2023-12-01

Activity Patterns Of Whiptail Lizards (aspidoscelis) Found In The Northern Chihuahuan Desert

Guillermo Alvarez
University of Texas at El Paso

Recommended Citation
Alvarez, Guillermo, "Activity Patterns Of Whiptail Lizards (aspidoscelis) Found In The Northern Chihuahuan Desert" (2023). *Open Access Theses & Dissertations*. 3954.
https://scholarworks.utep.edu/open_etd/3954

ACTIVITY PATTERNS OF WHIPTAIL LIZARDS (*ASPIDOSCELIS*) FOUND IN THE NORTHERN CHIHUAHUAN DESERT

GUILLERMO ALVAREZ

Doctoral Program in Ecology and Evolutionary Biology

APPROVED:

Jerry Johnson, Ph.D., Chair

Vicente Mata-Silva, Ph.D.

Michael Moody, Ph.D.

Ken Boykin, Ph.D.

Stephen L. Crites, Jr., Ph.D.
Dean of the Graduate School

ACTIVITY PATTERNS OF WHIPTAIL LIZARDS (*ASPIDOSCELIS*) FOUND IN THE NORTHERN CHIHUAHUAN DESERT

by:

GUILLERMO ALVAREZ M.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

Department of Biological Sciences
THE UNIVERSITY OF TEXAS AT EL PASO
December 2023

ACKNOWLEDGEMENTS

Very special thanks to Dr. Johnson, who trusted me to challenge unknown aspects about whiptails, for providing all the knowledge of the early ‘Cnemidophorologists’, and for sharing the resources found at Indio Mountains Research Station. This project was supported by UTEP’s internal funding to Jerry Johnson’s Lab, STEMGrow, and start-up funds from Dr. Mata-Silva. Assistance with fieldwork was provided by interns Daniel Muñoz, Jonatan Salinas, and Adolfo Bernal, who participated in the Chihuahuan Desert Biodiversity Research Experiences for Undergraduate students, funded by the University of Texas at El Paso. In learning about parthenogens, the teachings of Dr. Walsh were greatly appreciated. Research at RBWP was possible thanks to Hellen Geller and interns Patricia Aguirre, Matthew Jimenez, Gavin Welsh, and Giovanni Del Campo. Thanks also to Paul Hotchkin, Dr. Golding, and UTEP’s Center for Environmental Resource Management. I am grateful for the early Herpetology lessons from Dr. Harings. Thanks to Dr. Milligan for his advice. Also, thanks to Dr. Caldwell for her teachings as an undergrad, later as her technician and grad student. Also, thanks for the support to NMSU’s equipment rental program department, Las Cruces BLM, and the Texas Parks and Wildlife Department.

The assistance and feedback prior to the proposal defense from Dr. Moody helped shape the project into its final form and is greatly appreciated. I also appreciate Dr. Boykin for mentoring me and sharing his ideas before the project even started, but also for his continued support. This project would not have been possible without the guidance, field rescue, help, and motivation received from Dr. Vicente Mata-Silva. Lastly, this research, and everything in my life were only possible thanks to the support of my partner Scarlet Sellers, my brothers, and my mother.

ABSTRACT

Traditional lizard pitfall traps were modified to allow organisms to escape, while collecting valuable ecological data. Modified camera traps were capable of detecting the same species as traditional traps in a semi-arid environment, without posing the associated mortality risks. Pitfall-camera traps were used to sample the activity of the Side-blotched Lizard (*Uta stansburiana*) and the Southwestern Fence Lizard (*Sceloporus cowlesi*) in an urban wetland during four continuous years. Evaluations on activity pattern and the activity overlap between the two species revealed extensive overlap, with minor but significant seasonal shifts mediating coexistence. Traps were also effective at detecting other reptiles, invertebrates, and rodents. The same method was effective at discerning the activity patterns of closely related and potentially competing, sympatric whiptail lizards (*Aspidoscelis*). The capability of the improved sampling method was evaluated by surveying four separate sites in the northern Chihuahuan Desert where the hybrid Common Checkered Whiptail (*A. tesselata*) and its progenitor, the Marbled Whiptail (*A. marmorata*) coexist. The relative diversity was the highest at the Indio Mountains Research Station, Culberson County, Texas. Regardless, no differences were observed in the activity pattern of the whiptail species studied, except for a significant seasonal shift exhibited by the unisexual, Common Checkered Whiptail (*A. tesselata*), possibly explained by an increase in overlap within sites with high activity detected on individuals of the Marbled Whiptail (*A. marmorata*).

TABLE OF CONTENTS

INTRODUCTION

CHAPTER 1: EFFECTIVENESS OF PITFALL TRAPS WITH MOTION-ACTIVATED CAMERAS (PITCAMS) IN THE STUDY OF TERRESTRIAL LIZARDS AND SNAKES

CHAPTER 2: DAILY AND SEASONAL ACTIVITY PATTERNS OF LIZARDS FOUND IN AN URBAN WETLAND PARK

CHAPTER 3: ACTIVITY PATTERNS OF WHIPTAIL LIZARDS (ASPIDOSCELIS) FOUND IN THE NORTHERN CHIHUAHUAN DESERT

LIST OF TABLES

LIST OF FIGURES

INTRODUCTION

CURRENT SAMPLING TECHNIQUES

The diversity of lizards and snakes is rapidly declining due to their sensitivity to habitat loss and degradation (Keinath et al. 2017; Uetz 2018). For many reptiles, data on their ecology is simply not available due to limitations of traditional sampling methods (IUCN 2022; Welbourne et al. 2020). Developing cost-effective techniques to obtain ecological data of lizards and snakes is of concern, as commonly used methods such as pitfall traps and active searches, which are selective, are also associated with mortality rates (Christy et al. 2010; Enge 2001; Garden et al. 2007; Silvy 2012). Pitfall traps consist of buried containers with the rim right at ground level (Campbell and Christman 1981) and are sometimes used in combination with drift fences (Gibbons and Semlitsch 1981). Pitfall traps are very common in surveys of lizards, snakes, and amphibians (Enge 2001), and have been effectively used to calculate population dynamics (Kuhnz et al. 2005; Sutton et al. 2014) and to estimate overall diversity (Campbell and Christman 1981). Using a standardized method could also improve contrasts between different sites, or between surveys conducted by different researchers or over different years.

Nonetheless, installation, maintenance, and sampling of pitfall traps is labor intensive (Sung et al. 2011), and traps must be visited frequently each day to reduce mortality and predation (Ellis 2015; Enge 2001; Ferguson et al. 2008; Karraker 2001). Mortality associated with pitfall traps is often not reported (Enge 2001) but has been documented in studies where traps were not checked daily (Degraaf and Rudis 1990; Enge 2001). In studies where traps were checked daily, lower mortality rates have been reported (Gibbs 1998; Enge 2001). Many other examples of trap mortality have been discussed (Enge 2001; Hobbs and James 1999; Karraker

2001; Pearce et al. 2005; Read et al 2018). Having some form of shade or covering and checking traps regularly are the most common ways of reducing mortality (Hobbs and James 1999). Placing a coverboard on top of a pitfall trap technically constitutes a combination of sampling techniques, artificial refugia and pitfall traps, two methods used to sample lizards, snakes, and amphibians. Such hybrid method could be considered artificial refugia, which by attracting and concentrating organisms, they can be vulnerable to predation and temperature effects (Burghardt 2012; Putman 1995). Once captured, if set for release, handling of reptiles by researchers can have long term effects on some species (Fauvel et al. 2012; Holding et al. 2014; Langkilde and Shine 2006). Furthermore, characteristics of drift fences such as height, length, and arrangement can affect which species are captured (Bury and Corn 1987; Campbell and Christman 1981; Greenberg et al. 1994; Vogt and Hine 1982). Also, home range, activity pattern, and microhabitat can affect the effectiveness of pitfall traps (Bury and Corn 1987; Enge 2001). Due to different capture rates for different species and removal by predation, it is difficult to estimate accurate relative abundances (Bury and Raphael 1983; Enge 2001).

CAMERA-TRAPS

Technological advances have increased the use of camera-traps in biological research and have been effective for studying various vertebrates to answer a broad range of questions (Meek at al. 2014; Swann et al. 2004). Camera-traps have been effective at estimating abundance (Karanth et al. 2006), occupancy (O’Connell et al. 2006), activity patterns (de Almeida Jácomo et al. 2004; Mori et al. 2020), and behavior (Bauer et al. 2005) in mammals, but are not widely used for reptiles (Cochran and Schmitt 2009; McCallum 2013; O’Connell et al. 2011). Camera-traps have been shown more cost effective than traditional methods (De Bondi et al. 2010; Paull et al. 2012) due to the capability to obtain continuous data from various sites, and also reduce risk of mortality associated with temperature and predation by not trapping the animal (De Bondi et al. 2010; Swann et al. 2004). Despite those advances, only a few studies have successfully used camera-traps to monitor reptile species (Welbourne 2013; Welbourne et al. 2017).

Recently, the implementation of passive infrared sensors (PIR) has made motion-activated cameras more energy efficient, compact, and cheaper than older versions. These cameras are triggered by detecting small differences in the temperature of the background and a passing animal (Welbourne et al. 2016). Potentially, small mammals and ectotherms could be undetected due to their small thermal signature (Welbourne et al. 2015). However, there is evidence suggesting that under certain conditions, PIR cameras can detect and record reptiles (Welbourne 2013; Welbourne et al. 2017). For example, Welbourne (2013) used camera-traps to survey large snakes and varanid lizards in an Australian savannah, with each camera positioned under a protective shield from direct sunlight. Because the temperature of the reptiles was similar to the temperature of the surrounding substrate, motion-activated cameras failed to detect every reptile. To resolve this issue, Welbourne (2013) developed a Camera Overhead Augmented Temperature (COAT) protocol, utilizing a different substrate, such as wood chips, in the background of the camera's field of view. This protocol has been implemented effectively to sample reptiles (Dundas et al. 2019; Welbourne et al. 2015; Welbourne et al. 2017). Unfortunately, further modification is required to record nocturnal lizards and snakes (Welbourne et al. 2020). Initial cost of equipment associated with an array of camera-traps, such as cameras, power supply, memory cards, and mounting hardware, can be high and susceptible to theft in public places (Clarin et al. 2014). Nonetheless, if successfully deployed, camera-traps can monitor reptiles for longer periods than traditional methods, minimizing the effect that weather events may have on impeding sampling using traditional methods (Moseby and Read 2001; Read and Moseby 2001; Welbourne et al. 2020). In a recent study using this technology, two crepuscular and nocturnal species were the only reptile species detected at higher rates using traditional transect searches than camera traps (Welbourne et al. 2020). A potential solution to ensure nocturnal detection has been proposed by programming cameras to operate using a time-lapse feature at night (Welbourne et al. 2020). Unfortunately, not all accessible cameras offer programmable capabilities, and such increased programmed captures also diminishes battery life and memory card space. Although the species of interest in the research presented herein are diurnal, a secondary objective of this chapter included documenting how the specific conditions and modifications to the camera-traps impact the detection capabilities of PIR cameras for nocturnal species.

LIZARD PITFALL TRAPS

Current sampling methods such as active searches are capable of providing the exact time of capture, but are intrusive and labor intensive as they require searching, chasing, and capturing of individuals (Christy et al. 2010; Fauvel et al. 2012; Holding et al. 2014; Langkilde and Shine 2006). Traditional lizard pitfall traps only provide ranges of the time of each capture and not the exact time an individual enters the trap, and in the case of larger reptiles or predators, when they escape and if subjects were consumed. For example, if traps are checked every four hours by researchers, the time of capture for the organisms can only be associated within those time blocks and not the exact times when they entered the trap. In addition, some individuals are able to escape, while others are trapped and cannot avoid predation or injury when the trap is visited by a predator, or a larger organism (Ferguson et al. 2008). The very first step in the development of a sampling method capable of providing exact capture times, was to modify traditional pitfall traps to allow organisms to enter and escape the container freely. Secondly, traditional pitfall traps were modified following the guidelines of the COAT protocol (Welbourne 2013) to ensure a temperature contrast between the bottom of the container and the external surrounding substrate was attainable and that would allow the use of motion-activated cameras to detect lizards and snakes. The primary hypothesis was that lizard pitfall traps implemented with motion-activated cameras (camera-traps) would record a greater number of total reptile species than traditional lizard pitfall traps. It was expected that the number of observations would be very similar to traditional traps since the use of the camera did not alter the trap externally. After implementing and improving the effectiveness of traditional pitfall traps, the major research goal was to use camera-traps as a less intrusive sampling method to determine the activity patterns of overlapping lizards known to cooccur in an urban wetland, the Common Side-blotched Lizard (*Uta stansburiana*) and the Southwestern Fence Lizard (*Sceloporus cowlesi*).

Ecological research using modified pitfall camera-traps was carried out in an urban wetland from 2018 through 2021 at the Rio Bosque Wetlands Park (RBWP; 31°64’34’’N, 106°30’08’’W) located in El Paso County, Texas southeast of the city of El Paso (www.utep.edu/cerm/rio-bosque/rio-bosque-home.html). This public park is an enclosed area of 150 hectares (ha) surrounded by irrigation canals and the Rio Grande, the international border between the U.S. and Mexico. Water in the canals and drainage system within the park originates from the Bustamante Water Treatment Facility (BWTF) with flow levels dependent on effluent from the city. During the years of the investigation, the border wall was constructed and nearby lots were modified for development from 2019 through 2021. The area is dominated by several introduced plant species, such as Salt Cedar (*Tamarix chinensis*), Bermudagrass (*Cynodon* *dactylon*), and Russian Thistle (*Kali tragus*). Overall reptile diversity and density at RBWP is low compared to other areas of the Chihuahuan Desert. A secondary objective of this methodology was to document the activity of lizards, snakes, invertebrates, rodents, and other organisms detected by camera-traps at RBWP. This investigation revealed potential methodological improvements that allow for the detection of nocturnal species, at least in conditions similar to those observed in the Chihuahuan Desert. Previous studies have shown that yearly fluctuations in the abundance of Side-blotched Lizard (*U. stansburiana*) are correlated with precipitation from the previous season (Parker and Pianka 1975; Turner et al. 1970), thus important to monitor the same site over multiple consecutive years. This is a potential advantage of the implemented methodology.

URBAN ECOSYSTEMS

As habitat fragmentation and degradation increases due to rapid urbanization (Keinath et al. 2017; Uetz 2018), surviving reptile species detected in small habitat patches near urban areas, such as RBWP may be increasingly important to protect (Delaney et al. 2021). Urban development is the fastest form of habitat transformation and a major threat to global biodiversity (Grimm et al. 2008; McKinney 2006; Newbold et al. 2015). A wetland like RBWP provides habitat to species of lizards and snakes in an otherwise urban environment. Traffic on roads, urban structures, highly disturbed habitats, or large vacant or barren areas limit dispersal and gene flow between populations. Over time, urbanization can lead to genetic drift in sexually reproducing species, diminished recolonization, and eventually local extinction (Beninde et al. 2015; LaPoint et al. 2015). Overall, these areas and conditions may be detrimental to sexual species but can be more easily colonized by asexual ones (Haag and Ebert 2004; Schall 1978; Wright and Lowe 1968), a condition further discussed in the last chapter of this dissertation.

Nonetheless, many species thrive in urban ecosystems and become residents. Some adjust to the demands of urban habitats through evolutionary adaptation or through behavioral plasticity (McDonnell and Hahs 2015). Preserving the lizard and snake diversity within RBWP is of importance to other species present in the park and surrounding areas as these play important ecological roles. Simply put, amphibians and reptiles are efficient consumers of terrestrial arthropods (Medica 1967) but are better at converting food into biomass than birds and mammals, therefore, represent a more nutritionally valuable food for predators (Burton and Likens 1975). Populations of lizards and snakes might be of particular interest in the management of the existing lizard predators such as Burrowing Owls (*Athene cunicularia*), various hawks (Accipitridae), and the Greater Roadrunner (*Geococcyx californianus*) found within RBWP (www.utep.edu/cerm/rio-bosque/rio-bosque-home.html). Therefore, monitoring lizard populations in these habitats may be of interest to wildlife managers considering the potential cascading effects across trophic levels (Diaz et al. 2006). Similar to refuge size and corridors, recent studies have also found that high diversity in small patches of habitat can have significant value to the conservation of biodiversity (Delaney et al. 2021; McCoy and Mushinsky 1992; Vandergast et al. 2009). If populations affected by urbanization become too small or are extirpated, the urban landscape might prevent recolonization (Hanski 1999) and simultaneously introduce exotic predators and competitors (Shochat et al. 2010). For example, in urban environments of Southern California, invasive Argentine ants have outcompeted native ant species reducing their availability to the Blainville’s Horned Lizard (*Phrynosoma blainvillii*; Delaney et al. 2021). Unfortunately, only large species such as mammals can move across patches within the cityscape, while smaller species are restricted by roads (Brehme et al. 2018). Increased overlap in activity period may be experienced by lizards and snakes occupying small patches of habitat available such as RBWP, thus estimating the overlap and differences in activity patterns of cooccurring species may be relevant to their conservation.

ACTIVITY PATTERNS

Investigations of activity patterns of lizards are complex as lizards partition resources by foraging in different places, feeding on different prey, and by modifying their activity period (Pianka 1973). This is very important to insectivorous lizards such as whiptail lizards which depend on termites as their primary food source. The pronounced correlation between moisture, plant arthropod productivity, and the surface activity of termites has been well documented (Anderson 1994; Pianka 1970; Wright and Vitt 1993). Additionally, temperature has been reported to influence the physiological, ecological, and behavioral characteristics (activity pattern) of reptiles (Avery and Mynot 1990; Huey 1982). For example, initiation and cessation of daily activity of reptiles has been documented to be strongly determined by temperature (Huey 1982; Pianka 1970). For some species, temperatures in desert environments have been reported to influence the activity pattern of lizards into a bimodal pattern in the summer (Adolph and Porter 1993; Grant and Dunham 1988). In the current study, using implemented pitfall traps with motion-activated cameras which can monitor lizard assemblages continuously, the exact time of initiation and cessation of activity was determined for cooccurring species.

Considering that activity is critically connected to the thermal environment and the ecology of lizards, activity patterns are potentially shaped by natural selection (Fox 1978). For example, survival rates *U. stansburiana* have been correlated with their temporal activity patterns (Fox 1978; Turner et al. 1970). Lizards are reportedly active less than their maximum activity potential, suggesting a marked trade-off between the costs and benefits of activity (Niewiarowski and Dunham 1994; Simon and Middendorf 1976). This is of particular interest to investigate in overlapping species as it is possible that under certain conditions, the activity of one species may impact the activity of the other and impact its survival.

Indeed, both endogenous and exogenous factors influence activity patterns, and in some cases, external stimuli may mask endogenous rhythms and cause a suppression or increase in activity (Zug et al. 2001). For example, dehydration and high temperatures are shown to suppress activity, while hunger may increase it (Adolph and Porter 1993; Huey 1982). In these particular cases, masking is defined as a process that distorts the internal circadian rhythm, even if these distortions originate from inside or outside the organism (Rietveld et al. 1993).

Previous investigations have studied resource partitioning and competition along the gradients of food, habitat, and time (Schoener 1974). These comparisons arise mainly from the principles presented by the niche theory (Chase 2011; Hutchinson 1957; Pianka 2017), where the partitioning of food or other resource may be the result of direct utilization differences, or indirect, from habitat, or time segregation. The emphasis of the current research lies in detecting temporal variability among the species studied. Potentially, through temporal segregation, whiptails may reduce negative competition mediating the coexistence of cooccurring species (Pianka 2017; Schoener 1974). The effect of temperature on the ecology and activity pattern of lizards is further complicated by the ability of lizards to thermoregulate. In other words, diurnal lizards can alter their temperature and maintain a relatively high body temperature (T_b) through behavioral and physiological mechanisms (Adolph and Porter 1993; Avery and Mynot 1990;

Huey 1982). In further detail, T_b during inactivity has been shown to be influenced by air and substrate temperature, which significantly limit thermoregulatory options (Adolph and Porter 1993; Huey 1982). Of course, during activity, the amount of time per day that a lizard can be at its preferred T_b is also restricted by the thermal environment (Adolph and Porter 1993; Van Damme et al. 1991). Therefore, modifying the time of activity is a major mechanism of thermoregulation of lizards (Huey 1982), and the focus of the investigations described in this dissertation.

ASEXUAL REPRODUCTION

In a cumulative fashion, the energy that ultimately is devoted to reproduction depends on the energy budget which in turn is dependent on activity time. For example, energy acquisition depends on the rate at which resources are collected and by the rate at which they are processed (Adolph and Porter 1993). Also, daily prey captures should increase with activity time assuming that lizards are foraging while active (Anderson and Karasov 1988; Karasov and Anderson 1984). Another potential benefit is that energy assimilation should increase with activity time because rates of digestion are improved at or near activity T_b (Van Damme et al. 1991). Thus, energy assimilated minus energy expended is energy that could be allocated to reproduction, growth, or storage (Adolph and Porter 1993). Such energy ultimately depends on activity time over daily and seasonal periods (Anderson and Karasov 1988). Investigations using a method capable of estimating activity patterns of lizard species may indirectly be estimating differences in the relative energy budgets of overlapping species. For example, such continuous data is relevant to estimate activity patterns of cooccurring whiptail lizards with different modes of reproduction. Traditional methods such pitfall traps have failed at recording the exact time organisms were captured, as the traps were checked periodically every few hours (Enge 2001).

Whiptail lizards (Family: Teiidae, Genus: *Aspidoscelis*) have very short daily and seasonal activity periods (Wright and Vitt 1993), and emerge and retreat at specific times during the day (Huey 1982; Pianka 1970; 2017; Winne and Keck 2004). The genus *Aspidoscelis* (formerly included in the genus *Cnemidophorus*; Reeder et al. 2002) contains species distributed from the US to Central America. In the Chihuahuan Desert, they have a very short daily activity pattern, averaging three hours for some species (Wright and Vitt 1993). Also, whiptails have been reported to have a short seasonal activity of only two to three months (Wright and Vitt 1993). Evaluations of competitive exclusion between the unisexual, the Common Checkered Whiptail (*A. tesselata*) and its congener, the Marbled Whiptail (*A. marmorata*) have been mainly determined using demographic measurements (Wright and Lowe 1968; Wright and Vitt 1993) and diet overlap (Mata-Silva et al. 2013). Removal experiments suggest the presence of the parthenogen does not affect the density of the bisexual species, possibly due to the recent origin of the unisexual species (Cosentino et al. 2019). Whiptail lizards are a taxonomically rich and widespread group with high species richness in the southwestern United States and northern Mexico (Wright and Vitt 1993). The genus is characterized by having many parthenogenetic species with often assemblages having the parthenogen and parental species cooccurring. Because of this widely reported coexistence, many studies have investigated the patterns of resource partitioning that allow such overlap. Ecological investigations of the genus have revealed that many sympatric species eat the same prey items, occupy the same microhabitat, and are active during the same time of the day (Cuellar 1977; 1979; Milstead 1961; Mitchell 1979). The overlap across similar niche dimensions appears to challenge the principle of competitive exclusion, which states that two or more species cannot coexist permanently when they possess identical ecological needs (Levin 1970). The Marbled Whiptail Lizard (*A. marmorata*) and the hybrid species, Common Checkered Whiptail (*A. tesselata*) are found in sympatry across many areas in the northern Chihuahuan Desert including on Indio Mountains Research Station (IMRS; 30°46’37”N, 105°00’58” W), Culberson County, Texas located southeast of Van Horn (https://www.utep.edu/indio/). This area contains vegetation typical of the northern Chihuahuan Desert (Worthington et al. 2021), and has the highest reptile diversity of all the sites in the study including several whiptail species like the Chihuahuan Spotted Whiptail (unisexual; *A. exsanguis*), Little Striped Whiptail (*A. inornata*), Common Checkered Whiptail (unisexual; *A. tesselata*), and the Marbled Whiptail (*A. marmorata*; Worthington et al., 2021). Another area of sympatry investigated is located in El Paso County, Texas, in the Franklin Mountains State Park (FMSP; 31°90’81’’N, 106°52’54’’W; https://tpwd.texas.gov/state-parks/franklin-mountains). The specific research areas within this study site are surrounded by hiking and biking trails with one area on the west side between the Franklin Mountains and Interstate 10, adjacent to Transmountain Road near an active concrete quarry (https://www.jobematerials.com/). The other area is on the east side of the Franklin Mountains located between a residential area, Martin Luther King Road, and the Franklin Mountains. Reptile diversity is relatively high and several different species of whiptail lizards cooccur in this area including the unisexual Common Checkered Whiptail (*A. tesselata*), Chihuahuan Spotted Whiptail (*A. exsanguis*), bisexual Marbled Whiptail (*A. marmorata*), and the Little Striped Whiptail (*A. inornata*; Painter et al. 2017).

Another research area included in the whiptail study was a location within the Organ Mountains Desert Peaks National Monument (OMDPNM; 32°32’25’’N, 106°57’38’’W) in Doña

Ana County, New Mexico near the city of Las Cruces (www.blm.gov/visit/omdp). This study site also has vegetation typical of the Chihuahuan Desert, with research plots in the lowland desert area between the eastern residential zone of Las Cruces and Baylor Canyon Road. This area currently allows cattle grazing and is accessible to hiking, mountain biking, and off-road vehicles. Reptile diversity is relatively high, with potentially the highest diversity of whiptail species for all the sites. Whiptail lizard species known from this area include: the unisexual Common Checkered Whiptail (*A. tesselata*), Chihuahuan Spotted Whiptail (*A. exsanguis*), Desert Grassland Whiptail (*A. uniparens*), New Mexico Whiptail (*A. neomexicana*), the bisexual Marbled Whiptail (*A. marmorata*), and Little Striped Whiptail (*A. inornata*; Painter et al. 2017).

GEOGRAPHIC PARTHENOGENESIS

The Common Checkered Whiptail (*A. tesselata*) is the resulting hybrid from *A. marmorata* and *A. septemvittata* (Cordes and Walker 2006; Reeder et al. 2002; Wright and Lowe 1968; formerly referred as *A. tigris marmorata* and *A. gularis septemvittata*, respectively). The Marbled Whiptail (*A. marmorata*) like other whiptails, is a diurnal, intensive forager found in the deserts of the southwestern United States (Degenhardt et al. 2005) and spends a significant amount of time deliberately searching for prey under plants (Pianka 2017). The origin of the hybrid has been explained to have been driven by recent changes in the plant community of the desert grassland. Specifically, it has been suggested that when the grassland was converted to shrubland, the lizard diversity increased as lizards that were usually confined to marginal habitats began exploiting nearby areas (Peterson and Whitford 1987). In particular, *Cnemidophorus tigris* (now regarded as *A. marmorata* in part of its range) is a dominant species in the Chihuahuan Desert shrubland that would have been present at lower densities in the grassland habitat of the past. Today, the Western Whiptail (*A. tigris*) is a separate and recognized whiptail species known to hybridize with other whiptails in New Mexico (Painter et al. 2017). The major habitat changes that occurred in the southwest USA during the late 1800's and early 1900's were caused by livestock overgrazing (Dick-Peddie 1993), which resulted in more frequent drought and altered fire regimes (Bestelmeyer et al. 2018; Van Auken 2000). The parthenogen (*A. tesselata*) likely evolved no more than 200 years ago when overgrazing in the southwestern USA and northern Mexico first facilitated contact between the parental species (Lowe et al. 1970). Currently, the maternal progenitor, *A. marmorata* occurs only in the Chihuahuan Desert in southern New Mexico, western Texas, and northern Mexico, while *A. tesselata* has drastically expanded its home range more than 90% than its paternal progenitor in Texas, and more than 50% than its maternal progenitor in New Mexico (Degenhardt et al. 2005).

Unisexual organisms such as whiptail lizards are of particular interest to evolutionary biologists because of their departure from the most common mode of reproduction in animals (Bell 1982; Maynard-Smith 1978). Field research on asexual organisms may help determine the ecological conditions that control the advantages and disadvantages of sexual reproduction (Lively and Morran 2014; Neiman et al. 2018). Furthermore, ecological evaluations of successful asexual populations may help identify the mechanisms underlying geographic parthenogenesis (Vandel 1928). Geographic parthenogenesis refers to a pattern of distribution where the asexual species occupy areas at higher latitudes and altitudes, on islands or island-like habitats, xeric environments, marginal, stressful, disturbed, and transient areas when compared to their bisexual relatives (Cuellar 1979; Vandel 1928). Several hypotheses have been developed to explain their ecological success and the current distribution and survival of extant asexual species. For example, the hypothesis of 'reproductive assurance' suggests that parthenogens have an advantage by not being mate limited. Thus, parthenogens persist in marginal habitats with low densities (Cuellar 1977). The hypothesis of ‘biotic interactions’ suggests that sexual species are better at adapting to biotic pressures such as predators and parasites due to sexual recombination (Maynard-Smith 1978). Therefore, parthenogens should persist only where biotic pressures are weaker than abiotic ones, even if those conditions only support low population numbers (Haag and Ebert 2004). Of particular interest to the current research is a hypothesis developed specifically from observations on whiptail lizards, the ‘weed hypothesis’, which suggests that parthenogenetic whiptails are only successful in disturbed, marginal, and ecotonal habitats (Schall 1978; Wright and Lowe 1968; Wright and Vitt 1993). In particular, as the southwest region of North America has experienced severe climate and plant community changes, and that as a result, the unstable habitats were more effectively colonized by parthenogenetic whiptails due to wider ecological tolerances and other enhanced colonizing properties (Wright and Lowe 1968; Schall 1978). This implies that parthenogens are poor competitors with limited adaptability (Cuellar 1977; 1979).

Despite the expectations of the ‘weed hypothesis’, the literature reports many instances of parthenogenetic species cooccurring with bisexual ones (Case 1983; Cuellar 1977; Cuellar and McKinney 1976; Germano and Hungerford 1981; Medica 1967; Milstead 1961; 1965; Mitchell 1979; Smith 1989; Walker 1987). Parthenogenetic whiptails are still described as species that can only occur in disturbed habitats due to their colonization ability and tendency to avoid competition with sexual species (Cuellar 1977; 1979; Wright and Lowe 1968). Additionally, it has been proposed that parthenogens can increase their population size more rapidly as there is no energy expenditure associated with producing males (Case and Taper 1986; Maynard-Smith 1978). Schall (1977) suggested that parthenogenetic whiptails used different thermoregulatory behaviors as they are hypothesized to occupy a broader range of habitats when compared to bisexual species. Despite numerous evaluations and the greater reproductive potential and colonizing abilities of parthenogens, there is no evidence where they outcompete sexual species in undisturbed habitat (Glesener and Tilman 1978), while in other cases, responses in abundance are similar to sexual species in disturbed habitats (Cosentino et al. 2019). For example, the unisexual *A. uniparens* is associated with areas recently treated with herbicides for shrub removal, while *A. marmorata* is more abundant in the previously disturbed shrubland (Cosentino et al. 2013). Interestingly, studies on whiptail lizards have documented density fluctuations across years. For example, Milstead (1965) reported a density increase in *A. marmorata* (cited as *C. tigris*) from 45 per ha^{-1} to 185 per ha^{-1} due to rainfall. Similarly, Turner et al. (1969) reported an increase of 8 to 20 per ha^{-1}. Severe fluctuations have been observed in *A. tesselata* the following year after reduced food availability (Whitford and Creusere 1977). As an example, *A. exsanguis* (cited as *C. exsanguis*) which are more commonly found in mesic habitat within mountain slopes readily move and become established in lower and wetter habitats. Similarly, *A. inornata* (cited as *C. inornatus*) became established 2 km away from its original center due to increased available moisture (Medica 1967). It is important to investigate activity patterns of lizards in extreme thermal environments such as the Chihuahuan Desert under field conditions because a potential and discernible reduction in activity length has been hypothesized to be advantageous since the replenishment of water are limited under such arid conditions (Bowker 1993; Porter et al. 1973).

Investigations of the Marbled Whiptail (*A. marmorata*) and the Common Checkered Whiptail (*A. tesselata*) species pair have revealed no significant differences in adult body mass, but almost total overlap in prey number and volume (Mata-Silva et al. 2013). Other researchers have hypothesized that body size is a determinant of whiptail assemblages (Case 1983), and it appears that size is increasingly important as the number of *Aspidoscelis* species increases. It may be important to consider that size differences may be important at different times and sampling methods able to detect their continuous activity are needed. For example, in one study, the gravid individuals of the parthenogen, *A. tesselata* were significantly bigger than the gravid females of *A. marmorata* in New Mexico (Taylor et al. 2001), while another report suggests that sympatry occurs in a cyclical manner (Scudday 1971), further highlighting the need for continuous multi-year monitoring. Moreover, extensive research of whiptail assemblages in transitional and ecotonal habitats, has suggested that cooccurrence is transitory (Case 1983). Due to different literature sources providing support for contrasting views, the dynamics of the specific factors that allow coexistence of these closely related and very similar species remains unclear. For example, Mata-Silva et al. (2010) and Taylor et al. (2001) found *A. tesselata* to have larger clutch sizes than *A. marmorata*, while Schall (1978) did not. Similarly, Mata-Silva et al. (2008) determined that individuals of *A. tesselata* had significantly more endoparasites than their maternal progenitor *A. marmorata*. A more interesting and promising focus of analysis is behavioral differences such as activity period. In fact, behavioral differences have been described in some species (Echternacht 1967; Hotchkin and Riveroll Jr. 2005). Potentially, resource partitioning may be due to differences in foraging behavior including time spent foraging (Echternacht 1967; Scudday and Dixon 1973). Such differences in activity period, as a result of increased risk of predation associated with an increased activity length, may explain a report by Pilz (1983) where *A. marmorata* comprised 23% and 32% of the diet of nestling Swainson's Hawks (Accipitridae), while *A. tesselata* composed only 1% of the diet, for each of the two years of the study. Slight changes in populations have been documented when one species is removed from an overlapping area (Price 1986), but changes were small and after several years from the removal. Specific differences in activity period duration may be the result of differences in metabolic rates associated with differences between reproductive males and females, with males having a longer activity period and more intense activity per hour (Anderson and Karasov 1981; Karasov and Anderson 1984). Thus, an important aspect of the current research sampling method is the ability to monitor the activity of lizards in different sites across multiple years.

CHAPTER 1: EFFECTIVENESS OF PITFALL TRAPS IMPLEMENTED WITH MOTION-ACTIVATED CAMERAS (PITCAMS) IN THE STUDY OF TERRESTRIAL LIZARDS AND SNAKES

INTRODUCTION

Developing cost-effective methods that provide ecological data from lizards and snakes is an urgent concern as conservation strategies cannot be determined for many reptiles due to data deficiency on basic aspects of their ecology and natural history (McDiarmid et al. 2012). Sampling methods, such as active searches, are labor intensive, require prolonged field visits, and can require thousands of personnel hours (Christy et al. 2010; Garden et al. 2007; Silvy 2012). Capturing and handling of reptiles causes stress that has long-term effects on the survival of some species (Fauvel et al. 2012; Holding et al. 2014; Langkilde and Shine 2006). Currently, the most common method for sampling lizards are pitfall traps (Ali et al. 2018; Richardson et al. 2018), which consist of buried containers with a coverboard suspended a few centimeters above ground level, sometimes used with drift fences to increase their effectiveness (McDiarmid et al. 2012). Traps can be covered when not in use, and then reopened during sampling (Garden et al. 2007). Once opened, traps must be visited frequently to minimize the risk of mortality due to temperature and predation (Ellis 2015; Enge 2001; Ferguson et al. 2008; Karraker 2001). Although installation and maintenance of pitfall traps are labor intensive (Sung et al. 2011), they are effective at capturing nocturnal, fossorial, and cryptic species, but fail to capture longer snakes, larger lizards, and other animals able to escape (Thompson et al. 2005; Todd et al. 2007).

Technological advances have increased the use of motion-activated cameras in biological research, especially for mammals (Swann et al. 2004). Camera traps can effectively estimate abundance (Karanth et al. 2006), occupancy (O’Connell et al. 2006), activity patterns (de Almeida Jácomo et al. 2004), and behavior (Bauer et al. 2005). Even though initial costs associated with cameras, memory cards, and batteries can be high, data collection can be continuous, from multiple concurrent sites, and over long periods of time. Advantages of camera-traps include their ability to be deployed in most habitats and weather conditions, can document date and exact time the animal is observed, and eliminate the need to trap the animal, which reduces mortality (De Bondi et al. 2010; Welbourne et al. 2017). Nevertheless, camera-traps are not common in reptile surveys (Cochran and Schmitt 2009; O’Connell et al. 2011). Welbourne et al. (2015) observed reptiles, including large snakes (SVL 1500–2000 mm) and small skinks (SVL 50 mm) in a semi-arid environment. Other studies have found camera traps more effective than active searches for the grassland Earless Dragon (*Tympanocryptis pinguicolla*; Hunter et al. 2012). Camera traps are more effective for sampling diurnal than nocturnal species under certain environmental conditions (Welbourne et al. 2015; 2017). Camera traps are advocated to be effective in reptile surveys if enough thermal contrast between the animal and the background surface exists (Welbourne 2013; 2016). During the current study, the use of pitfall traps with motion-activated cameras to survey lizards and snakes was compared to traditional pitfall traps alone in a Chihuahuan Desert environment by contrasting the number of observations per trap, total number of species detected, and overall costs associated with each method during one active season.

MATERIALS AND METHODS

Study Site.—Research was conducted at the Indio Mountains Research Station (IMRS; 30°46’37” N, 105°00’58” W), Culberson County, located southeast of Van Horn, Texas (Fig. 1;

https://www.utep.edu/indio/). Vegetation at IMRS is typical of the Chihuahuan Desert (Johnson 2000). Lizard species that are found within IMRS include the Eastern Collared Lizard (*Crotaphytus collaris*), Texas Banded Gecko (*Coleonyx brevis*), Greater Earless Lizard (*Cophosaurus texanus*), Round-tailed Horned Lizard (*Phrynosoma modestum*), Crevice Spiny Lizard (*Sceloporus poinsettii*), Southwestern Fence Lizard (*S. cowlesi*; Leaché and Reeder 2002), Tree Lizard (*Urosaurus ornatus*), Side-blotch Lizard (*Uta stansburiana*), Great Plains Skink (*Plestiodon obsoletus*), Four-lined Skink (*P. tetragrammus*), Chihuahuan Spotted Whiptail (*Aspidoscelis exsanguis*), Little Striped Whiptail (*A. inornata*), Checkered Whiptail (*A. tesselata*), and the Marbled Whiptail (*A. marmorata*; Johnson 2000). Snakes found within IMRS are the Glossy Snake (*Arizona elegans*), Trans-Pecos Rat Snake (*Bogertophis subocularis*), Western Hook-nosed Snake (*Gyalopion canum*), Gray-banded Kingsnake (*Lampropeltis alterna*), Coachwhip Snake (*Masticophis flagellum*), Whipsnake (*M. taeniatus*), Gopher Snake (*Pituophis catenifer*), Long-nosed Snake (*Rhinocheilus lecontei*), Big Bend Patch-nosed Snake (*Salvadora deserticola*), Mountain Patch-nosed Snake (*S. grahamiae*), Ground Snake (*Sonora semiannulata*), Southwestern Black-headed Snake (*Tantilla hobartsmithi*), Plains Black-headed Snake (*T. nigriceps*), Chihuahuan Desert Lyre Snake (*Trimorphodon wilkinsonii*), Western Diamond-backed Rattlesnake (*Crotalus atrox*), Rock Rattlesnake (*C. lepidus*), Eastern Black-tailed Rattlesnake (*C. ornatus*), Ring-neck Snake (*Diadophis punctatus*), Chihuahuan Night Snake (*Hypsiglena jani*), Trans-Pecos Threadsnake (*Rena segrega*), and the Black-necked Garter Snake (*Thamnophis cyrtopsis*; Crother 2017; Johnson 2000).

Figure 1. Study site used in the research conducted at Indio Mountains Research Station, Culberson County, Texas.

***Traditional Pitfall Traps and Pitfall Camera-Traps.*—**Traditional pitfall traps consisted of a buried 20 liter plastic container with a coverboard positioned 4 cm above ground level; drift fences were not employed in this study (Fig. 2). For drainage, a total of 20 orifices (2 mm) were drilled on the bottom of each container. Traps implemented with motion-activated cameras also had a piece of hardware mesh (60 cm by 20 cm) attached to the inside container allowing organisms to escape. Each camera (Fig. 1.3; Moultrie® Alabaster, Alabama; Game Spy 6MP Trail Camera) was set with a 15 second delay between videos and was mounted with the lens facing downward. Cameras used were temperature activated, relying on a temperature differential between the organism and the background. Traps were installed prior to reptile emergence. Lizards and snakes were surveyed during months of increased activity, from 6 May - 26 August of 2018, in two areas of similar vegetation composition and elevation using traditional and camera approaches. Each array was located more than three kilometers apart and was further subdivided into three (150 m by 50 m) blocks with each block separated by a buffer zone of 100 meters. The traditional array was open to survey during each visit to the field site, while the camera-trap array was continuously surveyed throughout the season. In the traditional pitfall trap array, each block contained 10 traps arranged in two rows of five, with each trap located 20 meters apart, for a total of 30 traps; traps were opened in the morning upon arrival, checked every four hours, and closed prior to leaving the study site. In the camera-trap array, each block contained three traps with motion-activated cameras located 50 meters apart, for a total of nine traps; batteries and memory cards were replaced a total of four times during the season. There were a total of 780 traditional trap days and a total of 927 camera trap days.

Figure 2. External view of a traditional pitfall trap with no drift fences used in the study.

Figure 3. Inside view of a traditional pitfall trap equipped with a motion-activated camera (Moultrie® Game Spy 6MP Trail Camera) and hardware mesh allowing organisms to escape.

Statistical Analysis.—In the traditional pitfall trap array, we measured species, sex, snout-to-vent length (SVL), total length (TL), mass, date, and capture time (morning/evening) for all lizards. In the camera-trap array, lizards and snakes observed in videos were identified to species level, and whenever possible, sex was determined for adults and sexually dimorphic species. Estimated SVL and TL measurements were recorded for lizards identified in video recordings using ImageJ® software (Rasband 2016), using segments in the wire mesh in each trap as a known standard length. For each observation, the exact time of entrance and exit of the trap were recorded using the time stamp feature of the camera. Measurements of SVL and TL obtained by hand from the pitfall traps were compared to measurements estimated from camera footage for the most abundant lizard species. The total number of individuals observed and the total number of species from each sampling method were contrasted using Shannon's Diversity Index (Shannon and Weaver 1963). The total number of lizard captures between the two separate arrays were compared using a t-test by considering only lizard captures from dates when both methods were concurrently deployed. Further comparisons are limited due to differences in sampling methods. Using the exact time of entrance provided by the camera-traps, the diurnal activity of the three most frequently observed species was estimated. Fisher's exact test was conducted to determine whether the two most numerous lizard species captured by the camera-traps were active at significantly different times. For all statistical tests, $\alpha = 0.05$ was used. All tests were conducted using the statistical software R (R Development Core Team, 2021). At a minimum, non-target species, such as invertebrates and rodents were identified to order level.

RESULTS

Quality of Images Obtained Using Pitfall Camera-Traps.—The motion-activated cameras, using a preset resolution and 15 second delay between videos provided sufficient footage of lizards and snakes to allow identification to species level and sex for sexually dimorphic species. High resolution images were obtained of both diurnal and nocturnal species (Fig. 4 and Fig. 5). Furthermore, such images were time stamped allowing for the effective comparison of exact times of captures between observed subjects. We could not determine the sex of snakes and non-sexually dimorphic species. The 10-second length of the videos, which often recorded multiple videos of the same organism, and the short distance between the lens and the subject resulted in 100% of the videos used in SVL estimations for lizards. A t-test found no statistical difference between the average SVL estimated from video recordings (74.03 ± 10.31 mm) and measurements taken from captured individuals (73.67 ± 8.73 mm; $t_{(57,\ 0.05)} = 0.888$, $P = 1.674$) of *A. marmorata*, the most frequently recorded species observed in both sampling methods. We performed no tests on other species due to low sample sizes in one or both sampling methods.

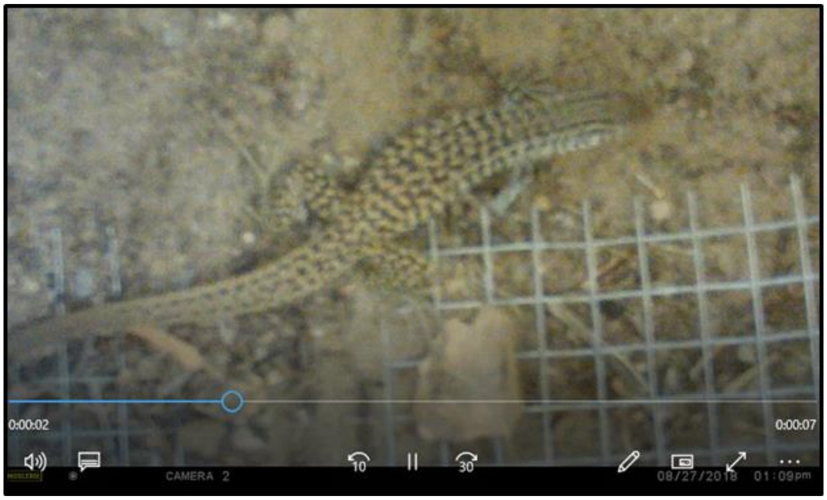

Figure 4. Image of a documented capture belonging to a diurnal species, the Common Checkered Whiptail (*Aspidoscelis tesselata*) obtained from a pitfall trap modified with a motion-activated camera (Moultrie® Game Spy 6MP Trail Camera).

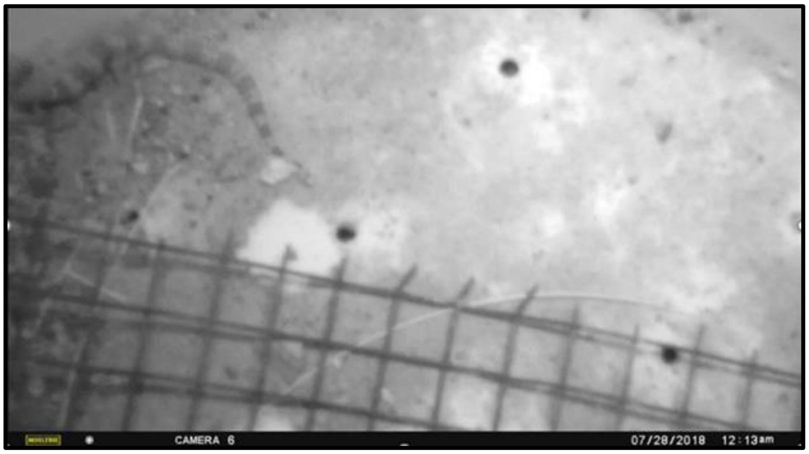

Figure 5. Image of a documented capture belonging to a nocturnal species, the Texas Banded Gecko (*Coleonyx brevis*) obtained from a pitfall trap modified with a motion-activated camera (Moultrie® Game Spy 6MP Trail Camera).

***Total Images and Trap Captures.*—**Overall, the use of pitfall traps with motion-activated cameras resulted in higher effective trap days, as these traps were open continuously and not only when researchers were present. Thus, the deployment of nine pitfall traps with motion-activated cameras resulted in a total of 927 effective trap days. In contrast, concurrent sampling using thirty traditional pitfall traps and a high number of field visits (14) resulted in 780 effective trap nights (Table 1). Pitfall traps implemented with motion-activated cameras detected a higher number of individual observations and total number of species per trap compared to traditional methods. Sampling using camera-traps detected a total number of 98 squamate observations including 87 lizard, and 11 snake observations. In contrast, a total of 72 observations were collected from the traditional pitfall trap array, including 70 lizards, and two snakes (Table 1). We performed a t-test considering only the captures obtained in days when both methods were simultaneously deployed, and no statistical difference was detected between the average number of lizards captured per trap recorded in the blocks of the traditional traps (2.4 ± 0.2) and those from traps equipped with motion-activated cameras (2.55 ± 0.7; $t_{(5, 0.05)} = 0.752$, $P = 2.015$). Overall, camera-traps captured higher diversity than traditional pitfall traps. Traditional pitfall traps detected six lizard and two snake species, while camera-traps detected eight lizard and seven snake species (Table 1). The number of lizards captured per trap was very similar between the two methods. In contrast, the number of snakes per trap observed using pitfall traps with cameras was higher when compared to traditional pitfall traps (Table 1). Diversity as estimated using Shannon's diversity index, was higher for the array using camera-traps when compared to the array of traditional pitfall traps (Table 1). We observed the highest diversity of snake species using the pitfall traps with cameras when compared to traditional pitfall traps (Table 2). One species of lizard, *A. inornata*, was observed in higher frequency using traditional traps than with traps that had cameras (Table 2). Sampling of the traditional pitfall trap array resulted in a total of 91 non-target observations composed of 82 invertebrates, and nine rodents. Sampling of the pitfall traps with cameras resulted in 95 total non-target observations, with 87 invertebrate sightings and eight rodents.

Table 1. Comparison of sampling methods in lizard and snake capture.

	Sampling Method	
	Pitfall Traps (n = 780 trap days)	Camera Traps (n = 927 trap days)
Individual Lizards	70	87
Individual Snakes	2	11
Lizard Species	6	8
Snake Species	2	7
Lizards/Trap Day	0.090	0.094
Snakes/Trap Day	0.003	0.012
Shannon's Diversity Index (*H*)	2.079	2.565

Table 2. Total number of captures recorded by pitfall and camera-traps.

Species	Pitfall Trap	Camera-trap
Aspidoscelis inornata	29	5
Aspidoscelis marmorata	24	35
Aspidoscelis tesselata	2	1
Coleonyx brevis	2	2
Cophosaurus texanus	6	26
Crotaphytus collaris	0	7
Phrynosoma modestum	7	10
Urosaurus ornatus	0	1
Bogertophis subocularis	0	2
Crotalus atrox	0	2
Hypsiglena jani	0	1
Masticophis flagellum	0	1
Masticophis taeniatus	0	3
Rhinocheilus lecontei	1	0
Salvadora deserticola	0	2
Sonora semiannulata	1	0
Total	72	98

***Activity Patterns.*—**Using the exact time of entry provided by the camera-traps, the diurnal activity of the three most frequently observed species was determined (Fig. 6). Activity peaks were estimated for the lizards *A. marmorata*, and *C. texanus*, which were bimodal and unimodal respectively, and distributed at different times of the day for each species (Fig. 6). The third most frequently recorded species, *P. modestum*, does not appear to have a pronounced daily activity peak (Fig. 6). Fisher's exact test was conducted to examine whether the two most numerous lizard species captured by camera-traps were active at significantly different times. The data used were restricted to lizards captured between 0600 and 1759 h and time was divided into periods of three-hour blocks. Proportions of *A. marmorata* and *C. texanus* captures were not equally distributed throughout the day ($p < 0.05$). Post-hoc tests indicated that captures were significantly different between 1200 – 1459 h (Fig. 7), where *C. texanus* captures were more abundant. As data collection using traditional pitfalls was restricted to morning and evening collections, fine-scale analysis of activity period cannot be conducted on data utilizing this capture method.

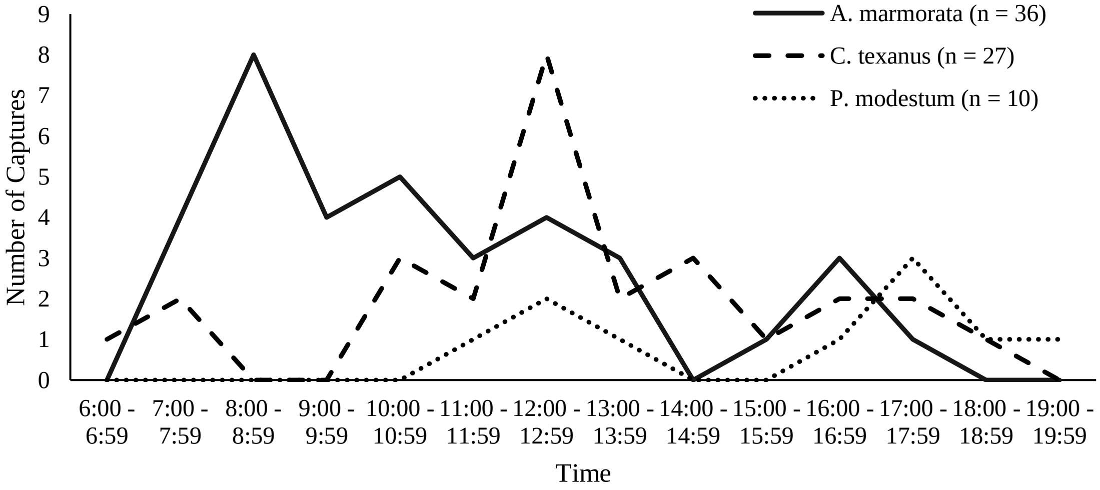

Figure 6. Frequency of captures by time period of the most abundant lizard species. Other species were not included due to low sample size.

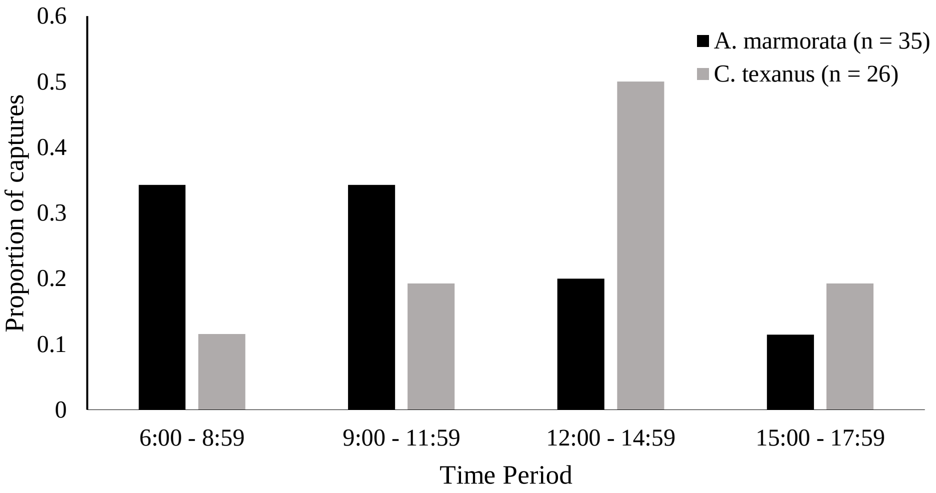

Figure 7. Proportion of diurnal captures in *Aspidoscelis marmorata* and *Cophosaurus texanus*. Time periods beyond 18:00 h contained 1 or fewer captures and were not analyzed. * Significant at the 0.05 level.

DISCUSSION

Detection Efficiency of Lizards and Snakes.—Camera-traps were effective at detecting small and large organisms, as well as diurnal and nocturnal species. This method could eliminate the negative effects of chasing, capturing, and handling animals (Langkilde and Shine 2006). The use of camera-traps does not require searching, capturing, or handling large or venomous snakes, also decreasing risks for researchers (Beaupre and Greene 2012). Success in detecting ectothermic species such as reptiles may rely on the type of camera used, as a sufficient temperature contrast must exist between the background surface and the organism for the sensor to trigger the camera (Welbourne et al. 2016). To overcome this issue, Welbourne (2013) developed the Camera Overhead Augmented Temperature (COAT) protocol, using a heat-gaining substrate to create a temperature differential between the reptile and the background. Due to this required temperature differential, other environments have been less effective in the detection of nocturnal reptiles (Richardson et al. 2018; Welbourne et al. 2016). In this Chihuahuan Desert study, it was possible to detect small and nocturnal species (geckos) despite the smaller thermal signature of smaller species (Swann and Perkins 2014). This is likely due to a sufficient thermal contrast between the background surface and the organisms due to the bottom of the container being shielded from the sun and in contact with soil at 60 centimeters below the surface.

Monitoring Lizards and Snakes Using Camera-Traps.—In this study, camera-traps yielded similar number of lizard observations and more snake observations compared to traditional pitfall traps, indicating greater effectiveness than pitfall traps alone. The total number of lizard observations per trap day was similar between the two methods, but overall higher diversity was observed with camera-traps (Tables 1 and 2). Camera-traps sampled a broader spectrum of fauna including large lizards, snakes, and invertebrates that usually escape pitfall traps (Michael et al. 2012; Silvy 2012), potentially eliminating the need for separate surveys for taxa previously excluded (Garden et al. 2007). Information that could not be gained from camera-traps include sex for some species, gravidity in females, identification of unique markings, and weight of the organism. The ability to also record data without physical capture may make camera-traps more ethical compared to traditional pitfall traps (Burghardt et al. 2012; Putman 1995). The collection of more precise activity data will yield greater information in estimating daily and seasonal activity patterns. Future advances in camera technology may provide better image resolution to allow individual identification for more ethical mark-recapture studies of reptiles (Edwards and Gardner 2010; Perera and Perez-Mellado 2004).

***Cost Effectiveness.*—**Overall, camera-traps were more cost-effective than the surveys conducted using traditional pitfall traps as it required fewer field visits and less personnel. Cost for fuel and materials was $868.30 USD for the traditional trap array and $797.80 USD for the camera-trap array. Costs associated with fuel were estimated at $33.45 USD per round trip to the field station. Establishing and visiting the camera-trap array to replace batteries and memory cards required four visits ($133.80 USD) while establishing, opening, and closing traps at the traditional array required 14 visits ($468.30 USD). Cost of materials used in the camera-trap array totaled $464.00 USD (cameras, buckets, boards, and hardware), and consumables for one season amounted to an approximate $200.00 USD (batteries and memory cards). Cost of the materials used in the traditional trap array was approximately $400.00 USD (buckets, boards, and hardware). Surveys using the traditional array also required overnight stay at the study site and the assistance of multiple individuals to operate traps, thus resulting in increased costs in labor, food, and lodging.

ACKNOWLEDGEMENTS

Special thanks to Daniel Muñoz, Jonatan Salinas, and Adolfo Bernal for their help with fieldwork and who participated in the Chihuahua Desert Biodiversity Research Experiences for Undergraduate students, funded by the University of Texas at El Paso. This project was partially supported by UTEP startup funding to Dr. Vicente Mata-Silva and internal funding to Dr. Jerry Johnson's Lab. Research was conducted under IACUC protocol A -201004-1 356592-8.

CHAPTER 2: ACTIVITY PATTERNS OF LIZARDS FOUND IN THE RIO BOSQUE WETLAND PARK

INTRODUCTION

Developing cost-effective methods that provide ecological data from lizards and snakes found near cities is an urgent concern as rapid urban development and habitat transformation continue to diminish global biodiversity (Grimm et al. 2008; McDiarmid et al. 2012; McKinney 2006; Newbold et al. 2015). As habitat degradation increases (Delaney et al. 2021; Keinath et al. 2017; Uetz 2018), protecting surviving reptile species detected in habitat patches near urban areas, such as the Rio Bosque Wetlands Park (RBWP) may be increasingly important (Delaney et al. 2021). In El Paso, Texas, RBWP represents a patch of habitat for lizards and snakes being impacted by urbanization. Urban areas have historically been understudied in ecology (Delaney et al. 2021). However, there is growing evidence that many species thrive near urban areas (McDonnell and Hahs 2015). Lizards, snakes, and amphibians found in RBWP are of particular interest as consumers of terrestrial arthropods (Medica 1967). Importantly, they are better at converting food into biomass than birds or mammals, therefore representing a more nutritionally available food source for predators (Burton and Likens 1975). This might be of particular interest considering the existing population of Burrowing Owls (*Athene cunicularia*), various hawks (Accipitridae), and Greater Roadrunner (*Geococcyx californianus*) within RBWP (www.utep.edu/cerm/rio-bosque/rio-bosque-home.html.).

The commonly used active searches as sampling methods of lizards and snakes are labor intensive, require prolonged field visits, are not cost-effective, and can amount to thousands of personnel hours (Christy et al. 2010; Garden et al. 2007; Silvy 2012). Furthermore, capturing and handling of small lizards and snakes causes stress that has long-term effects on the survival of some species (Fauvel et al. 2012; Holding et al. 2014; Langkilde and Shine 2006). Currently, the most common method for sampling lizards are pitfall trap arrays (Ali et al. 2018; Richardson et al. 2018), which consist of buried containers with a wooden coverboard positioned a few centimeters above ground level and are often used with drift fences (McDiarmid et al. 2012). Once opened, traps must be visited frequently to minimize the risk of mortality due to temperature and predation (Ellis 2015; Enge 2001; Ferguson et al. 2008; Karraker 2001). Although installation and maintenance is labor intensive (Sung et al. 2011), pitfall traps are effective at capturing most small diurnal and nocturnal species, but fail to capture longer snakes, larger lizards, and animals capable of escaping (Thompson et al. 2005; Todd et al. 2007).

Cameras have been reported effective in the assessment of activity patterns of vertebrates (Mori et al. 2020; Ridout and Linkie 2009) and more cost-effective than traditional methods (De Bondi et al. 2010; Paull et al. 2012) due to the ability to obtain continuous data. Camera-traps also reduce exposure and predation mortality by not trapping the animal (De Bondi et al. 2010; Swann et al. 2004). Despite those advances, only a few studies have used camera-traps to monitor reptiles (Welbourne 2013; Welbourne et al. 2017). More recently, the implementation of passive infrared sensors (PIR) has made motion-activated cameras more energy efficient, more compact, and cost-effective than older versions. These cameras are triggered by detecting small differences in the temperature of the background and a passing organism (Welbourne et al. 2016). Using such technology, small mammals and ectotherms could potentially be undetected due to their small thermal signature (Swann et al. 2004; Welbourne et al. 2015). However, there has been sufficient evidence suggesting that under certain conditions, PIR cameras can effectively detect reptiles (Welbourne 2013; Welbourne et al. 2017). For example, Welbourne (2013) utilized downward-facing cameras to survey large snakes and lizards in an Australian savannah. As expected, the temperature of the reptiles was similar to that of the surrounding substrate and cameras failed to detect every reptile. To overcome this, Welbourne (2013), developed a Camera Overhead Augmented Temperature (COAT) protocol, altering the background by using a different substrate such as wood chips. Such protocol with slight modifications has been used in several reptile investigations successfully since then (Dundas et al. 2019; Welbourne et al. 2015). Reptiles were effectively surveyed using camera-traps, including large snakes (SVL 1500–2000 mm) and small skinks (SVL 50 mm) in a semi-arid environment (Welbourne et al. 2015). Other studies have found camera-traps more effective than active searches for the grassland Earless Dragon (*Tympanocryptis pinguicolla*; Hunter et al., 2012). Unfortunately, further modification is required to record nocturnal lizards and snakes more reliably (Welbourne et al. 2020).

The main research objective was to determine the activity patterns of overlapping lizards found in this Chihuahuan Desert wetland remnant in an urban setting using a recently developed, less intrusive methodology that employs modified lizard pitfall traps with PIR-activated cameras. Focus species included the Common Side-blotched Lizard (*Uta stansburiana*), the Southwestern Fence Lizard (*Sceloporus cowlesi*), and the Little Striped Whiptail (*A. inornata*). Sampling using camera-traps is capable of providing exact times of capture and has been evaluated (Chapter 1; *under review*) to offer the opportunity to analyze quantitative differences in activity patterns. The assumption was that coexistence of these species is facilitated by behavioral differences, in this case, differences in their activity period.

MATERIALS AND METHODS

Study Site.─Research was conducted in the Rio Bosque Wetlands Park (RBWP; 31°64’34’’N, 106°30’08’’W) located southeast of El Paso, Texas (www.utep.edu/cerm/rio-bosque/rio-bosque-home.html). This public park is an enclosed 150-hectare area surrounded by irrigation canals and the Rio Grande, which represents the international border between the U.S. and Mexico. Vegetation within the park is typical of a Chihuahuan Desert wetland area. However, the vegetation within the wetland has been recovering from various disturbances including grazing, farming, and the most recent channelization. In general, the site is mostly characterized by Saltbush (*Atriplex canecens*), Honey Mesquite (*Prosopis glandulosa*), Jimmy Weed (*Isocoma spp.*), and Saltcedar (*Tamarix chinensis*). Riparian scrub includes Wolfberry (*Lycium berlandieri*), Spiny Aster (*Chloracantha spinosa*), Coyote willow (*Salix exigua*), and Arrow Weed (*Pluchea sericea*). Documented lizards within RBWP include the Texas Horned Lizard (*Phrynosoma cornutum*), the Southwestern Fence Lizard (*S. cowlesi*), Side-blotched Lizard (*U. stansburiana*), Great Plains Skink (*Plestiodon obsoletus*), Chihuahuan Spotted Whiptail (*Aspidoscelis exsanguis*), and the Little Striped Whiptail (*A. inornata*). Snakes found in RBWP include the Glossy Snake (*Arizona elegans*), Chihuahuan Nightsnake (*Hypsiglena jani*), Desert Kingsnake (*Lampropeltis splendida*), Great Plains Ratsnake (*Pantherophis emoryii*), Coachwhip (*Masticophis flagellum*), Gopher Snake (*Pituophis catenifer*), Longnose Snake (*Rhinocheilus lecontei*), Smith’s Black-headed Snake (*Tantilla hobartsmithi*), and the Checkered Garter Snake (*Thamnophis marcianus*).

Pitfall Camera-Traps.─Lizard pitfall traps used in this study consisted of a buried 20-liter plastic container with a wooden coverboard positioned four centimeters above ground level; drift fences were not employed. Considering the potential flooding within the wetland, a total of 20 orifices (2 mm in diameter) were drilled on the bottom of each container for drainage. Lizard traps were implemented with a motion-activated camera and had a piece of hardware mesh (60 cm x 20 cm) attached to the inside container allowing organisms to escape following the same protocol established in the first chapter of this dissertation and following closely the COAT protocol (Welbourne 2013). Each camera (Moultrie® Alabaster, Alabama; Game Spy 6MP Trail Camera) was programmed with a 15 second delay between videos and was mounted with the lens facing down into the container. All traps were installed prior to reptile emergence. The survey was conducted from 20 March 2018 through 23 September 2021. The survey period was sometimes interrupted by flooding of the area, theft, and malfunction of the cameras, thus not technically continuous for all traps. Estimations of observations per number of traps deployed had to be adjusted for the actual number of traps running. Each of the nine camera-traps was located approximately 500 meters apart. Batteries and memory cards were replaced a total of six times during the season. Data from camera-traps reported herein included the period when the first and last lizard observations were recorded for each year. Nonetheless, camera-traps were deployed beyond the active range of lizards and snakes resulting in the documentation of rodents, as well.

Overall Diversity.—Total number of camera-trap captures of lizards, snakes, rodents, and invertebrates were summarized for each year included in the study. Lizards and snakes observed in videos were identified to species level, and whenever possible, sex was determined for adults and sexually dimorphic species. At a minimum, non-target species such as invertebrates and rodents were identified to order level. For each observation, the exact time was recorded using the time stamp feature of the camera. Videos belonging to the same species recorded from the same trap within 30 minutes were excluded from diversity and activity analyses to reduce pseudoreplication bias (Mori et al. 2022) unless it was confirmed using individual size and color variations to be a different individual. Overall diversity of lizards and snakes was estimated by comparing the total number of independent captures documented and the total number of species from each year using Shannon's Diversity Index (Shannon and Weaver 1963).

Activity Patterns and Activity Overlap.—Seasons were defined as those falling within the calendar dates of spring (March 1 – May 31) and summer (June 1 – Aug 31). A minimum sample size of >10 was utilized in all comparisons. All capture times were converted to radians prior to analysis. Military time was converted to proportions of a 24-hour day by dividing time by 24. Radians were then calculated by multiplying values by 2π. The coefficient of overlap was used to quantify the amount of overlap between two pairs of activity periods using the R package *overlap* (Linkie and Ridout 2011; Ridout and Linkie 2009). This method was used to estimate the probability density function of activity period patterns nonparametrically using kernel density. Capture times from cameras were considered as random samples from a continuous distribution. All statistics were performed using R statistical software (R Development Core Team 2021). The coefficient of overlap (Δ_1) was estimated for all interactions, as appropriate for small sample sizes <75 observations (Ridout and Linkie 2009). Resulting values range from 0 (no overlap) to 1 (identical overlap). The precision of Δ_1 was estimated by computing the mean and standard deviation from 999 bootstrap samples. Significant differences between activity distributions were analyzed with a nonparametric multisample Mardian-Watson-Wheeler test (MWW; Batschelet 1981) implemented in the R package *circular* (Agostinelli and Lund 2022).

As the coefficient of overlap ($\Delta_{1)}$ is primarily a descriptive method, nonparametric tests for significance such as MWW tests are utilized (Monterroso 2014). When multiple pairwise comparisons of MWW tests were implemented, type I errors were controlled with the Bonferroni correction (McDonald 2009), where the significance level (0.05) was divided by the number of pairwise tests conducted.

RESULTS

Overall Diversity.—The total number of observations obtained from each group varied greatly across years, with the year 2019 having the highest number of recorded observations, while 2020 and 2021 were lower (Table 3). With a total of 573 observations, invertebrates were the most common group detected using pitfall camera-traps, but no further additional activity period analyses were conducted. Lizards were the second most common group detected with a total of 481 independent observations (Table 3). Recordings from 'other' organisms and rodents were also summarized for each year of the study, but no further analyses were conducted (Table 3). Invertebrates were the only group surveyed that exhibited an increase in observations during 2018 and 2019, prior to the years of excessive rain and flooding observed at the park. In contrast, rodent observations were highest during 2018 to then decrease the following year. Rodents also had the highest number of observations of any other group in the flooded years (Table 3). The least number of observations were recorded from organisms that entered the traps in rare occasions and were classified as 'other'. These observations included two unintended amphibian species, the American Bullfrog (*Lithobates catesbeianus*) and Couch's Spadefoot (*Scaphiopus couchi*). Other unexpected, but more frequent species documented included the Cottontail (*Sylvilagus audubonii*), and the Cactus Wren (*Campylorhinchus brunneicapillus*). Observations of diurnal and nocturnal snake species amounted to a total of 50 independent recordings and were also summarized for each year, respectively (Table 3).

Table 3. Total captures per group detected at RBWP.

	2018	2019	2020	2021	Total
Lizards	223	186	10	62	481
Snakes	15	21	2	12	50
Invertebrates	135	378	31	29	573
Rodents	194	47	44	63	348
Other	15	4	1	5	25
Total	582	636	88	171	1477

The Side-blotched Lizard (*U. stansburiana*), the Southwestern Fence Lizard (*S. cowlesi*), and the Little Striped Whiptail (*A. inornata*) were the most frequently observed lizards (Table 4). The Common Checkered Whiptail (*A. tesselata*) was recorded in the first two years of the study, while the Chihuahuan Spotted Whiptail (*A. exsanguis*) was recorded only during the first and the last years of the study (Table 4). Unique detections throughout the four years of the survey included a single observation of the Great Plains Skink (*P. obsoletus*), Great Plains Ratsnake (*P. emoryi*), and the Chihuahuan Nightsnake (*H. jani*; Table 4). The most frequently observed snakes were the Long-nosed Snake (*R. lecontei*) and the Gopher Snake (*P. catenifer*), both absent during 2020 (Table 4). The Coachwhip (*M. flagellum*) and the Glossy Snake (*A. elegans*) were the only snake species recorded in three of the four years of the study (Table 4). The Checkered Garter Snake (*T. marcianus*) was observed only during the flooding years at RBWP, likely as a result of the overflowing channels and resulting standing water near the traps which was not the case in 2018 and 2019 (Table 4).

Table 4. Number of reptile observations from species detected at RBWP from 2018-2021.

		2018	2019	2020	2021	Total
Common Side-blotched Lizard	*U. stansburiana*	135	128	4	10	277
Southwestern Fence Lizard	*S. cowlesi*	14	41	5	38	98
Little Striped Whiptail	*A. inornata*	66	14	0	11	91
Common Checkered Whiptail	*A. tesselata*	4	3	0	0	7
Chihuahuan Spotted Whiptail	*A. exsanguis*	4	0	0	3	7
Great Plains Skink	*P. obsoletus*	0	0	1	0	1
Long-nosed Snake	*R. lecontei*	1	4	0	9	14
Gopher Snake	*P. catenifer*	2	8	0	0	10
Coachwhip	*M. flagellum*	5	2	1	0	8
Glossy Snake	*A. elegans*	4	1	0	1	6
Desert Kingsnake	*L. splendida*	1	3	0	0	4
Big Bend Patchnose Snake	*S. deserticola*	1	2	0	0	3
Checkered Gartersnake	*T. marcianus*	0	0	1	1	2
Great Plains Ratsnake	*P. emoryi*	0	1	0	0	1
Chihuahuan Nightsnake	*H. jani*	1	0	0	0	1

According to estimates of standardized diversity indices (Shannon and Weaver 1963), the diversity detected using camera-traps was low and remained unchanged for all years even when the number of detections decreased (Table 5). Despite changes in the number of observations, the number of lizard species was similar each year from 2018 through 2021, while the number of detected snake species decreased (Table 5). The highest number of lizard species recorded in a single year was five, while the highest number of snake species was seven (Table 5). In total, there were six lizard species and nine different snake species recorded throughout the study. The slightly highest recorded diversity index value (1.40 *H*') was observed in 2021 corresponding to one of the years with a low number of lizard and snake observations (Table 5).

Table 5. Relative reptile diversity detected at RBWP (Shannon and Weaver 1963).

	Lizard observations	Lizard species	Snake observations	Snake species	*H*'
2018	223	5	15	7	1.26
2019	186	4	21	7	1.26
2020	10	3	2	2	1.35
2021	62	4	12	3	1.40

Activity Patterns.―Using the exact time of capture from each independent observation, the activity pattern for each of the three most frequently detected species was determined (Fig. 8). The Side-blotched Lizard (*U. stansburiana*) exhibited a significant shift in activity in the summer compared to its activity in the spring, a pattern observed in each of the years surveyed (Fig. 8A). In the summer, the estimated range of activity of *U. stansburiana* was wider than its estimated activity in the spring (Fig. 8A). In the summer, the activity peak of *U. stansburiana* was observed to shift to a later time in the day, when compared to the estimated peak in the spring (Fig. 8A). The Southwestern Fence Lizard (*S. cowlesi*) exhibited a shift in activity in 2021 from its recorded pattern observed in 2018 and 2019 (Fig. 8B). The breadth of activity observed in *S. cowlesi* was similar across all years, but it was determined that the activity peak recorded in the last year of the study shifted to an earlier time in the day (Fig. 8B). The activity pattern of *A. inornata* was statistically unchanged from the beginning of their active season through their last days of reported activity for every year they were recorded (Fig. 8C).

Activity Overlap.―The activity period pattern of *U. stansburiana* was revealed to have considerable overlap with the activity pattern of *A. inornata* and *S. cowlesi* in the spring (Fig. 9A and 9B). In the spring, the three lizard species were active over the same period of time and had similar activity peaks illustrated by the high overlap estimates. In the summer, the peak of activity of *U. stansburiana* shifted significantly towards a later time in the day resulting in reduced activity overlap with *A. inornata* (Fig 9C), and with the activity period of the *S. cowlesi* (Fig. 9D). The activity period pattern observed in *A. inornata* was determined to be unchanged through the seasons and across the years of the study (Fig. 8C) and estimated to differ significantly when compared to the activity period of *S. cowlesi* (Fig. 9E).

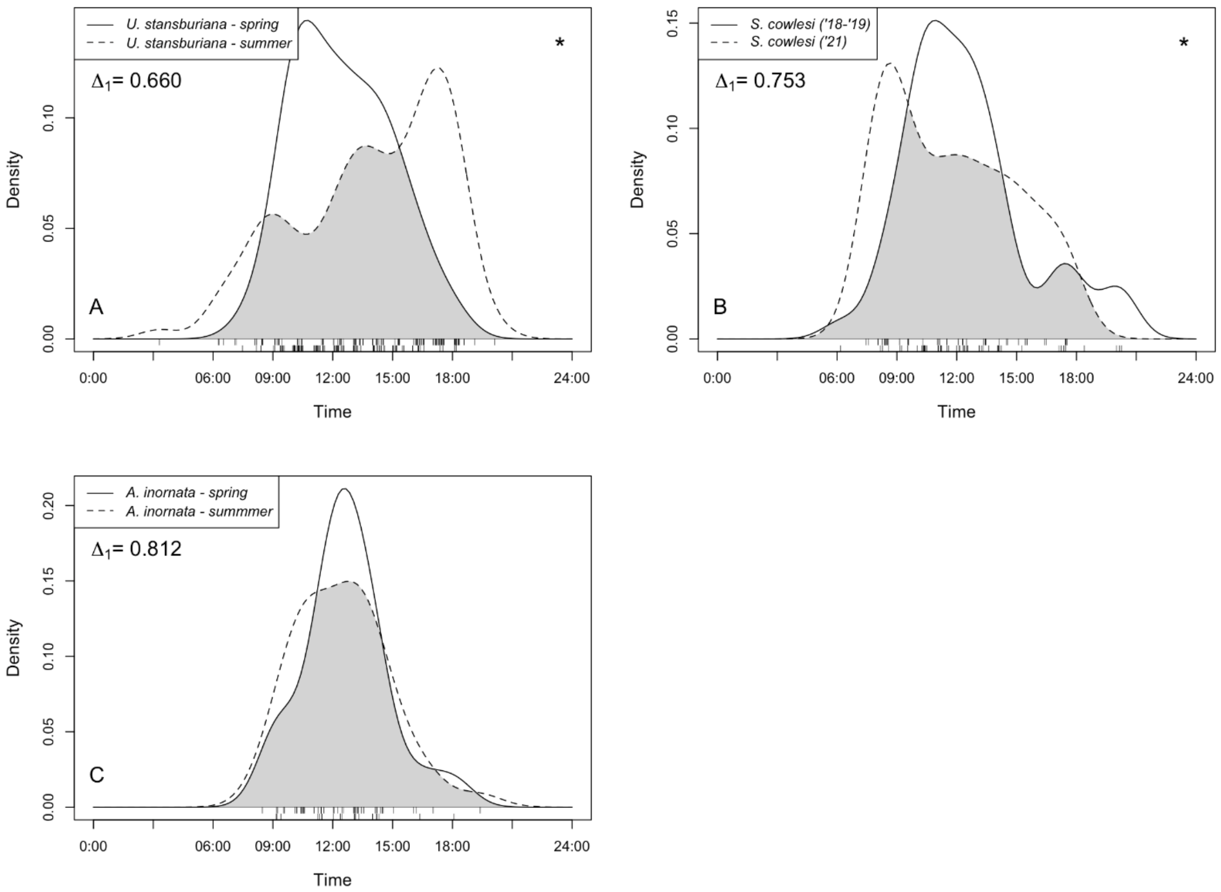

Figure 8. Daily activity patterns for each of the three most frequently observed species in the Rio Bosque Wetlands Park from 2018 through 2021. **A)** Overlap contrast between the documented spring activity pattern of the Common Side-blotched Lizard (*U. stansburiana*) and its pattern exhibited during the summer (Δ_1= 0.660 ± 0.057, W = 32.83, $_{df = 2}$, *p* value < 0.05). **B)** Overlap contrast in the activity patterns exhibited by the Southwestern Fence Lizard (*S. cowlesi*) in 2018 and 2019, compared to 2021 (Δ_1= 0.753 ± 0.071, W = 6.06, $_{df = 2}$, p-value = 0.04802). **C)** Contrast in the activity period pattern in the spring and summer of the Little Striped Whiptail (*A. inornata*; Δ_1= 0.812 ± 0.071, W = 2.49, $_{df = 2}$, p value = 0.2873). *Patterns are significantly different.

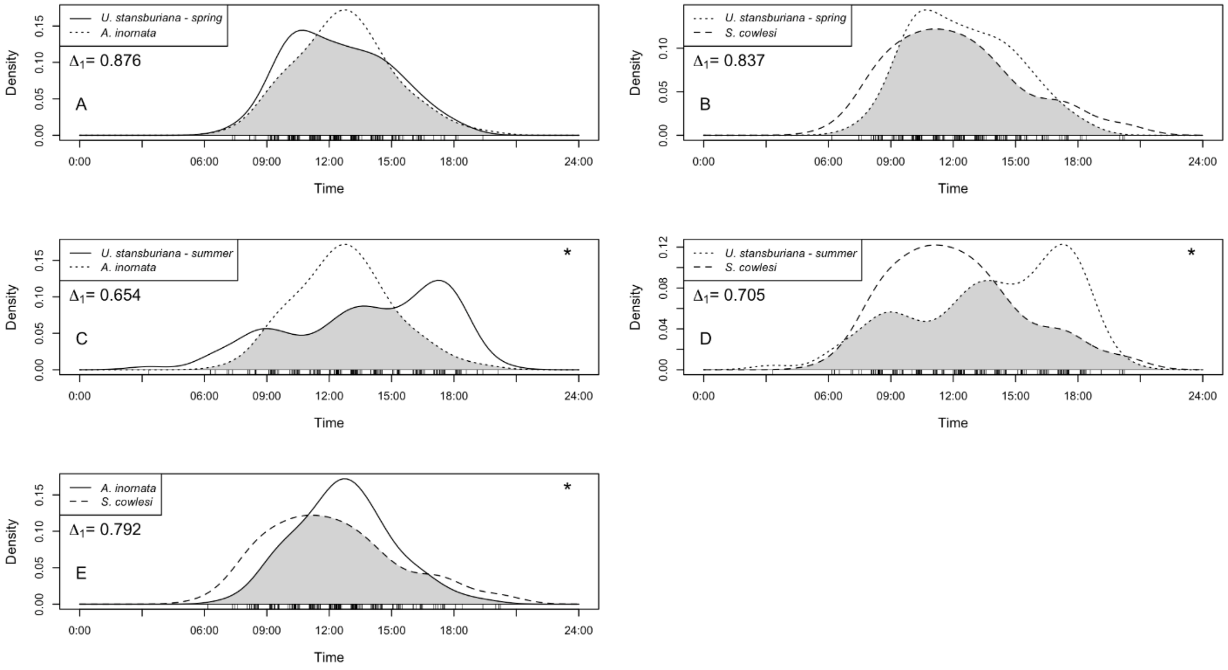

Figure 9. Assessment of activity overlap between the three most common species documented at RBWP from 2018 through 2021. A) Contrast between the activity period of the Common Side-blotched Lizard (U. stansburiana) in the spring and the activity period of the Little Striped Whiptail (*A. inornata*; Δ_1= 0.876 ± 0.043, W = 4.56, $_{\text{df = 2}}$, *p* value =0.102). B) Estimate of activity overlap between the Common Side-blotched Lizard (*U. stansburiana*) in the spring and the activity period of the Southwestern Fence Lizard (*S. cowlesi*; Δ_1= 0.837 ± 0.046, W = 2.13, $_{\text{df = 2}}$, *p* value = 0.342). C) Overlap estimate of the activity period of the Common Side-blotched Lizard (*U. stansburiana*) in the summer and the activity period of the Little Striped Whiptail (*A. inornata*; Δ_1= 0.654 ± 0.056, W = 34.08, $_{\text{df = 2}}$, *p* value < 0.001). D) Activity overlap estimate of the activity period of the Common Side-blotched Lizard (*U. stansburiana*) in the summer and the activity pattern observed in the Southwestern Fence Lizard (*S. cowlesi*; Δ_1= 0.705 ± 0.058, W = 23.67, $_{\text{df = 2}}$, *p* value < 0.001). E) Overlap estimate of the activity period of the Little Striped Whiptail (*A. inornata*) and the activity period of the Southwestern Fence Lizard (*S. cowlesi*; Δ_1= 0.792 ± 0.056, W =10.70, $_{\text{df = 2}}$, *p* value =0.004).

DISCUSSION

Lizard Pitfall Camera-Traps.—Pitfall traps equipped with motion-activated cameras were effective at documenting the target species, the Common Side-blotched Lizard (*U. stansburiana*), the Southwestern Fence Lizard (*S. cowlesi*), and the Little Striped Whiptail (*A. inornata*), among other species of lizards, snakes, invertebrates, and rodents. Detections were possible by following the COAT protocol developed by Welbourne (2013) to create the necessary temperature contrast between the reptile and the background. Because of this required temperature differential, other studies have been less effective especially in the detection of nocturnal reptiles (Richardson et al. 2018; Welbourne et al. 2016). In this urban wetland investigation, due to the background being shielded from direct sunlight by the coverboard, buried, and near the sensor, it was possible to detect small and nocturnal species, despite their smaller thermal signature (Swann and Perkins 2014; Welbourne et al. 2015). For example, species recorded included the Chihuahuan Nightsnake (*H. jani*), a nocturnal and crepuscular forager (Degenhardt et al. 2005). Additionally, snakes, which are known to escape unrecorded from traditional pitfall traps (Enge 2001; Ferguson et al. 2008; Thompson et al. 2005; Todd et al. 2007) were effectively documented including the Big Bend Patch-nosed Snake (*S. deserticola*), which was first recorded in 2018 and represents the first documented record for the wetland (www.utep.edu/cerm/rio-bosque/rio-bosque-home.html).

The development of cost-effective methods that provide ecological data from lizards and snakes in urban areas is an urgent concern due to the accelerated development and habitat degradation which diminish global biodiversity (Grimm et al 2008; McDiarmid et al. 2012; McKinney 2006; Newbold et al. 2015). In this study, the use of pitfall camera-traps did not increase risks associated with chasing, capturing, and handling of animals (Beaupre and Greene 2012; Langkilde and Shine 2006). For example, predation by snakes of captured lizards, if unable to escape (Enge 2001; Ferguson et al. 2008). With predation as a major factor in the demographics of *U. stansburiana* (Wilson 1991), methods that allow subjects to escape, that have the capability of detecting known predators, and that are able to record predation events may have an advantage over traditional pitfall traps and may also be considered more ethical (De Bondi et al. 2010; Paull et al. 2012; Putman 1995). Additionally, camera-traps were more cost-effective than traditional sampling methods as it required limited personnel and only a reduced number of field visits (De Bondi et al. 2010; Paull et al. 2012; Swann et al 2004). In this study, several snake species were effectively recorded, including some lizard predators, the Coachwhip (*M. flagellum*), Glossy Snake (*A. elegans*), and Long-nosed Snake (*R. lecontei*; Degenhardt et al. 2005; Halstead et al. 2008; Whiting et al. 1992; Wright and Wright 1957). Sample sizes of snake observations in each year of this study were insufficient to include in the activity overlap analyses and were also beyond the scope of the study. In contrast, large sample sizes of several species of rodents and invertebrates were collected, but not included in the analysis as this objective was also beyond the scope of the study. Camera-traps have been previously reported effective in detecting rodents (Swingle et al. 2004) and invertebrates (Hobbs and Brehme 2017), but further field research is needed to evaluate actual detectability rates for many species.

Activity Patterns.—Traditional sampling methods have reported similar activity patterns to those in this study for the three subject species, *U. stansburiana*, *S. cowlesi*, and *A. inornata* (Degenhardt et al. 2005; Fox 1978; Wright and Vitt 1993), but most investigations have focused on a single species and have limited capacity for analytical contrasts between species. In this study, continuous data was used to calculate and statistically contrast the activity period patterns of multiple species by estimating their coefficient of overlap (Δ_1; Linkie and Ridout 2011; Ridout and Linkie 2009). The only species to demonstrate a significant shift in activity from spring to summer was *U. stansburiana* (Fig. 8A). For *U. stansburiana*, the activity peak in the spring was around 1100h then shifted to around 1600h in the summer (Fig. 8A). Similar seasonal shifts in activity have been previously reported (Fox 1978) and have been explained to be driven primarily by the increased summer temperatures as hotter midday conditions are avoided by some lizard species (Adolph and Porter 1993; Pianka 1975). However, the direction of this shift was in the opposite direction of the activity peak of a similar and cooccurring species, *S. cowlesi*. The observed shift in the activity period of *U. stansburiana* may result in a reduction in predation and competition in the summer with *S. cowlesi*, which has an activity peak earlier in the day (Fig. 9D). The Southwestern Fence Lizard (*S. cowlesi*) has been reported to consume hatchlings of smaller lizards including *U. stansburiana*, which emerge in mid-June (DeMarco et al. 1985; Degenhardt et al. 2005; Dixon and Medica 1966; Turner et al. 1970). Moreover, both species are commonly found in sympatry and are described as sit-and-wait foragers that eat similar items, including flies, grasshoppers, insect larvae, ants, wasps, spiders, termites, and beetles (Barbault and Maury 1981; Best and Gennaro 1984; Dixon and Medica 1966; Douglas 1966; Ferner 1976; Parker and Pianka 1975; Toliver and Jennings 1975).

For a large part of 2020, extensive and lasting flooding observed at the wetland affected most areas within it including the exact locations where the traps had been installed. The floods modified three of the nine original trap locations, making these areas unrecognizable from their previous state. Two new locations were setup with traps in the fall of 2020 only to have the cameras stolen shortly after being installed. These cameras were redeployed in the Fall of 2021; no new locations were added after that. Only *S. cowlesi* showed a significant change in activity period following the disturbance to the wetland, most likely driven by the discharge from the BWTF in 2020 (Fig 8B). Specifically, the activity peak observed once the area recovered, had significantly shifted to an even earlier time of the day. The results show that *S. cowlesi* shifted its activity pattern after these major changes to the wetland by having an earlier activity peak while *U. stansburiana* did not. This may reflect a more efficient exploitation by *S. cowlesi* to a new preferable time to be active and forage, assuming this space has not yet been occupied (Pianka 1975).

This shift in the activity period of *S. cowlesi* did result in significantly reduced overlap with *U. stansburiana* (Fig. 9D) in the summer. Although, the activity overlap between *A. inornata* and *S. cowlesi* was considered high (Δ_1=0.792; Ridout and Linkie 2009), their activity patterns were statistically different mainly due to differences in activity peak and not in the range of activity. The different and intense wide-foraging behavior of *A. inornata* may contribute to their considerable overlap with the other two species, which are considered sit-and-wait foragers (Anderson and Karasov 1981). Prey items of *A. inornata* are similar to those consumed by the other two species in this study, but whiptail lizards feed mostly on termites (Anderson 1994; Degenhardt et al. 2005; Milstead 1974; Wright and Vitt 1993). As a result, the high overlap values of activity of *A. inornata* and the other species may not impact them due to different foraging strategies (Degenhardt et al. 2005; Fox 1978; Pianka 1966; Wright and Vitt 1993).

In fact, population overlap of *U. stansburiana*, *S. cowlesi*, and *A. inornata* is common in Texas, New Mexico, Arizona, and Colorado (Degenhardt et al. 2005). Areas where these species occur include natural habitats such as riparian corridors, xeric environments, desert grasslands, desert woodlands, sand dunes (Degenhardt et al. 2005; Stebbins 1985; Tinkle 1967), and in urban habitats and areas surrounded by extensive urban development (Ackley et al. 2015; Cosentino et al. 2013; Flores et al. 2023). As habitat degradation increases (Delaney et al. 2021; Keinath et al. 2017; Uetz 2018), the protection of surviving reptile species found in habitat patches, such as the Rio Bosque Wetlands Park (RBWP) may be increasingly important (Delaney et al. 2021). In this study, nine snake species and six lizard species were detected representing a valuable patch of habitat for reptiles being impacted by urbanization. It is important to investigate the effects of urbanization in areas such as RBWP, which is a refugia to several organisms. There is evidence of many species thriving in habitats impacted by urbanization (McDonnell and Hahs 2015). The results of this study show specific responses to urbanization and disturbance at RBWP, as excess water and prolonged flooding reduced the total number of observations and changed the number of species detected. Additionally, the seasonal shift observed in the Common Side-Blotched Lizard (*U. stansburiana*), which remained consistent throughout the years of the study, may be explained by differences in lizard species to preferentially adjust their activity in one direction or another to remain a longer time at a more optimal period of the day (Fox 1978). Similarly, the significant change in activity of the Southwestern Fence Lizard (*S. cowlesi*) post-disturbance to an earlier activity peak when activity of the other abundant lizard species is low, may be evidence of a quicker exploitation by the Southwestern Fence Lizard (*S. cowlesi*) towards an optimal activity time when compared to the other species present (Pianka 1975).

ACKNOWLEDGEMENTS

Research at RBWP was possible thanks to Hellen Geller, project manager of STEMGrow at UTEP. Special thanks to the interns Patricia Aguirre, Matthew Jimenez, Gavin Welsh, and Giovanni Del Campo for their assistance with fieldwork. Thanks also to Paul Hotchkin and Dr. Golding. This project was funded partially by the Department of Education HIS STEMGrow PO31C160235. Also, I appreciate the support from UTEP's Center for Environmental Resource Management in facilitating access and use of the wetland. Research was conducted under IACUC protocol A -201004-1 356592-8.

CHAPTER 3: ACTIVITY PATTERNS OF WHIPTAIL LIZARDS (*ASPIDOSCELIS*) FOUND IN THE NORTHERN CHIHUAHUAN DESERT

INTRODUCTION

Unisexual species were hypothesized to have a common distribution pattern referred to as 'la parthénogenèse géographique', or 'geographic parthenogenesis', and should inhabit islands or island-like environments, higher altitudes, higher latitudes, xeric landscapes, and ecotonal or disturbed habitats (Vandel 1928). Unisexual parthenogens occur in 19 out of 34 animal phyla, including 70 vertebrates, but no mammals or birds (Avise et al. 1992). As an example of unisexual vertebrates, parthenogenetic whiptail lizards (Family: Teiidae Genus: *Aspidoscelis*) are abundant across Arizona, New Mexico, Texas, southern Utah, Colorado, and northern and central Mexico (Painter et al. 2017; Wright and Vitt 1993). These all-female lizards have been a model organism to investigate the ecology and evolution of 'geographic parthenogenesis' as most occupy transitional, ecotonal, disturbed, marginal, dryer and warmer environments compared to their sexual relatives (Schall 1978; Wright and Vitt 1993).

Several hypotheses, including the 'weed hypothesis' suggest that the unstable, disturbed, marginal, and ecotonal habitats created from overgrazing within the past 200 years, have been more effectively colonized by unisexual whiptails due to their wider ecological tolerances and enhanced colonizing properties when compared to their sexual progenitors (Bestelmeyer et al. 2018; Schall 1978; Van Auken 2000; Wright and Lowe 1968). However, the genus *Aspidoscelis* is characterized by assemblages where both the parthenogen and parental species cooccur. For example, the Marbled Whiptail Lizard (*A. marmorata*) and the Common Checkered Whiptail (unisexual; *A. tesselata*) are found in sympatry across many areas in the northern Chihuahuan

Desert and many studies have investigated the resource partitioning that allows coexistence among parthenogens and their sexual relatives (Case 1983; Cuellar 1977; Cuellar and McKinney 1976; Degenhardt et al. 2005; Germano and Hungerford 1981; Medica 1967; Milstead 1961; 1965; Mitchell 1979; Smith; 1989; Walker 1987). Ecological investigations of the genus have reported that in general, many sympatric whiptail species eat the same prey items, occupy the same microhabitat, have similar foraging behaviors, and are active during the same time of the day (Cuellar 1977; 1979; Milstead 1961; 1965; Mitchell 1979; Wright and Vitt 1993). The overlap across similar niches appears to challenge the principle of competitive exclusion, which states that two or more species cannot coexist permanently if they possess identical ecological needs (Levin 1970). Due to resource partitioning, activity patterns of lizards are complex (Adolph and Porter 1993; Pianka 1973). Tests of those hypotheses and estimates of competitive exclusion between the unisexual *A. tesselata*) and its congener, *A. marmorata* have been mainly focused on demographic measurements (Schall 1978; Wright and Lowe 1968; Wright and Vitt 1993) and diet overlap (Mata-Silva et al. 2013).

Developing cost-effective methods to obtain ecological data of lizards and snakes is of urgent concern, as traditional methods such as pitfall traps and active searches are labor intensive, selective, and can have considerable mortality rates to target and non-target organisms (Christy et al. 2010; Enge 2001; Garden et al. 2007; Silvy 2012). Data obtained using traditional sampling methods used to estimate activity period has very limited analytical capacity when attempting to detect differences in activity patterns of cooccurring whiptail species because some species in the Chihuahuan Desert have estimated average daily activity periods of less than five hours (Wright and Vitt 1993). For example, when using traditional pitfall traps, the exact time for each captured animal is unknown and can only be associated with the time at which the trap was revisited by researchers, which is usually every few hours (Enge 2001). Additionally, when sampling using traditional pitfall traps, predation by larger lizards or snakes capable of escaping the trap cannot be accurately accounted for, unless each event is observed (Ferguson et al. 2008).

Camera-traps are commonly used to address questions related to diversity, abundance, and density (O'Connell et al. 2011), and are increasingly being used to evaluate activity period patterns (Ridout and Linkie 2009). Previous studies have relied on summary statistics to describe activity patterns by classifying a species as diurnal, nocturnal, crepuscular, or cathemeral based on the proportion of photos obtained in discrete time periods (Maffei et al. 2004; Oliveira-Santos et al. 2008), or by graphing the total number or proportion of photos obtained in 1-hour blocks (Maffei et al. 2005). More recently, statistical methods for specifically analyzing circular data have been developed to test for differences in activity periods and comparison among species (Oliveira-Santos et al. 2013; Ridout and Linkie 2009). Despite those advances, only a few studies have effectively used camera-traps to study reptiles (Welbourne 2013; Welbourne et al. 2017). Recently, the implementation of passive infrared sensors (PIR) has made motion-activated cameras more energy efficient, more compact, and cheaper than older versions. These cameras are triggered by detecting small differences in the temperature of the background and a passing animal (Welbourne et al. 2016). Potentially, small mammals and ectotherms could go undetected due to their small thermal signature (Swann and Perkins 2014; Welbourne et al. 2015). However, there is substantial evidence suggesting that under certain conditions, this type of camera can successfully detect and record the activity of reptiles (Welbourne 2013; Welbourne et al. 2017). For example, Welbourne (2013) used camera-traps to survey large snakes and varanid lizards in an Australian savannah, with each camera positioned under a protective shield from direct sunlight. Because the temperature of the reptiles resembled the temperature of the surrounding substrate, motion-activated cameras failed to detect every reptile. Welbourne (2013) developed a Camera Overhead Augmented Temperature (COAT) protocol, utilizing a different substrate, such as wood chips to alter the background of the camera's field of view. This protocol has been implemented effectively to sample reptiles (Dundas et al. 2019; Welbourne et al. 2015; Welbourne et al. 2017).

The main research objective was to characterize the activity period patterns of sympatric whiptail species and conduct statistical contrasts between the Common Checkered Whiptail (unisexual; *A. tesselata*) and its parental species the Marbled Whiptail (*A. marmorata*) using pitfall traps implemented with motion-activated cameras. The estimated activity range and activity peak for whiptails was described using methods developed by Oliviera-Santos et al. (2013). To compare sexual and asexual *Aspidoscelis* congeners, the coefficient of overlap (Δ_1) was estimated based on the activity pattern of each species (Ridout and Linkie 2009) and evidence of temporal niche partitioning between these species was investigated. The coefficient of overlap (Δ_1) provides estimates for each species interaction with values ranging from zero (no overlap) to one (identical overlap; Ridout and Linkie 2009). In this study, overlap values ranging from 0.500 to 0.750 are considered mid to high overlap values, while values above 0.750 are deemed high. The first hypothesis was that high overlap of activity period patterns between the parthenogen and the progenitor species occurs across all sites included in the study. Secondly, despite high coefficient overlap between the parthenogen and the Marbled Whiptail Lizard (*A. marmorata*), it was hypothesized that coexistence of assemblages of the parthenogen, its progenitor, and other whiptail species is facilitated by differences in the activity pattern periods.

MATERIALS AND METHODS

Pitfall-Camera Traps.—Lizard pitfall traps used in this study consisted of a buried 20-liter plastic container with a wooden coverboard positioned four centimeters above ground level, while drift fences were not employed. For drainage, 20 orifices (2 mm in diameter) were drilled on the bottom of each container. Lizard pitfall traps were implemented with a motion-activated camera and a piece of hardware mesh (60 cm x 20 cm) attached to the bottom and the side of the container allowing organisms to escape. Each camera (Moultrie® Alabaster, Alabama; Game Spy 6MP Trail Camera) was set with a 15 second delay between videos and mounted facing down into the bottom of the container. All traps were installed prior to reptile emergence. Camera-trap ranges of sampling reported herein were restricted to the periods when the first and last lizard observation were recorded within each year. Camera-traps were deployed beyond the active range of lizards and snakes resulting in the documentation of rodents. Camera-traps were deployed at all sites from 20 March 2018 through 23 September 2021. The survey period was sometimes interrupted by flooding, theft, and malfunction of the cameras, thus not technically continuous for all traps at each site. Estimations of observations per number of traps deployed had to be adjusted for the actual number of traps running. Batteries and memory cards were replaced a total of seven times during the season at each site.

Study Sites.—Research focused on whiptail lizards (*Aspidoscelis*) was conducted at the Indio Mountains Research Station (IMRS; 30°46’37” N, 105°00’58” W), Culberson County, southeast of Van Horn, Texas (https://www.utep.edu/indio/). A total of nine traps were used in the survey of whiptail lizards, but this site had cameras deployed from 2018 through 2021, as it was part of a preliminary study. This site has relatively high reptile diversity including several whiptail species such as the Chihuahuan Spotted Whiptail (unisexual; *A. exsanguis*), Little Striped Whiptail (*A. inornata*), Checkered Whiptail (unisexual; *A. tesselata*), and the Marbled Whiptail (*A. marmorata*; Crother 2017; Johnson 2000).

A separate site located in El Paso, Texas is placed in the Franklin Mountains State Park (FMSP; 31°90’81’’N, 106°52’54’’W; https://tpwd.texas.gov/state-parks/franklin-mountains). Vegetation is typical of the Chihuahuan Desert and very similar in composition to IMRS. In this site, a total of six pitfall camera-traps were used to survey this area from 2019 through 2021. In contrast to IMRS, this study site is a public park characterized by hiking and biking trails frequently visited by locals. In the west, FMSP is bordered by Interstate 10 and found adjacent to Transmountain Road. There is also an active concrete quarry (https://www.jobematerials.com/) located near the west boundary of FMSP and another quarry on the northeast boundary. The area on the east side is bordered by a residential area in the northeast of El Paso, near Martin Luther King Road. Lizard and snake diversity is high including several species of whiptail lizards are known to cooccur in this area. Whiptails in FMSP include the Common Checkered Whiptail (unisexual; *A. tesselata*), Chihuahuan Spotted Whiptail (unisexual; *A. exsanguis*), and Marbled Whiptail (*A. marmorata*), and the Little Striped Whiptail (*A. inornata*; Painter et al. 2017).

An additional research area was located within the Organ Mountains Desert Peaks National Monument (OMDPNM; 32°32’25’’N, 106°57’38’’W) in Doña Ana County, New Mexico near the city of Las Cruces (www.blm.gov/visit/omdp). This study site also has vegetation typical of the Chihuahuan Desert and is similar in composition to the other study sites. In this site, nine pitfall camera-traps were placed in the lowland desert area between the eastern residential zone of Las Cruces and Baylor Canyon Road. This site was included in the survey with cameras deployed from 2019 through 2021. This area currently allows cattle grazing and is accessible to hiking, mountain biking, and off-road vehicles. Overall reptile diversity is relatively high, with potentially the highest diversity of whiptail species. Whiptail lizard species known from this area include: the unisexual Common Checkered Whiptail (unisexual; *A. tesselata*), Chihuahuan Spotted Whiptail (unisexual; *A. exsanguis*), Desert Grassland Whiptail (unisexual; *A. uniparens*), New Mexico Whiptail (unisexual; *A. neomexicana*), the Marbled Whiptail (*A. marmorata*), and Little Striped Whiptail (*A. inornata*; Degenhardt et al. 2005; Painter et al. 2017).

Whiptail data from a separate reptile study using the same standardized method from a separate study conducted at the Rio Bosque Wetlands Park (RBWP; 31°64’34’’N, 106°30’08’’W) from 2018 through 2021 were also included in this study. RBWP is located southeast of El Paso, Texas (www.utep.edu/cerm/rio-bosque/rio-bosque-home.html). This public park is an enclosed 150-hectare (ha) area surrounded by irrigation canals and the Rio Grande, which acts as the international border between the U.S. and Mexico. Vegetation within the park is typical of Chihuahuan Desert wetland areas. The vegetation has been recovering from grazing, farming, and the most recent channelization. The site includes Saltbush (*Atriplex canecens*), Honey Mesquite (*Prosopis glandulosa*), Jimmy Weed (*Isocoma spp.*), and Saltcedar (*Tamarix chinensis*). Riparian scrub includes Wolfberry (*Lycium berlandieri*), Spiny Aster (*Chloracantha spinosa*), Coyote Willow (*Salix exigua*), and Arrow Weed (*Pluchea sericea*). Whiptail species within RBWP include the Chihuahuan Spotted Whiptail (*A. exsanguis*) and the Little Striped Whiptail (*A. inornata*).

Overall Diversity.—Lizards and snakes observed in videos were identified to species level, and whenever possible, sex was determined for adults and sexually dimorphic species. At a minimum, non-target species such as invertebrates and rodents were identified to order level. Total number of camera-trap captures from lizards, snakes, rodents, and invertebrates were summarized for each year. For each observation, the exact time was recorded using the time stamp feature of the camera. Videos belonging to the same species recorded from the same trap within 30 minutes were removed from diversity and activity analyses to reduce pseudoreplication bias (Mori et al. 2022) unless confirmation of being a different individual using size and pattern differences. Overall diversity of lizards and snakes was estimated by comparing the total number of individuals documented and the total number of species from each year using Shannon's Diversity Index (Shannon and Weaver 1963).

Activity Patterns and Activity Overlap.—Seasons were defined as those falling within the calendar dates of spring (March 1 – May 31) and summer (June 1 – Aug 31). A minimum sample size of >10 was utilized in all comparisons. All capture times were converted to radians prior to analysis. Military time was converted to proportions of a 24-hour day by dividing time by 24. Radians were then calculated by multiplying values by 2π. The coefficient of overlap was used to quantify the amount of overlap between two pairs of activity using the R package *overlap* (Linkie and Ridout 2011; Ridout and Linkie 2009). This method was used to estimate the probability density function of activity patterns nonparametrically using kernel density. Capture times from cameras were considered random samples from a continuous distribution. All statistics were performed using R statistical software (R Development Core Team 2021). The coefficient of overlap (Δ_1) was estimated for all interactions, as appropriate for small sample sizes <75 observations (Ridout and Linkie 2009). Resulting values range from 0 (no overlap) to 1 (complete overlap). The precision of Δ_1 was estimated by computing the mean and standard deviation from 999 bootstrap samples. Significant differences between activity distributions were analyzed with a nonparametric multisample Mardian-Watson-Wheeler test (MWW; Batschelet 1981) implemented in the R package *circular* (Agostinelli and Lund 2022). As the coefficient of overlap is primarily a descriptive method, nonparametric tests for significance such as MWW tests are utilized (Monterroso 2014). When multiple pairwise comparisons of MWW tests were implemented, type I errors were controlled with the Bonferroni correction (McDonald 2009), where the significance level (0.05) was divided by the number of pairwise tests conducted.

RESULTS

Overall Diversity.—A total of 762 lizard captures were recorded using camera-traps from 2019 through 2021 with 467 of those observations belonging to whiptail lizards. The majority of lizard observations (416) were obtained from IMRS, while only 66 were collected in FMSP (Table 6). Similarly, IMRS was also the site with the highest number of snake observations (Table 6). The rodents were the group with the highest number of total documented observations with a total of 992 independent observations. Similarly, a total of 694 observations of invertebrates were recorded from 2019 through 2021 (Table 6). The total number of captures detected from each reptile species documented in IMRS, FMSP, and OMDP were summarized for each year of the study, including sampling from a preliminary sampling season at IMRS in 2018 (Table 7). In total, 30 different species of diurnal and nocturnal lizards and snakes were detected by the camera-traps across all sites and years included in the study. Overall, the highest number of independent observations belonged to the Marbled Whiptail Lizard (*A. marmorata*) followed by the Greater Earless Lizard (*C. texanus*), and the parthenogen, Common Checkered Whiptail (*A. tesselata*; Table 7). Only the unisexual whiptail was recorded in all three of the sites (IMRS, FMSP, and OMDP) across all years of the study, while lizard species such as the New Mexico Whiptail (*A. neomexicana*) and the Ornate Tree Lizard (*U. ornatus*) were only documented once. Similarly, the Texas Horned Lizard (*P. cornutum*) was recorded only two times throughout the study (Table 7). A total of 19 recordings were collected of the nocturnal Texas Banded Gecko (*C. brevis*; Degenhardt et al. 2005) with 18 of those obtained in IMRS and a single recording from FMSP (Table 7).

The most commonly documented snake species was the Big Bend Patch-nosed Snake (*S. deserticola*) with a total of 25 separate observations. The second most frequently recorded snake was the Striped Whipsnake (*M. taeniatus*) with 19 observations and 6 additional observations belonging to a similar species, the Coachwhip (*M. flagellum*; Table 7), both considered lizard predators known to be able to catch and feed on whiptail lizards (Halstead et al. 2008). A total of four snake species were observed only once, including the Long-nosed Snake (*R. lecontei*), Plains Black-headed Snake (*T. nigriceps*), Black-necked Garter Snake (*T. cyrtopsis*), and the Rock Rattlesnake (*C. lepidus*; Table 7). A total of 16 recordings of large venomous snakes were collected during the study belonging to three different rattlesnake species (*Crotalus spp*.). Also, a total of 15 observations of the mildly venomous (Chiszar and Smith 2002), nocturnal and crepuscular Chihuahuan Nightsnake (*H. jani*; Degenhardt et al. 2005; Stebbins 1985) were recorded (Table 7).

The estimated reptile diversity values of the pitfall camera-trap captures were consistent for all three sites across all years of the investigation (Table 8). Diversity index values were higher in IMRS for three of the four years of the study due to the high number of snake species observed (Table 8), while FMSP exhibited the highest diversity index recorded in 2020 (*H*'=2.17; Table 8). The OMDP site had a similar number of lizards to IMRS, but always a lower number of snake species for every year of the study (Table 8).

Table 6. Number of captures for each major group detected using camera-traps 2019-2021.

	2019			2020			2021			Total			
	IM	FM	OM	IM	FM	OM	IM	FM	OM	IM	FM	OM	Total
Lizards	201	22	152	111	24	61	104	20	67	416	66	280	762
Snakes	34	6	11	16	9	2	10	3	2	60	18	15	93
Invertebrates	202	43	68	145	91	23	64	32	26	411	166	117	694
Rodents	218	43	145	196	118	37	79	120	36	493	281	218	992
Other	18	14	18	7	15	8	4	3	0	29	32	26	87

Table 7. Total number of captures of each reptile species detected during the survey.

	IMRS	IMRS			FMSP			OMDPNM			
Lizards	2018	2019	2020	2021	2019	2020	2021	2019	2020	2021	TOTAL
A. marmorata	34	61	52	22	0	4	3	78	27	23	304
A. tesselata	1	19	12	18	8	6	11	25	6	8	114
A. inornata	5	21	4	8	0	2	0	0	1	4	45
A. exsanguis	0	0	0	0	0	0	0	0	3	0	3
A. neomexicana	0	0	0	0	0	0	0	1	0	0	1
S. cowlesi	0	2	1	1	0	0	0	12	2	19	37
S. magister	0	0	0	0	0	0	0	0	10	5	15
U. stansburiana	0	0	0	0	0	0	0	4	1	0	5
C. texanus	27	68	23	49	10	0	1	30	11	5	224
C. collaris	7	16	8	0	4	3	0	0	0	0	38
C. brevis	2	9	4	3	0	1	0	0	0	0	19
P. modestum	10	3	2	0	0	0	0	0	0	0	15
P. cornutum	0	0	0	0	0	0	0	0	0	2	2
P. obsoletus	0	2	4	3	0	8	5	0	0	0	22
U. ornatus	1	0	0	0	0	0	0	0	0	0	1
Snakes											
M. taeniatus	3	8	5	1	0	2	0	0	0	0	19
S. deserticola	2	11	4	1	0	2	2	2	1	0	25
H. jani	1	6	3	3	0	0	0	0	1	1	15
B. subocularis	2	1	0	0	1	1	0	0	0	0	5
P. catenifer	0	0	0	0	2	0	0	1	0	0	3
M. flagellum	1	1	0	1	0	0	0	2	0	1	6
S. semiannulata	0	1	0	0	0	0	1	0	0	0	2
A. elegans	0	0	0	2	0	0	0	2	0	0	4
R. lecontei	0	0	1	0	0	0	0	0	0	0	1
T. nigriceps	0	1	0	0	0	0	0	0	0	0	1
T. cyrtopsis	0	0	0	1	0	0	0	0	0	0	1
C. atrox	2	2	1	0	3	3	0	2	0	0	13
C. lepidus	0	0	1	0	0	0	0	0	0	0	1
C. viridis	0	0	0	0	0	0	0	2	0	0	2
R. segrega	0	2	1	1	0	1	0	0	0	0	5

Table 8. Relative reptile diversity detected at each site from 2018-2021.

	Lizard Observations	Lizard Species	Snake Observations	Snake Species	Reptile Species	*H*'
IMRS						
2018	87	8	10	5	13	1.86
2019	201	9	34	9	18	2.10
2020	111	9	16	7	16	1.98
2021	104	7	10	7	14	1.76
FMSP						
2019	22	3	6	3	6	1.55
2020	24	6	9	5	11	2.17
2021	20	4	3	2	6	1.43
OMDP						
2019	152	6	11	6	12	1.57
2020	61	8	2	2	10	1.70
2021	67	7	2	2	9	1.75

Activity Patterns of Whiptail Lizards.─Recordings belonging to the Marbled Whiptail (*A. marmorata*), Common Checkered Whiptail (*A. tesselata*), and the Little Striped Whiptail (*A. inornata*) were summarized and the average number of independent observations from each whiptail species was also calculated (Table 9). The number of observations of each species varied greatly across all study sites. For example, the Marbled Whiptail (*A. marmorata*) was observed three times more frequently than the unisexual, the Common Checkered Whiptail (*A. tesselata*; Table 9). Moreover, the Common Checkered Whiptail (*A. tesselata*), where the Marbled Whiptail (*A. marmorata*) was also documented, was only detected at a higher rate in FMSP; it was also observed in RBWP, but it was outnumbered by the Little Striped Whiptail (*A. inornata*; Table 9). Observations of the Marbled Whiptail Lizard (*A. marmorata*) were the highest recorded for any species in the study in 2019 at OMDP (Table 9). The estimated seasonal activity range was estimated using the total number of days of activity, which was calculated by using the first and last recorded day of activity for each season where more than five independent observations were available from each whiptail species (Table 10). Only the observations belonging to the Little Striped Whiptail (*A. inornata*) that originated from RBWP were included in the estimation of seasonal activity range, since not enough observations from the Common Checkered Whiptail (*A. tesselata*), or other whiptail species were available from this site (Table 10). The estimated total number of active days per season were almost identical in the sexual Marbled Whiptail (*A. marmorata*) and the parthenogen, the Common Checkered Whiptail (*A. tesselata*), while the range of the Little Striped Whiptail (*A. inornata*) was considerably wider (Table 10).

Table 9. Total number of whiptail lizard captures detected in all sites including RBWP from 2018-2021.

	A. marmorata	*A. tesselata*	*A. inornata*
IMRS			
2018	34	1	5
2019	61	19	21
2020	52	12	4
2021	22	18	8
FMSP			
2019	-	8	-
2020	4	6	2
2021	3	11	-
OMDP			
2019	78	25	-
2020	27	6	1
2021	23	8	4
RBWP			
2018	-	4	66
2019	-	3	14
2020	-	-	-
2021	-	-	11
Total	304	121	136
Average	33.78	10.08	13.6
SD	23.95	6.95	18.41

Table 10. Estimates of activity duration (days) of whiptail lizard detected in all sites including RBWP from 2018-2021.

	A. marmorata	*A. tesselata*	*A. inornata*
IMRS			
2018	90	-	145
2019	165	148	216
2020	111	169	138
2021	172	131	242
FMSP			
2019	-	144	-
2020	141	100	-
2021	-	98	-
OMDP			
2019	161	152	-
2020	107	101	-
2021	112	-	-
RBWP			
2018	-	-	224
2019	-	-	146
2020	-	-	-
2021	-	-	122
Total	1059	1043	1233
Average	132.37	130.37	176.14
SD	29.24	25.71	45.48

The seasonal activity range for the three whiptails species investigated was also summarized using a Gantt chart to illustrate the overlap of their activity and the dates when the activity was recorded (Fig. 10). Using the exact emergence date (Julian days) documented for the parthenogen and its parental species at each site within each season, the activity of the parthenogen was recorded later than that of its progenitor. In six of the seven observed concurrent seasons, *A. marmorata* was recorded an average of 10.57 days later than the first observations of *A. tesselata*. The data available on entire seasonal ranges, and their estimated dates of activity is limited, thus not explored any further. Instead, differences in activity period patterns for each whiptail species were estimated using contrasts of their activity overlap (Linkie and Ridout 2011; Meredith and Ridout 2014).

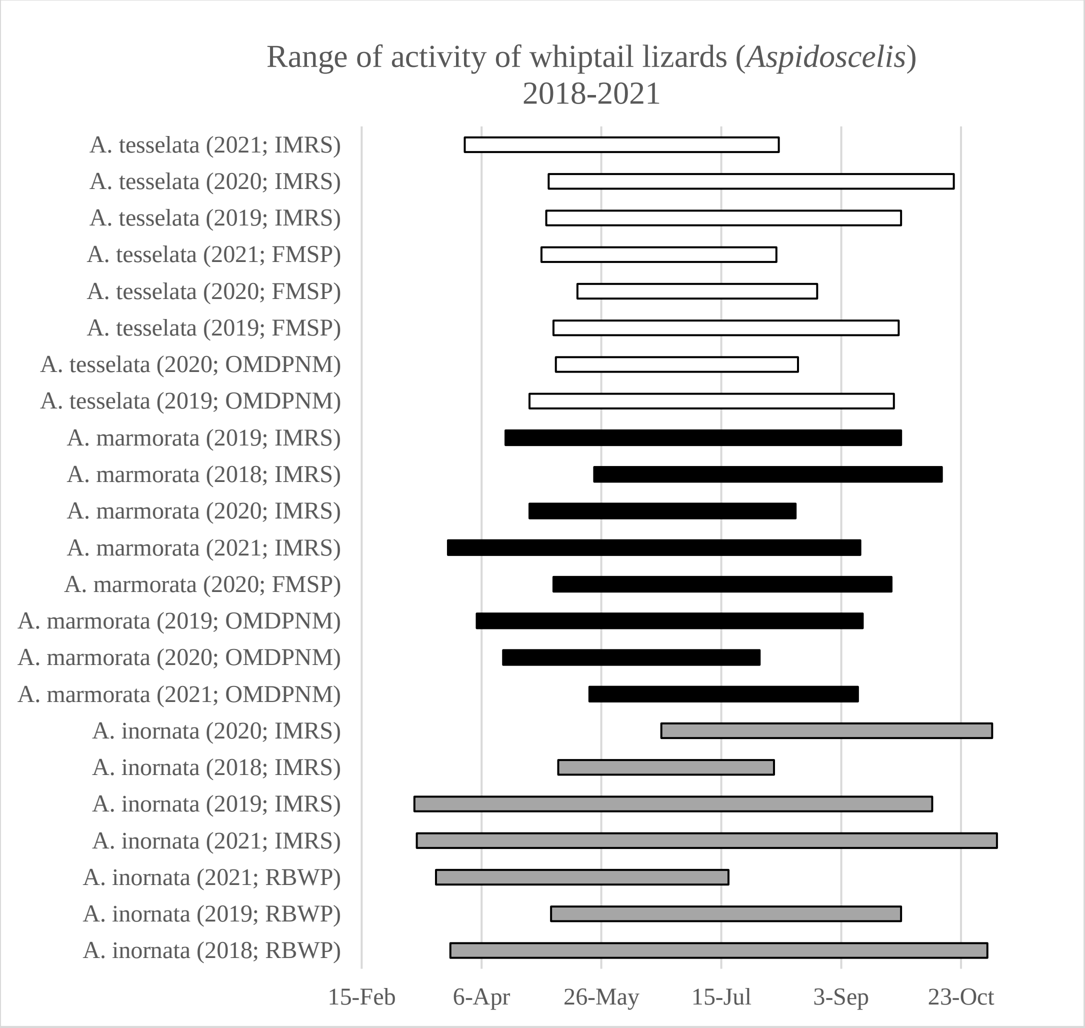

Figure 10. Gantt chart showing the overlap in seasonal activity of the three whiptail species detected using camera-traps from 2018-2021.

Daily activity patterns of the subject whiptail species were estimated and differences within each species for each site evaluated (Fig. 11). Most whiptail species in all sites had a consistent activity pattern during the spring and summer seasons, except *A. tesselata* in OMDP site (Fig. 11B) where the summer activity pattern for the parthenogen overlapped with its activity pattern in the spring only about 50% ($\Delta_1 = 0.502$; Fig. 11B). Since only one species exhibited a shift within its season, the combined observations from each season were contrasted across sites for all the other species and the results of their overlap estimations were summarized accordingly

(Fig. 12). No significant differences in the activity period patterns were detected, as all activity patterns were very similar to each other regardless of the site or season, except for the activity period of *A. tesselata* (Fig. 11B) at OMDP. The highest value of overlap was recorded for *A. marmorata* at IMRS and OMDP (Δ_1= 0.856; 12B). Similarly, the estimate of contrast recorded for *A. tesselata* in IMRS and FMSP, was relatively high (Δ_1= 0.803; 12F).

Furthermore, using estimates of activity overlap (Δ_1) between whiptail species (Fig. 13) it was revealed that the investigated whiptails have a very similar activity pattern to each other, except in the case of spring activity period documented of *A. inornate* and the daily activity period pattern of *A. marmorata* (Fig. 13A). The lowest value of overlap (Δ_1=0.682) between species was observed in the spring activity period of *A. inornata* and *A. marmorata* (Fig. 13A). The highest values of overlap were estimated for the parthenogen, *A. tesselata* and its maternal progenitor, *A. marmorata* during the spring (Δ_1= 0.855; Fig. 13D) and in the summer (Δ_1= 0.832; Fig. 13F). Overall, the range of activity reported for all three species was very similar. Although, not statistically tested, the range of activity of *A. inornata* did extend to earlier times during the spring, and into later times during the summer when compared to the other whiptail species (Fig. 13A and 13B).

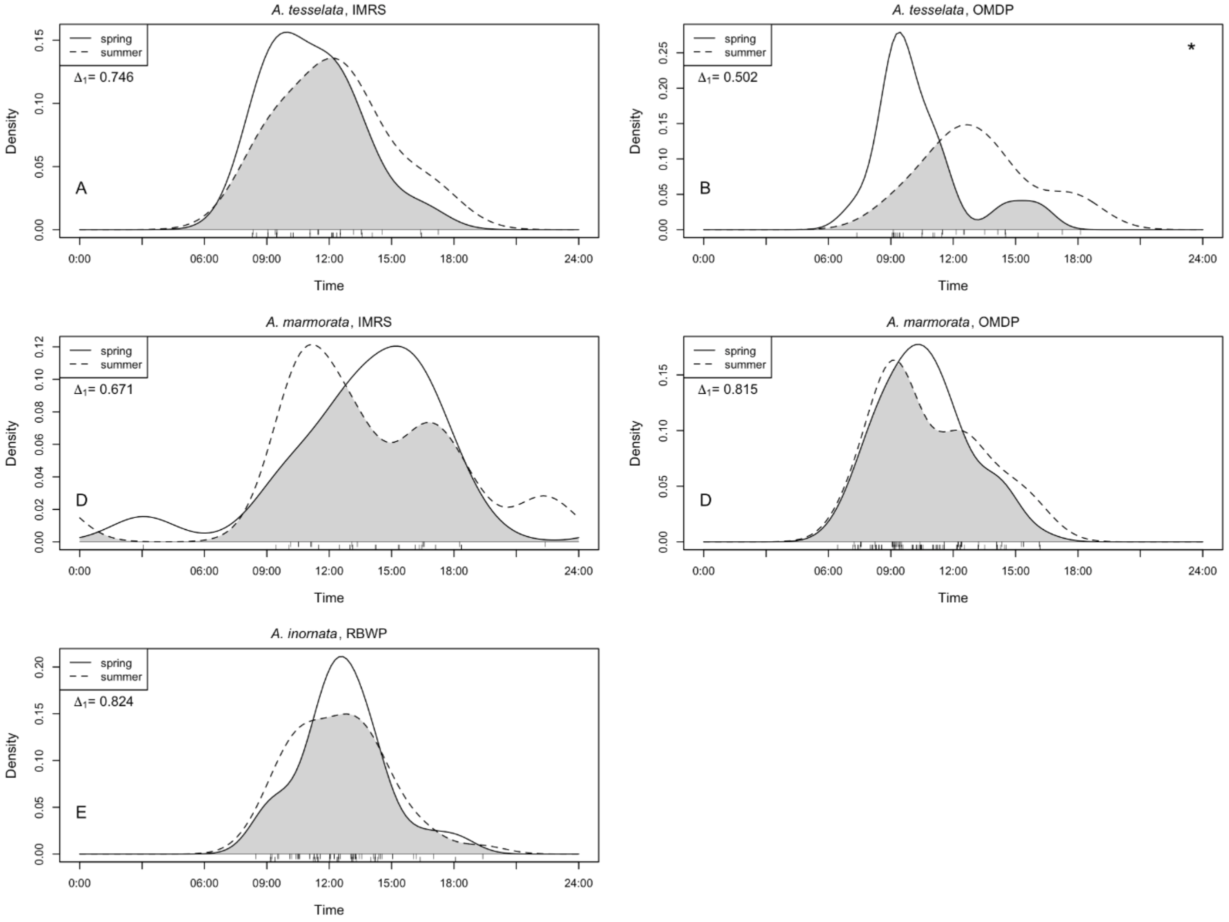

Figure 11. Overlap (Δ_1) within each season of the activity patterns for the whiptail species documented at each of sites from 2018 through 2021, respectively. **A)** Overlap of the spring and summer activity patterns belonging to the Common Checkered Whiptail (*A. tesselata*) from IMRS ($\Delta_1 = 0.746 \pm 0.103$, W = 1.912, $_{\text{df} = 2}$, *p* value = 0.3843). **B)** Overlap of the spring and summer activity patterns belonging to the Common Checkered Whiptail (*A. tesselata*) from OMDP ($\Delta_1 = 0.502 \pm 0.135$, W = 9.474, $_{\text{df} = 2}$, *p* value = 0.0087). **C)** Overlap of the spring and summer activity periods of the Marbled Whiptail (*A. marmorata*) from IMRS ($\Delta_1 = 0.671 \pm 0.113$, W = 2.545, $_{\text{df} = 2}$, *p* value = 0.2801). **D)** Overlap of the spring and summer activity patterns belonging to the Marbled Whiptail (*A. marmorata*) from OMDP ($\Delta_1 = 0.683 \pm 0.058$, W = 5.246, $_{\text{df} = 2}$, *p* value = 0.07255). **E)** Overlap of the spring and summer activity patterns belonging to the Little Striped Whiptail (*A. inornata*) from RBWP ($\Delta_1 = 0.815 \pm 0.070$, W = 2.545, $_{\text{df} = 2}$, *p* value = 0.2801). *Statistically different.

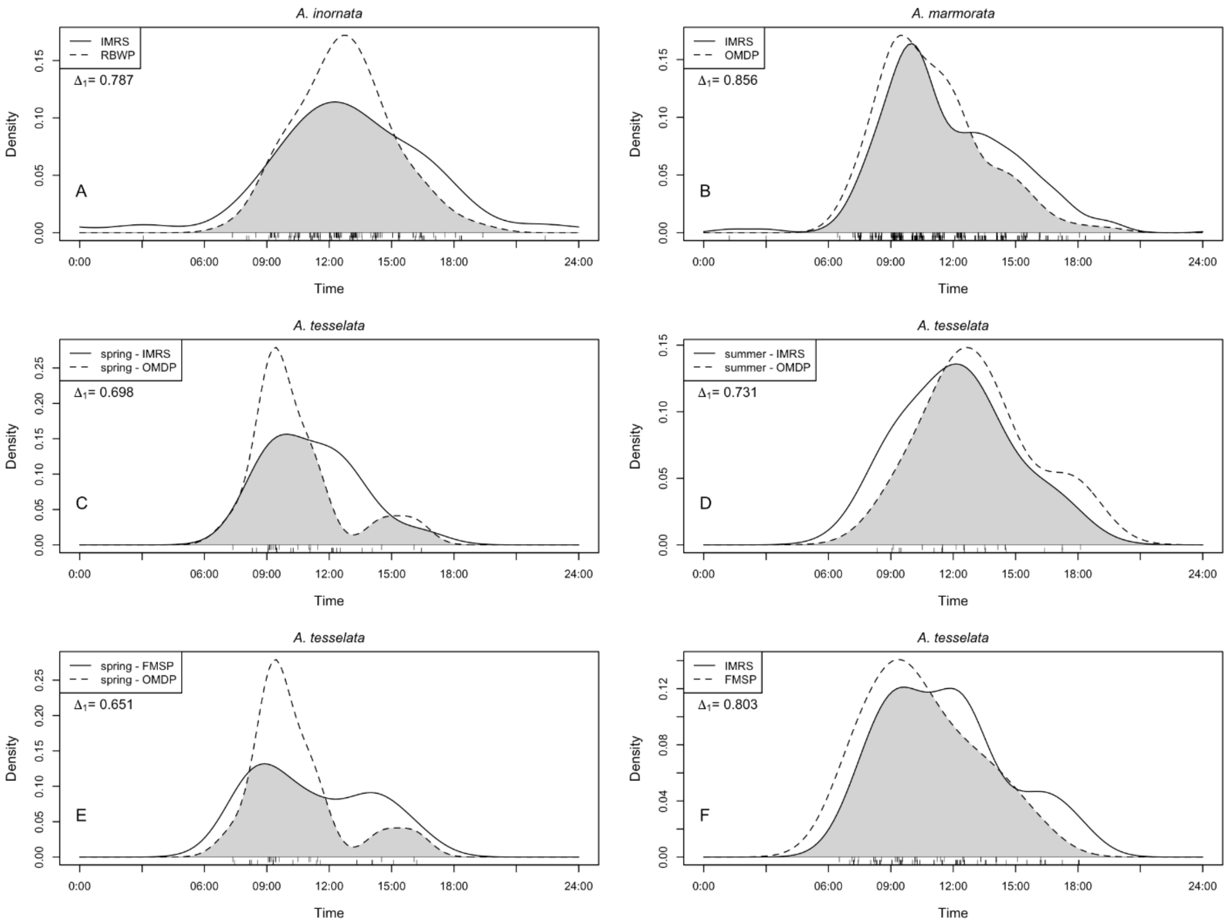

Figure 12. Estimates of activity period overlap (Δ_1) when entire season patterns were compared across sites. **A)** Overlap of the activity period documented for the Little Striped Whiptail (*A. inornata*) in IMRS and RBWP (Δ_1= 0.787 ± 0.061, W = 3.925, $_{df = 2}$, *p* value = 0.1925). **B)** Overlap of the activity pattern documented for the Marbled Whiptail (*A. marmorata*) in IMRS and OMDP (Δ_1= 0.856 ± 0.039, W = 1.373, $_{df = 2}$, *p* value = 0.5032). **C)** Overlap of the spring activity pattern documented for the Common Checkered Whiptail (*A. tesselata*) in IMRS and OMDP (Δ_1= 0.698 ± 0.108, W = 3.3666, $_{df = 2}$, *p* value = 0.1858). **D)** Overlap of the summer activity pattern documented for the Common Checkered Whiptail (*A. tesselata*) in IMRS and OMDP (Δ_1= 0.731 ± 0.105, W = 0.1164, $_{df = 2}$, *p* value = 0.9434). **E)** Overlap of the spring activity pattern documented for the Common Checkered Whiptail (*A. tesselata*) in FMSP and OMDP (Δ_1= 0.651 ± 0.122, W = 3.559, $_{df = 2}$, *p* value = 0.1687). **F)** Overlap of the activity pattern documented for the Common Checkered Whiptail (*A. tesselata*) in IMRS and FMSP (Δ_1= 0.803 ± 0.070, W = 0.8879, $_{df = 2}$, *p* value = 0.6415). *Statistically different.

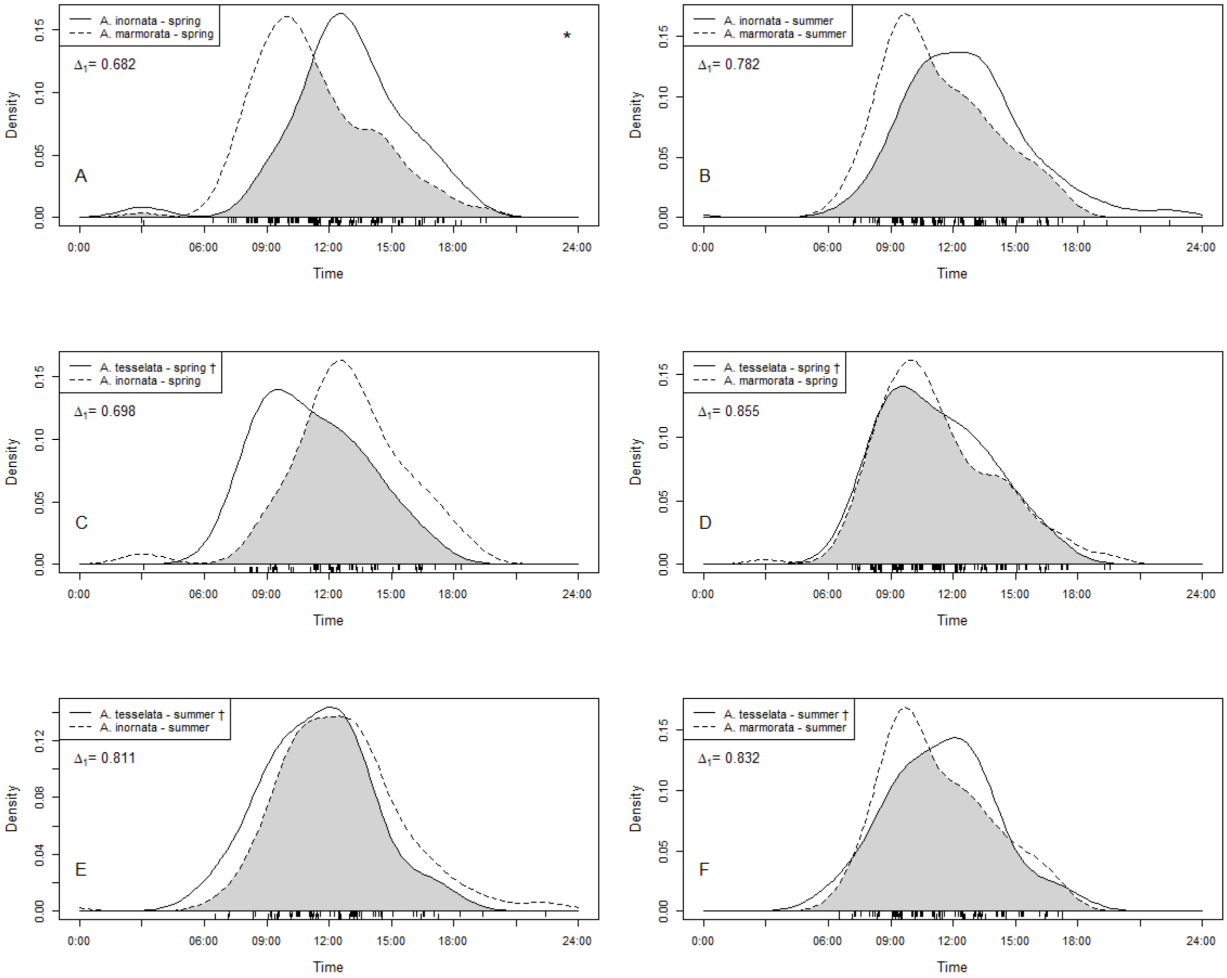

Figure 13. Estimates of activity pattern overlap (Δ_1) between species excluding the activity pattern of the Common Checkered Whiptail (*A. tesselata*) as it was the only one to exhibit a seasonal shift at one of the sites. **A)** Overlap of the spring activity pattern documented for the Little Striped Whiptail (*A. inornata*) and the Marbled Whiptail (*A. marmorata*; Δ_1= 0.682 ± 0.064, W = 18.271, $_{df = 2}$, *p* value = 0.0001078). **B)** Overlap of the summer activity pattern documented for the Little Striped Whiptail (*A. inornata*) and the Marbled Whiptail (A. marmorata; Δ_1= 0.782 ± 0.059, W = 7.8709, $_{df = 2}$, *p* value = 0.01954). **C)** Overlap of the spring activity pattern documented for the Common Checkered Whiptail (*A. tesselata*) and the Little Striped Whiptail (*A. inornata*; Δ_1= 0.698 ± 0.086, W = 5.2164, $_{df = 2}$, *p* value = 0.07367). **D)** Overlap of the spring activity pattern documented for the Common Checkered Whiptail (*A. tesselata*) and the Marbled Whiptail (*A. marmorata*; Δ_1= 0.855 ± 0.049, W = 0.1111, $_{df = 2}$, *p* value = 0.9459). **E)** Overlap of the summer activity pattern documented for the Common Checkered Whiptail (*A. tesselata*) and the Little Striped Whiptail (*A. inornata*; Δ_1= 0.811 ± 0.063, W = 0.31745, $_{df = 2}$, *p* value = 0.8532). **F)** Overlap of the summer activity pattern documented for the Common Checkered Whiptail (*A. tesselata*) and the Marbled Whiptail (*A. marmorata*; Δ_1= 0.832 ± 0.059, W = 1.8763, $_{df = 2}$, *p* value = 0.3914). *Statistically different.

When the activity pattern exhibited in the spring by the Common Checkered Whiptail (*A. tesselata*) from OMDP was compared to the activity patterns estimated for the other species, the only statistical difference was found when contrasted with the spring activity pattern of *A. inornata* (Fig. 14). Conversely, the highest relative overlap (Δ_1= 0.763) was observed when comparing the summer activity pattern of *A. tesselata* from OMDP to the summer activity pattern of *A. inornata* (Fig. 14C).

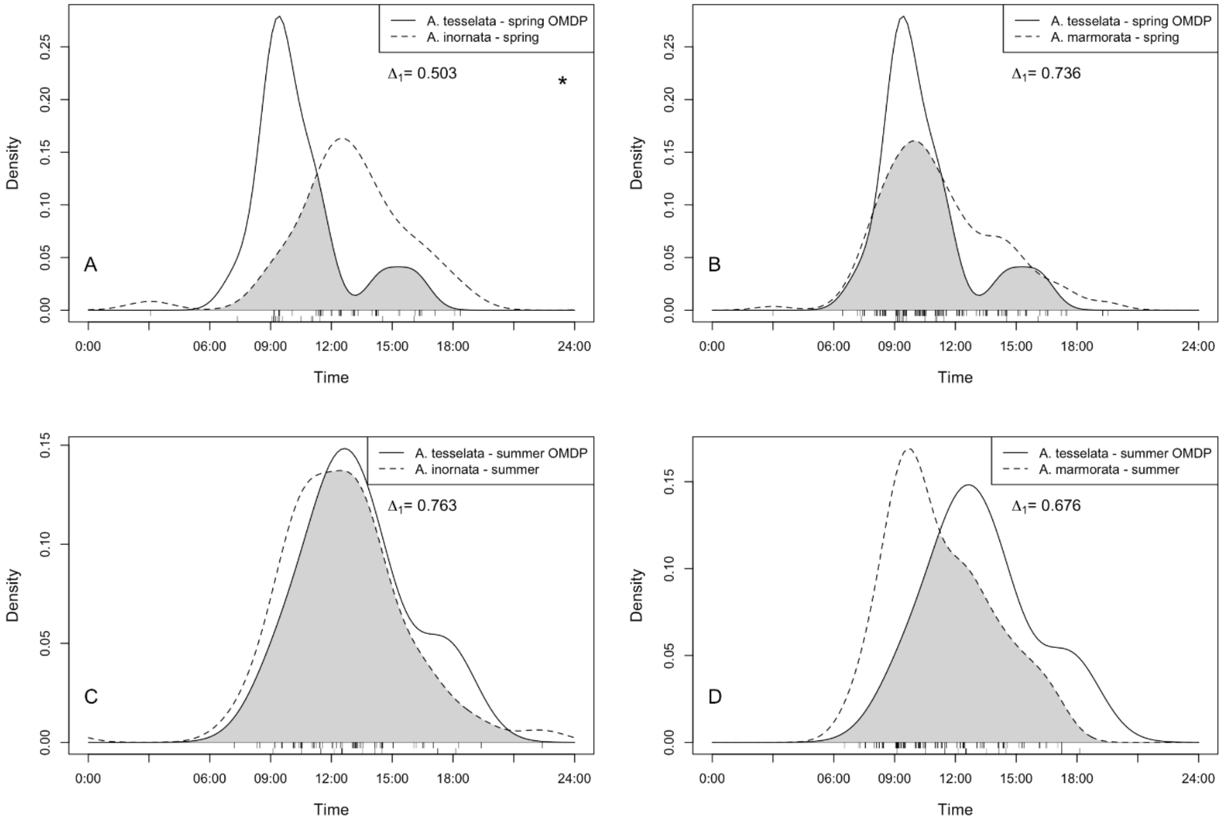

Figure 14. Activity overlap estimates (Δ_1) including observations from the parthenogen the Common Checkered Whiptail (*A. tesselata*) between all species documented in the study. **A)** Overlap of the spring activity pattern documented for the Common Checkered Whiptail (*A. tesselata*) from OMDP and the Little Striped Whiptail (*A. inornata*; Δ_1= 0.503 ± 0.114, W = 15.265, $_{df = 2}$, *p* value = 0.0004846). **B)** Overlap of the spring activity pattern documented for the Common Checkered Whiptail (*A. tesselata*) from OMDP and the Marbled Whiptail (*A. marmorata*; Δ_1= 0.736 ± 0.093, W = 3.8891, $_{df = 2}$, *p* value = 0.1431). **C)** Overlap of the summer activity pattern documented for the Common Checkered Whiptail (*A. tesselata*) and the Little Striped Whiptail (*A. inornata*; Δ_1= 0.763 ± 0.093, W = 0.4245, $_{df = 2}$, *p* value = 0.8085). **D)** Overlap of the summer activity pattern documented for the Common Checkered Whiptail (*A. tesselata*) and the Marbled Whiptail (*A. marmorata*; Δ_1= 0.676 ± 0.102, W = 4.245, $_{df = 2}$, *p* value = 0.1197). *Statistically different.

DISCUSSION

***Lizard Pitfall Camera-Traps.*—**In this study, modified pitfall camera-traps were effective at detecting the target species of whiptail lizards, as well as other small, large, diurnal, and nocturnal organisms. Cameras with Passive Infrared Sensors (PIR) required sufficient temperature contrast between the background surface and the organism for the sensor to trigger the camera (Welbourne 2013; Welbourne et al. 2016). To ensure the temperature contrast exists and the sensor detects a moving reptile, Welbourne (2013) developed the Camera Overhead Augmented Temperature (COAT) protocol, by altering the background substrate to create a temperature differential. Even using the COAT protocol, surveys in various environments have not been as effective in the detection of nocturnal species (Richardson et al. 2018; Welbourne et al. 2016). In this Chihuahuan Desert study, it was possible to detect small and nocturnal species despite their relatively small thermal signature due to the background being shielded from direct sunlight by the coverboard, and due to the closeness of the sensor to the subjects (Swann and Perkins 2014; Welbourne et al. 2015). Nocturnal and crepuscular species detected included the Chihuahuan Nightsnake (*H. jani*) and the Texas Banded Gecko (*C. brevis*) among other small species (Degenhardt et al. 2005; Stebbins 1985).

Using camera-traps could eliminate the negative effects on some species associated with chasing, capturing, and handling (Langkilde and Shine 2006). Additionally, camera-traps may be considered more ethical due to the reduced risk of predation, damage by larger organisms, and mortality due to temperature, because the lizards are able to escape (De Bondi et al. 2010; Enge 2001; Ferguson et al. 2008; Putman 1995). In this study, several large lizards and snakes reported as lizard predators were recorded including the Big Bend Patch-nosed Snake (*S. deserticola*), Striped Whipsnake (*M. taeniatus*), and the Coachwhip (*M. flagellum*; Degenhardt et al. 2005;

Halstead et al. 2008; Painter et al. 2017). Furthermore, the use of camera-traps may also reduce the risk to researchers associated with handling of venomous snakes (Beaupre and Greene 2012). Several recordings of large venomous snakes were collected in the current study belonging to three different species of rattlesnakes (*Crotalus spp*.; Johnson 2000; Painter et al. 2017). Additionally, a small species considered mildly venomous was also detected, the Chihuahuan Nightsnake (*H. jani*) in IMRS and FMSP (Chiszar and Smith 2002; Johnson 2000). Large organisms that may cause physical damage to small lizards when captured in pitfall traps detected by the camera-traps included the Desert Cottontail (*Sylvilagus audubonii*) and Rock Squirrel (*Spermophilus variegatus*). Also, birds that could potentially prey on trapped lizards were recorded including the Greater Roadrunner (*Geococcyx californianus*), Black-throated Sparrow (*Amphispiza bilineata*) and the Cactus Wren (*Campylorhynchus brunneicapillus*).

Pitfall camera-traps effectively documented the target whiptail species, the Marbled Whiptail (*A. marmorata*), the Common Checkered Whiptail (*A. tesselata*), the Little Striped Whiptail (*A. inornata*), among other species of lizards, snakes, invertebrates, and rodents. Due to limitations in the long-term capability of the pitfall camera-traps to identify individuals across years, estimates of population sizes should only be considered an approximation of actual population sizes. However, the number of captures was very similar to the number of *A. marmorata* and *A. tesselata* collected individuals reported from previous studies conducted at IMRS (Mata-Silva 2010; 2013). Despite such disadvantages, traditional pitfall traps have been commonly used in surveys of lizards, snakes, and amphibians (Enge 2001) to calculate population dynamics (Kuhnz et al. 2005; Sutton et al. 2014) and estimates of overall diversity (Campbell and Christman 1981). For example, using traditional pitfall traps, organisms that can escape like large lizards and snakes (Thompson et al. 2005; Todd et al. 2007) also have the potential of entering the trap and consuming a smaller captured organism without being detected by researchers (Ferguson et al. 2008) resulting in an inaccurate assessment of diversity.

Non-target Organisms.—Traditional lizard pitfall traps have also been reported to be effective in the sampling of amphibians (Corn 1990; Enge 2001; Greenberg et al. 1994) and although pitfall camera-traps at IMRS were located more than 3 km from the nearest known area to retain water, several recordings of amphibians were documented including the Texas Toad (*Anaxyrus speciosus*) and the Great Plains Narrow-mouthed Toad (*Gastrophryne olivacea*). Similarly, after heavy rains, observations of the Red-spotted Toad (*A. punctatus*) were recorded every year at FMSP. There were no amphibian species observed at OMDP possibly due to being the only site with cattle which may have inhibited the presence of amphibians during the study (Smalling et al. 2021).

Recordings of invertebrates were also summarized, and whenever possible, individuals were identified as a minimum to order and family. Most recordings may potentially allow for further identification even for small organisms. However, analyses beyond the summaries presented herein on invertebrates were beyond the scope of the study. As expected, most recordings belonged to terrestrial species, but some flying species were also documented using pitfall camera-traps. For example, Tarantula Hawk (*Hemipepsis spp*.), bees (Apidae), and moths (Lepidoptera) were common during all years across all study sites. Species observed in all the the sites included the Solifuge (*Eremobates spp*.), Desert Centipede (*Scolopendra polymorpha*), Vinegaroon (*Mastigoproctus giganteus*), Striped Bark Scorpion (*Centruroides vittatus*), Burrowing Wolfspider (*Geolycosa spp*.), Tarantulas (*Aphenopelma* spp.), and Desert Millipede (*Orthoporus ornatus*), among many others. Under Chihuahuan Desert conditions and mainly due to the proximity of the camera sensor to the bottom of the pitfall traps, detections of small and nocturnal organisms including small invertebrates were successfully recorded. In fact, pitfall traps have been recently used in sampling of invertebrates (Bertoia et al. 2023), but additional investigations are needed to assess further the detectability of invertebrates when pitfall traps are implemented with PIR-activated cameras.

Similarly, rodent recordings were also identified to order and family as a minimum, and whenever possible to genus and species. The observations from each year were also summarized, but no further analyses were conducted. Rodents were frequently detected, and a closer look revealed that the observations only belonged to four species at IMRS and three species at the other two sites. Species observed included the Cotton Rat (*Sigmodon hispidus*), Rock Pocket Mouse (*Chaetodipus spp*.), the Rock Squirrel (*S. variegatus*), the White-throated Woodrat (*Neotoma leucodon*), and Kangaroo Rat (*Dipodomys spp*.). Traditional pitfall traps are commonly used as effective sampling methods for small rodent species (Bury and Corn 1987; Swingle et al. 2004), thus rodents were expected to enter the traps, but were not the subject of the investigation. Additionally, under the conditions of the study, successful recordings of small mammals with small thermal signatures (Swann et al. 2004) were possible mainly due to the short distance of the lens to the background surface and because the bottom is further isolated from surface temperatures as the traps are buried 60 cm (Welbourne 2013; Welbourne et al. 2016).

Overall Reptile Diversity.—A total of 30 different species of diurnal and nocturnal lizards and snakes were detected across all sites included in the study. Pitfall camera-traps may be considered more cost-effective than traditional sampling methods due to their capability to survey multiple species, over multiple concurrent seasons, and multiple sites (De Bondi et al. 2010; Paull et al. 2012). Furthermore, improved assessments of diversity may be possible as camera-traps are capable of detecting organisms known to escape traditional traps, such as snakes and larger lizards (Campbell and Christman 1981; Enge 2001). Camera-traps effectively provided observations used in the estimation of standardized diversity index values (Shannon and Weaver 1963). Relative diversity was very consistent for each site included in the study with more reptile species recorded in IMRS, while diversity was lower in OMDP (Shannon and Weaver 1963). Higher diversity index values in IMRS can be explained by the higher number of lizard observations belonging to several lizard species consistently detected. Secondly, higher diversity in this site can be explained by the high number of snake species observed. In fact, IMRS is considered to have a higher number of species when compared to other areas within the northern Chihuahuan Desert (Johnson 2000; Painter et al. 2017). In this study, out of the 33 known species of lizards and snakes found at IMRS, camera-traps detected a total of 23. The Chihuahuan Desert is considered one of the most diverse arid regions in the world (Cotera et al. 2004) and it appears that such high diversity was captured due to the continuous monitoring of camera-traps.

Activity Patterns and Activity Overlap of Whiptail Lizards.─Only the observations from the Marbled Whiptail (*A. marmorata*), Common Checkered Whiptail (A. *tesselata*), and the Little Striped Whiptail (*A. inornata*) were included in the evaluation of the temporal niche analysis. Other whiptail species were detected too infrequently, including the Chihuahuan Spotted Whiptail (*A. exsanguis*) and the New Mexico Whiptail (*A. neomexicana*). The most frequently recorded whiptail was *A. marmorata* followed by *A. tesselata*, then *A. inornata*. Additionally, activity data from *A. inornata* and *A. tesselata* from a separate investigation conducted concurrently at RBWP, using the same camera-trap methodology was included in the whiptail activity analysis portion of the study. The number of observations from each whiptail species was often low, but always reached the minimum required number of observations necessary for the estimation of activity period patterns and subsequent overlap contrasts (Ridout and Linkie 2009). The assessment of population density fluctuations using pitfall camera-traps was not the main research objective. In fact, traditional pitfall traps have been reported (Enge 2001) to have several limitations when calculating population dynamics (Kuhnz et al. 2005; Sutton et al. 2014) and estimating overall diversity (Campbell and Christman 1981). Nonetheless, traditional pitfall traps have been commonly used in reptile surveys to estimate diversity and population dynamics (Campbell and Christman 1981Enge 2001; Kuhnz et al. 2005; Sutton et al. 2014). The use of camera-traps may contribute to resolve some of those limitations such as the ability to record removal by predation and document organisms able to escape from traditional traps (Ferguson et al. 2008; Thompson et al. 2005; Todd et al. 2007). Unfortunately, detectability rates of cameras for many species of reptiles is limited (Dundas et al. 2019; Welbourne et al. 2015; Welbourne et al. 2017).

The Marbled Whiptail (*A. marmorata*) was observed three times more frequently than the Common Checkered Whiptail (*A. tesselata*) in IMRS and OMDP throughout the study. In both sites, the number of observations closely resembled the total number of individuals collected during investigations conducted years earlier at IMRS (Mata-Silva 2010; 2013). In most studies conducted on *A. marmorata* and *A. tesselata*, or similar species pairs, have consistently reported a lower number of observations of the parthenogen species (Schall 1978; Wright and Lowe 1968; Wright and Vitt 1993). In this study, *A. tesselata* was detected at a higher rate only in FMSP (Table 9). At RBWP, observations of the parthenogen were very low, and while its maternal progenitor was absent from this site, observations of *A. inornata* were consistently higher (Table 9). Parthenogenetic whiptails have been hypothesized to be successful only in areas distinct from their parental and other related sexual species (Wright and Lowe 1968; Vandel 1928), but this assumption of 'geographic parthenogenesis' and more specifically of the 'weed hypothesis', continues to be unvalidated over many areas in the northern Chihuahuan Desert where *A. marmorata* and *A. tesselata* cooccur (Cuellar 1977; Lowe 1968; Wright and Lowe 1968; Wright and Vitt 1993). Under laboratory conditions, artificial rearing of parthenogens has led to them outnumbering sexual species in as fast as three years (Cole 1984). An additional assumption of the 'weed hypothesis' is that parthenogens are better at colonizing disturbed habitats (Lowe 1968; Wright and Lowe 1968), but several studies have not supported this assumption (Bestelmeyer et al. 2018; Cosentino et al. 2019). Considering that all sites in this study represent disturbed habitat, the consistent proportion of observations of parthenogens and their maternal species across the years may be a reflection of their reported similarities when colonizing or occupying these areas. However, the number of observations of the parthenogen did exceed that of the sexual progenitor in FMSP and could potentially be explained by differences in the major disturbances ongoing at each site. For example, FMSP is surrounded by active quarries (https://www.jobematerials.com/), roads, and residential development (Brehme et al. 2018), while OMDPNM and IMRS are not.

Pitfall camera-traps were used effectively to calculate the total number of active days in each season for the whiptail species in this study. The seasonal activity range was determined by using the first and last recorded days of activity for each season with more than five independent observations for each species. The reported average total number of active days per season of *A. marmorata* was almost identical to the average days of activity documented by the parthenogen (Table 10). In this study, the activity range of *A. marmorata* and the parthenogen, spanned over the same narrow time each season as frequently reported by previous surveys (Winne and Keck

2004; Wright and Vitt 1993). However, the low number of concurrent seasonal ranges available for comparison hinders traditional methods for rigorous analytical evaluations (Enge 2001). Camera-traps and their ability to collect continuous observations allowed for the detection of statistical differences in activity period patterns for each whiptail using coefficient of overlap estimates (Linkie and Ridout 2011; Meredith and Ridout 2014). The range of activity of *A. inornata* was considerably wider than the other whiptail species (Table 10) with observations as late as November and is consistent with previous reports on the activity period of this species (Degenhardt et al. 2005; Schall 1993).

A major advantage of camera-traps over traditional methods was the ability of traps to be deployed prior to the emergence of reptiles and beyond the published ranges of activity (Wright and Vitt 1993). As a result, differences in the emergence and cessation of activity were effectively determined using the first and last day (Julian days) of reported activity for each species. In six of the seven observed seasons, *A. marmorata* emerged an average of 10.57 days earlier than the parthenogen (Table 10). The average number of active days for both species was very similar, 132.37 and 130.37, respectively, thus an average of 10.57 days represented approximately 8% of the entire yearly activity (Table 10). A difference in the timing of emergence from overwintering retreats may lead to differences in the sizes of lizards active at a given time, in prey availability, time to reach maturity, and affect when hatchlings emerge (Adolph and Porter 1993; Wright and Vitt 1993). Such differences then may result in a decrease in the overlap of activity and partially contribute to the coexistence of the species (Bateman et al. 2010). Partial explanation for such pattern could be due to size differences between the males of *A. marmorata* and the all-female *A. tesselata*, as body sizes may be correlated with fat storage, and in turn, on the length of overwintering periods of whiptail lizards, which are relatively long compared to other lizards (Adolph and Porter 1993; Winne and Keck 2004; Wright and Vitt 1993).

Differences in emergence and cessation of activity may also be explained by differences in energy expenditures reported in sexual and asexual species, such as foraging effort prior to overwintering. For example, sexual whiptails have been reported to have an increased energy expenditure associated with looking for mates, holding territories, and copulating, while asexual species do not and can potentially allocate that energy, if available, for growth or storage for overwintering (Adolph and Porter 1993; Anderson and Karasov 1984; Pianka 1970; Wright and Vitt 1993). Furthermore, aggressive behaviors such as supplanting, chasing, and fighting, associated with competition over food items have been documented to be more common in the sexual whiptail species when compared to several parthenogens (Leuck 1985). Although, pseudocopulation in captivity of all-female whiptails has been reported including a single event in *A. tesselata* (Crews and Fitzgerald 1980), further laboratory research has failed to observe pseudocopulation in this species and was concluded that such behavior may be rare, if present, under natural conditions (Moore et al. 1985). Further research may be needed to fully understand the rate of pseudocopulation and its effect on activity of parthenogens.

All whiptail species in the study had a short and similar activity period during the spring and summer seasons. In some lizard species, the summer activity has been reported to change more into a bimodal distribution or shifted directionally in avoidance of midday summer temperatures (Adolph and Porter 1993; Grant and Dunham 1988). For whiptail lizards, the activity period in the summer has been reported to be unchanged from the activity period in the spring and characterized by a short range of activity and a pronounced activity peak approximately during the hottest time of the day (Winne and Keck 2004; Wright and Vitt 1993).

Such short activity periods have been considered a major characteristic of whiptail species (Wright and Vitt 1993). In this study, an exception was detected in the activity pattern of *A. tesselata* at OMDPNM (Fig. 11B). In OMDPNM when the spring activity pattern for this species differed significantly from the pattern documented in the summer and had an estimated overlap coefficient of approximately 50% (Fig. 11B). Considering the shift of *A. tesselata* to an activity peak later in the day, might be partially driven by midday summer temperatures as reported in other lizard species (Adolph and Porter 1993; Grant and Dunham 1988). The pattern was observed every year of the study for this species and only in OMDPNM, which may indicate that such shift was in response to unique biotic or abiotic conditions in OMDPNM. Major differences of OMDPNM that may have influenced the activity period of *A. tesselata* include active cattle grazing as it is well-documented to affect the diversity and activity of lizards (Cordier et al. 2021; Read and Cunningham 2010). Additionally, OMDPNM was the site reported to have the highest number of overlapping asexual whiptail lizard species (Painter et al. 2017). Previous studies have reported that the number of whiptail species other than the sexual progenitor determines the distribution and abundance of *A. tesselata* (Wright and Lowe 1968).

No significant differences in seasonal activity period patterns were detected when contrasts between species across sites were calculated (Fig. 12). In other words, the activity period for each species was the same regardless of the study site when observations from spring and summer were combined. High similarity between activity periods of whiptails has been previously reported and has been explained to be driven by their high energy expenditure associated with their intense wide-foraging strategy (Wright and Vitt 1993). For whiptails in temperate zones, the seasonal activity of adults has been reported to be no more than five months (Fitch 1958; McCoy 1965; Pianka 1970; Turner et al. 1969; Wright and Vitt 1993). The activity of adults usually is suspended in mid to late August, while juveniles remain active longer (Milstead 1957; Parker 1972; Routman and Hulse 1984; Wright and Vitt 1993). Additionally, the lack of differentiation in the activity of overlapping, and related whiptail species may be evidence in support of their recent origin and the absence of secondary isolating mechanisms (Wright and Vitt 1993). Previous studies have reported similar activity period patterns for whiptail lizards, but because of traditional investigations rely on summary statistics and arbitrary time-block classifications, have failed to test for statistical differences (Maffei et al. 2004; 2005; Oliveira-Santos et al. 2008). The challenge of traditional pitfall traps is the inability to provide the exact time of each capture, since the times of capture can only be associated with the time when the traps are checked by researchers, which is every few hours, sometimes longer periods than the entire average daily activity of whiptails (Enge 2001; Wright and Vitt 1993). In contrast, camera-traps provided the exact time each organism was observed under field conditions and facilitated the use of recently developed statistical methods for specifically analyzing activity period patterns (Oliveira-Santos et al. 2013; Ridout and Linkie 2009; Winne and Keck 2004).

Furthermore, activity period contrasts revealed the three whiptail species had very similar activity patterns, except in the case of the spring activity period of *A. inornata* and *A. marmorata* (Fig. 13A). Similarly, it was determined that the activity patterns of the parthenogen and *A. inornata* in the spring were also statistically different (Fig. 14A). Both results may indicate that *A. inornata* altered its activity pattern in the spring and effectively reduced the overlap with each of the other two whiptails. The smallest of the whiptail species studied, *A. inornata*, with a Snout-to-Vent-Length (SVL) of 50-65 mm (Degenhardt et al. 2005) was reported to have a wider range of activity (176.14 average days) compared to the other two species of whiptails (130.37 and 132.37 days; Table 10). The body size of whiptail species has been previously reported to determine which species coexist (Case 1983). A wide range of activity has been previously reported in *A. inornata* (Schall 1993). Significant shifts in activity peak in the spring and a wider seasonal activity period may result in partial reduction of overlap and contribute to the coexistence of *A. inornata* in sites where two or more whiptail species are present, a common situation in the northern Chihuahuan Desert (Case 1983; Cuellar 1977; Cuellar and McKinney 1976; Wright and Vitt 1993). In sexual whiptail species, social behavior of adults during the peak of the reproductive season has been shown to impact foraging behavior, but the energetic cost of reduced feeding was not found to be significant, as the energy budgets of the lizards were still met (Anderson 1994; Anderson and Karasov 1988; Wright and Vitt 1993). Reduced feeding time in mating whiptails may be overcome due to their flexible foraging strategy enabling them to maintain a high prey intake rate (Anderson 1994; Wright and Vitt 1993). In this study, the shift in *A. inornata* could be evidence of increased foraging activity in compensation for the energy expenditure associated with social behaviors during the reproductive season, which for this species, coincides with when the reported shift occurred (Degenhardt et al. 2005).

In this study, the activity patterns of the parthenogen and the progenitor species were statistically identical (Figs. 13 and 14). In fact, the highest values of overlap detected were estimated for *A. tesselata* and *A. marmorata* during the spring (Δ_1= 0.855; Fig. 13D) and in the summer (Δ_1= 0.832; Fig. 13F). The coexistence of the parthenogen and the parental species may be facilitated by the lower number of observations recorded of the parthenogen (Table 9) and its estimated later emergence when compared to *A. marmorata* (Fig. 10). Coexistence of similar whiptail assemblages has been documented and explained to be facilitated by differences in size, overwintering survival, clutch size, and time to reach maturity, even though activity patterns are very similar (Bateman et al. 2010).

CONCLUSION

Contrary to the ‘weed hypothesis’ (Schall 1978), parthenogens have been reported to have very narrow food niches that are almost identical to those of sexual whiptail species. For example, high values of diet overlap (0.90 and 0.94) in several parthenogens and their sexual relatives have been reported (Schall 1993). Other studies have determined similar diet overlap values over 0.90 in parthenogens and related sexual species in New Mexico and Texas (Mata-Silva et al. 2013; Medica 1967; Milstead 1965). Several studies have reported the absence of microhabitat segregation and concluded that parthenogens occupy the same foraging areas as sexual species (Cosentino et al. 2013; Price 1986). Additionally, high overlap on activity time have also documented values ranging from 0.80 to 0.98 (Schall 1993). Similar times of activity are expected because whiptail species in the northern Chihuahuan Desert have very similar preferred body temperatures (Schall 1977). High overlap across the niche dimensions of food, space, and time appears to challenge the principle of competitive exclusion, which hypothesizes that two or more species cannot coexist permanently if they have identical ecological needs (Levin 1970; Schoener 1974). In lizards, coexistence of species is achieved by partition of resources by feeding on different prey, foraging in different areas, and by having different activity period patterns (Pianka 1973). In summary, the ecological “twins” (Price 1986), the Common Checkered Whiptail (*A. tesselata*) and the Marbled Whiptail (*A. marmorata*) feed mostly on termites (Mata-Silva et al. 2013; Medica 1967; Milstead 1965), are found in the same microhabitats (Cuellar 1979; Price 1986) and have almost identical daily activity patterns (Schall 1993). As a combined result, the superior colonizing ability of parthenogens proposed by the ‘weed hypothesis’ continues to be unsupported (Cosentino et al. 2019; Price 1986; Schall 1978; Wright and Lowe 1968; Schall 1978). For highly overlapping species, competition may be avoided by complex and possibly unresolved processes (MacArthur and Levins 1967; Schoener 1974).

In this study, the overlap in daily activity period was relatively high between *A. tesselata*, *A. marmorata*, and *A. inornata*, but not complete. The coexistence of similar whiptails may be feasible in assemblages where the overlap in the three niche dimensions is not complete and when the overlap value of at least one niche dimension is lower than the other two (Dias and Rocha 2007). For example, similar cooccurring whiptail species from northeastern Brazil had an estimated activity period overlap of 0.93, a microhabitat overlap of 0.97, and an overlap in food of 0.89. Although not significant, it was concluded that coexistence is facilitated by a reduced overlap in the food niche dimension when compared to the higher overlap observed in microhabitat and activity (Dias and Rocha 2004).

Studies of *A. tesselata* and *A. marmorata* have described overlap values in food of 0.90 (Medica 1967; Milstead 1965; Schall 1993) and an overlap value of 0.82 in microhabitat use (cited as *C. tigris*; Schall 1993). In this study, the overlap values showed that activity period overlap was not complete as the values ranged from 0.503 to 0.855. Although different methods were used, the overlap values across the three niche dimensions reported *A. tesselata* and *A. marmorata* were relatively lower and more variable than the values reported from Brazil (Dias and Rocha 2007). According to the findings of this study, since overlap values are reportedly higher in food and microhabitat, a reduced overlap in activity period patterns may be the most important niche dimension contributing to the coexistence of whiptail assemblages including of *A. tesselata*, *A. marmorata*, and *A. inornata*.

ACKNOWLEDGEMENTS

Assistance with fieldwork for this project was provided by interns Daniel Muñoz, Jonatan Salinas, and Adolfo Bernal, who participated in the Chihuahua Desert Biodiversity Research Experiences for Undergraduate students, funded by the University of Texas at El Paso. Special thanks to Dr. Brook Milligan for his advice. This project was partially supported by UTEP's internal funding to Jerry Johnson's Lab. Very special thanks to NMSU's equipment rental program department. Research was conducted under IACUC protocol A -201004-1 356592-8. Thanks to Jesarey Barela, Natural Research Specialist at Las Cruces BLM office (Permit reference number 6220; NM), and Nicolas Havlik, Texas Parks and Wildlife Department (Permit #R1-16; 2019-2021).

REFERENCES

Ackley, J. W., M. J. Angilletta, D. DeNardo, B. Sullivan, and J. Wu. 2015. Urban heat island mitigation strategies and lizard thermal ecology: landscaping can quadruple potential activity time in an arid city. *Urban ecosystems* 18:1447-1459.

Adolph, S. C., and W. P. Porter. 1993. Temperature, activity, and lizard life histories. *The American Naturalist*, *142*:273-295.

Agostinelli, C. and U. Lund. 2022. R package 'circular': Circular Statistics (version 0.4-95). URL https://r-forge.r-project.org/projects/circular/

Ali, W., A. Javid, S. M. Bhukhari, A. Hussain, S. M. Hussain, and H. Rafique. 2018. Comparison of Different Trapping Techniques used in Herpetofaunal Monitoring: A Review. *Punjab University Journal of Zoology*, *33*(1): 57–68.

Anderson, R. A. 1994. Functional and population responses of the lizard *Cnemidophorus tigris* to environmental fluctuations. *American Zoologist*, *34*:409-421.

Anderson, R. A., and W. H. Karasov. 1981. Contrasts in energy intake and expenditure in sit-and-wait and widely foraging lizards. *Oecologia*, *49*, 67-72.

Anderson, R. A., and W. H. Karasov. 1988. Energetics of the lizard *Cnemidophorus tigris* and life history consequences of food-acquisition mode. *Ecological monographs*, *58*(2), 79-110.

Aschoff, J. 1966. Circadian activity pattern with two peaks. *Ecology*, *47*(4), 657–662.

Avery, R. A., and A. Mynott. 1990. The effects of temperature on prey handling time in the common lizard, *Lacerta vivipara*. *Amphibia-Reptilia*, *11*(2), 111-122.

Barbault, R., and M. E. Maury. 1981. Ecological organization of a Chihuahuan Desert lizard community. Oecologia 51:335-342.

Bateman, H. L., H. L. Snell, A. Chung-MacCoubrey, and D. M. Finch. 2010. Growth, activity, and survivorship from three sympatric parthenogenic whiptails (Family Teiidae). *Journal of Herpetology*, *44*:301-306.

Batschelet E.1981. Circular statistics in ecology. Academic Press, London.

Bauer, J. W., K. A. Logan, L. L. Sweanor, and W. M. Boyce. 2005. Scavenging behavior in puma. *The Southwestern Naturalist*, *50*:466–471.

Bell, G. 1982. The Masterpiece of Nature: The Evolution and Genetics of Sexuality. University of California Press, Berkeley, CA.

Beninde, J., M. Veith, and A. Hochkirch. 2015. Biodiversity in cities needs space: a meta-analysis of factors determining intra-urban biodiversity variation. *Ecology letters*, *18*:581-592.

Bertoia, A., T. Murray, B. C. Robertson, and J. M. Monks. 2023. Pitfall trapping outperforms other methods for surveying ground-dwelling large-bodied alpine invertebrates. *Journal of Insect Conservation*, 1-14.

Best, T. L., and A. L. Gennaro. 1984. Feeding ecology of the lizard, *Uta stansburiana*, in southeastern New Mexico. *Journal of Herpetology*, 291-301.

Bestelmeyer, B. T., D. P. Peters, S. R. Archer, D. M. Browning, G. S. Okin, R. L. Schooley, and N. P. Webb. 2018. The grassland–shrubland regime shift in the southwestern United States: Misconceptions and their implications for management. *BioScience*, *68*:678-690.

Beaupre, S.J., and H.W. Greene. 2012. Handling live reptiles: leave your ego at the door. Pp. 130–134 in M.S. Foster ed., Dealing with live reptiles. In R. W. McDiarmid, M. S. Foster, C. Guyer, J. W. Gibbons, N. Chernoff, eds. Reptile biodiversity: standard methods for inventory and monitoring. University of California Press, Ltd., Berkeley, California, USA.

Bolger, D. T., A. C. Alberts, R. M. Sauvajot, P. Potenza, C. McCalvin, D. Tran, and M. E. Soulé, M. E. 1997. Response of rodents to habitat fragmentation in coastal southern California. *Ecological Applications* 7:552-563.

Bowker, R.G. 1993.Thermoregulation of the lizards Cnemidophorus exsanguis and C. velox: some consequences of high body temperatures. Biology of the Whiptail Lizards (Genus Cnemidophorus) (eds J.W. Wright & L.J. Vitt), pp. 117–133. Oklahoma Museum of Natural History, Norman.

Brehme, C. S., S. A. Hathaway, and R. N. Fisher. 2018. An objective road risk assessment method for multiple species: ranking 166 reptiles and amphibians in California. *Landscape Ecology*, *33*:911-935.

Burghardt, G. M. 2012. Ethical considerations in working with reptiles. In Foster M.S. (Ed.), Dealing with live reptiles. In: McDiarmid RW, Foster MS, Guyer C, Gibbons JW, Chernoff N, editors. Reptile Biodiversity: Standard Methods for Inventory and Monitoring. Berkeley, California, USA: University of California Press, Ltd. p. 127–30.

Burton, T. M., and G. E. Likens. 1975. Energy flow and nutrient cycling in salamander populations in the Hubbard Brook Experimental Forest, New Hampshire. *Ecology*, *56*(5), 1068-1080.

Bury, R. B., and P. S. Corn. 1987. Evaluation of pitfall trapping in northwestern forests: trap arrays with drift fences. *The Journal of wildlife management*, 112-119.

Bury, R. B., and M. G. Raphael. 1983. Inventory methods for amphibians and reptiles, p. 416–419. *Bell J, F an& T Atterbury (eds.). Renewable Resource Inventories for Monitoring Changes and Trends. SAF*, 83-14.

Campbell, H. W., and S. P. Christman. 1981. Field techniques for herpetofaunal community analysis. *Herpetological Communities. Wildlife Research Report*, *13*:193-200.

Case, T. J. 1983. Niche overlap and the assembly of island lizard communities. *Oikos*, 427-433.

Case, T. J., and M. L. Taper. 1986. On the coexistence and coevolution of asexual and sexual competitors. *Evolution*, *40*:366-387.

Chase, J. M. 2011. Ecological niche theory. *The theory of ecology*, 93-107.

Chiszar, D., and H. M. Smith. 2002. Colubrid envenomations in the United States. *Journal of Toxicology: Toxin Reviews*, *21*:85-104.

Christy, M. T., A. A. Yackel Adams, G. H. Rodda, J. A. Savidge, and C. L. Tyrrell. 2010. Modelling detection probabilities to evaluate management and control tools for an invasive species. *Journal of Applied Ecology*, *47*:106-113.

Clarin, B. M., E. Bitzilekis, B. M. Siemers, and H. R. Goerlitz. 2014. Personal messages reduce vandalism and theft of unattended scientific equipment. *Methods in Ecology and Evolution*, *5*:125-131.

Cochran, P. A., and S. J. Schmitt. 2009. Use of remote cameras to monitor rock ledge microhabitat of timber rattlesnakes (*Crotalus horridus*). *Bull. Chicago Herpetological Soc, 44*:161–165.

Cole, C. J. 1984. Unisexual lizards. *Scientific American*, *250*:94-101.

Cordes, J. E., and J. M. Walker. 2006. Evolutionary and systematic implications of skin histocompatibility among parthenogenetic teiid lizards: three color pattern classes of *Aspidoscelis dixoni* and one of *Aspidoscelis tesselata*. *Copeia*, 14-26.

Cordier, J.M., R. Aguilar, J. N. Lescano, G. C. Leynaud, A. Bonino, D. Miloch, R. Loyola, and J. Nori. 2021. A global assessment of amphibian and reptile responses to land-use changes. *Biological conservation, 253,* p.108863.

Corn, P. S. 1990. *Sampling methods for terrestrial amphibians and reptiles* (Vol. 256). US Department of Agriculture, Forest Service, Pacific Northwest Research Station.

Cosentino, B. J., R. L. Schooley, B. T. Bestelmeyer, H. Campos, and L. M. Burkett. 2019. Does habitat disturbance promote geographical parthenogenesis in whiptail lizards? *Evolutionary Ecology*, *33*:839–853

Cosentino, B. J., R. L. Schooley, B. T. Bestelmeyer, and J. M. Coffman 2013. Response of lizard community structure to desert grassland restoration mediated by a keystone rodent. *Biodiversity and Conservation*, *22,* 921-935.

Cotera, M., E. Guadarrama, J. Brenner, A. M. Arango, M. E. García, A. Ganem, G. Bell, S. Yanoff, T. Sullivan, S. Nájera, P. and Gronmeyer. 2004. Ecoregional conservation assessment of the Chihuahuan Desert. PRONATURA Noreste and The Nature Conservancy, World Wildlife Found.

Crews, D., and K. T. Fitzgerald. 1980. “Sexual” behavior in parthenogenetic lizards (Cnemidophorus). *Proceedings of the National Academy of Sciences*, *77*:499-502.

Crother, B.I. (Ed.). 2017. Scientific and Standard English Names of Amphibians and Reptiles of North America North of Mexico, with Comments Regarding Confidence in Our Understanding pp. 1‒102. SSAR Herpetological Circular 43.

Cuellar, O. 1977. Animal parthenogenesis. *Science, 197*(4306): 837–843.

Cuellar, O. 1979. On the ecology of coexistence in parthenogenetic and bisexual lizards of the genus Cnemidophorus. *American Zoologist*, *19*:773-786.

Cuellar, O., and C. O. McKinney. 1976. Natural hybridization between parthenogenetic and bisexual lizards: detection of uniparental source of skin grafting. *The Journal of experimental zoology*, *196*:341-350.

de Almeida Jácomo, A. T., Silveira, L., and J. A. F. Diniz-Filho. 2004. Niche separation between the maned wolf (Chrysocyon brachyurus), the crab-eating fox (Dusicyon thous) and the hoary fox (Dusicyon vetulus) in central Brazil. *Journal of Zoology*, *262*:99–106.

De Bondi, N., J. G. White, M. Stevens, and R. Cooke. 2010. A comparison of the effectiveness of camera trapping and live trapping for sampling terrestrial small-mammal communities. *Wildlife Research*, *37*:456–465.

Degenhardt, W. G., C. W. Painter, A. H. Price, and R. Conant. 2005. *Amphibians and reptiles of New Mexico*. UNM Press.

Degraaf, R. M., and D. D. Rudis. 1990. Herpetofaunal species composition and relative abundance among three New England forest types. *Forest Ecology and Management*, *32*:155-165.

Dias, E. J. D. R., and C. F. D. D. Rocha. 2007. Niche differences between two sympatric whiptail lizards (*Cnemidophorus abaetensis* and *C. ocellifer*, Teiidae) in the restinga habitat of northeastern Brazil. *Brazilian Journal of Biology*, *67*:41-46.

Díaz, S., J. Fargione, F. S. Chapin III, and D. Tilman, D. 2006. Biodiversity loss threatens human well-being. *PLoS biology*, *4*(8), e277.

Dick-Peddie, W. A. 1993. *New Mexico vegetation: past, present, and future*. UNM Press.

Dixon, J. R., and P. A. Medica. 1966. Summer food of four species from the vicinity of White Sands, New Mexico. Los Angeles Co. Mus. Nat. Hist. Contrib. Sci. 121:1-6.

Douglas, C. L. 1966. Amphibians and reptiles of Mesa Verde National Park, Colorado. Univ. Kansas Publ. Mus. Nat. Hist. 15:711-744.

Dundas, S. J., K. X. Ruthrof, G. E. S. J. Hardy, and P. A. Fleming. 2019. Pits or pictures: a comparative study of camera traps and pitfall trapping to survey small mammals and reptiles. *Wildlife Research*, *46*:104–113.

Echternacht, A. C. 1967. Ecological relationships of two species of the lizard genus Cnemidophorus in the Santa Rita Mountains of Arizona. *American Midland Naturalist*, 448-459.

Edwards, A., and C. Gardner. 2010. Individual markings are a reliable non-invasive means of identification over time in blotched blue-tongued lizards, Tiliqua nigrolutea. *Herpetofauna*, *40*:26–29.

Ellis, M. V. 2015. Protecting trapped animals from heat exposure: the influence of shading on temperature within small metal box traps. *Australian Journal of Zoology*, *63*:253–257.

Enge, K. M. 2001. The pitfalls of pitfall traps. *Journal of Herpetology*, 467–478.

Fauvel, T., F. Brischoux, M. J. Briand, and X. Bonnet. 2012. Do researchers impact their study populations? Assessing the effect of field procedures in a long term population monitoring of sea kraits. *Amphibia-Reptilia*, *33*:365–372.

Ferguson, A. W., F. W. Weckerly, J. T. Baccus, and M. R. J. Forstner. 2008. Evaluation of predator attendance at pitfall traps in Texas. *The Southwestern Naturalist*, *53*:450–457.

Ferner, J. W. 1976. Notes on natural history and behavior of Sceloporus undulatus erythrocheilus in Colorado. Amer. Midl. Nat. 96:291-302.

Fitch, H. S. 1958. Natural history of the six-lined racerunner (*Cnemidophorus sexlineatus*). University of Kansas.

Flores, J., J. A. Rivera, J. J. Zúñiga-Vega, H. L. Bateman, and E. P. Martins. 2023. Specific Habitat Elements (Refuges and Leaf Litter) Are Better Predictors of Sceloporus Lizards in Central Mexico Than General Human Disturbance. *Herpetologica*, *79*:48-56.

Frey, S., J. T. Fisher, A. C. Burton, and J. P. Volpe. 2017. Investigating animal activity patterns and temporal niche partitioning using camera-trap data: challenges and opportunities. In *Remote Sensing in Ecology and Conservation* (Vol. 3, Issue 3, pp. 123–132).

Fox, S. F. 1978. Natural selection on behavioral phenotypes of the lizard *Uta stansburiana*. *Ecology*, *59*:834-847.

Garden, J. G., C. A. McAlpine, H. P. Possingham, and D. N. Jones. 2007. Using multiple survey methods to detect terrestrial reptiles and mammals: what are the most successful and cost-efficient combinations? *Wildlife Research*, *34*:218–227.

Gehlbach, F. R. 1956. Annotated records of southwestern amphibians and reptiles. Trans. Kansas Acad. Sci. 59:364-372.

Germano, D. J., and C. R. Hungerford. 1981. Reptile population changes with manipulation of Sonoran Desert shrub. *The Great Basin Naturalist*, 129-138.

Gibbs, J. P. 1998. Amphibian movements in response to forest edges, roads, and streambeds in southern New England. *The Journal of Wildlife Management*, 584-589.

Glesener, R. R., and D. Tilman. 1978. Sexuality and the components of environmental uncertainty: clues from geographic parthenogenesis in terrestrial animals. *The American Naturalist*, *112*:659-673.

Grant, B. W., and A. E. Dunham. 1988. Thermally imposed time constraints on the activity of the desert lizard *Sceloporus merriami*. *Ecology*, *69*:167-176.

Greenberg, C. H., D. G. Neary, and L. D. Harris. 1994. A comparison of herpetofaunal sampling effectiveness of pitfall, single-ended, and double-ended funnel traps used with drift fences. *Journal of Herpetology*, 319-324.

Grimm, N. B., S. H. Faeth, N. E. Golubiewski, C. L. Redman, J. Wu, X. Bai, and J. M. Briggs. 2008. Global change and the ecology of cities. *Science*, *319*:756-760.

Haag, C. R., and D. Ebert. 2004. A new hypothesis to explain geographic parthenogenesis. *Annales Zoologici Fennici*, 539–544.

Halstead, B.J., H. R. Mushinsky, and E. D. McCoy. 2008: Sympatric *Masticophis flagellum* and *Coluber constrictor* select vertebrate prey at different levels of taxonomy. Copeia 2008: 897-908.

Hanski, I. 1999. Habitat connectivity, habitat continuity, and metapopulations in dynamic landscapes. *Oikos*, 209-219.

Hobbs, M. T., and C. S. Brehme. 2017. An improved camera trap for amphibians, reptiles, small mammals, and large invertebrates. *PloS one*, *12*(10), e0185026.

Hobbs, T. J., and C. D. James. 1999. Influence of shade covers on pitfall trap temperatures and capture success of reptiles and small mammals in arid Australia. *Wildlife Research*, *26*:341-349.

Holding, M. L., J. A. Frazier, S. W. Dorr, S. N. Henningsen, I. T. Moore, and E. N. Taylor. 2014. Physiological and behavioral effects of repeated handling and short-distance translocations on free-ranging Northern Pacific rattlesnakes (Crotalus oreganus oreganus). *Journal of Herpetology*, *48*:233–239.

Hotchkin, P., and H. Riveroll Jr. 2005. Comparative escape behavior of Chihuahuan Desert parthenogenetic and gonochoristic whiptail lizards. *The Southwestern Naturalist*, 50:172-177.

Huey, B. R. 1982. Temperature, physiology, and the ecology of reptiles. *Physiological ecology*, 25-95.

Hunter, D., W. Osborne, and S. Sarre. 2012. A trial use of camera traps detects the highly cryptic and endangered grassland earless dragon Tympanocryptis pinguicolla (Reptilia: Agamidae) on the Monaro tablelands of New South Wales, Australia. *Herpetological Review*, *43*:249–252.

Hutchinson, G. E. 1957. Concluding remarks. Cold Spring Harbor Symposia on Quantitative Biology 22:415–427.

IUCN. 2022. The IUCN Red List of Threatened Species. Version 2022-2. https://www.iucnredlist.org. Accessed on [10 April 2023].

Johnson, J. D. 2000. Indio Mountains Research Station: a place of learning in the desert. Chihuahuan Desert Discovery 45: 4–5.

Jones, L. L., and R. E. Lovich. 2009. *Lizards of the American Southwest: a photographic field guide*. Rio Nuevo Publishers.

Karanth, K. U., J. D. Nichols, N. S. Kumar, and J. E. Hines. 2006. Assessing tiger population dynamics using photographic capture–recapture sampling. *Ecology, 87*:2925–2937.

Karasov, W. H., and R. A. Anderson. 1984. Interhabitat differences in energy acquisition and expenditure in a lizard. *Ecology*, *65*:235-247.

Keinath D. A., D. F. Doak, K. E. Hodges, L. R. Prugh, W. Fagan, C. H. Sekercioglu, et al. 2017.

A global analysis of traits predicting species sensitivity to habitat fragmentation. Global Ecology and Biogeography 26:115–27.

Karraker, N. E. 2001. String theory: reducing mortality of mammals in pitfall traps. *Wildlife Society Bulletin*, 1158–1162.

Kuhnz, L. A., R. K. Burton, P. N. Slattery, and J. M. Oakden. 2005. Microhabitats and population densities of California legless lizards, with comments on effectiveness of various techniques for estimating numbers of fossorial reptiles. *Journal of herpetology*, *39*:395-402.

Langkilde, T., and R. Shine. 2006. How much stress do researchers inflict on their study animals? A case study using a scincid lizard, *Eulamprus heatwolei*. *Journal of Experimental Biology*, *209*:1035–1043.

LaPoint, S., N. Balkenhol, J. Hale, J. Sadler, and R. van der Ree. 2015. Ecological connectivity research in urban areas. *Functional ecology*, *29*:868-878.

Leaché, A. D., and T. W. Reeder. 2002. Molecular systematics of the eastern fence lizard (*Sceloporus undulatus*): a comparison of parsimony, likelihood, and Bayesian approaches. *Systematic biology, 51*:44-68.

Leuck, B. E. 1985. Comparative Social Behavior of Bisexual and Unisexual Whiptail Lizards (*Cnemidophorus*). *Journal of Herpetology, 19*:492–506.

Levin, S. A. 1970. Community equilibria and stability, and an extension of the competitive exclusion principle. *The American Naturalist*, *104*:413-423.

Linkie, M., and M. S. Ridout. 2011. Assessing tiger–prey interactions in Sumatran rainforests. *Journal of Zoology*, *284*:224-229.

Lively, C. M., and L. Morran. 2014. The ecology of sexual reproduction. *Journal of Evolutionary Biology*, *27*:1292-1303.

Lowe, C. J., J. W. Wright, C. J. Cole, and R. L. Bezy.1970. Natural hybridization between the teiid lizards *Cnemidophorus sonorae* (parthenogenetic) and *Cnemidophorus tigris* (bisexual). *Systematic Zoology*, *19*:114-127.

MacArthur R., and R. Levins. 1967. The limiting similarity, convergence, and divergence of coexisting species. *The american naturalist*, *101*:377-385.

Maffei, L., E. Cuéllar, and A. Noss. 2004. One thousand jaguars (*Panthera onca*) in Bolivia's Chaco? Camera trapping in the Kaa-Iya National Park. *Journal of Zoology*, *262*:295–304.

Maffei, L., A. J. Noss, E. Cuéllar, and D. I. Rumiz. 2005. Ocelot (*Felis pardalis*) population densities, activity, and ranging behaviour in the dry forests of eastern Bolivia: Data from camera trapping. *Journal of Tropical Ecology*, *21*:349–353.

Mata-Silva, V., C. R. Bursey, and J. D. Johnson. 2008. Gut parasites of two syntopic species of whiptail lizards, *Aspidoscelis marmorata* and *Aspidoscelis tesselata* from the northern Chihuahuan Desert. *Boletin de la Sociedad Herpetologica Mexicana*, *16*:1-4.

Mata-Silva, V., J. D. Johnson, and A. Ramirez-Bautista. 2013. Comparison of diets of two syntopic lizards, *Aspidoscelis marmorata* and *Aspidoscelis tesselata* (Teiidae), from the northern Chihuahuan Desert of Texas. *The Southwestern Naturalist*, *58*:209–215.

Mata-Silva, V., A. Ramírez-Bautista, and J. D. Johnson. 2010. Reproductive characteristics of two syntopic whiptail lizards, *Aspidoscelis marmorata* and *Aspidoscelis tesselata*, from the northern Chihuahuan Desert. *The Southwestern Naturalist*, *55*:125-129.

Maynard-Smith, J. 1978. The Evolution of Sex. Cambridge University Press, Cambridge

McCallum, J. 2013. Changing use of camera traps in mammalian field research: habitats, taxa and study types. *Mammal Review*, *43*:196–206.

McCoy, C. J. 1965. Life history and ecology of *Cnemidophorus tigris septentrionalis* (Doctoral dissertation, University of Colorado).

McCoy, E. D., and H. R. Mushinsky. 1992. Rarity of organisms in the sand pine scrub habitat of Florida. *Conservation Biology*, *6*:537-548.

McDiarmid, R. W. (Ed.). 2012. *Reptile biodiversity: standard methods for inventory and monitoring*. Univ of California Press.McDonald J. H. 2009. Handbook of biological statistics, 2nd edn. Sparky House Publishing, Baltimore.

McDonnell, M. J., and A. K. Hahs. 2015. Adaptation and adaptedness of organisms to urban environments. *Annual review of ecology, evolution, and systematics*, *46*:261-280.

McKinney, M. L. 2006. Urbanization as a major cause of biotic homogenization. *Biological conservation*, *127*:247-260.

Medica, P. A. 1967. Food habits, habitat preference, reproduction, and diurnal activity in four sympatric species of whiptail lizards (*Cnemidophorus*) in south central New Mexico. *Bulletin, Southern California Academy of Sciences*, *66*:251-276.

Meek, P.D., G. Ballard, A. Claridge, R. Kays, K. Moseby, T. O'brien, A. O'connell, J. Sanderson, D. E. Swann, M. Tobler, and S. Townsend. 2014. Recommended guiding principles for reporting on camera trapping research. *Biodiversity and conservation*, *23*:2321-2343.

Meredith, M., and M. Ridout. 2014. Overview of the overlap package. *R. Proj*, 1–9.

Michael, D.R., R.B. Cunninham, C.F. Donnelly, and D.B. Lindenmayer. 2012. Comparative use of active searches and artificial refuges to survey reptiles in temperate eucalypt woodlands. Wildlife Research 39:149–162.

Milstead, W. W. 1957. Some aspects of competition in natural populations of whiptail lizards (genus *Cnemidophorus*). *Texas J. Sci*, *9*:410-447.

Milstead, W. W. 1961. Observations of the activities of small animals (Reptilia and Mammalia) on a quadrat in southwest Texas. *American Midland Naturalist*, 127-138.

Milstead, W. W. 1965. Changes in competing populations of whiptail lizards (Cnemidophorus) in southwestern Texas. *American Midland Naturalist*, 75-80.

Milstead, W. W. 1974. The Black Gap whiptail lizards after twenty years. In *Transactions of the Symposium on Biological Resources of the Chihuahuan Desert Region: United States and Mexico,* 523-532.

Mitchell, J. C. 1979. Ecology of southeastern Arizona whiptail lizards (Cnemidophorus: Teiidae): population densities, resource partitioning, and niche overlap. *Canadian Journal of Zoology*, *57*:1487-1499.

Monterroso, P., P. C. Alves, and P. Ferreras. 2014. Plasticity in circadian activity patterns of mesocarnivores in Southwestern Europe: Implications for species coexistence. *Behavioral Ecology and Sociobiology*, *68*:1403–1417.

Moore, M. C., J. M. Whittier, A. J. Billy, and D. Crews. 1985. Male-like behaviour in an all-female lizard: relationship to ovarian cycle. *Animal Behaviour*, *33*:284-289.

Mori, E., A. Andreoni, F. Cecere, M. Magi, and L. Lazzeri. 2020. Patterns of activity rhythms of invasive coypus *Myocastor coypus* inferred through camera-trapping. *Mammalian biology*, *100*:591-599.

Mori, E., G. Mazza, C. Pucci, D. Senserini, R. Campbell-Palmer, M. Contaldo, and A.Viviano. 2022. Temporal activity patterns of the Eurasian beaver and coexisting species in a Mediterranean ecosystem. *Animals*, *12*:1961.

Moseby, K. E., and J. L. Read. 2001. Factors affecting pitfall capture rates of small ground vertebrates in arid South Australia. II. Optimum pitfall trapping effort. *Wildlife Research*, *28*:61-71.

Neiman, M., P. G. Meirmans, T. Schwander, and S. Meirmans. 2018. Sex in the wild: How and why field-based studies contribute to solving the problem of sex. *Evolution*, *72*:1194-1203.

Newbold, T., L. N. Hudson, S. L. Hill, S. Contu, I. Lysenko, R. A. Senior, L. Börger, D. J. Bennett, A. Choimes, B. Collen, and J. Day. 2015. Global effects of land use on local terrestrial biodiversity. *Nature*, *520*:45-50.

Niewiarowski, P. H., and Dunham, A. E. 1994. The evolution of reproductive effort in squamate reptiles: costs, trade-offs, and assumptions reconsidered. *Evolution*, *48*, 137-145.

O'Connell, A. F., J. D. Nichols, and K. U. Karanth. 2011. *Camera traps in animal ecology: methods and analyses* (Vol. 271). Springer.

O'Connell Jr, A. F., N. W. Talancy, L. L. Bailey, J. R. Sauer, R. Cook, and A. T. Gilbert. 2006. Estimating site occupancy and detection probability parameters for meso-and large mammals in a coastal ecosystem. *The Journal of Wildlife Management*, *70*:1625–1633.

Oliveira-Santos, L. G. R., M. A. Tortato, and M. E. Graipel. 2008. Activity pattern of Atlantic Forest small arboreal mammals as revealed by camera traps. *Journal of Tropical Ecology*, *24*:563–567.

Oliveira-Santos, L. G. R., C. A. Zucco, and C. Agostinelli. 2013. Using conditional circular kernel density functions to test hypotheses on animal circadian activity. In *Animal Behaviour,* 85:269–280.

Painter, C. W., J. N. Stuart, J. T. Giermakowski, and L. J. S. Pierce. 2017. Checklist of the amphibians and reptiles of New Mexico, USA, with notes on taxonomy, status, and distribution. *Western Wildlife*, *4*:29–60.

Parker, W. S. 1972. Ecological Study of the Western Whiptail Lizard, *Cnemidophorus tigris gracilis*, in Arizona. *Herpetologica*, 360-369.

Parker, W. S., and E. R. Pianka. 1975. Comparative ecology of populations of the lizard *Uta stansburiana*. *Copeia*, 615-632.

Paull, D. J., A. W. Claridge, and R. B. Cunningham. 2012. Effective detection methods for medium-sized ground-dwelling mammals: a comparison between infrared digital cameras and hair tunnels. *Wildlife Research*, *39*:546–553.

Perera, A., and V. Perez-Mellado. 2004. Photographic identification as a non invasive marking technique for Lacertid lizards. Herpetological Review 35:349–350.

Peterson, D. K., and W. G. Whitford.1987. Foraging behavior of *Uta stansburiana* and *Cnemidophorus tigris* in two different habitats. *The Southwestern Naturalist*, 427-433.

Pianka, E. R. 1966. Convexity, desert lizards, and spatial heterogeneity. *Ecology*, *47*:1055-1059.

Pianka, E. R. 1970. Comparative autecology of the lizard *Cnemidophorus tigris* in different parts of its geographic range. *Ecology, 51*:703-720.

Pianka, E. R. 1973. The structure of lizard communities. *Annual review of ecology and systematics*, *4*:53-74.

Pianka, E. R. 2017. Ecology and natural history of desert lizards: analyses of the ecological niche and community structure (Vol. 5153). Princeton University Press.

Pilz, W. R. 1983. *Nesting ecology and diet of Swainson's Hawk in the Chihuahuan Desert, South-central New Mexico* (Master's thesis, New Mexico State University).

Price, A. H. 1986. The Ecology and Evolutionary Implications of Competitions and Parthenogenesis in Cnemidophorus (United States, Mexico; Doctoral dissertation, New Mexico State University).

Porter, W. P., J. W. Mitchell, W. A. Beckman, and C. B. DeWitt. 1973. Behavioral implications of mechanistic ecology: thermal and behavioral modeling of desert ectotherms and their microenvironment. *Oecologia*, *13*:1-54.

Putman, R. J. 1995. Ethical considerations and animal welfare in ecological field studies.

Biodiversity & Conservation, *4*:903–915.

R Development Core Team. 2021. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org.

Rasband, W. S. ImageJ, U. S. National Institutes of Health, Bethesda, Maryland, USA, https://imagej.nih.gov/ij/, 1997-2016.

Read, J. L., and R. Cunningham. 2010. Relative impacts of cattle grazing and feral animals on an Australian arid zone reptile and small mammal assemblage. *Austral Ecology*, *35*:314-324.

Read, J. L., and K. E. Moseby. 2001. Factors affecting pitfall capture rates of small ground vertebrates in arid South Australia. I. The influence of weather and moon phase on capture rates of reptiles. *Wildlife Research*, *28*:53-60.

Reeder, T. W., C. J. Cole, and H. C. Dessauer. 2002. Phylogenetic relationships of whiptail lizards of the genus Cnemidophorus (Squamata: Teiidae): a test of monophyly, reevaluation of karyotypic evolution, and review of hybrid origins. *American Museum Novitates*, *2002*:1-61.

Richardson, E., D. G. Nimmo, S. Avitabile, L. Tworkowski, S. J. Watson, D. Welbourne, and S. W. J. Leonard. 2018. Camera traps and pitfalls: an evaluation of two methods for surveying reptiles in a semiarid ecosystem. *Wildlife Research*, *44*:637–647.

Ridout, M. S., and M. Linkie. 2009. Estimating overlap of daily activity patterns from camera trap data. *Journal of Agricultural, Biological, and Environmental Statistics*, *14*:322-337.

Rietveld, W. J., D. S. Minors, and J. M. Waterhouse. 1993. Circadian rhythms and masking: an overview. *Chronobiology international*, *10*:306-312.

Routman, E. J., and A. C. Hulse. 1984. Ecology and reproduction of a parthenogenetic lizard, *Cnemidophorus sonorae*. *Journal of Herpetology*, 381-386.

Rowcliffe, J. M., J. Field, S. T. Turvey, and C. Carbone. 2008. Estimating animal density using camera traps without the need for individual recognition. *Journal of Applied Ecology*, 1228-1236.

Schall, J. J. 1977. Thermal ecology of five sympatric species of Cnemidophorus (Sauria: Teiidae). *Herpetologica*, 261-272.

Schall, J. J. 1978. Reproductive strategies in sympatric whiptail lizards (Cnemidophorus): two parthenogenetic and three bisexual species. *Copeia*, 108–116.

Schall, J. J. 1993. Community ecology of Cnemidophorus lizards in southwestern Texas: a test of the weed hypothesis. *Biology of whiptail lizards (Genus Cnemidophorus). Oklahoma Mus. Nat. Hist, Norman Oklahoma* 319-343.

Scudday, J. F., and J. R. Dixon. 1973. Diet and feeding behavior of teiid lizards from Trans-Pecos, Texas. *The Southwestern Naturalist*, 279-289.

Schoener, T. W. 1974. Resource Partitioning in Ecological Communities: Research on how similar species divide resources helps reveal the natural regulation of species diversity. *Science*, *185*:27-39.

Scudday, J. F. 1971. *The biogeography and some ecological aspects of the teiid lizards (Cnemidophorus) of Trans-Pecos Texas*. Texas A&M University.

Shannon, C.E. and W. Weaver. 1963. The Mathematical Theory of Communication. University Illinois Press, Urbana, 117 pp.

Shochat, E., S. B. Lerman, J. M. Anderies, P. S. Warren, S. H. Faeth, and C. H. Nilon. 2010. Invasion, competition, and biodiversity loss in urban ecosystems. *BioScience*, *60*:199-208.

Silvy, N. J. 2012. *The wildlife techniques manual. 1. Research*. Johns Hopkins University Press.

Simon, C. A., and G. A. Middendorf. 1976. Resource partitioning by an iguanid lizard: temporal and microhabitat aspects. *Ecology, 57*:1317-1320.

Smalling, K.L., J. C. Rowe, C. A. Pearl, L. R. Iwanowicz, C. E. Givens, C. W. Anderson, B. McCreary, and M. J. Adams. 2021. Monitoring wetland water quality related to livestock grazing in amphibian habitats. *Environmental Monitoring and Assessment*, *193*:1-17.

Smith, D. D. 1989. A comparison of food habits of sympatric *Cnemidophorus exsanguis* and *Cnemidophorus gularis* (Lacertilia, Teiidae). *The Southwestern Naturalist*, *34*:418-420.

Sung, Y.-H., N. E. Karraker, and B. C. H. Hau. 2011. Evaluation of the effectiveness of three survey methods for sampling terrestrial herpetofauna in South China. *Herpetological Conservation and Biology*.

Sutton, W. B., Y. Wang, C. J. Schweitzer, and D. A. Steen. 2014. Lizard microhabitat and microclimate relationships in southeastern pine-hardwood forests managed with prescribed burning and thinning. *Forest Science*, *60*:180-190.

Swann, D. E., C. C. Hass, D. C. Dalton, and S. A. Wolf. 2004. Infrared-triggered cameras for detecting wildlife: an evaluation and review. *Wildlife Society Bulletin*, *32*:357–365.

Swann, D.E., and N. Perkins. 2014. Camera trapping for animal monitoring and management: a review of applications. Pp. 3–11 in P. Meek, P. Fleming, G. Ballard, P. Banks, A. Claridge, J. Sanderson and D. Swann, eds. Camera Trapping Wildlife Management and Research. CSIRO Publishing, Melbourne, Australia.

Swingle, J. K., E. D. Forsman, and S. G. Sovern. 2004. A method for live-trapping tree voles. *Northwestern Naturalist*, *85*:134-135.

Taylor, H. L., C. J. Cole, L. M. Hardy, H. C. Dessauer, C. R. Townsend, J. M. Walker, and J. E. Cordes. 2001. Natural hybridization between the teiid lizards *Cnemidophorus tesselatus* (parthenogenetic) and *C. tigris marmoratus* (bisexual): assessment of evolutionary alternatives. *American Museum Novitates*, *2001*:1-65.

Thompson, S. A., G. G. Thompson, and P. C. Withers. 2005. Influence of pit-trap type on the interpretation of fauna diversity. *Wildlife Research*, *32*:131–137.

Toliver, M. E., and D. T. Jennings. 1975. Food habits of *Sceloporus undulatus tristichus* Cope (Squamata: Iguanidae) in Arizona. *Southwest Nat*, 20:1-11.

Todd, B., C. Winne, J. Willson, and J. Gibbons. 2007. Getting the Drift: Examining the Effects of Timing, Trap Type and Taxon on Herpetofaunal Drift Fence Surveys. *American Midland Naturalist 158.*

Turner, F. B., G. A. Hoddenbach, P. A. Medica, and J. R. Lannom. 1970. The demography of the lizard, *Uta stansburiana* Baird and Girard, in southern Nevada. *The Journal of Animal Ecology*, 505-519.

Turner, F. B., P. A. Medica, J. R. Lannom Jr, and G. A. Hoddenbach. 1969. A demographic analysis of fenced populations of the whiptail lizard, Cnemidophorus tigris, in southern Nevada. *The Southwestern Naturalist*, 189-201.

Uetz P. Species numbers (as of March 2018) http://www.reptile-database.org: The Reptile Database; [http://www.reptile-database.org/db-info/SpeciesStat.html.

Van Auken, O. W. 2000. Shrub invasions of North American semiarid grasslands. *Annual review of ecology and systematics*, *31*:197-215.

Van Damme, R., D. Bauwens, and R. F. Verheyen. 1991. The thermal dependence of feeding behaviour, food consumption and gut-passage time in the lizard Lacerta vivipara Jacquin. *Functional Ecology*, 507-517.

Vandel, A. 1928. *La parthénogenèse géographique. Contribution à l'étude biologique et cytologique de la parthénogenèse naturelle. Bull. Biol. France Belg. 62:164-281.*

Vandergast, A. G., E. A. Lewallen, J. Deas, A. J. Bohonak, D. B. Weissman, D. B., and R. N. Fisher. 2009. Loss of genetic connectivity and diversity in urban microreserves in a southern California endemic Jerusalem cricket (Orthoptera: Stenopelmatidae: *Stenopelmatus* n. sp.“santa monica”). *Journal of Insect Conservation*, *13*:329-345.

Vogt, R. C., and R. L. Hine. 1982. Evaluation of techniques for assessment of amphibian and reptile populations in Wisconsin. *Herpetological communities*, *13*:201-217.

Walker, J. M. 1987. Distribution and habitat of the parthenogenetic whiptail lizard, Cnemidophorus laredoensis (Sauria: Teiidae). *American Midland Naturalist*, 319-332.

Welbourne, D. 2013. A method for surveying diurnal terrestrial reptiles with passive infrared automatically triggered cameras. *PloS One*, *6*, e18965.

Welbourne, D. J., A. W. Claridge, D. J. Paull, and A. Lambert. 2016. How do passive infrared triggered camera traps operate and why does it matter? Breaking down common misconceptions. *Remote Sensing in Ecology and Conservation*, *2*:77–83.

Welbourne, D. J., A. W. Claridge, D. J. Paull, and F. Ford. 2020. Camera-traps are a cost-effective method for surveying terrestrial squamates: A comparison with artificial refuges and pitfall traps. *PLoS One*, *15*(1), e0226913.

Welbourne, D. J., C. MacGregor, D. Paull, and D. B. Lindenmayer. 2015. The effectiveness and cost of camera traps for surveying small reptiles and critical weight range mammals: a comparison with labour-intensive complementary methods. *Wildlife Research*, *42*:414–425.

Welbourne, D. J., D. J. Paull, A. W. Claridge, and F. Ford. 2017. A frontier in the use of camera traps: surveying terrestrial squamate assemblages. *Remote Sensing in Ecology and Conservation*, *3*:133–145.

Wilson, B. S. 1991. Latitudinal variation in activity season mortality rates of the lizard *Uta stansburiana*. *Ecol. Monogr.* 61:393-414.

Winne, C. T., and M. B. Keck. 2004. Daily activity patterns of Whiptail Lizards (Squamata: Teiidae: Aspidoscelis): a proximate response to environmental conditions or an endogenous rhythm?. *Functional Ecology*, 314-321.

Whitford, W. G., and F. M. Creusere. 1977. Seasonal and yearly fluctuations in Chihuahuan Desert lizard communities. *Herpetologica*, 54-65.

Whiting, M. J., B. D. Greene, J. R. Dixon, A. L. Mercer, and C. C. Eckerman. 1992. Observations on the foraging ecology of the western coachwhip snake, *Masticophis flagellum testaceus*. *The Snake*, 24:157-160.

Worthington, R. D., J. D. Johnson, C. S. Lieb, and W. Anderson. 2021. Biotic Resources of Indio Mountains Research Station (IMRS) Southeastern Hudspeth County, Texas: A Handbook for Students and Researchers. The University of Texas at El Paso, El Paso, Texas. Updated Version, 27 September 2021. 1-94 pp. Original Version Fall 2004, Privately Printed.

Wright, A. J., and A. A. Wright. 1957. Handbook of Snakes of the United States and Canada by states and provinces. *Amer. Midl. Nat.* 48:574-603.

Wright, J. W., and C. H. Lowe.1968. Weeds, polyploids, parthenogenesis, and the geographical and ecological distribution of all-female species of Cnemidophorus. *Copeia*, 128–138.

Wright, J. W., and L. J. Vitt. 1993. Biology of whiptail lizards (genus *Cnemidophorus*). Oklahoma Museum of Natural History, Norman, Oklahoma, USA. 417.

Zar, J. H. 1999. *Biostatistical analysis*. Pearson Education India.

Zug, G. R., L. Vitt, and J. P. Caldwell. 2001. *Herpetology: an introductory biology of amphibians and reptiles*. Academic press.

CURRICULUM VITAE

Guillermo received his Bachelor of Science with a concentration in Biology from New Mexico State University in 2012. Guillermo continued to pursue his Master of Science degrees in Plant and Environmental Science and a separate one in Conservation Ecology in 2015. Throughout his graduate career, Guillermo has gained extensive teaching experience. Lecturer positions held at New Mexico University include Herpetology and Management of Aquatic and Terrestrial Ecosystems. Throughout his research, Guillermo has mentored four students in various herpetological sampling techniques. Such students have successfully presented the results of their independent investigations as part of the UTEP/EPCC STEMgrow BRIDGE program in 2019 and 2020. Additionally, Guillermo has held the position of teaching assistant in Environmental Physiology of Fishes. Guillermo also has experience as a teaching assistant in GIS for Natural Resource Managers. Guillermo has more than 10 years as a teaching assistant in the Organismal Biology Laboratory. Throughout his research, Guillermo has presented his work at the Southwestern Association of Naturalists 64th Annual Meeting (2017). Also, in the American Fisheries Society Joint Annual Meeting (2014) and at the Hellenic Mediterranean University in Athens, Greece (2013). Guillermo has published manuscripts on amphibians, parthenogenetic whiptails, pesticides, drought, ecological services, acequias, climate, and conservation.