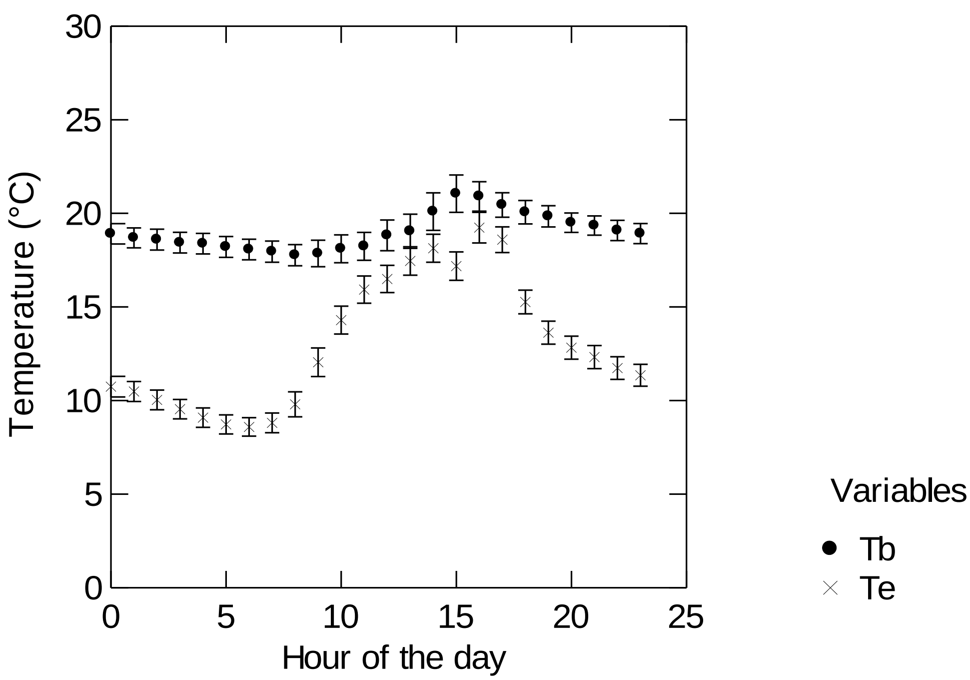

FIG. 7. Hourly Tb profile of six individual *C. lepidus* during winter 2009-2010 (n = 3515). Error bars denote standard error.

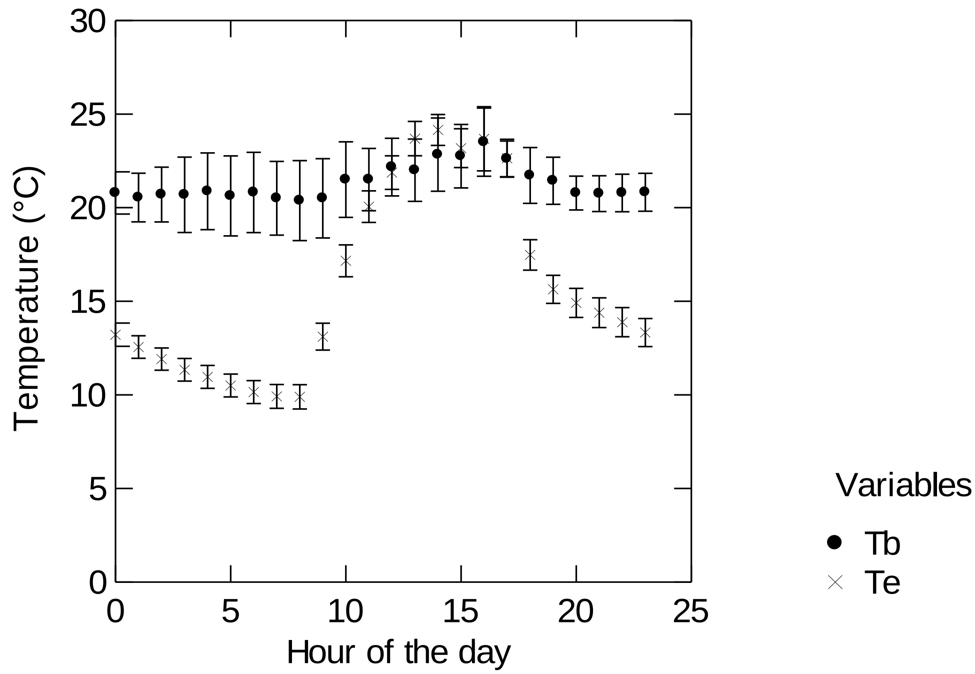

FIG. 8. Hourly Tb profile of six individual *C. lepidus* during November, 2009 (n = 906). Error bars denote standard error.

During January rattlesnakes had the highest body temperatures (20.0-21.0 °C) between 1900 and 2100 hrs (Fig. 10). During February rattlesnakes had the highest body temperatures (24.3-27.1 °C) between 1100 and 1600 hrs (Fig. 11). During March, rattlesnakes remained the warmest (27.7-33.3 °C) between 1100 and 1400 hrs (Fig.12).

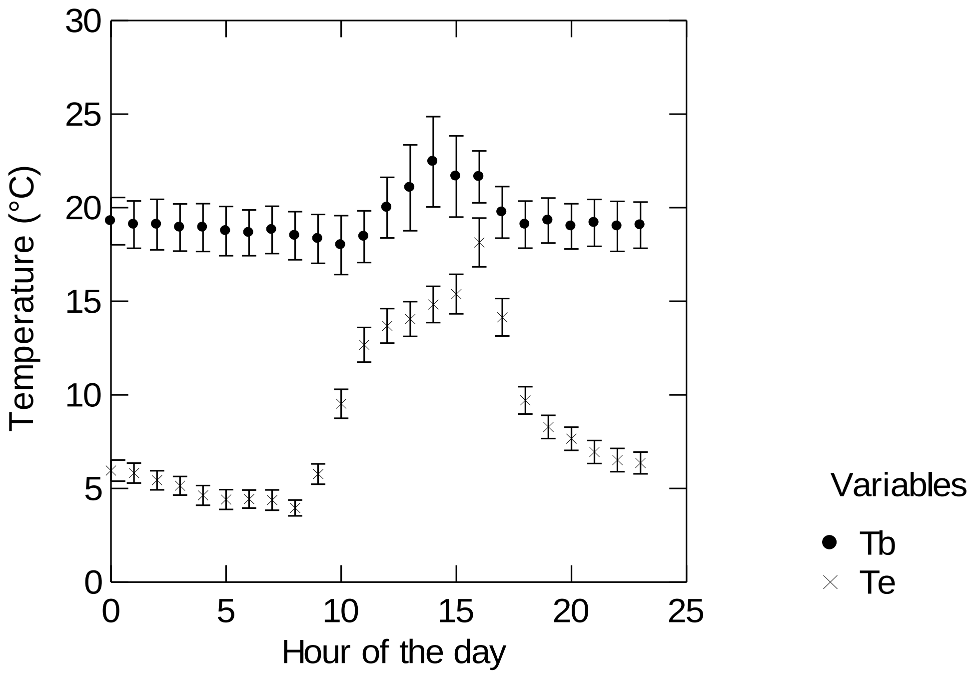

FIG. 9. Hourly Tb profile of six individual *C. lepidus* during December, 2009 (n = 913). Error bars denote standard error.

The body mass lost from nine individuals during the winters of 2007-2010 is recorded in Table 5. Average body mass lost was 13.9 ± 4.40 g (10.9% of body weights) and ranged from 1.0 to 44.6 g. Comparison of body mass before and after winter was statistically significant ($t = 2.841$, $df = 7$, $p = 0.025$, $n = 8$).

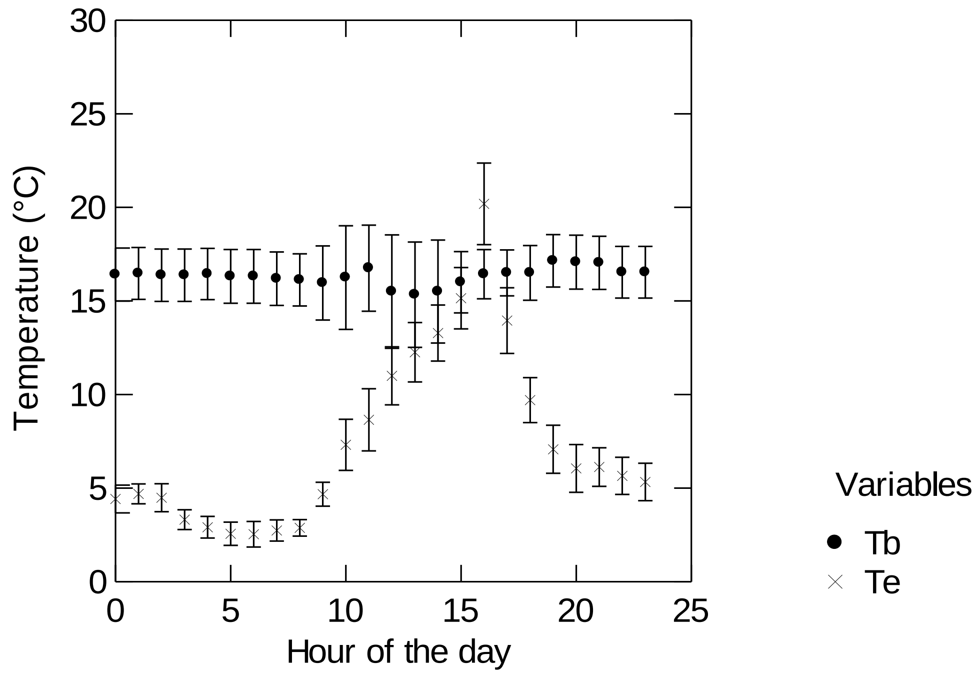

FIG. 10. Hourly Tb profile of six individual *C. lepidus* during January, 2010 (n = 373). Error bars denote standard error.

With respect to selecting slope directions for overwintering shelters by 12 *C. lepidus* during 2007-2010, eight overwintered on southeast facing slopes, two overwintered on west facing slopes, one other spent the winter on a southwest facing slope, and another individual selected a northwest facing slope. Results from the GIS ArcMap analysis (Table 6) revealed that southwest facing slopes are the most abundant (17%) in the study area, followed by south (16%), east (15%) and west (15%). On the other hand, north facing slopes are the least available (4%), followed by northwest (9%), and northeast facing slopes (10%). Distribution of the pixel frequencies was statistically significant ($X^2 = 18416.300$, df = 7, $p < 0.001$). Ground temperature readings from the eight cardinal slopes directions during winter of 2010-2011 (Fig. 13), indicate

that in general, southern facing slopes were warmer than slopes facing other directions, with the highest ground temperatures recorded on the southeast facing slope.

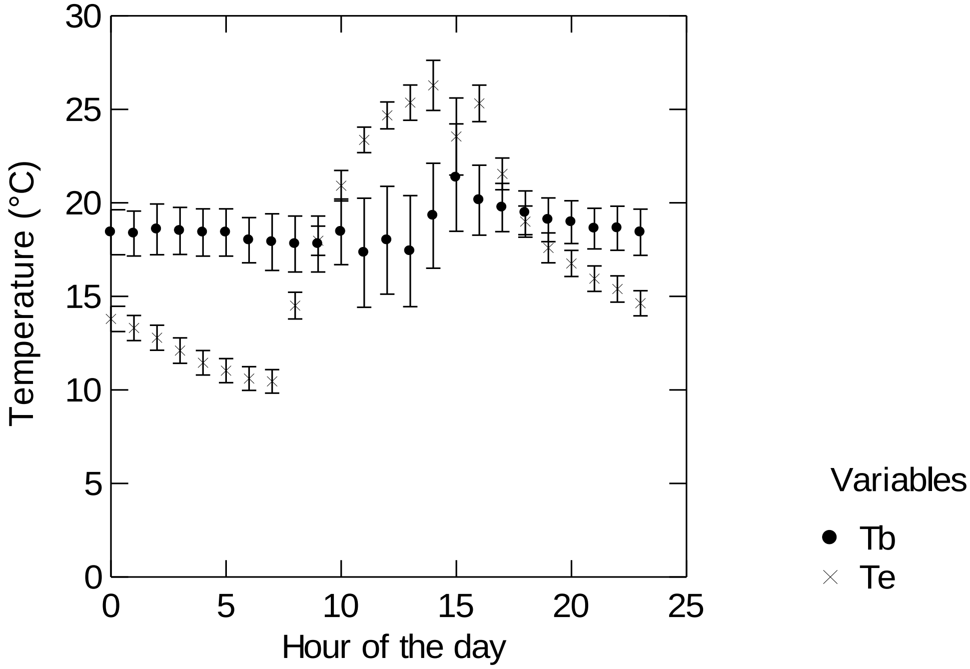

FIG. 11. Hourly Tb profile of six individual *C. lepidus* during February, 2010 (n = 803). Error bars denote standard error.

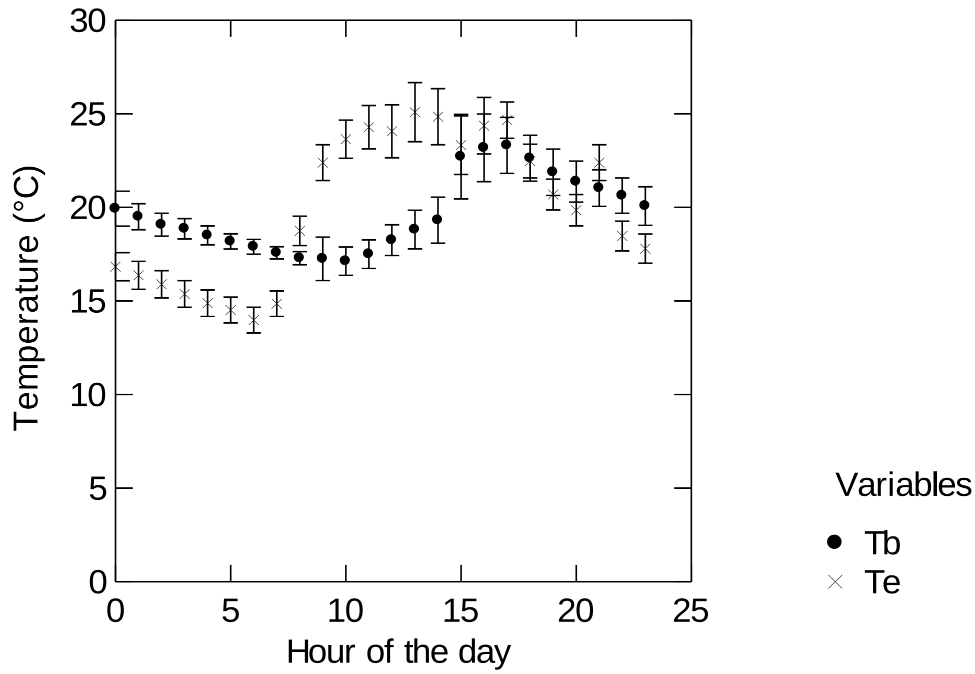

FIG. 12. Hourly Tb profile of six individual *C. lepidus* during March, 2010 (n = 898). Error bars denote standard error.

TABLE 5. Body mass lost for nine individual *C. lepidus* during winters 2007-2010 on IMRS. * = Rattlesnake was monitored in two different winters.

Snake ID	Sex	Before	After	Mass (g) lost	Percentage
003	♀	99.5	85.3	14.2	14.3
004	♀	118.0	105.2	12.8	10.8
001	♂	161.7	147.8	13.9	8.6
002	♂	149.6	146.7	2.9	1.9
021	♂	135.1	90.5	44.6	33.0
022	♂	123.2	122.2	1.0	0.8
023	♂	103.0	85.8	17.2	16.7
024	♂	170.9	154.2	16.7	9.8
003*	♀	96.9	95.0	1.9	2.0
Average	-	-	-	13.9	10.9

TABLE 6. Total numbers of pixels and percentage of land coverage for each facing slope at IMRS estimated with ArcMap GIS (n = 168537 pixels).

Facing slope	Number	Percentage
N	6565	4.0
NE	17695	10.0
E	24849	15.0
SE	23599	14.0
S	26178	16.0
SW	29492	17.0
W	24903	15.0
NW	15256	9.0

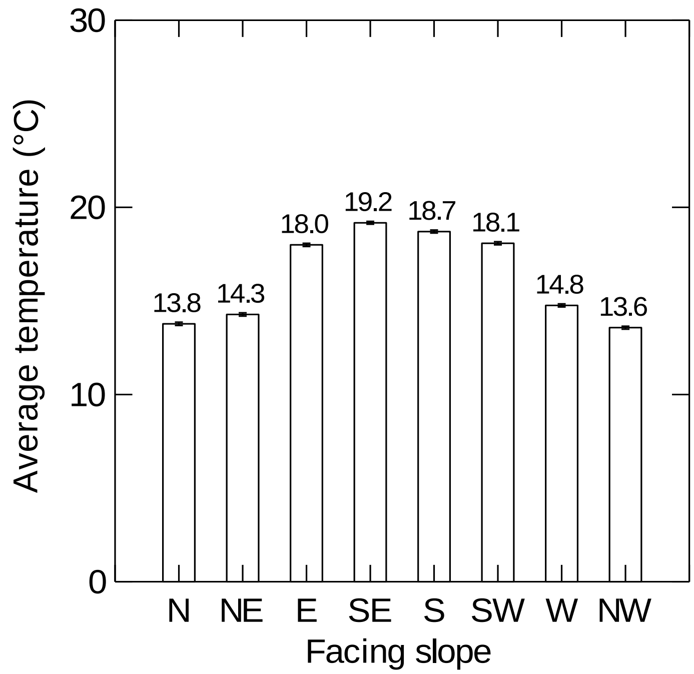

FIG. 13. Average ground temperatures (15 cm deep) from the eight slopes directions recorded every two hours during the winter of 2010-2011 (November-March) on IMRS (n = 28992). Error bars denote standard error.

DISCUSSION

Results demonstrated that 12 *C. lepidus* on IMRS averaged about five months from November through early April overwintering at a single shelter site. Similar results were found for populations of *C. atrox* (Repp, 1998; Taylor et al., 2004; Schuett et al., 2005, 2006; Taylor and DeNardo, 2005) in southern Arizona, for *C. cerate*s in the Mojave Desert of California (Brown and Lillywhite, 1992; Secor, 1992), *C. molossus* in the Chiricahua Mountains of Arizona, in the upland Chihuahuan Desert scrub (Greene et al., 2002), and for a population of *Sistrurus catenatus* in northwestern Missouri (Seigel and Pilgrim, 2002). However, the overwintering period of *C. lepidus* on IMRS lasts longer than populations of *C. ruber* and *C. oreganus* in southern California (Dugan et al., 2008; Brown, 2008), and *C. atrox*, *C. molossus*, and *C. tigris*, in southern Arizona (Beck, 1995); the latter species overwintered three months only (December-February). On the contrary, the overwintering period of *C. lepidus* was shorter when compared to populations located in places at higher latitudes or elevations, such as *C. viridis* in northern New Mexico (Jacob and Painter, 1980), *C. mitchellii* in Nevada (Glaudas and Rodriguez-Robles, 2011), *C. oreganus* in northern Idaho (Diller and Wallace, 1984), and *C. horridus* in North Carolina (Sealy, 2002), all of which spend about six months hibernating. Populations of *C. oreganus* in Utah (Hirth, 1966), *C. oreganus* in British Columbia, Canada (Macartney et al., 1990), *C. oreganus* in Idaho (Cobb and Peterson, 2008), *C. viridis* in Saskatchewan, Canada (Ganon and Secoy, 1985), *C. horridus* in Virginia (Martin, 1992), *S. catenatus* in southeastern Michigan (Moore and Gillingham, 2006), and *C. horridus* in northeastern U. S. (Galligan and Dunson, 1979; Brown, 1982, 1992, 2008; Martin, 1992, 2002) spend around seven months overwintering, and some species are reported to spend even longer time hibernating (about eight to nine months), including *S. catenatus* in southeastern Colorado

(Wastell and Mackessy, 2011), and *C. viridis* in Wyoming (Duvall et al., 1985). Thus, overwintering periods of rattlesnakes in North America, including IMRS, seem to be based on temperature factors relating to latitude, elevation, and also to localized ecological conditions in related geographic areas.

All 12 individuals *C. lepidus* on IMRS overwintered singly on separate slopes. Although other *C. lepidus* were never observed overwintering on the same slope, three individuals (one *C. atrox* and two *C. molossus*) were observed singly in different instances and locations nearby (within 2 m). It has been assumed that rattlesnakes in areas with relatively mild temperatures have a greater propensity to find potential overwintering shelters with the appropriate thermal conditions favoring solitary overwintering (Reed and Douglas, 2002). Solitary overwintering behavior has been observed for most populations of rattlesnakes living in the southwestern U.S., such as *C. atrox* (Beck, 1995; Taylor and DeNardo, 2005; Repp, 1998; Schuett et al, 2006), *C. molossus* and *C. tigris* (Beck, 1995), and *C. abyssus* (Reed and Douglas, 2002) in Arizona, and *C. cerastes* (Brown and Lillywhite, 1992; Secor, 1992,1994), *C. oreganus* (Dugan et al., 2008), *C. ruber* (Dugan et al., 2008; Brown, 2008), and *C. scutulatus* (Cardwell, 2007) in California. The same situation was reported for a population of *S. catenatus* in southeastern Colorado (Wastell and Mackessy, 2011). Communal denning behavior has been reported for populations of *C. atrox* in southwestern Oklahoma (Landreth, 1973), *C. lutosus* in Nevada and Utah (Hamilton and Nowak, 2009) *C. oreganus* in northwestern Utah (Hirth, 1966), *C. oreganus* in British Columbia, Canada (Macartney et al., 1990), and *C. viridis* in north-central New Mexico (Jacob and Painter, 1980), and in Colorado (Klauber, 1997). Communal denning was also reported for *C. horridus* in New York (Brown, 1982, 2008), North Carolina (Sealy, 2002), and New Jersey (Smith et al., 2008). Sexton et al. (1992) hypothesized that latitude 38°N was the

dividing line between winter denning behavior and migration patterns of snake populations in North America. However, some populations of rattlesnakes located below latitude 38°N (e.g., *C. atrox*, Repp and Schuett, 2008 and Hamilton and Nowak, 2009; and *C. molossus*, Hamilton and Nowak, 2009) in Arizona have been reported to display communal overwinter behavior, but those accounts were associated instead with higher elevations. Thus, denning singly seems to generally hold true for rattlesnakes in warmer regions of North America below 38°N latitude, but snakes in the same latitudes at higher elevations tend also to den communally. Therefore, empirical data again points to temperature as a major factor controlling denning behavior.

FIG. 14. Typical overwintering site of *C. lepidus* on IMRS.

With respect to body temperatures (Tb), on average *C. lepidus* on IMRS maintained rather cool average body temperature (19.2°C) during the entire winter period. The average Tb was roughly 4°C higher than the average environmental temperature (14.8°C) at ground level; and 10°C lower than their summer average Tb (ca. 29°C). Compared to other studies that have reported Tb during the winter period, *C. lepidus* had an average Tb similar to individuals of *C. pricei* (18.5°C; Prival et al., 2003), and *C. molossus* (20.3°C) in Arizona (Beck, 1995). However, *C. lepidus* had a higher average Tb than individuals of *C. atrox* (14.5°C) and *C. tigris* (15.3°C) studied by Beck (1995) in Arizona. Those differences were likely due to specific thermoregulation behavior such as basking and physical position of overwintering sites. Average Tb of *C. lepidus* also was 8.6°C higher than the Tb reported for a population of *C. viridis* located in the northern plains of New Mexico (Jacob and Painter, 1980), 8.7°C higher than a population of *C. horridus* in New York (Brown, 1982), and 10.3°C higher than a population of *C. oreganus* in southeastern Idaho (Cobb and Peterson, 2008). Although average Tb was slightly different for each individual *C. lepidus* (Table 3), temperatures in all rattlesnakes were statistically significant (Table 4). These differences are likely the results of the specific characteristics of the shelters selected and the thermoregulatory behavior achieved by each individual during cold periods. For instance, individual 003 had the lowest average Tb, possibly because it was located on a slope that was partially blocked from the sun by other slopes, thereby limiting the amount of solar radiation absorbed by its shelter. Furthermore, individual 003 was never observed outside basking during the entire winter period.

Comparing diurnal and nocturnal winter body temperatures found that individuals of *C. lepidus* were slightly warmer during day light hours (Figs. 4, 7-12). A factor that contributed to a higher diurnal Tb was the ability for rattlesnakes to come out and bask when outside

temperatures were higher than inside the shelters (Fig. 15). On some warmer days, especially in early November and late March, rattlesnakes would reach body temperatures above 30 °C. Beaupre (1993) observed individuals of *C. lepidus* in the Big Bend region basking and some of them were active on the surface during the winter months. This was also observed for individuals of *C. molossus* by Beck (1995), when apparently some individuals were also able to feed. Although feeding was never observed in *C. lepidus* on IMRS during the winter period, water consumption through rain harvesting from the body was observed for one individual positioned outside its shelter during a cold and windy day on 16 February 2008 when the air temperature was only 5 °C.

FIG. 15. Male *C. lepidus* (024) basking outside its overwintering shelter on 5 March 2010.

All Rock Rattlesnakes during the overwintering period lost an average of 10.9% of their total body mass (Table 5). Individual 021 showed the highest percentage (33.0%) of body mass

loss, which was likely attributed to the effects of a predatory injury on its dorsum, probably received while basking during March 2010. It is probable that this rattlesnake expended more energy during the healing process, and not representative of weight loss under normal circumstances. By excluding this individual from the analysis, the average mass loss for the other eight individuals was less (8.1%). Similar mass loss percentages were found in a population of *C. oreganus* (9.4%) in Idaho (Cobb and Peterson, 2008), and for a population of *C. viridis* (11.0%) in Utah (Hirth, 1966). However, when compared to a population of adult and juvenile *C. viridis* in Colorado, *C. lepidus* in the present study lost more mass than adults (4%), but less than juveniles (20%), (Klauber, 1997).

Crotalus lepidus on IMRS overwintered mostly on southeastern facing slopes. Studies reporting slope direction during winter periods have indicated that southern facing slopes are commonly chosen by rattlesnakes (Brown, 1982; Graves and Duvall, 1990; Macartney et al., 1990; Beck, 1995; Sealy, 2002; Dugan et al., 2008; Hamilton and Nowak, 2009). Rattlesnakes tend to prefer southern facing slopes because they receive more solar radiation during the winter period (Hamilton and Nowak, 2009, Walton et al., 2005), so consequently rattlesnakes located on southern slopes experience more optimal temperatures for longer periods of time. The estimated percentage of area of available slopes on IMRS (Table 6) indicated that southeastern facing slopes were not the most abundant, so it appears that rattlesnakes select that direction for specific reasons. Results from ground temperature records (Fig. 13) showed that the southeastern facing slope was the warmest in the study area, followed by south, southwest, and east facing slopes. So far, it has been suggested that rattlesnakes locate their overwintering slopes by a combination of three mechanisms: solar orientation (Landreth, 1973), scent tracking (Duvall et al., 1992), and the use of the pit organs (Sexton et al., 1992). In the study reported herein, intensity and duration

of solar radiation as a heat source seems to play a major role for selecting winter shelters sites by Rock Rattlesnakes.

In summary, information presented here provided an insight on the winter ecology of *C. lepidus* at IMRS. Data suggested that warmer southern facing slopes are preferred by Rock Rattlesnakes during winter periods. Although these wintering habitats are not frequently used in the summer activity season by *C. lepidus* on IMRS, it is important that they be included in protection and conservation plans that aim to address the survivability of the species in Chihuahuan Desert habitats. However, due to the small sample size used in this study, it is recommended that future monitoring on IMRS includes more individuals, especially adult females, to substantiate consistency of winter behaviors in *C. lepidus* populations. Because body temperatures were obtained mostly from one winter season (2009-2010), it remains to be seen if there is a temporal temperature change due to climatic fluctuations. Consequently, future monitoring of winter body temperatures may help to elucidate if the overwintering period of *C. lepidus* is being affected by global climate change. Also, the behavior of juveniles during the cold period remains unknown. Because *C. lepidus* has a large geographic range that includes significant latitudinal variance, and variation in elevation from desert flats to high mountains, both of which affects temperature and landscape characteristics, an analysis of *C. lepidus* range-wide is needed to fully understand all parameters of wintering behavior within the species.

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SYNTHESIS

Without any doubt, the study presented herein demonstrated once more the great amount of ecological information obtainable through the use of radiotelemetric techniques, especially from secretive species, such the Rock Rattlesnake, *Crotalus lepidus*. The field data acquired in this study revealed that *C. lepidus* on IMRS is active from early April to early November. It is active at night and early morning hours throughout hot summer months, but become more diurnally active during early spring and late fall when nighttime temperatures are lower. Individuals within the study area have an average home range encompassing 13.6 ha and move on average 8.5 meters per day; males move farther than females. Males also have larger home ranges due precisely to the influence of female mate searches. Future studies of this species on the western slopes of IMRS should compare home ranges obtained in this study with those of individuals living on the eastern slopes, which are located at higher elevations and receive more precipitation. The data also indicate that arroyos play important roles on daily activities of *C. lepidus,* especially those containing a constant amount of vegetation during the warm season for reproduction and feeding behaviors. Individuals selected some microhabitats non-randomly, so it is most likely that only microhabitats with specific characteristics fulfill the preferred requirements of this species in the study area. *Crotalus lepidus* undergoes courtship and copulation unimodally in August and September. Unfortunately mating behavior also coincides with fatalities in males because of deliberate movement into more open spaces, making them more susceptible to predation. Although there are many potential predators suspects on IMRS, it remains unknown what specific animals kill small size rattlesnakes, such as *C. lepidus*. The only female observed around the time she gave birth (20 July 2008) was located with her neonates on a steep slope at the edge of her home range. This supports the hypothesis that *C. lepidus* females

provide parental care shortly after birth and the timing also suggests that the species on IMRS have a gestation period of nearly a year; courtship and copulation in late summer and giving birth the following midsummer.

Crotalus lepidus on IMRS overwinters for approximately five months; from early November to late March or early April). Not all Rock Rattlesnakes arrive or leave their overwintering shelters on the same dates, probably because of differential temperatures at separate sites. Because winter seasons are usually mild, rattlesnakes are able to leave their dens and thermoregulate during warm days, but were not observed to feed. The preferred winter shelter is located on southeastern facing slopes, which are the warmest during the winter period on IMRS. During the overwintering period *C. lepidus* loses around 10% of body mass. A larger sample of individuals would be desired to determine if mass loss during winter is consistent. It also remains to be seen how much body temperatures vary across different winter seasons.

During this study I was also able to observe individuals performing rain-harvesting behavior on two occasions, one in the summer and the other during winter; indicating that *C. lepidus* will collect water when available from its body or surrounding substrate in an environment with unpredictable weather patterns such as in the Chihuahuan Desert. Those two observations however, are the first ever reported for *C. lepidus* from any part of its geographic range.

Regrettably, because only a small number of rattlesnakes of the correct size were radiotracked in this study, caution should be considered when drawing final conclusions. Besides, the study area is only a restricted locality when compared to the entire geographic distribution of the species. My results also question the measure of abundance of *C. lepidus* on

IMRS. The difficulty finding rattlesnakes was probably exacerbated by their cryptic coloration, nocturnal activity, small body size, and by the low propensity for individuals to rattle. Consequently, stating that *C. lepidus* is not abundant on IMRS, as described for the species in other areas, has not been completely answered. It is important that future studies include more females and juveniles to determine more precisely the complete ecological limits of this population on IMRS.

In spite of all the confronted difficulty, the data gathered in this study contains important baseline information for future comparative studies on IMRS and for other populations of Rock Rattlesnakes across their geographic range in desert settings. To date, few investigations have addressed ecological requirements of *C. lepidus* in its natural habitats, and none have gone into the depth presented herein for populations on IMRS during the entire yearly interval. There is no doubt that the natural environments of many populations of Rock Rattlesnakes from throughout its geographic range are under great pressures from human-based disturbances. The information gleaned from this study is critical for use by conservation groups and environmental advocates involved in conserving and protecting not only Rock Rattlesnakes, but their required habitats as well. Critical habitat loss is probably the primary reason why Chihuahuan Desert environments are being adversely affected by human intervention, so determining the natural ecological limits of species like *C. lepidus* are instrumental in determining the future viability of the biota occurring in this fragile region of the United States and Mexico. Environmental protection should become a major focus of academic, governmental, and political efforts to sustain regional ecological stability; especially considering that future prospects of habitat destruction and climate change are inevitable if nothing is done to forestall the progression. Even though perseverance of *C. lepidus* is just a small aspect of the overall environmental health of the

Chihuahuan Desert, learning about its needs and behaviors are important links in the ecological chain regulating a continuously flourishing bionetwork. Hopefully the information presented herein will be used to help accomplish these important goals.

CURRICULUM VITAE

Vicente Mata-Silva was born on December 24, 1973 in Río Grande Oaxaca, México. The sixth son of Vicente Mata Pérez and Elena Silva Sandoval. Vicente attended the Universidad Nacional Autónoma de México and obtained his Bachelor of Science Degree in Biology in 2000; his Bachelor thesis focused on comparing herpetofaunistic richness in habitats with different degree of human related disturbance, in Puebla, México. Vicente attended The University of Texas at El Paso and obtained his Master of Science Degree in Biology in 2005. Under the advice of Dr. Jerry D. Johnson, Vicente wrote his Master's thesis focusing primarily on the diet of two syntopic whiptail species of lizards, one unisexual and the other bisexual, from the northern Chihuahuan Desert on Indio Mountains Research Station. Vicente had a Graduate Teaching Assistant position while working on both M. S. and Ph.D. programs at The University of Texas at El Paso. While working on his Ph.D., Vicente was awarded with the Frank B. Cotton State Fund Scholarship (2007), the Krutilek Fellowship (2008), the Dodson Dissertation Fellowship (2011) and a grant from T&E (2008). To date, Vicente has authored and coauthored 24 peer-reviewed scientific publications concerning ecology, natural history, geographic distribution, and conservation of the herpetofauna from México and southwestern United States, most of which were produced as a graduate student at the University of Texas at El Paso.

Vicente is a member of the Southwestern Association of Naturalists, Society for the Study of Amphibians and Reptiles, Sociedad Herpetológica Mexicana, A. C., and Society of Sigma Xi.

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