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Behavioral Ecology Of A Desert Ambush Predator: Assessing Movement Patterns, Habitat And Microhabitat Use, And The Innate Feeding Response Of Eastern Black-Tailed Rattlesnakes (Crotalus ornatus) In The Northern Chihuahuan Desert

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BEHAVIORAL ECOLOGY OF A DESERT AMBUSH PREDATOR: ASSESSING MOVEMENT PATTERNS, HABITAT AND MICROHABITAT USE, AND THE INNATE FEEDING RESPONSE OF EASTERN BLACK-TAILED RATTLESNAKES (*Crotalus ornatus*) IN THE NORTHERN CHIHUAHUAN DESERT

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2020

Dedication

For my family

BEHAVIORAL ECOLOGY OF A DESERT AMBUSH PREDATOR: ASSESSING MOVEMENT PATTERNS, HABITAT AND MICROHABITAT USE, AND THE INNATE FEEDING RESPONSE OF EASTERN BLACK-TAILED RATTLESNAKES (*Crotalus ornatus*) IN THE NORTHERN CHIHUAHUAN DESERT

by

JAMES DAVID EMERSON, B.S.

DISSERTATION

Presented to the Faculty of the Graduate School of
The University of Texas at El Paso
In Partial Fulfillment
of the Requirements
for the Degree of

DOCTOR OF PHILOSOPHY

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Abstract

Research on the ecology and evolution of rattlesnakes has been sporadic over the past 80 years, but has seen recent expansion into the diverse fields of physiology, physiological ecology, life history, behavioral ecology, ethology, reproductive biology, chemical ecology, venom biochemistry and medicine, conservation, and many other subdisciplines. The development of small, implantable VHF radiotransmitters in the 1980s revolutionized research in the field of behavioral ecology for rattlesnakes, which are uniquely suited for radiotelemetry studies because they possess several morphological, physiological, and behavioral characteristics that are unique among terrestrial vertebrates. The widespread application of radiotelemetry by the mid-1980s advanced the model organism status of rattlesnakes for classes of questions that were difficult to address with other taxa. Radiotelemetry has been responsible for notable insights into several areas of rattlesnake behavioral ecology, including movement and habitat associations, predation and sensory ecology, defensive behavior, and rattlesnake socioecology. Ultimately, research in these areas of rattlesnake behavioral ecology is necessary in order to guide informed conservation plans for this ecologically important group of organisms. Thus, the following research attempts to accomplish the following objectives: 1) I utilized radiotelemetry to determine movement patterns of *C. ornatus* on the Indio Mountains Research Station, including the estimation of home range sizes, identification of core use areas, and examining seasonal and sexual patterns in movement metrics; 2) I used data collected during radiotelemetry to determine seasonal and sexual patterns of habitat and microhabitat use of *C. ornatus*; and 3) I presented naive young snakes with aqueous extracts from the integument of known and suspected prey items to determine innate prey preferences of *C. ornatus*.

Recently, accelerated rates of taxonomic change have outpaced the subsequent ecological research that is necessary to inform conservation objectives for newly described or revalidated species. Black-tailed rattlesnakes in the southwestern United States are an example, with *Crotalus ornatus*, which was recently revalidated, occurring east of the Continental Divide, and *C. molossus* occupying the range west of the Continental Divide. This created a void in our ecological knowledge about *C. ornatus* because historical research on black-tailed rattlesnakes in the United States was mostly conducted at study sites west of the Continental Divide. Thus, radiotelemetry was used to monitor *C. ornatus* on Indio Mountains Research Station (IMRS) in the Trans-Pecos ecoregion of Texas for at least one active season from May 2015 through August 2018. Mean (±1 SE) home range size for all individuals was 22.84 ± 4.49 ha, mean movement frequency was 0.73 ± 0.03, and mean daily movement rate was 9.28 ± 0.93 m/day. Male snakes had larger home range sizes, larger core use areas, higher movement frequencies, and higher movement rates than female snakes. Female movement rates peaked in June, although movement rates were statistically similar for all months. Male movement rates were significantly greater during August, with slight peaks in July and June that were approaching significance. Multinomial logit models were used to analyze habitat use patterns, while controlling for subject, habitat availability, and season. Models predicted that snakes were most likely to be found in arroyo and rocky slope habitats, despite the limited availability of these habitats within snake home ranges. Microhabitats were also used non-randomly, with *C. ornatus* preferring areas composed primarily of rock and vegetative ground

cover and seeking refuge in rocky structure or under dense vegetation. This study presents the first detailed information about habitat and microhabitat use, along with patterns of movement and home range size for *C. ornatus*.

Chemical signals are left behind as organisms move throughout the environment. Chemical eavesdropping is the use of these signals by other organisms to gain information about the animals that they share the ecosystem with. There are two main avenues of chemical eavesdropping: 1) prey species using the signals to avoid predation by gaining information about potential predators, and 2) predators using the signals to gain information about prey species and identify fertile hunting areas. Despite its utility for predators, chemical eavesdropping has usually been examined from the perspective of potential prey items. Thus, the final goal of this study was to determine if *C. ornatus* differentiates among chemical cues from potential prey items when choosing ambush spots. Naive neonate snakes were raised in captivity, then placed in an arena where they were presented with aquatic extracts from the integument from 10 known and suspected prey items and a tap water control, after which their reactions to the chemical extracts were recorded, and they were given a tongue-flick-ambush score (TFAM) based on their behavior towards the chemical cue. Ten neonate *C. ornatus* were put through each of the 11 trials, and based on TFAM scores, snakes differentiated among the chemical cues ($F_{df=9, df=10} = 19.149$, $P < 0.001$). Snakes showed preference for native small mammal and lizard prey over larger native mammals, native amphibians, native invertebrates, and non-native small mammals. The snakes used in this study have never been exposed to wild prey stimuli in their native ecosystem and have fed exclusively on non-native mammalian prey

in captivity, thus their preference for native small mammals and lizards indicates an innate basis for prey preference.

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Chapter 1: An introduction to the behavioral ecology of rattlesnakes

1.1: Introduction

During the past 80 years, studies on the ecology and evolution of rattlesnakes have been sporadic, with a few noteworthy landmark publications (Gloyd 1940, Klauber 1972, Campbell and Lamar 1989, Campbell and Brodie 1992, Campbell and Lamar 2004, Hayes et al. 2008, Schuett et al. 2016, Dreslik et al. 2017). This literature reflects the recent expansion of rattlesnake research into diverse fields such as physiology, physiological ecology, life history, behavioral ecology, ethology, reproductive biology, chemical ecology, venom biochemistry and medicine, conservation, and many other subdisciplines. The aim of this review is to provide the groundwork of the behavioral ecology of rattlesnakes, which guide the research objectives in the following chapters.

Behavioral ecology is a broad and integrative field utilizing diverse studies of movement, habitat use, sensory ecology, defense, and socioecology, among other areas (Beaupre and Duvall 1998). The development of small implantable very high frequency (VHF) radiotransmitters in the 1980s revolutionized snake ecology (Beaupre 2016). Rattlesnakes possess several morphological, physiological, and behavioral characteristics that are unique among terrestrial vertebrates, which have made them ideal candidates for radiotelemetry studies, resulting in their suitability and contributions to the fields related to behavioral ecology (Reinert and Cundall 1982, Reinert 1992, Beaupre and Duvall 1998). Refinement of implantation techniques facilitated the widespread application of radiotelemetry by the mid-1980s (Reinert and Cundall 1982, Weatherhead and Anderka 1984, Hardy and Greene 1999, Hardy and Greene

2000, DeNardo 2012), which advanced the model organism status of rattlesnakes for classes of questions that were difficult to address with other taxa (Beaupre and Duvall 1998). Ironically, the characteristics of rattlesnakes that made them ideal candidates for VHF radiotransmitters now limit our ability to utilize more modern advances in animal tracking, leaving VHF radiotelemetry as the preferred method for ongoing behavioral ecology research (Beaupre 2016).

1.2: Movements and Habitat Associations

Understanding how animals move within the ecosystem is critical to developing an informative ecological body of knowledge to guide conservation efforts. Animal movements may be thought of as a tradeoff between the need to acquire resources and factors that restrict those movements (Bronmark et al. 2008). Consideration of this tradeoff is particularly important for species that face additional movement constraints, such as the length of the active season, which constrains the movement of ectotherms in temperate climates, including many rattlesnake species (Bauder et al. 2017). Important resources, including prey, potential mates, thermoregulatory sites, and hibernacula often vary spatio-temporally in distribution, influencing animal movements (McIntyre and Wiens 1999, Klaassen et al. 2006, Filipa-Loureiro et al. 2007, Noyce and Garshelis 2011). These movements may also be constrained by other factors, such as size and vagility, energetic requirements, predation, abiotic conditions, habitat composition and configuration, and anthropogenic disturbances (Daltry et al. 1998, Johnston and Frid 2002, Alerstam et al. 2003, Fortin et al. 2005, Coulon et al. 2008, Shepard et al. 2008, Bartelt et al. 2010, Cushman et al. 2011). Species whose movements are strongly constrained by natural factors may also be more susceptible to the negative effects of anthropogenic disturbance, such as restricted movement along small corridors, preventing access to resources within those corridors, thereby reducing dispersal, and leading to an overall decrease in population viability (Epps et al. 2007, Sawyer et al. 2009, Bauder et al. 2017).

Because of their large size, relatively slow pace of movement, and their easy observability, rattlesnakes are ideal candidates for VHF radiotelemetry studies, which allow for detailed analysis of movement and habitat associations. The population-specific databases produced by these studies are invaluable for creating sound management policies and have contributed to an increased understanding of animal movement and habitat utilization. Studies have utilized descriptive statistical methods to illuminate nonrandom habitat associations in multiple species (*Sistrurus catenatus*, *Agkistrodon contortrix*, and *Crotalus horridus*) and have revealed that single species can show seasonal and geographic differences in habitat associations (*S. catenatus*). In addition, these studies have shown that the potentially competitive species *A. contortrix* and *C. horridus* may reduce competition by separating themselves in space, with *C. horridus* utilizing complex structural components out of proportion to their availability (Reinert 1993).

Macartney et al. (1988) found that seasonal movements to and from overwintering refugia, or dens, may be extensive and dramatic. However, they are not always extensive, as some taxa undergo “ranging” movements, in which the animals never move very far away from dens, but rather simply come and go as the season progresses. When the movements away from dens are dramatic, animals may migrate over 5 km from dens to specific habitat units along fixed-bearing paths (Duvall et al. 1985, King and Duvall 1990). Some species, such as *S. catenatus* and *C. horridus*, demonstrate successive activity centers as they travel (Brown et al.

1982, Reinert and Zappalorti 1988). The activity centers are small units of habitat, in which individuals may search for prey, seek temporary refugia to undergo ecdysis, seek conspecifics or potential mates, or utilize microhabitat for optimal thermoregulatory characteristics. King and Duvall (1990) defined these bouts of movement between successive habitat units in time and space as “functionally dedicated episodes of activity.” For example, *C. viridis* has been shown to have one episode of activity dedicated to the location of prey patches (Duvall et al. 1990) and another episode of activity where male snakes exhibit mate searching behavior (Duvall and Schuett 1997). The identification of discreet episodes of activity makes it possible to combine successive episodes of movement, resulting in the construction of activity budgets that encompass entire seasonal migrations. This provides the opportunity for bioenergetic and cost-benefit analyses to input data directly into microevolutionary models and address multivariate selection in progress (Duvall et al. 1992, Duvall et al. 1993, Arnold and Duvall 1994). Thus, constructing seasonal activity budgets has opened the doors for the study of proximate and ultimate causation in behavior (Duvall and Beaupre 1998).

Competition with sympatric snake species and subsequent partitioning of resources is another important factor influencing rattlesnake movement and habitat use. Differential resource use in the form of niche partitioning allows ecologically similar species to coexist (Gause 1934, Schoener 1974, Pfenning et al. 2006, Dugan and Hayes 2017). Niche partitioning typically occurs along four major niche axes: 1) spatial separation; 2) temporal avoidance; 3) dietary differentiation; and 4) differential use of thermal resources (Shoener 1974, Luiselli 2006). The current view for snakes, including vipers, is that extensive niche partitioning occurs, with sympatric species primarily partitioning food resources, which is atypical among vertebrates (Toft 1985). However, Luiselli (2006) found that, while many snake families partition food resources, sympatric viperids usually partition space, suggesting that prey availability may not be a source of exploitive interspecific competition (Reichenbach and Dalrymple 1980). Studies among viperids of the southwestern United States, although limited, seem to support the theory of habitat partitioning by sympatric viper species (Luiselli 2006, Steen et al. 2007, Dugan et al. 2008, Martinez-Freiria et al. 2008), including among sympatric populations of *C. atrox*, *C. molossus*, and *C. scutulatus* in the Sonoran Desert (Pough 1966, Reynolds and Scott 1982, Mendelson and Jennings 1992) and among sympatric *C. atrox*, *C. molossus*, and *C. tigris* in Arizona (Beck 1995). Additionally, ecological niche modeling indicates that the range of *C. pyrrhus* is limited by *C. stephensi* through competition (Lawing et al. 2012). Dugan and Hayes (2017) suggest that differential niche use between *C. ruber* and *C. helleri* in southern California has likely resulted from non-competitive mechanisms, and that resources within their study system are not sufficiently limited to promote competition. They hypothesize that, if competitive niche portioning exists, it probably occurs subtly on multiple niche axes, but likely more so via differential habitat use.

1.3: Predation and Sensory Ecology

Rattlesnake sensory ecology and behavior demonstrated while in ambush posture within prey patches has received most of the research attention, while studies on how snakes locate specific prey patches has been largely neglected. The ability to detect electromagnetic radiation in the infrared region of the spectrum through paired heat-sensing facial pits allows rattlesnakes to respond to prey and other stimuli, in addition to visual prey detection and stimuli response. Based on the sensitivity and arrangement of the pits, it is thought that small, warm-bodied mammals and local thermal habitat features create a three-dimensional heat image seen by rattlesnakes (Beaupre and Duvall 1998).

Nasal and vomeronasal olfaction are powerful chemical senses that play an important role in the predatory ecology of rattlesnakes (Chiszar et al. 1983, Kardong 1986, Ford and Burghardt 1993). Many field studies across numerous species, including *C. atrox*, *C. cerastes*, *C. horridus*, *C. oreganus*, *C. ruber*, and *C. scutulatus*, have documented the basic behavioral pattern of relatively short bouts of chemosensory searching followed by long periods of waiting in stereotyped ambush coils (Reinert and Cundall 1982, Reinert et al. 1984, Clark 2006, Wittenberg 2012, Putman et al. 2016, Clark 2016). The rattlesnake relies on these sensory mechanisms to trail envenomated prey accurately after the strike, envenomation, and release of the prey item (Golan et al. 1982). Post-envenomation, some pitviper species have shown the ability to differentiate between envenomated and non-envenomated prey items, often preferring envenomated prey over non-envenomated prey (Greenbaum et al. 2003, Greenbaum 2004). Greenbaum et al. (2003) found that *A. contortrix* could also differentiate between prey that was envenomated by conspecifics from different geographic regions, and some individuals differentiated between prey envenomated by other sympatric pitviper species (*A. piscivorus* and *Sistrurus catenatus*). Additionally, *C. viridis* and *S. miliarus* respond to the odors of common prey species by adopting ambush coils, both in the laboratory and the field (Duvall et al. 1990, Roth et al. 1999b, Theodoratus and Chiszar 2000, Bevelander et al. 2006). Neonate *C. horridus* raised in captivity have been shown to discriminate among chemical cues from potential prey items, showing preference for those from their native prey (Clark 2004b). Additionally, ontogenetic shifts in prey chemical cue discrimination have been observed, as captive *C. helleri* adopt ambush coils towards lizard chemical cues as juveniles and shift their preference to rodent prey chemical cues as adults (LaBonte 2008). Captive *C. viridis* also demonstrated this ontogenetic shift, tongue flicking more towards lizard chemical cues as juveniles, shifting their preference to rodent chemical cues as adults (Saviola et al. 2012). There is also evidence that prey preference seems to be an innate development, not dependent on body size or experience. Saviola et al. (2013) found that individuals with stunted growth showed prey responses typical of their chronological age, not size. Greenbaum (2004) found that *A. contortrix* from population with different staple diets (small mammals, frogs, and lepidopteran larvae) all preferred small mammal prey in behavioral trials. Furthermore, Holding et al. (2016) demonstrated that 5-year old captive *S. miliarus* preferred chemical cues from native lizard prey, despite being raised exclusively on a diet of laboratory mice.

In addition to using chemical cues from prey to inform predation strategies, it is likely that rattlesnakes can integrate chemical information from other sources as well. It is possible that individuals pay attention to conspecific-derived chemical cues and use this as a source of environmental information (Clark 2007). Other vertebrate species have been shown to use conspecific information to assess their environment (Valone 2007, Bonnie and Earley 2007), and small mammals can use social cues to transmit food preferences (Posadas-Andrews and Roper 1983). Chemical cues are used by snakes in the genus *Thamnophis* to assess the body condition of conspecifics during courtship (Shine et al. 2003). Thus, given their sensitivity to conspecific cues during mating and courtship, it is likely that rattlesnakes can integrate conspecific chemical cues in assessing local prey resources as well (Clark 2016).

Research has shown that chemical cues are sufficient for selecting ambush sites, but visual cues are also likely to be important. However, data examining the role of vision in snake predatory behavior are limited. When presented with chemical and/or visual cues from live mice, *C. enyo*, *C. viridis*, and *S. catenatus* only exhibited elevated tongue-flicking when the live mouse was visible, and the rate of tongue-flicking increased if both visual and chemical cues were present (Chiszar et al. 1991). In captivity, Duvall et al. (1990) found that *C. viridis* will adopt ambush coils next to soiled bedding from mice (chemical cue), but their responses were much stronger when presented with a live mouse residing in the bedding (chemical and visual cue). Hennessy and Owings (1988) concluded that visual cues from live squirrels were probably an important component of ambush site selection after observing *C. oreganus* hunting Ground Squirrels.

1.4: Defense

The tail rattling and antagonistic behavior that rattlesnakes often exhibit for defense is often misinterpreted as aggression (Duvall et al. 1985). The significance, complexity, and sequential escalation of stereotypical rattlesnake defense behavior was first described in detail by Klauber (1972). Rattlesnakes incorporate passive elements, such as crypsis, as an immobile defense tactic, and active elements of defense, such as the stereotyped defense coil posture combined with tail rattling. These behaviors occur sequentially, covarying predictably with ecological and social context, and the intensity of the predator threat (Duvall et al. 1985). Additionally, rattlesnake defense behavior has been shown to vary based on reproductive status and body temperature (Goode and Duvall 1989, Graves 1989).

Striking with envenomation typically occurs only when a rattlesnake is at maximum defensive escalation (Duvall et al. 1985, Goode and Duvall 1989). Free-ranging *C. viridis* that were threatened vigorously, but were not contacted physically, only struck out in defense less than 2% of the time, and were more likely to hide their head under a coil of the body (6% of the time) than attempt a self-defense bite. However, when the snakes were grasped gently and repeatedly with foam covered tongs, the percentage of defensive bites rose to approximately 39% (Duvall et al. 1985).

When presented with painted wooden models of *Lampropeltis getula* that were coated with skin chemicals extracted from the kingsnakes, *C. tigris* and *C. mitchellii* demonstrated a consistent defense behavior in retaliation to the potential ophidian predator, suggesting that rattlesnake defensive behavior is highly evolved and context specific. The active defense display included the lifting of mid-body coils from the substrate, referred to as “body bridging,” and elevated body temperature (Beaupre and Duvall 1998).

1.5: Socioecology

As a group, rattlesnakes have long been thought to be non-gregarious, with large aggregations, including more than 500 individuals, occurring only in denning aggregations (Graves and Duvall 1990, Graves and Duvall 1995). However, despite these large aggregations, it has been reported that rattlesnakes do not engage in complex social or cooperative social interactions (Gregory 1982). There is still very little information on the individual-based social interactions that occur at these communal dens (Repp 1998, Amarello 2012, Clark et al. 2012). Most of the knowledge base for these communal dens concerns the environmental conditions, such as temperature, and geologic features, rather than the individual snakes (Sexton et al. 1992, Hamilton and Nowak 2009, Gienger and Beck 2011). There are only limited long-term data on ingress, egress, and social activities of individual snakes at these den sites because of limited long-term, highly detailed studies on the social interaction of individual snakes in nature (Sexton et al. 1992, Amarello 2012, Clark et al. 2012, Clark et al. 2014). However, the field of rattlesnake socioecology is ever expanding, and as more studies are conducted, it seems that all snakes, including rattlesnakes, communicate, are social, and have culture (Doody et al. 2013). Additionally, for almost 20 years, researchers have argued that snakes have complex communication systems and live complex social lives (Greene et al. 2002, Amarello 2012, Clark et al. 2012, Clark et al. 2014, Lillywhite 2014), however there remains no detailed review of social behavior in reptiles (Doody et al. 2013).

Communication is broadly defined as the transfer of information from one individual to another (Carpenter 1977), in which selection favors both the production of the initial communication signal and the reception of that signal by a receiver (Lewis and Gower 1980). All sociality in snakes must involve communication, including sensory modalities such as vision, touch, vibration, and chemosensation, primarily via the vomeronasal sense organs, with olfactory and taste systems (Halpern and Martinez-Marcos 2003, Filaramo and Schwenk 2009, Mason and Parker 2010, Lillywhite 2014). In pitvipers and other lineages of snakes with infrared detection organs, thermal information is also likely to be a source of communication (Lillywhite 2014). Additionally, snakes may use mechanoreceptors and free nerve endings in the integument to communicate and process social information (Lillywhite 2014). Other sensory modalities, such as hearing, seem to be of secondary importance (Gillingham 1987, Young and Aguiar 2002, Young 2003, Lillywhite 2014).

The phenomenon of communal denning has been covered at length (Klauber 1972, Sexton et al. 1992, Graves and Duvall 1995), but nearly all reports lack details of social behavior at the level of the individual (Clark 2004c, Amarello 2012, Clark et al. 2014). Gregory (1984) proposed three mutually inclusive hypotheses regarding communal denning: 1) Availability of suitable den sites low; 2) Enhancement of thermoregulation from high numbers of individuals (thermal inertia); and 3) Increased opportunities for mating success from having individuals in close proximity.

Most publications only address the use of communal dens by rattlesnakes as hibernacula. However, there are several western species, such as *C. cerberus* and *C. concolor*, that use communal dens as birthing rookeries (Graves and Duvall 1995, Amarello et al. 2011) or nurseries for newly born rattlesnakes (Amarello et al. 2011, Parker et al. 2013). One to two months prior to parturition, gravid *C. viridis* are known to aggregate in small groups at microhabitat units that are called birthing rookeries or creches. The individuals that make up these aggregations had a more uniform, higher body temperature than solitary conspecifics. This thermal inertia may facilitate more rapid embryo development and reduce developmental anomalies in neonates. This behavior may constitute mutualistic thermoregulatory cooperation, which represents one of the simplest forms of social cooperation known in nature (Graves and Duvall 1995). Furthermore, observations suggest that prey availability, such as lizards, may keep young-of-the-year and juvenile rattlesnakes at den sites for a period of up to several years

(Schuett et al. 2016). Also, adult rattlesnakes, particularly females, may occupy den sites year-round when undergoing gestation (Graves and Duvall 1995, Schuett et al. 2016).

Group living (i.e. denning) has both costs and benefits (Hamilton 1964, Alexander 1974, Wittenberger 1981). Benefits include increased vigilance, predator defense, access to mates, and control over other resources (Wittenberger 1981). Costs include limited resource use and the close proximity of individuals facilitates the spreading of parasites and disease (Wittenberger 1981, Alcock 1998, Dugatkin 2009). Inclusive fitness theory predicts that the benefits of group living will be greater when they are composed of kin rather than unrelated individuals (Hamilton 1964). Clark (2004c) demonstrated that pairs of female siblings in the species *C. horridus* were more likely to associate with each other than non-related females. Males, both related and not, were less gregarious. Subsequently, kin-based aggregations were identified in natural populations of *C. horridus* (Clark et al. 2012). Females and juvenile snakes were found to aggregate with related individuals under certain conditions, but notably showed no kin preference in winter denning, although previous studies on the same species have shown that individuals occupying the same den have a higher degree of relatedness than those from neighboring winter dens (Bushar et al. 1998). A high degree of philopatry has also been documented with *C. horridus*, in which individuals born at or near a particular den often return to that identical site throughout their lives (Brown 1993). However, when Clark et al. (2008) examined the genetic structure of this species at specific dens, they found significant gene flow between most dens, with approximately 30% of paternity assignment involving individuals between dens, indicating that gene flow largely occurs through dispersal of males during the late summer and early fall mating season. Selection of den sites by *C. atrox* in the Suizo

Mountains in Arizona seems to be by social choice, kin-based, or a combination of the two. The dens are a mix of kin-based groups and non-kin groups, characterized by low genetic relatedness, but nonetheless strongly connected individuals that associate at certain times of the year (Clark et al. 2014).

1.6: Conservation

Ultimately, more research on the behavioral ecology of rattlesnakes is needed to create informed management objectives in order to guide the conservation of rattlesnakes and the ecosystems in which they inhabit (Dodd 1993, Dodd 2016). Rattlesnakes are threatened by habitat loss, urbanization, persecution, disease, introduction of invasive exotic species, and climate change, all of which is compounded by human indifference and intolerance resulting from ophidiophobia (Gibbons et al. 2000, Burghardt et al. 2009, Nowak and Greene 2016, Funk et al. 2017, Spear et al. 2017, Stengle et al. 2017). For example, in the United States there is continued sanctioning of rattlesnake roundups, which are clearly detrimental to the long-term stability of this group of snakes, especially *C. adamanteus, C. atrox*, and *C. horridus* (Fitzgerald and Painter 2000). This is especially concerning given how important rattlesnakes are to desert food webs, often serving as top predators in these ecosystems (Fitch 1982, Reynolds and Scott 1982, Greene 1997, Nowak et al. 2008, Loughran et al. 2014). Additionally, they are of cultural importance, notably appearing in folklore and literature left behind by indigenous inhabitants of the southwestern United States (Klauber 1972, Dilworth 1996, Nabhan 2003, Silko 2010, Sasaki et al. 2011). Venomous snakes also provide direct utility to humans from the wealth of pharmacological research on snake venoms, which to date has developed several novel drugs that are used to treat common human ailments, including defibrinogenating agents derived from the venoms of *Callesolasma rhodestoma*, *Bothrops atrox*, and *C. adamanteus*, pain relievers from the venoms of *Ophiophagus hannah*, *C. durissus*, and *Naja kaouthia*, and anti-cancer treatments from the venom of *Agkistrodon contortrix* (Vonk et al. 2011). However, declines in snake populations have not received the same level of attention as the declines in other groups of herpetofauna, such as amphibians and sea turtles (Norris 2007, Ernst and Lovich 2009).

1.7: Primary Objectives

The above summary only scratches the surface of the current research on the behavioral ecology of rattlesnakes, but highlights many of the principles that guide the research objectives in the following chapters. With that in mind, the following chapters will address three primary research objectives:

1) Utilize radiotelemetry to determine movement patterns of *C. ornatus* at the Indio Mountains Research Station, including the estimation of home range sizes, identification of core use areas, and examining seasonal and sexual patterns in movement metrics.
2) Using data collected during radiotelemetry, determine seasonal and sexual patterns of habitat and microhabitat use of *C. ornatus.*
3) Present naive young snakes with aqueous extracts from the integument of known and suspected prey items to determine innate prey preference of *C. ornatus*.

Chapter 2: Movement, home range size, and habitat use of Eastern Black-tailed Rattlesnakes (*Crotalus ornatus*) in the northern Chihuahuan Desert

2.1 Abstract

Despite its wide distribution throughout the northern Chihuahuan Desert, very little is known about the ecology or behavior of the Eastern Black-tailed Rattlesnake (*Crotalus ornatus*). The body of knowledge was largely based on research conducted on the former conspecific (*C. molossus*), thus the revalidation of *C. ornatus* widened the void in our understanding of the species. The aim of this study was to elucidate movement patterns, space use, and habitat use by *C. ornatus* in the northern Chihuahuan Desert of far west Texas. Radiotelemetry was used to monitor individual snakes for at least one active season from May 2015 through August 2018. Mean (±1 SE) home range size for all individuals was 22.84 ± 4.49 ha, mean movement frequency was 0.73 ± 0.03, and mean daily movement rate was 9.28 ± 0.93 m/day. Male snakes had larger home range sizes, larger core use areas, higher movement frequencies, and higher movement rates than female snakes. Although female movement peaked in June, overall monthly movement rates were similar. Male movement peaked during August, with lesser peaks in movement, although not statistically significant, in July and June. Multinomial logit models were used to analyze habitat use patterns of *C. ornatus*, while controlling for subject, habitat availability, and season. Despite limited availability within snake home ranges, most observations of snakes occurred in arroyos or on rocky slopes. Microhabitat was also used non-

randomly, with snakes seeking cover in rocky refugia or under dense vegetation, rather than areas containing high proportions of gravel or plant litter. This study presents the first detailed information about habitat and microhabitat use, along with patterns of movement and home range size for the recently revalidated *C. ornatus*.

2.2 Introduction

Movement patterns and habitat use represent fundamental aspects of snake biology and ecology, reflecting individual responses to spatio-temporal fluctuations in the distribution of resources in the environment (Plummer and Congdon 1994, Johnson 2000, Smith et al. 2009). Detailed knowledge of species' spatial requirements is critical for developing appropriate management strategies when the need for conservation initiatives arise (Dodd 1993, Webb and Shine 1997, Fitzgerald et al. 2002, Dodd 2016), particularly for species that occur within suboptimal habitats (Parent and Weatherhead 2000, Lomas et al. 2015) or are the targets of direct human persecution, such as many snakes (Maritz et al. 2016). The utilization of radiotelemetry to study snake behaviors (e.g., Reinert 1992, Greene 1997, Gardiner et al. 2013) has previously provided insights into the impacts of sex, body size, and seasons on habitat use and movement (Whitaker and Shine 2003, Roth 2005, Blouin-Demers et al. 2007, Glaudas and Rodrıguez-Robles 2011). However, there is a dearth of information regarding the spatial and behavioral ecology of many snake species.

Crotalus ornatus, a wide ranging, medium-sized (762–1067 mm snout-vent length) rattlesnake species found in the northern Chihuahuan Desert, was recently reinstated as a valid species by Anderson and Greenbaum (2012). Historically, ecological research on black-tailed rattlesnakes in the United States has been conducted on populations in Arizona (Beck 1995, Hardy and Greene 1999a, Nowak 2009), which are now recognized as a different species (*C. molossus*), leaving only limited ecological information available for *C. ornatus*. At its current pace, the rate of taxonomic change has exceeded the rate at which ecological information has been gathered for newly described or revalidated species, and the inability of ecological research to keep up with taxonomic change greatly hampers conservation efforts in a rapidly changing world (Garnett and Christidis 2017). Therefore, my objective was to provide a detailed assessment of the movement patterns, estimate home range size, and examine habitat and microhabitat use by *C. ornatus* in the Trans-Pecos ecoregion of west Texas, near the border between the United States and Mexico.

Based on patterns of other rattlesnake species in the southwestern United States, I predicted that male *C. ornatus* will have larger home range sizes, move more frequently, and have higher movement rates than female snakes. Space use has been recently documented for the other rattlesnake species present in the study area (Mata-Silva et al. 2018, DeSantis et al. 2019), so based on body size, I hypothesized that *C. ornatus* would have larger home range sizes than *C. lepidus*, and smaller home range sizes than *C. atrox*. No previous studies reported estimates of home range size or movements for *C. ornatus*, so I made general comparisons with its former conspecific *C. molossus*, which is thought to occupy a similar niche west of the Continental Divide (Werler and Dixon 2000, Ernst and Ernst 2012, Persons et al. 2016).

Additionally, I compared space use of *C. ornatus* with the other two rattlesnake species present at the study area, *C. lepidus* and *C. atrox*. Only general information is known for *C. ornatus* habitat use patterns, but individuals are typically encountered in rock dominated habitats, such as rocky hillsides with numerous crevices, stony ridges, rock-slides, and dry rocky streambeds (Werler and Dixon 2000, Ernst and Ernst 2003, Campbell and Lamar 2004, Dixon and Werler 2005, Persons et al. 2016). I, therefore, predicted that *C. ornatus* at Indio Mountains Research Station (IMRS) would favor rocky habitats (i.e., rocky slopes and alluvial rocky slopes) and microhabitats characterized by rock and gravel substrates over other available habitat and microhabitat features.

2.3 Methods

2.3.1 Study Area

The study was conducted at the Indio Mountains Research Station (IMRS; centered on 30.75°N, 105.00°W; datum = WGS84), a 16,000-ha parcel of the northern Chihuahuan Desert that is overseen by the University of Texas at El Paso. IMRS headquarters is ~40 km southwest of Van Horn, Texas, in southeastern Hudspeth County (Fig. 2.1). Relevant characteristics of IMRS can be found below, and a detailed description of the study site can be found in Worthington et al. (2020).

The Indio Mountains run from north to south, resulting in primarily east- and west-facing slopes. Substrates are primarily composed of intermittent conglomerate, limestone, sandstone, and igneous rock, or combinations of the above in areas where they adjoin. Flat alluvial fans radiate from the steeper mountainous terrain that are transected by large and small arroyos, which drain the mountainous areas into the Green River to the east and the Rio Grande to the south and southwest. During the active season for *C. ornatus* (March–October) within the study period (May 2015–August 2018), mean daily temperature was 25.5°C, with a mean daily maximum and minimum of 32.3°C and 18.4°C, respectively. Average annual precipitation on IMRS is 235 mm, most of which is rainfall during the June-October summer monsoon season.

The vegetation on IMRS is typical Chihuahuan Desert scrubland, dominated by Creosote Bush (*Larrea tridentata*), White-thorn Acacia (*Vachellia constricta*), Catclaw (*Senegalia greggii*), Honey Mesquite (*Prosopis glandulosa),* Desert Christmas Cactus (*Cylindropuntia leptocaulis*) and Engelmann's Prickly-pear (*Opuntia engelmannii*) on alluvial flats and along arroyos. Rocky slopes and outcrops are characterized by Lechuguilla (*Agave lechuguilla*), Pitaya (*Echinocereus enneacanthus*), Ocotillo (*Fouquieria splendens*), Sotol (*Dasylirion leiophyllum*), Torrey's Yucca (*Yucca treculeana*), Eve's Needle (*Yucca faxoniana*), and Purple Prickly Pear (*Opuntia macrocentra*). Grasses such as Black Gramma (*Bouteloua eriopoda*), Arizona Cottontop (*Digitaria californica*), and Tanglehead (*Heteropogon contortus*) are found scattered throughout the above associations.

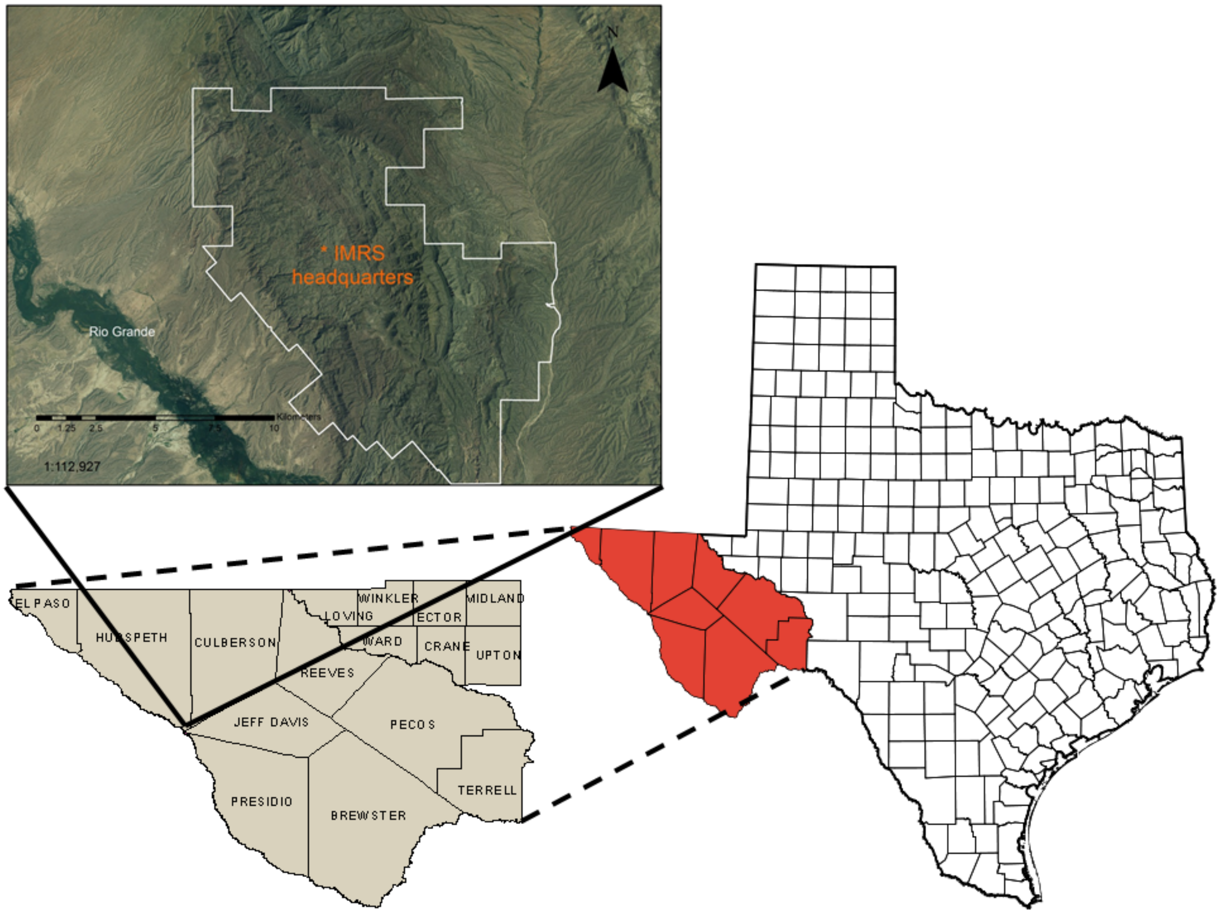


Figure 2.1: Map showing the location of the Indio Mountains Research Station, Hudspeth County, Texas.

2.3.2 Study Subjects and Transmitter Implantation

Data were collected for this study from May 2015 through August 2018. Active searches for rattlesnakes were conducted over the course of 2–4 days per week from March through October. In total, 25 individuals (10 females and 15 males) suitable for telemetry were found during active searches, which consisted of walking transects of ~4 km through suitable habitat, primarily during morning (0600–1000h) and evening (1900–2400h). Of these 25 monitored individuals, only 15 contributed data for statistical analyses. One male was killed by an unknown predator shortly after release, 1 female never exited her overwintering refuge and was presumed dead, and 8 individuals (2 females and 6 males) experienced premature transmitter failure before sufficient data had been collected. Individuals were considered suitable based on size (≥100 g), with small individuals (100–200 g) being implanted with 5 g radiotransmitters, and large individuals (>200 g) being implanted with 10 g radiotransmitters (Holohil Systems Ltd., Models SB-2T and SI-2T). Suitable size was determined so that transmitters weighed ≤5% of the body mass of the snake at the time of implantation. Implantation procedures followed those of Reinert and Cundall (1982) and Hardy and Greene (1999b, 2000). Post-surgery, snakes were released at the site of original capture within 24–48 h of transmitter implantation.

2.3.3 Home Range and Movement Patterns

To allow for recovery and acclimation, data collection began one week after release for each snake. Relocations occurred every two to three days during the active season (March–October) and biweekly during the inactive season (November–February) using R-1000 telemetry receivers and a RA-150 Yagi directional antenna (Communication Specialists Inc.). Locations were recorded in Universal transverse Mercator (UTM) with a hand-held global positioning system (Garmin: eTrex 30x).

For each month of the active season, daily movement rate was calculated (m/day = total distance moved by an individual divided by the number of days monitored; Beaupre 1995). For this study, I selected a suite of commonly presented home range estimators, including the 100% Minimum Convex Polygon (MCP) (Row and Blouin-Demers 2006) and 50% fixed-kernel Utilization Distribution (UD; core use areas) with the plug-in bandwidth matrix (Bauder et al. 2015, Bauder et al. 2016). I selected the plug-in bandwidth matrix for UD home ranges because it was demonstrated to be robust to variation in sampling with spatial data collected on a congener of *C. ornatus* (*C. oreganus*) (Bauder et al. 2015). Movement metrics and home range sizes were calculated in R using the packages *adehabitat*, *adehabitatHR*, and *adehabitatLT* (Calenge 2006, Program R v3.6.3, R Core Team 2020).

2.3.4 Habitat and Microhabitat Use

The following dominant topographic features were used to define habitat types (Fig. 2.2): alluvial flats, alluvial slopes, alluvial rocky slopes, rocky slopes, and arroyos. Alluvial flats and alluvial slopes are primarily gravel and sand dominated habitats almost completely lacking rocky substrates and large rocks (>50 mm diameter); alluvial rocky slopes are eroding slopes with a mixture of loose gravel (<50 mm diameter) and rocky substrates; rocky slopes are represented by steep hillsides with rimrock, exposed bedrock, and frequent rock outcroppings; and arroyos are temporary watercourses that drain the mountainous terrain with dense stands of shrub vegetation extending ~5 m in diameter on each side of the bare ground at the arroyo bottom. Plant associations within habitat types follows Henrickson and Johnston (1983) and Diamond (1993).

To test whether the patterns of habitat use by snakes were associated with availability of each habitat type within individual home ranges, I used a subject-random sampling method by pairing 407 used locations with 407 random locations across all *C. ornatus* home ranges. Random sites were obtained by moving a random distance at a random bearing from the location of the subject (Sperry and Taylor 2008). The range of random distances was based on the observed range of typical daily movement distances made by *C. ornatus* during the study (10–300 m), and random distances and bearings were obtained using a random number generator (http//www.random.org).

Microhabitat type was classified during all snake relocations. I also quantified ground cover composition in a 1-m^2 area centered at each of the locations (Reinert 1984). Ground cover elements that were factored into the composition (%) included vegetation, rocks, gravel, sand, and vegetation litter. However, sand was not included in analyses of ground cover composition because it accounted for <1% of the ground cover types. A photograph was taken of each microhabitat and used for detailed inspection of structural attributes and ground cover composition. I used the same 407 subject–random paired sites to compare ground cover composition between used and available microhabitats. Locations used more than once by a snake were only included once in the analyses, and sites that snakes were actively crossing when encountered were not included in analyses (Reinert 1984; Blouin-Demers and Weatherhead 2001).

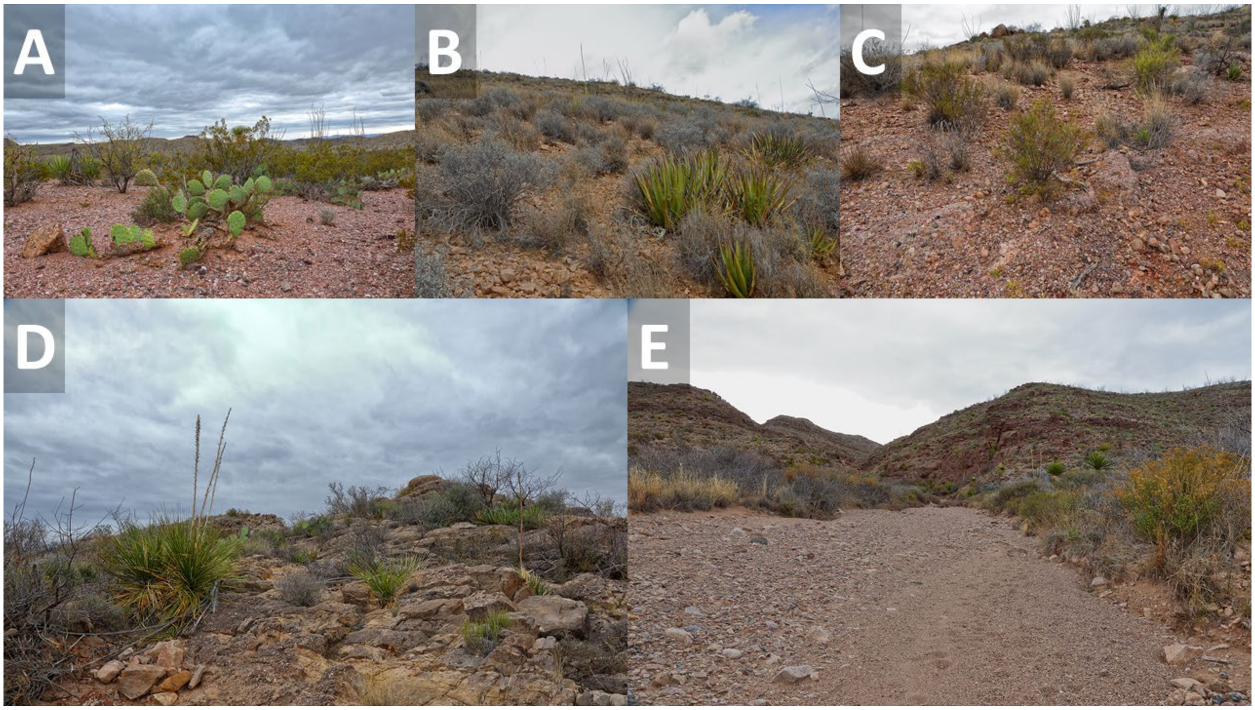


Figure 2.2: Representative photographs of habitat classifications at Indio Mountains Research Station, Hudspeth County, Texas: (A) alluvial flat, (B) alluvial slope, (C) alluvial rocky slope, (D) rocky slope, (E) arroyo.

2.3.5 Statistical Analyses

All statistical tests were performed using R statistical software (v3.6.3; R Core Team 2020), with α set at 0.05. Because of the relatively small sample of *Crotalus ornatus* (*n* = 15), I analyzed the data using both parametric and nonparametric tests. A one-way analysis of variance (ANOVA) was used to test for differences in movement rates, movement frequency, and home range sizes as a function of sex. A repeated-measures ANOVA was used to test for monthly differences in movement rates for each sex. A repeated-measures multivariate ANOVA and Wilk's lambda were used to test for differences among and between ground cover composition at used and random sites. To investigate patterns of habitat use while accounting for dependencies attributable to repeated measures and the availability of each habitat type within snake home ranges, I examined multinomial logit models with maximum likelihood estimation with two predictor variables: (1) habitat availability and (2) season (spring = March–May; summer = June–October). Snake ID was input as a random factor. The reference level for habitat was ‘‘arroyo,’’ and for season it was ‘‘summer.’’ I used the Akaike Information Criterion (AIC) for model selection with a forward stepwise selection process based on minimum AIC criteria. Model results are reported using model-based odds ratios and associated profile likelihood confidence limits. All habitat use analyses were conducted using the *multinom* function in the *nnet* package (Venables and Ripley 2002).

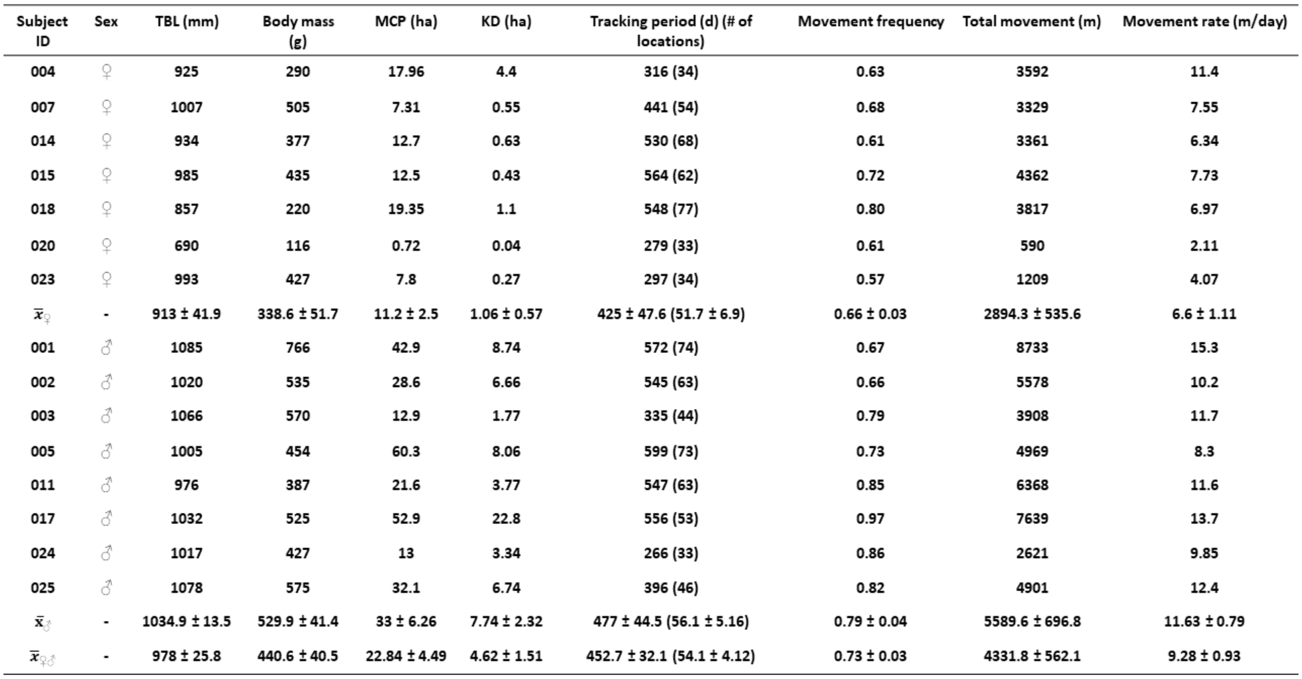
2.4 Results

2.4.1 Home Range and Movement Patterns

From May 2015 to August 2018, 15 *Crotalus ornatus* (seven female, eight male) were radiotracked during at least one active season (March through October). The duration of tracking ranged from 266 to 599 d (Table 2.1), with the number of locations ranging from 33 to 77 ($\bar{x}$ ± 1 SE = 54.1 ± 4.12). Mean home range size was 22.84 ± 4.49 ha for all individuals and ranged from 0.72 to 60.3 ha. Home range size was significantly larger for males (*n* = 8), with a mean home range size of 33 ± 6.26 ha, compared to female snakes (*n* = 7) with a mean home range size of 11.2 ± 2.5 ha ($F_{\mathrm{df1,\,df14}}$ = 9.469, *P* = 0.00882; Fig. 2.3). The mean 50% KD area was also significantly larger for males than females (7.74 ± 2.32 compared to 1.06 ± 0.57 ha; $F_{\text{df1, df14}} = 6.876$, $P = 0.0211$). For all individuals, the mean 50% KD area was 4.62 ± 1.51 ha. All snakes overwintered in rock piles or crevices on rocky slopes within their home range. Most snakes became active by early to mid-March, with two individuals becoming active in February. Individuals typically reached winter refugia by mid-November, with a single instance of a snake remaining active until early-December.

Mean movement frequency for all snakes was 0.73 ± 0.03 (Table 2.1), with males moving more frequently than females (0.79 ± 0.04 and 0.66 ± 0.03 respectively; $F_{\text{df1, df14}} = 7.532$, $P = 0.0167$; Fig. 2.3). Males also exhibited a higher movement rate than females, moving 11.63 ± 0.79 m/d compared to 6.66 ± 1.11 m/d for female snakes ($F_{\text{df1, df14}} = 16.7$, $P = 0.00128$). For all individuals, the mean movement rate was 9.28 ± 0.93 m/d. Female movement rates were highest in June and July, but were statistically similar across all months ($F_{\text{df7, df39}} = 0.8004$, $P = 0.5924$). For males, monthly movement rates varied significantly ($F_{\text{df7, df47}} = 4.9164$, $P < 0.001$), with the highest movement rates being observed in August ($P = 0.0036$). Following August, movement rates in June ($P = 0.06787$) and July ($P = 0.052$) were approaching significance, but still did not differ statistically from other months of the active season. Movement rates for both sexes were lowest during the month of September (Fig. 2.4).

Table 2.1: Sex, morphometrics, size of home range and core use area, and movement measures for Eastern Black-tailed Rattlesnakes (*Crotalus ornatus*) radiotracked at Indio Mountains Research Station, Hudspeth County, Texas, from May 2015 through August 2018. Body size is reported as total body length (TBL), and size of home range and core use areas are based on minimum convex polygon (MCP) and 50% kernel utilization distribution (KD) estimators.



Subject ID	Sex	TBL (mm)	Body mass (g)	MCP (ha)	KD (ha)	Tracking period (d) (# of locations)	Movement frequency	Total movement (m)	Movement rate (m/day)
004	♀	925	290	17.96	4.4	316 (34)	0.63	3592	11.4
007	♀	1007	505	7.31	0.55	441 (54)	0.68	3329	7.55
014	♀	934	377	12.7	0.63	530 (68)	0.61	3361	6.34
015	♀	985	435	12.5	0.43	564 (62)	0.72	4362	7.73
018	♀	857	220	19.35	1.1	548 (77)	0.80	3817	6.97
020	♀	690	116	0.72	0.04	279 (33)	0.61	590	2.11
023	♀	993	427	7.8	0.27	297 (34)	0.57	1209	4.07
$\bar{x}_{♀}$	-	913 ± 41.9	338.6 ± 51.7	11.2 ± 2.5	1.06 ± 0.57	425 ± 47.6 (51.7 ± 6.9)	0.66 ± 0.03	2894.3 ± 535.6	6.6 ± 1.11
001	♂	1085	766	42.9	8.74	572 (74)	0.67	8733	15.3
002	♂	1020	535	28.6	6.66	545 (63)	0.66	5578	10.2
003	♂	1066	570	12.9	1.77	335 (44)	0.79	3908	11.7
005	♂	1005	454	60.3	8.06	599 (73)	0.73	4969	8.3
011	♂	976	387	21.6	3.77	547 (63)	0.85	6368	11.6
017	♂	1032	525	52.9	22.8	556 (53)	0.97	7639	13.7
024	♂	1017	427	13	3.34	266 (33)	0.86	2621	9.85
025	♂	1078	575	32.1	6.74	396 (46)	0.82	4901	12.4
$\bar{x}_{♂}$	-	1034.9 ± 13.5	529.9 ± 41.4	33 ± 6.26	7.74 ± 2.32	477 ± 44.5 (56.1 ± 5.16)	0.79 ± 0.04	5589.6 ± 696.8	11.63 ± 0.79
$\bar{x}_{♀♂}$	-	978 ± 25.8	440.6 ± 40.5	22.84 ± 4.49	4.62 ± 1.51	452.7 ± 32.1 (54.1 ± 4.12)	0.73 ± 0.03	4331.8 ± 562.1	9.28 ± 0.93

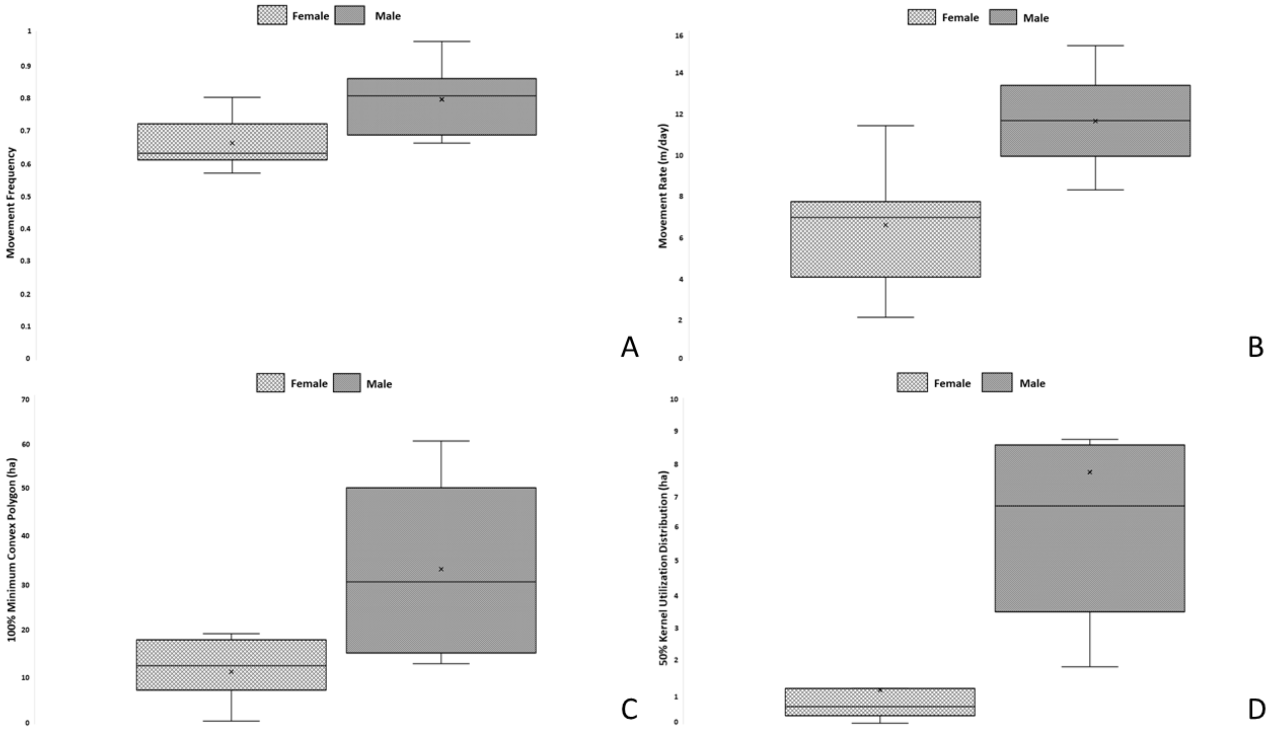


Figure 2.3: Movement and home range size comparisons between the sexes of Eastern Black-tailed Rattlesnakes (*Crotalus ornatus*; reported as mean ± 1 SE) at Indio Mountains Research Station, Hudspeth County, Texas: (A) movement frequency ($F_{\text{df1, df14}}$ = 7.532, P = 0.0167), (B) movement rate (m/day; $F_{\text{df1, df14}}$ = 16.7, P = 0.00128), (C) 100% minimum convex polygon home range estimate (ha; $F_{\text{df1, df14}}$ = 9.469, P = 0.00882), (D) 50% kernel utilization distribution estimation (ha; $F_{\text{df1, df14}}$ = 6.876, P = 0.0211).

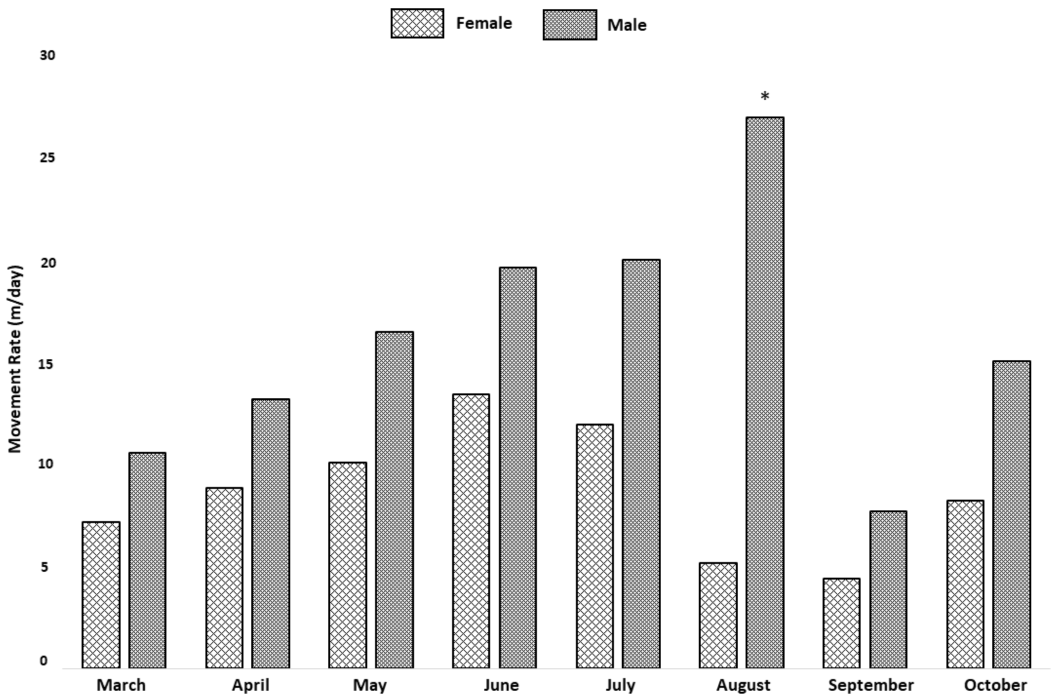


Figure 2.4: Monthly movement rates of female ($F_{\mathrm{df7,\ df39}}$ = 0.8004, *P* = 0.5924) and male ($F_{\mathrm{df7,\ df47}}$ = 4.9164, *P* < 0.001; August [*]: *P* = 0.0036) Eastern Black-tailed Rattlesnakes (*Crotalus ornatus*) at Indio Mountains Research Station, Hudspeth County, Texas.

2.4.2 Habitat and Microhabitat Use

Crotalus ornatus were more likely to be found in arroyo or rocky slope habitat, despite these being the least expansive of the habitat types available within their home ranges. Snakes were observed using arroyo habitat 182 times (44.7%) and rocky slope habitat on 179 occasions (44%), which together accounted for over 88% of total observations. *Crotalus ornatus* was observed on alluvial slopes 23 times (5.6%), 20 times on alluvial rocky slopes (4.9%), and 3 times (0.7%) in alluvial flat habitat (Table 2.2). Conversely, alluvial rocky slopes were estimated as the most expansive habitat available within snake home ranges, followed by alluvial flat and alluvial slope habitats, with rocky slope and arroyo habitats being predicted as the least available habitats. The best fitting multinomial logit model was the random slopes and intercepts model, controlling for snake ID (AIC = 636.98), and only included a single predictor variable: habitat availability within snake home ranges (Table 2.3). Because of the extremely low number of observations, the best fitting model excluded alluvial flat habitat. Overall, snakes were observed using arroyo and rocky slope habitat more frequently than would be expected based on the estimated availability of these habitat types within snake home ranges. Conversely, alluvial rocky slope was the most expansive habitat, but observations of snakes were infrequent here. Alluvial slope habitat was largely avoided by *C. ornatus* on IMRS.

Table 2.2: Number of observed and random points used in subject-random pairings for each habitat type at Indio Mountains Research Station, Hudspeth County, Texas.

Habitat	Observed (subject)	Available (random)
Alluvial flat	**3**	**87**
Alluvial slope	**23**	**86**
Alluvial rocky slope	**20**	**127**
Rocky slope	**179**	**59**
Arroyo	**182**	**48**

Table 2.3: Output by habitat type (reference level = arroyo) for the best fitting multinomial logit model (random slopes and intercepts model, controlling for snake ID; AIC=636.98) of habitat use by Eastern Black-tailed Rattlesnakes (*Crotalus ornatus*) at Indio Mountains Research Station, Hudspeth County, Texas, when accounting for habitat availability within snake home ranges. The best fitting model excluded alluvial flat habitat.

					Confidence interval	
Habitat type	**Odds ratio**	**SE**	**Z-statistic**	***P*-value**	**Lower (2.5%)**	**Upper (97.5%)**
Alluvial flat						
Intercept	**-41.13**	**15065.19**	**-0.0027**	**0.998**	**-29568.9**	**29486.65**
Availability	**18.09**	**10251.41**	**0.0018**	**0.999**	**-20074.7**	**20110.86**
Alluvial slope						
Intercept	**-11.76**	**1.66**	**-7.09**	**<0.001**	**-15.01**	**-8.51**
Availability	**13.93**	**2.42**	**5.75**	**<0.001**	**9.18**	**18.68**
Alluvial rocky slope						
Intercept	**-36.18**	**7.84**	**-4.61**	**<0.001**	**-51.54**	**-20.81**
Availability	**28.59**	**4.69**	**6.09**	**<0.001**	**19.38**	**37.79**
Rocky slope						
Intercept	**-3.05**	**0.50**	**-6.10**	**<0.001**	**-4.03**	**-2.07**
Availability	**3.96**	**1.26**	**3.15**	**0.002**	**1.50**	**6.43**

Radiotracked snakes were observed in 17 microhabitat types, with the majority of locations being under plants (under succulents = 17%, under shrub = 16%) or concealed in rocky refugia (in crevice = 17%, under rock = 13%; x^2 = 652.9, df = 16, *P* < 0.001; Table 2.4). Male snakes *(N* = 8) were observed in 15 different microhabitat types, most frequently being found under succulent vegetation (20%) and in crevices (16%), with locations under rock (14%) and under shrubs (13%; x^2 = 314.71, df = 14, *P* < 0.001) occurring at a slightly lower rate. Only male snakes were located more than 1 m off of the ground in shrubs and on grass; however, both microhabitat categories accounted for less than 1% of observations. Female snakes (*N* = 7) were also observed in 15 microhabitats; however, most locations were under shrubs (20%) or in crevices (18%; x^2 = 227.18, df = 14, *P* < 0.001). Observations of snakes on sand and on plant litter were unique to females, but each category accounted for less than 1% of observations. Ground cover composition (%) in 1-m^2 plots at each point of relocation was primarily composed of vegetation ($\bar{x}$ = 39.83 ± 1.83%) and rock (35.12 ± 2.01%), with gravel and plant litter (9.93 ± 0.73, and 9.84 ± 0.72%, respectively) being lesser components. When comparing used and random microhabitats, the repeated-measures MANOVA highlighted a difference in ground cover composition between the two categories (Wilk's λ = 0.52, *n* = 406, $F_{\mathrm{df1,\,df\,810}}$ = 188.78, *P* < 0.001; Table 2.5). Snakes used microhabitats with a greater abundance of vegetation and rock relative to random microhabitats, which consisted mostly of gravel. When examined on a monthly basis, this same pattern was maintained (Fig. 2.5). Although gravel and plant litter were present at observed microhabitats, they always accounted for <25% of ground cover.

2.5 Discussion

2.5.1 Home Range and Movement Patterns

Although the lack of consistent protocols (e.g., differences in geographic location, sample size, location frequency, and tracking period) makes detailed comparisons difficult and likely contributes to the variability between studies (Gregory et al. 1987), I estimated home range sizes of *Crotalus ornatus* and present comparisons with former conspecific *C. molossus*, which is thought to exhibit similar life history characteristics west of the Continental Divide. Although the literature is sparse, both sexes of *C. molossus* seem to exhibit smaller home range sizes than those demonstrated by *C. ornatus* at IMRS. In the Sonoran Desert of Arizona, Beck (1995) reported male *C. molossus* home ranges (0.93 and 3.41 ha) that were much smaller than male *C. ornatus* on IMRS, and a female home range (6.41 ha) that was slightly smaller than the mean for female *C. ornatus* on IMRS. Hardy and Greene (1999a) reported that *C. molossus* of both sexes in the Chiricahua Mountains of southeast Arizona have smaller home ranges (male = 21 ha, female = 3.75 ha) than *C. ornatus* on IMRS. In the Peloncillo Mountains of southwestern New Mexico, Smith et al. (2001) also reported a home range size (<0.1 ha) for *C. molossus* that is much smaller than those of *C. ornatus* on IMRS. At Tonto National Monument in Arizona, Nowak (2009) reported home range sizes (18.05 ha) for male *C. molossus* that were smaller than male *C. ornatus,* and a female that had a home range (6.33 ha) slightly smaller than those used by *C. ornatus* on IMRS.

In addition to comparing the home range sizes of *Crotalus ornatus* to those of a former conspecific, I compared them to the two other *Crotalus* species found on IMRS, *C. lepidus* and *C. atrox*. Mata-Silva et al. (2018) found that *C. lepidus* on IMRS had a smaller home range size (13.69 ha) and smaller core use area (2.83 ha) than *C. ornatus*. DeSantis et al. (2019) also found that both male and female *C. atrox* on IMRS have smaller home range sizes (male = 22.68 ha, female = 4.31 ha) and core use areas (male = 7.35 ha, female = 1.07 ha) than male and female *C. ornatus*. Although unclear at an interspecific level (Macartney et al. 1988), body size has been shown to positively correlate with space use within species (Blouin-Demers et al. 2007), which may explain why *C. lepidus* exhibits smaller space use metrics than *C. ornatus*. On IMRS, DeSantis et al. (2019) demonstrated that some *C. atrox* utilize human-made earthen tanks as resource hotspots, decreasing the home range sizes and core use areas of the snakes in these areas, which explains why a larger-bodied species would use less space than *C. ornatus*.

On IMRS, *Crotalus ornatus* usually became active for the year in early March, when they exited overwintering areas high on primarily south and west facing slopes. During this time, *C. ornatus* was often observed outside of refugia during the late morning (0900–1100h) and afternoon hours (1400–1800h). By late May, snakes shifted to primarily nocturnal behavior, leaving their refugia just before dusk, and returning by 0930 h the following morning. This shift in activity is likely tied to thermal constraints, as snakes typically retreated into shelters when ground temperatures exceeded 38°C, which is approaching the critical thermal maximum for many desert reptiles (~39–42°C; Brattstrom 1965).

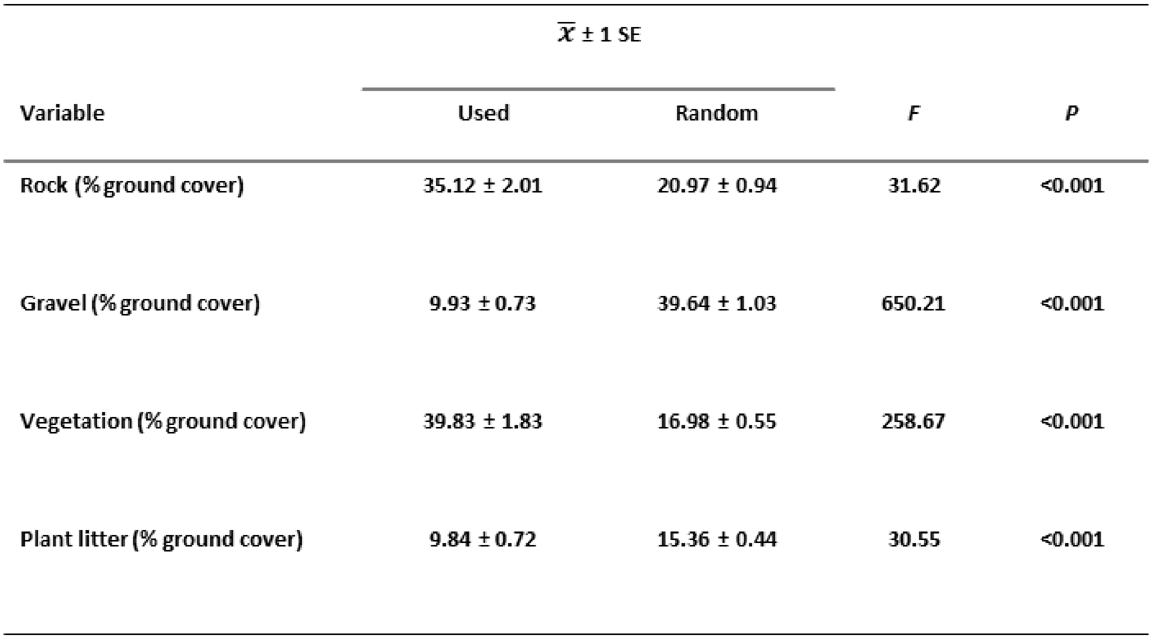
Overall, movement rates for *Crotalus ornatus* on IMRS increased through June and into July, before peaking in August (fig 2.4). Although not significant, female movement peaked in late June, which possibly reflects efforts by female snakes deposit lipid-based pheromone trails to attract males during the breeding season in the following months (Aldridge and Duvall 2002, Jellen and Aldridge 2014). Male movement rates increased in late June through July before peaking during the breeding season in August. This pattern is similar to the male mate-searching behavior documented in other rattlesnake species (Duvall and Schuett 1997, Glaudus and Rodriguez-Robles 2011). All observations of mating behavior were in July through August, which indicates that *C. ornatus* on IMRS follows a unimodal reproductive pattern. Both of the other rattlesnake species present on IMRS also follow a unimodal pattern of reproduction (Mata-Silva et al 2018, DeSantis et al. 2019), and the pattern has been observed in other

Table 2.4: Microhabitat types, number of observations (M8:F7), and proportional use by Eastern Black-tailed Rattlesnakes (*Crotalus ornatus*) at Indio Mountains Research Station, Hudspeth County, Texas.

	Observations					
Microhabitat	**Male**	**%**	**Female**	**%**	**Total**	**%**
In crevice	61	16	45	18	106	17
In woodrat midden	9	2	5	2	14	2
In rockpile	26	7	19	7	45	7
In shrub	3	<1	0	0	3	<1
On grass	1	<1	0	0	1	<1
On gravel	11	3	4	2	15	2
On plant litter	0	0	1	<1	1	<1
On rock	24	6	4	2	28	4
On sand	0	0	3	1	3	<1
Under grass	7	2	5	2	12	2
Under herbs	9	2	11	4	20	3
Under plant litter	18	5	28	11	46	7
Under log	1	<1	1	<1	2	<1
Under rock	52	14	31	12	83	13
Under shrub	48	13	50	20	98	16
Under succulent	76	20	34	13	110	17
Underground	31	8	14	5	45	7
Total	377	100	255	100	632	100

rattlesnake species in the southwestern United States, including *C. molossus* (Greene et al 2002, Schuett et al 2005), *C. oreganus* (Fitch and Gladding 1947), *C. pricei* (Prival et al 2002), *C. pyrrhus* (Klauber 1997, Goldberg 2000, Gartner and Reiserer 2003), *C. ruber* (Dugan et al 2008), and *C. willardi* (Holycross and Goldberg 2001).

Table 2.5: Ground cover of microhabitats used by Eastern Black-tailed Rattlesnakes (*Crotalus ornatus*) and random sites within snake home ranges at Indio Mountains Research Station, Hudspeth County, Texas. Test statistic and *P*-values from repeated measures multivariate analysis of variance are included.



	$\bar{x}$ ± 1 SE			
Variable	Used	Random	*F*	*P*
Rock (% ground cover)	35.12 ± 2.01	20.97 ± 0.94	31.62	<0.001
Gravel (% ground cover)	9.93 ± 0.73	39.64 ± 1.03	650.21	<0.001
Vegetation (% ground cover)	39.83 ± 1.83	16.98 ± 0.55	258.67	<0.001
Plant litter (% ground cover)	9.84 ± 0.72	15.36 ± 0.44	30.55	<0.001

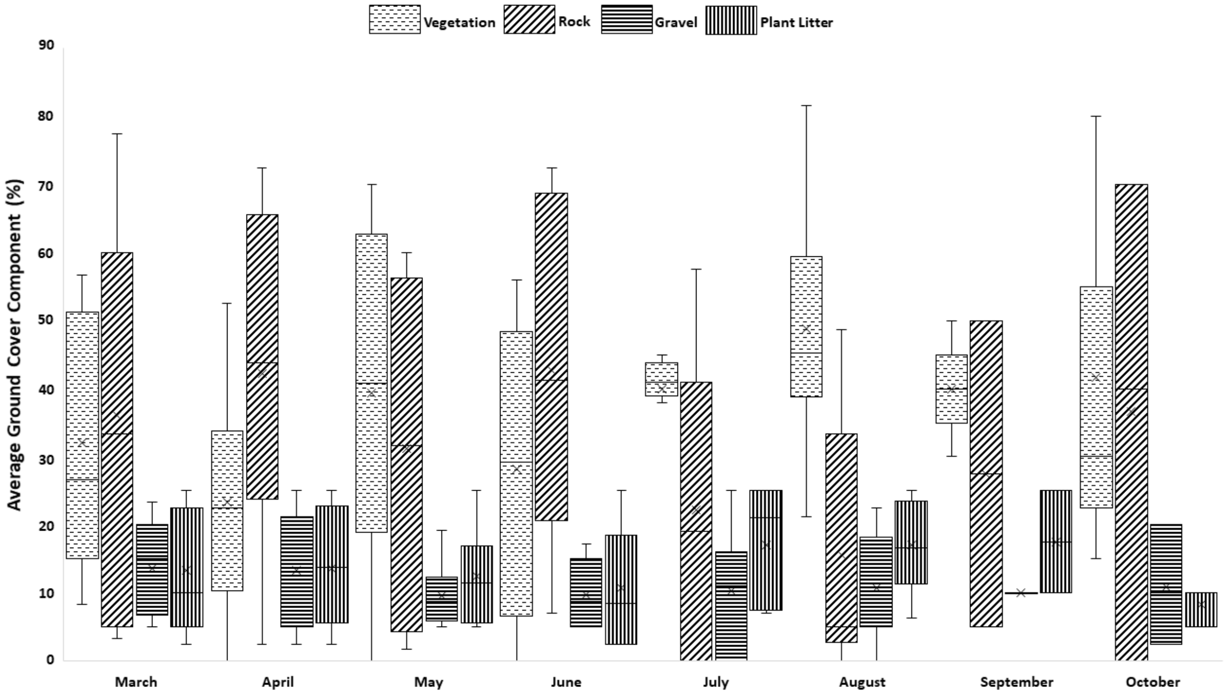


Figure 2.5: Monthly comparisons of microhabitat composition (reported as mean ± 1 SE) at sites used by Eastern Black-tailed Rattlesnakes (*Crotalus ornatus*; *n* = 632 observations) on Indio Mountains Research Station, Hudspeth County, Texas during the active season (March through October).

2.5.2 Habitat and Microhabitat Use

I predicted that *Crotalus ornatus* would favor rocky habitats (rocky slopes and alluvial rocky slopes) at IMRS, and while rocky slope habitat was important, arroyo habitat accounted for a slightly higher proportion of observations. Both alluvial rocky slope and alluvial slope habitat were generally avoided by *C. ornatus*, despite being more expansive within snake home ranges. There was no association between availability and use of alluvial slopes and alluvial rocky slopes. The complete avoidance of alluvial flat habitat is likely driven by a lack of plant diversity and structural complexity, which are important microhabitat features for *C. ornatus* on IMRS. Additionally, Mata-Silva et al. (2018) found that *C. lepidus* is also more likely to be found in arroyos than expected (55% of total observations), making arroyo habitat stand out as important to rattlesnakes at IMRS. It is assumed that habitats most often inhabited by rattlesnakes contain high prey densities (Beck 1995), which are associated with elevated hunting success. However, observations of foraging and feeding behavior were limited during this study, so this could not be determined as a driver of habitat selection. Other than prey presence, environmental factors and predator avoidance may play a role in habitat selection by rattlesnakes (Duvall et al. 1985, Reinert 1993). The Indio Mountains are comprised of mainly west facing slopes, thus *C. ornatus* may use arroyo and rocky slope habitats more frequently because the presence of ample refugia allows them to escape the extreme surface temperatures present on these slopes (Beck 1995).

Ground cover composition at used sites by *C. ornatus* on IMRS differed from random microhabitats. Vegetation and rock cover were the dominant ground cover composition at used microhabitats throughout the active season. Used sites also had gravel and vegetation litter as ground cover, but they were present in lesser proportions. My snakes were most frequently associated with “crevice” and “under succulent” microhabitats, with each accounting for 17% of total observations. After these microhabitats, “under shrub” (16%) and “under rock” (13%) were the most frequently used microhabitats. Most observations of male *C. ornatus* were “under succulent” (20%) or “in crevice” (16%), followed by “under rock” (14%) and “under shrub” (13%). Female snakes were most often observed “under shrub” (20%) and “in crevice” (18%), followed by “under succulent” (13%) and “under rock” (12%). It is likely that snakes were able to find a wide range of climatic conditions using these refugia, allowing for proper thermoregulation, while concealing themselves from predators.

Crotalus ornatus has been reported in a variety of habitats in Texas and is most often thought to be associated with rocky highland habitats in areas dominated by talus slopes, rocky side canyons, crevices in outcrops, and rocky riparian zones (Werler and Dixon 2000, Ernst and Ernst 2012). These observations are consistent with those found for *C. ornatus* on IMRS, however, most of the information on *C. ornatus* is anecdotal in nature, because the species was recently revalidated by Anderson and Greenbaum (2012) and historical black-tailed rattlesnake research was primarily focused at sites in Arizona, making this the first detailed account on the spatial ecology of *C. ornatus*. To better inform conservation objectives, future studies on *C. ornatus* should be conducted at other study sites across the geographic range in New Mexico, other sites in Texas, and in Mexico. Additionally, studies with larger sample sizes and/or emphasizing the behavior of juvenile snakes would greatly improve our understanding of this species. Although it is not listed as a species of concern in Texas and has yet to be evaluated as a recognized species by the International Union for Conservation of Nature (IUCN), large portions of its habitat in the Chihuahuan Desert are under continuing pressure from anthropogenic alterations, such as those associated with ranching, mining, and urbanization (Curtain et al. 2002, Hoyt 2002), in addition to the pressures of over-exploitation facing most rattlesnake species, such as persecution and unregulated take for events such as rattlesnake round-ups (Fitzgerald and Painter 2000).

Chapter 3: Eastern Black-tailed Rattlesnakes (*Crotalus ornatus*) innately discriminate among chemical cues from potential prey

3.1: Abstract

Chemical eavesdropping is a critical tool used by organisms to gain information about their environment and mediate interactions with other organisms within it, such as prey gaining information about predators and vice versa. However, most chemical eavesdropping studies focus on information used by prey species, not predators. The goal of this study was to assess whether or not a desert ambush predator, the Eastern Black-tailed Rattlesnake (*Crotalus ornatus*), differentiates among chemical cues from potential prey items when choosing ambush spots. Naive neonate *C. ornatus* were raised in captivity and placed in an arena where they were presented with aquatic extracts from the integument from 10 known and suspected prey items and a tap water control. Their reactions to the chemical extracts were recorded, and they were given a tongue-flick-ambush (TFAM) score based on their predatory behavior towards the chemical cue. Ten naive neonate *C. ornatus* were put through each of the 11 trials, and based on TFAM scores, snakes differentiated among the chemical cues ($F_{df=9,\ df=10} = 19.149$, $P < 0.001$). *Post hoc* pairwise tests indicated that snakes preferred native small mammal and lizard prey over larger native mammals, native amphibians, native invertebrates, and non-native small mammals. The snakes used in this study have never been exposed to wild prey stimuli in their native ecosystem and have fed exclusively on non-native mammalian prey in captivity, and thus

their preference for native small mammals and lizards indicates an innate basis for prey preference in *C. ornatus*.

3.2: Introduction

As organisms move through the environment, they leave chemical cues on the substrate, which can be used by prey to gain information about potential predators, and by predators to gain information about potential prey (Kats and Dill 1998, Burghardt 1990, Clark 2004b). Despite being a common method for predators to locate prey, most of the research in this area has focused on the ability of prey species to detect potential predators (Kats and Dill 1998, Clark 2004b).

Inadvertently leaving behind scent cues composed of chemicals resulting from the excretory process as prey animals move throughout the environment results in the unavoidable formation of scent trails. A variety of predators exploit these scent trails as sources of information about potential prey items. Most studies of chemosensory prey recognition have been conducted on active foraging species (Burghardt 1990, Stowe et al. 1995, Finelli et al. 2000, Koivula and Korpimaki 2001) despite their utility for sit-and-wait predators (Downes 1999, Roth et al. 1999a, Carroll 2000, Persons and Rypstra 2000, Clark 2004b). Because they seek to acquire different information when investigating scent trails, the behavior of ambush predators is likely to differ from that of active foragers.

Ambush predators must be able to identify species-specific cues left behind in the environment in order to identify ambush sites that are likely to yield hunting success. Many species of actively foraging squamate species are born with the ability to utilize chemical cues to discriminate among prey species (Burghardt 1990). Typically, these studies present the snake with a cotton-tipped applicator impregnated with the chemical cue from a potential prey species, then document the tongue-flicking response and propensity to bite the applicator (Cooper 1998). These studies have shown that active foraging snakes and lizards demonstrate the ability to discriminate among different prey chemical cues, and that the preferences vary geographically (Arnold 1981, Clark 2004b). Preferential targeting of certain prey would be beneficial to species, allowing the predator to focus on prey that is abundant, susceptible to capture, or energy rich.

However, ambush predators typically do not respond when presented with scent cues impregnated into a cotton-tipped applicator, including most iguanian and agamid lizards (Cooper 1995), and viperid snakes (Chiszar and Scudder 1980). This is likely because the scents are not presented in an ecologically relevant manner. Snakes that are primarily ambush predators move widely throughout the environment searching for chemical cues, which are then used in ambush site selection (Greene 1992). The use of chemical cues in the location of ambush sites has been demonstrated in the viperid species *Crotalus horridus*, *C. viridis*, and *Sistrurus miliarius*, and in the elapid species *Hoplocephalus bungaroides* (Duvall et al. 1990, Downes 1999, Roth et al. 1999a, Theodoratus and Chiszar 2000, Clark 2004b, Holding et al. 2016). Given the importance of chemosensory information to snakes in general, the use of chemical cues exhibited by these species is probably characteristic of most snakes that are sit-and-wait predators.

There have been a limited number of studies that examine the ability of an ambush predator to discriminate among chemical cues when selecting an ambush site, especially regarding crotaline study species. With this study, I demonstrated that neonate *Crotalus ornatus* innately discriminate among environmental chemical cues when selecting ambush sites. Based on the limited information available on the diet of *C. ornatus*, I predicted that they will show preference for native small mammals, such as *Dipodomys merriami*, *Chaetodipus intermedius*, and *Peromyscus eremicus*, over native invertebrates (*Scolopendra heros*), amphibians (*Anaxyrus punctatus*), lizards (*Cophosaurus texanus*) and larger small mammals (*Neotoma leucodon*, *Sigmodon hispidus*, and *Ammospermophilus interpres*), and over non-native mammal prey (*Mus musculus*).

3.3: Methods

For this experiment, I obtained 10 neonate *Crotalus ornatus* born in the laboratory between July 2017 and August 2018 to four wild-caught females that were part of an ongoing radiotelemetry study being conducted at the Indio Mountains Research Station (IMRS) in Hudspeth County, Texas. The experiment was conducted between May 2019 and February 2020. The snakes were maintained in the IMRS laboratory space and were kept with their mother until they underwent their natal shed, after which, they were housed individually in appropriately sized latching tubs with a hide area, heat mat on one end of the tub, and a water dish. They were maintained at 21–26°C under a 12L:12D light cycle. The experimental methodology of this research follows that introduced by Clark (2004b).

Each of the 10 experimental subjects were tested once each on a series of aqueous extracts from the integument of 8 vertebrate and 1 invertebrate species, in addition to being presented with a tap water control. The aqueous extracts were prepared by placing a living, intact animal into a water bath in the proportion of 1 ml water per gram of body mass for 10 minutes. Immediately following the water bath, extracts were separated into 10 ml units, and frozen until use.

Extracts were made from *Scolopendra heros* (Giant Desert Centipede), *Anaxyrus punctatus* (Red-spotted Toad), *Cophosaurus texanus* (Greater Earless Lizard), *Chaetodipus intermedius* (Rock Pocket Mouse), *Dipodomys merriami* (Merriam's Kangaroo Rat), *Neotoma leucodon* (White-throated Woodrat), *Sigmodon hispidus* (Hispid Cotton Rat), *Ammospermophilus interpres* (Texas Antelope Squirrel), *Peromyscus eremicus* (Cactus mouse), and *Mus musculus* (House Mouse). All of the animals used to make the extracts were wild caught, except for *M. musculus*, which was captive bred. Species were chosen because they 1) have been documented in the natural diet of *C. ornatus* (*C. intermedius*, *D. merriami*, *N. leucodon*, and *P. eremicus*), 2) have not been documented in the diet of *C. ornatus*, but have been documented in the diet of other desert dwelling rattlesnake species (*S. heros*, *A. punctatus*, *C. texanus*, *S. hispidus*, and *A. interpres*), and 3) a species not sympatric with *C. ornatus*, but closely related to natural prey (*M. musculus*).

For the experimental trials, snakes were placed in an open topped wooden enclosure (61 x 61 x 122 cm), lined with clean construction paper and containing a hide area, water dish, and 2 wooden blocks (4 x 7 x 20 cm; Fig. 3.1). Snakes were allowed to acclimate for 1 day prior to each trial. Clark (2004b) allowed snakes to acclimate for 3 days, but I conducted a pilot study indicating that 1 day was sufficient for *C. ornatus*. To begin each test, the wooden blocks were removed, and paper towels placed on each one. One paper towel, selected at random, was soaked in 10 ml of extract, while the other was soaked in 10 ml of tap water. Both wooden blocks were replaced in the enclosure and snakes were allowed to respond to the extracts for 2 hours, after which the paper towels were removed, and the trial ended. When placed back into the enclosure, the wooden blocks were situated approximately equidistant from the subject. This method of presenting artificial chemical trails allows for the presentation of similar chemical cues from a broad range of species. Clark (2004b) found that snakes exhibited similar responses to chemical extracts made from aqueous extracts and more naturalistic trails created by allowing a potential prey item to run across the substrate surface several times.

Each of the subjects was tested in a different random ordering of the 10 conditions (9 experimental and 1 control) and was tested no more than twice in a 30-day period, and at least 21 days after being fed. Individuals that were undergoing ecdysis were not tested until after the shed cycle was completed. During radiotelemetry, *C. ornatus* has been observed in ambush during the day and at night, so all trials were conducted during the light half of the light cycle and were recorded using a portable video camera for scoring purposes.

Videos were coded and scored blindly. Clark (2004b) outlines the procedure used for scoring the videos. The first encounter with the chemical extract was defined as the time from the initial encounter to the time that the snake removed its head from contact with the chemical extract for 60 seconds. The head of the snake did not have to contact the chemical extract for the entirety of the initial encounter as long as it was not out of contact for more than 60 seconds. I recorded the latency to encounter the chemical extract and the number of tongue-flicks that the snake delivered to the chemical extract during the encounter, where a tongue-flick was counted only if the tongue directly contacted the scent trail or was directly above the paper towel containing the extract. It was noted whether or not the snake adopted the stereotyped ambush posture response after contacting the chemical extract (Reinert et al. 1984). This response is a stereotyped and readily apparent behavior, with the snake assuming a tight coil adjacent to the chemical extract, with the head and neck oriented towards the scent trail in a ready-to-strike position. To quantify this behavior, an ambush posture was defined as the snake not moving, with the head and anterior one third of its body in a recoiled position, oriented toward and within 15 cm of the chemical extract, adopted within 2 minutes of tongue flicking the chemical trail, and maintained for at least 5 minutes (Clark 2004b). In most cases, ambush posture was maintained for the remainder of the trial once initially adopted.

For statistical analysis, I used the modified scoring system for snakes that are ambush predators proposed by Clark (2004b), in which he modified the widely used scoring system initially suggested by Cooper and Burghardt (1990) for active foraging snakes. The method produces a tongue-flick-ambush score (TFAM), where TF_{max} is the maximum number of tongue flicks emitted during the initial encounter of the chemical extract by any individual in any trial, TL is the trial length in minutes, and latency is the latency in minutes to adopt the ambush posture toward the chemical extract:

$$\mathrm{TFAM} = \mathrm{TF}_{max} + (\mathrm{TL} - \mathrm{latency})$$

This composite measure assumes that an ambush posture indicates a stronger response to the chemical extract than any number of tongue flicks, and that the latency to ambush posture decreases with increasing response to the chemical stimulus.

The responses of the subjects were tested for normality and compared with a randomized block analysis of variance (ANOVA), with snake identity as the blocking factor and Tukey's *a posteriori* test for pairwise comparisons (Program R v3.6.3, R Core Team 2020).

Figure 3.1: Overhead photograph showing the configuration of the 61 x 61 x 121 cm construction paper lined arena in which trials were conducted, with hide area and water dish

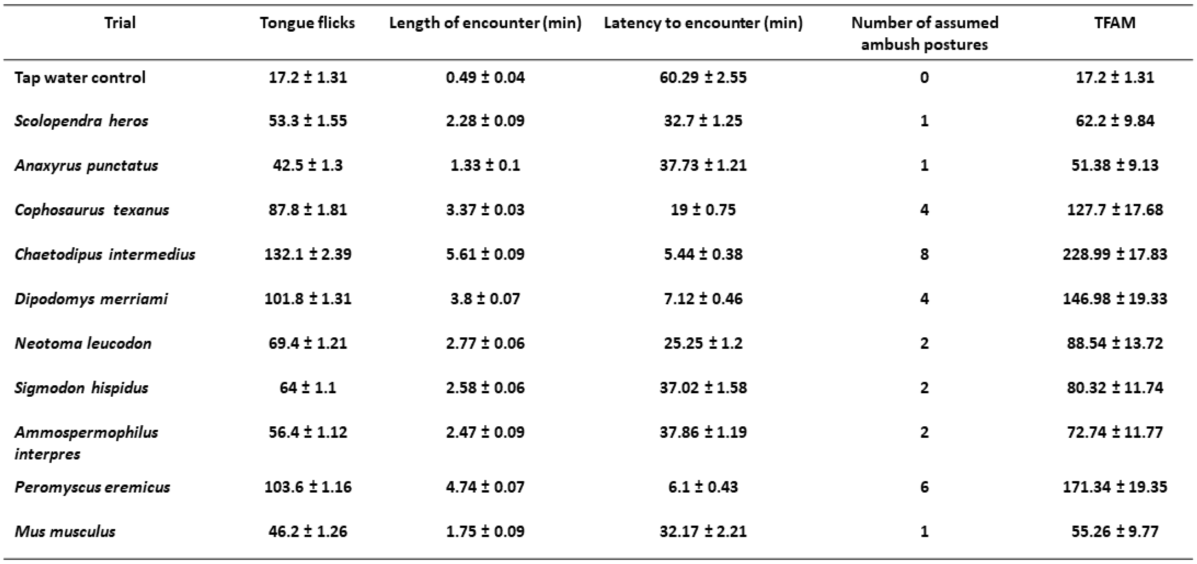
(bottom), the two wooden blocks (one with a paper towel soaked with a scent cue and the other paper towel with tap water), and a neonate *Crotalus ornatus* in ambush position during a trial.

3.4: Results

During trials, snakes exhibited the strongest tongue-flicking responses to chemical cues from *Chaetodipus intermedius*, *Peromyscus eremicus*, and *Dipodomys merriami*, whereas the weakest tongue-flicking rates occurred when presented with the tap water control (Table 3.1). Ambush posture was adopted at least once to all chemical cues, except for the tap water control, and was adopted most frequently to the chemical cues for *C. intermedius* (80% of trials) and *P. eremicus* (60% of trials; Table 3.1). Higher tongue-flicking rates and more assumptions of ambush posture were correlated with higher TFAM scores (Table 3.1).

The randomized block ANOVA used to compare average TFAM scores shows that snakes differentiated between treatments ($F_{df=9,\ df=10} = 19.149$, $P < 0.001$; Fig. 3.1). Tukey's test for pairwise *post hoc* comparisons revealed that snake responses were stronger to chemical cues from *C. intermedius*, *P. eremicus*, *D. merriami*, *Cophosaurus texanus*, and *Neotoma leucodon* than to the tap water control, and chemical cues from *Scolopendra heros, Anaxyrus punctatus*, *Sigmodon hispidus*, *Ammospermophilus interpres*, and *Mus musculus* were similar to the tap water control. In general, the response to chemical cues from native small mammal and lizard prey was stronger than that to native invertebrate and amphibian prey, and non-native small mammal prey, with the exceptions being the weaker responses shown to *S. hispidus* and *A. interpres* chemical cues (Table 3.2).

Table 3.1: Tongue-flicks, length of encounter, latency to encounter, ambush postures assumed and tongue-flick-ambush scores (TFAM) by naive neonate *Crotalus ornatus* in response to chemical cues from potential prey items.



Trial	Tongue flicks	Length of encounter (min)	Latency to encounter (min)	Number of assumed ambush postures	TFAM
Tap water control	17.2 ± 1.31	0.49 ± 0.04	60.29 ± 2.55	0	17.2 ± 1.31
Scolopendra heros	53.3 ± 1.55	2.28 ± 0.09	32.7 ± 1.25	1	62.2 ± 9.84
Anaxyrus punctatus	42.5 ± 1.3	1.33 ± 0.1	37.73 ± 1.21	1	51.38 ± 9.13
Cophosaurus texanus	87.8 ± 1.81	3.37 ± 0.03	19 ± 0.75	4	127.7 ± 17.68
Chaetodipus intermedius	132.1 ± 2.39	5.61 ± 0.09	5.44 ± 0.38	8	228.99 ± 17.83
Dipodomys merriami	101.8 ± 1.31	3.8 ± 0.07	7.12 ± 0.46	4	146.98 ± 19.33
Neotoma leucodon	69.4 ± 1.21	2.77 ± 0.06	25.25 ± 1.2	2	88.54 ± 13.72
Sigmodon hispidus	64 ± 1.1	2.58 ± 0.06	37.02 ± 1.58	2	80.32 ± 11.74
Ammospermophilus interpres	56.4 ± 1.12	2.47 ± 0.09	37.86 ± 1.19	2	72.74 ± 11.77
Peromyscus eremicus	103.6 ± 1.16	4.74 ± 0.07	6.1 ± 0.43	6	171.34 ± 19.35
Mus musculus	46.2 ± 1.26	1.75 ± 0.09	32.17 ± 2.21	1	55.26 ± 9.77

3.5: Discussion

The results of this study demonstrate that *Crotalus ornatus* utilize chemical cues left in the environment by prey species when identifying suitable spots for ambush sites. Vipers are most often characterized as sit-and-wait predators. However, Greene (1992) reviewed field observations of venomous snakes, and found that, guided by chemosensory cues, they often travel long distances until reaching a site where prey is abundant. Often, the snakes remain at these areas with concentrated prey for the remainder of the active season. He defined this technique as “mobile ambushing.” Another species of rattlesnake, *C. viridis*, is known to adopt ambush coils more readily when soiled bedding from potential prey is nearby (Duvall et al. 1990) and will more readily adopt ambush coils facing natural chemical trails left by the mice themselves (Theodoratus and Chiszar 2000). Additionally, Roth et al. (1999) found that free-ranging *Sistrurus miliarus* were attracted to transects that had been treated with aqueous washes from preferred prey items.

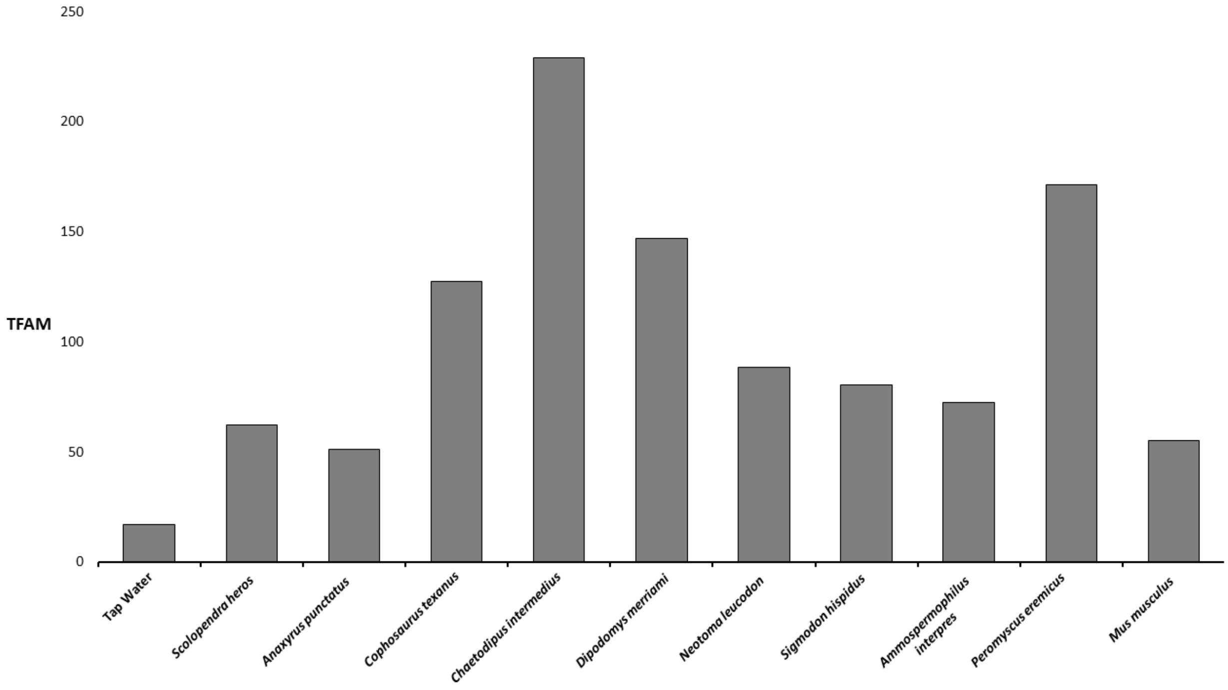
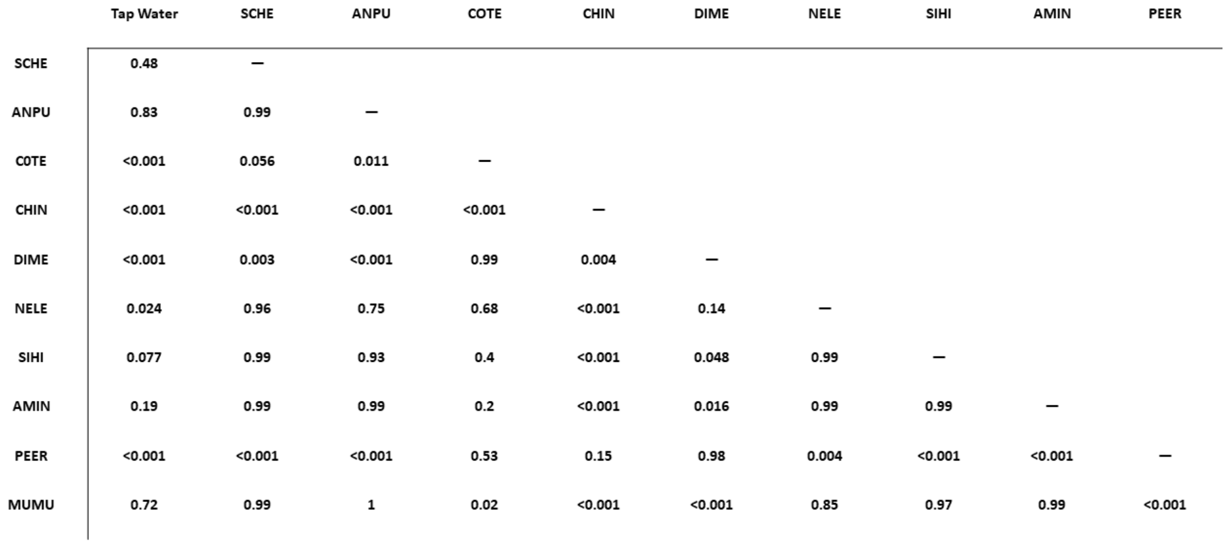


Figure 3.2: Mean tongue-flick-ambush scores (TFAM) by naive neonate *Crotalus ornatus* to chemical cues from potential prey items ($F_{\text{df=9, df=10}} = 19.149$, $P < 0.001$).

Table 3.2: Representative *P*-values of *post hoc* pairwise comparisons of tongue-flick-ambush scores (TFAM) using Tukey’s Test by naive neonate *Crotalus ornatus* in response to chemical cues from potential prey items (SCHE = *Scolopendra heros*, ANPU = *Anaxyrus punctatus*, COTE = *Cophosaurus texanus*, CHIN = *Chaetodipus intermedius*, DIME = *Dipodomys merriami*, NELE = *Neotoma leucodon*, SIHI = *Sigmodon hispidus*, AMIN = *Ammospermophilus interpres*, PEER = *Peromyscus eremicus*, MUMU = *Mus musculus*).



	Tap Water	SCHE	ANPU	COTE	CHIN	DIME	NELE	SIHI	AMIN	PEER
SCHE	0.48	–								
ANPU	0.83	0.99	–							
COTE	<0.001	0.056	0.011	–						
CHIN	<0.001	<0.001	<0.001	<0.001	–					
DIME	<0.001	0.003	<0.001	0.99	0.004	–				
NELE	0.024	0.96	0.75	0.68	<0.001	0.14	–			
SIHI	0.077	0.99	0.93	0.4	<0.001	0.048	0.99	–		
AMIN	0.19	0.99	0.99	0.2	<0.001	0.016	0.99	0.99	–	
PEER	<0.001	<0.001	<0.001	0.53	0.15	0.98	0.004	<0.001	<0.001	–
MUMU	0.72	0.99	1	0.02	<0.001	<0.001	0.85	0.97	0.99	<0.001

Although there is limited information available on the natural diet of *C. ornatus*, the results of this study parallel the published information. As predicted, snakes in this study showed a strong preference for native small mammal and lizard prey, notably for the small mammal species *Chaetodipus intermedius*, *Peromyscus eremicus*, and *Dipodomys merriami*. Likewise, when examining the stomach contents of individual *C. ornatus* in Chihuahua, Mexico, Reynolds and Scott (1982) found *C. intermedius* (25%), *P. eremicus* (16.7%), and *D. merriami*

(16.7%) to be the most frequently ingested prey items. Additionally, they found a large number of birds (16.7%) in the stomachs of *C. ornatus*, which were mostly ground-nesting species (Odontophoridae). Avian scent cues were not used as a part of this study but provide an interesting avenue for future research. Although published literature indicates a strong preference for native small mammal and avian prey, it is also likely that young *C. ornatus* feed on native lizards, as they are the right size and shape for a young individual to ingest with ease, and are abundant in the desert ecosystems inhabited by this species (Werler and Dixon 2000). This would explain the strong response to the *Cophosaurus texanus* scent cue in this study, which I did not predict prior to the experimental trials. Additional research in this area would be to repeat the experiment with different size classes of snakes to determine if any ontogenetic shifts in prey preference occur. Continuing annual trials on the same individual snakes used in this study would also demonstrate this shift in the absence of learning in a wild setting. Also, this study was conducted under diurnal conditions, whereas during radiotelemetry, *C. ornatus* was observed in ambush both diurnally and nocturnally, thus examining if any potential shifts in preference occur under nocturnal conditions would be informative.

This study also provides evidence that prey preference in *C. ornatus* is likely an innate, genetically determined characteristic. The individuals used in this study were captive raised for 1 to over 2 years exclusively on a diet of the non-native mammalian species *Mus musculus*, and still showed no detectable difference in preference between the familiar *M. musculus* prey cue and the tap water control. They were born in captivity to wild caught mothers, so they also never had the chance to learn to target native prey species in a wild setting. Holding et al. (2016) found similar results when comparing *S. miliarus* raised for 5 years on native lizard prey to those raised for 5 years on non-native mammalian prey. However, their study involved a rattlesnake species from a different genus than presented here, and there was a much wider taxonomic breadth between the native lizard prey and the non-native mammalian prey presented to their animals. The results here suggest a fine-tuned ability to innately differentiate between chemical cues from potential prey species belonging to the same taxonomic class by *C. ornatus*.

In snakes, prey preference has been used as a trait to examine both the adaptive genetic divergence in behavior (Arnold 1981, Drummond and Burghardt 1983, Aubret et al. 2006) and the contexts under which phenotypic plasticity occurs as the result of experience (Clark 2004a, Aubret et al. 2006, Waters and Burghardt 2013). Diet exposure periods ranging from 1 week to 1 year have shown evidence for phenotypic plasticity (Fuchs and Burghardt 1971) and genetic determination for prey preference (Burghardt and Hess 1968, Arnold 1977, Arnold 1981). Further research into this system could potentially provide both micro- and macroevolutionary perspectives on what determines variation in prey preference (Holding et al. 2016). Using comparative phylogenetic analyses could establish the plasticity of prey preference over evolutionary time, including identifying any broad ecological similarities of prey preference characteristics within lineages of snakes (Cooper 2008). Additionally, if paired with local estimates of prey availability and gene flow, population-level comparisons on the variation of prey preference within species would elucidate how geographic variation in selection dictates the evolution of plasticity (Arnold 1981, Golmulkiewicz et al. 2007).

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Appendix

Ethics statement:

All methods were carried out in accordance with relevant guidelines and regulations, and all research protocols were approved for the entire study period by the University of Texas at El Paso Animal Care and Use Committee (Protocols: A-201405-1 and A-201806-1) and Texas Parks and Wildlife (Scientific Permit Number SPR-0290-019).

R Code for Multinomial Logit Models for Habitat Use:

Chapter 2

#Multinomial Logit Models

```
> summary(dat)

> dat$H2=relevel(dat$Habitat,ref="Arroyo")

> dat$Season2=relevel(dat$Season,ref="Summer")

> m0=multinom(H2~A,data=dat)

> summary(m0)

> z=summary(m0)$coefficients/summary(m0)$standard.errors
```

```
> (p=(1-pnorm(abs(z)))*2)

#mlogit version

> m1=multinom(H2~A+ID+Season2,data=dat)

> stargazer(m1,type="text",out="m1.rtf")

> z=summary(m1)$coefficients/summary(m1)$standard.errors

> (p=(1-pnorm(abs(z)))*2)

> names(dat)

> table(dat$H2)

> dat2=mlogit.data(dat,choice="H2",alt.levels=levels(dat$H2),shape="wide",id="ID")

> dat2$A=as.numeric(dat2$A)

> dat2$A2=as.numeric(dat2$A*100)

> summary(dat2$A2)

> ml.0=mlogit(H2 ~  0 | A2 | 0, panel=FALSE,  data = dat2)

> summary(ml.0)

> exp(coef(ml.0))

> cl.mlogit(fm=ml.0,dat$ID)
```

```
> pnames=names(ml.0$coefficients)
> rparArg=rep('n',length(pnames))
> names(rparArg)=pnames
> ml.1=mlogit(H2 ~ 0|A2|0,rpar=rparArg,panel=TRUE,data = dat2)
> summary(ml.1)
> cl.mlogit(ml.1,dat$ID)
> ml.2=mlogit(H2 ~ 0|A2|0,rpar=rparArg[1:4],panel=TRUE,data = dat2)
> summary(ml.2)
> cl.mlogit(ml.2,dat$ID)
> lrtest(ml.0,ml.1,ml.2)
> scoretest(ml.1,ml.2)
#include residuals
>pnames=names(ml.0$coefficients)
>rparArg=rep('n',length(pnames))
>names(rparArg)=pnames
#random slopes and intercepts
>ml.1=mlogit(H2 ~ 0|A2|0,rpar=rparArg,panel=TRUE,data = dat2)
```

```
>summary(ml.1)

>cl.mlogit(ml.1,dat$ID)

#random intercepts

>ml.2=mlogit(H2 ~ 0|A2|0,rpar=rparArg[1:4],panel=TRUE,data = dat2)

>summary(ml.2)

>cl.mlogit(ml.2,dat$ID)

#other multinom mods

>m1=multinom(H2~A+ID+Season2,data=dat)

# weights:  25 (16 variable)

>summary(m1)

>stargazer(m1,type="text",out="m1.rtf")

>z=summary(m1)$coefficients/summary(m1)$standard.errors

>(p=(1-pnorm(abs(z)))*2)

#odds-ratios for best fitting model

> exp(coef(ml.1))
```

Image of *Crotalus ornatus* subjected to radiotelemtry at Indio Mountains Research Station:

Vita

James D. Emerson earned his B.S. in Wildlife Biology from West Texas A&M University (WTAMU) in 2010. He conducted research on snake communities in the Texas Panhandle while serving as a teaching assistant and mentoring undergraduates in wildlife biology at WTAMU from 2010–2013. James was an active member of The WTAMU Student Chapter of the Wildlife Society as an undergraduate and graduate student. He was also involved in public outreach during this time, presenting educational programs on native wildlife, herpetofauna, and biodiversity at local schools and youth organizations. During the summer of 2013, he initiated a project to examine the impacts of mineral development on native herpetofauna, including 4 state threatened species for the Texas Parks and Wildlife Department at the Chaparral Wildlife Management Area. Directly following that, he enrolled at UTEP to begin his Ph.D. in August 2013. While at UTEP, he was an assistant instructor for the department of biological sciences from 2013–2019, during which he mentored undergraduate students in order to get them experience biology and field biology. He received the Texas Public Educational Grant (2016–2018), the UTEP Grant for Graduate Students (2017–2018), the UTEP Summer Grant for Graduate Students (2019) and was awarded the Graduate Excellence Fellowship from 2019–2020. He has been first author or co-author on 16 presentations at professional conferences. James is currently a member of The Southwestern Association of Naturalists, The Herpetologists League, and The Wildlife Society. James' research interests broadly include the behavioral ecology, conservation biology, community dynamics, and natural history of reptiles and amphibians.

This dissertation was typed by James David Emerson.