FINAL PERFORMANCE REPORT

Federal Aid Grant No. F19AF001212 (T-112-R-1)

Assessment of Texas Horned Lizard Populations in Western Oklahoma

Oklahoma Department of Wildlife Conservation

October 1, 2019 through June 30, 2024

FINAL PERFORMANCE REPORT

State: Oklahoma **Grant Number:** F19AF01212 (T-112-R-1)

Grant Program: State Wildlife Grants

Grant Title: Assessment of Texas Horned Lizard Populations in Western Oklahoma

Grant Period: October 1, 2019 – June 30, 2024

Principal Investigator: Dr. Cameron D. Siler, Associate Curator for Herpetology, Sam Noble Museum; Assistant Professor of Biology, University of Oklahoma
Co-PI: Jessa L. Watters, Oklahoma Department of Transportation, University of Oklahoma
Co-PI: Katharine Marske, Associate Professor, School of Biological Sciences, University of Oklahoma
Graduate Research Assistant: Alexandria Fulton, School of Biological Sciences, University of Oklahoma

ABSTRACT:
We conducted reptile surveys focused on the Texas Horned Lizard (*Phrynosoma cornutum*) across three of the Oklahoma Department of Wildlife Conservation's wildlife management areas (WMAs) between early June and early August each year from 2021 through 2023. These wildlife management areas were Beaver River WMA (2021), Coooper WMA (2022), and Sandy Sanders WMA (2023). We implemented multiple survey techniques to evaluate their relative efficacies for detecting and enumerating Texas Horned Lizards. These were 1) Y-shaped drift fence and pitfall trap arrays, 2) visual surveys along transect lines, 3) visual surveys of marked plots, and 4) road-cruising surveys. Fortuitous encounters of horned lizards, primarily along roads, were recorded as well.

We captured 31 Texas Horned Lizards on Beaver River WMA. Four were captured by the drift fence arrays, four were captured during road cruising surveys, none were captured while walking transects, and 27 were captured during fortuitous encounters. Including these horned lizards, the survey team documented 256 individual reptiles and amphibians of 27 species during the field season. On Cooper WMA, 95 unique individual Texas Horned Lizards were captured – seven by the drift fence arrays, 29 during road cruising surveys, one during a plot survey, none during transect surveys, and 68 during fortuitous encounters. Altogether, 210 amphibians and reptiles of 18 species were documented on the WMA. The final field season was an abbreviated one and we worked on Sandy Sanders WMA where we captured 53 Texas Horned Lizards – one in a drift fence array, 27 during road cruising surveys, 12 during transect surveys, and 13 during fortuitous encounters. Including the horned lizards, 123 amphibians and reptiles of 19 species were documented.

Our results indicate that the road cruising survey technique, timed to occur during the peak periods of basking and movement, is the most efficient and effective method for surveying and potentially monitoring Texas Horned Lizards. The use of drift fence arrays and visual plot searches both appear to be ineffective with respect to encounters per unit effort and may lead to an underestimate of the abundance of lizards. Transect searches showed mixed results depending upon habitat conditions because the detection rate along transects may be affected by

the density of ground-level vegetation. In areas with dense herbaceous ground cover, horned lizard detections are lower and searching along transect lines is less effective. However, where ground-level vegetation is sparse and visibility is greater, transect surveys may be effective, although they still are more time intensive than road-based surveys. We were unable to perform a mark-recapture analysis at any of the study areas due to low recapture rates and detectability. While mark-recapture data would be useful for assessing population size and density, and can be generated from road cruising surveys, the number of replicates needed to generate sufficient data to perform a mark–recapture analysis may be cost prohibitive. At the spatial level of our road cruising survey routes (11.24–12.35 km), we found that seven survey events within the active season for Texas Horned Lizards would be the minimum number needed to determine with over 95% confidence that a continuous series of non-detections suggest that the site is unoccupied.

On the Cooper WMA study site, the most productive road-type for road cruising surveys was the one-lane gravel/dirt road, followed by two-track roads, and finally the two-lane gravel roads, which are busier and provide the lowest opportunity for lizard encounters. At our field sites (which have minimal traffic), we concluded that one observer was as effective as two observers during a road cruising survey; however, the abilities of individual observers to detect and capture Texas Horned Lizards clearly differ. We recommend ensuring that all observers survey each route or site an equal number of times or that the same observer perform all surveys to avoid introducing multi-observer bias. Standardized survey methodology for Texas Horned Lizards takes thoughtful planning but is necessary to produce the high-quality data needed to evaluate the state of their populations. To better understand the generalizability of these findings and optimize survey methods across varying conditions, we encourage similar studies to be conducted throughout the Texas Horned Lizard's range. Comparing results from different regions will help refine survey techniques and enhance our understanding of how these methods perform under diverse abiotic and biotic conditions.

OBJECTIVES:

Objective 1: Estimate the distribution, population density, and habitat requirements of *Phrynosoma cornutum* across three public conservation lands in western Oklahoma through intensive, three-month field surveys during the species' active season.

Objective 2: Develop and test standardized survey protocols for locating and monitoring *Phrynosoma cornutum* in the wild.

Objective 3: Evaluate the status of the SGCN species' primary food source (harvester ants) and monitor for the presence and prevalence of invasive species recognized as conservation threats (e.g., red fire ants) at each selected site.

Objective 4: Analyze population-level genetic diversity of the horned lizard to assess the long-term genetic viability of populations in western Oklahoma.

NEED:

The Oklahoma Department of Wildlife Conservation has designated the Texas Horned Lizard, *Phrynosoma cornutum*, as a Tier I Species of Greatest Conservation Need in the

Oklahoma Comprehensive Wildlife Conservation Strategy (ODWC 2016a). Through previous surveys, the historical distribution of this species is well-known in Oklahoma, but information regarding the current status and health of populations within in the state is limited to a few areas within its relatively large geographic range. There is a paucity of recent vouchered records and roughly 93% of all museum records for the species stem from surveys conducted prior to 1990 (Appendices I and II).

The Texas Horned Lizard is one of the most charismatic and enigmatic species of the American Southwest. The species is well-known for its distinctive horns, lateral spikes, and flattened body (Price 1990). Despite a range covering parts of Arizona, Colorado, Kansas, Missouri, New Mexico, Oklahoma, Texas, and northern Mexico, the species has experienced substantial population declines, particularly in the eastern portion of its historic range (Price 1990; Carpenter et al. 1993). These declines have been linked to a number of factors, including: (1) overexploitation for the pet trade (particularly in the first half of the 20^{th} century), (2) the spread of the invasive ants such as the red imported fire ant (*Solenopsis invicta*), and (3) human expansion into the plains, which has resulted in habitat loss, fragmentation, increased road mortality, and loss of their primary food source, harvester ants (*Pogonomyrmex* spp.) (Price, 1990; Carpenter et al. 1993; Donaldson et al. 1994). Due to increasing concerns regarding population-level declines for *P. cornutum*, many states have implemented regulations to limit collecting. Furthermore, in addition to its Tier I status in Oklahoma, the species is protected in this state under a year-round closed season that prohibits its collection and possession. It is also listed as a threatened species in the neighboring state of Texas (TPW 2018). Although the species has managed to persist in small, presumably isolated pockets in areas where human population levels are lower, as human encroachment continues, it is critical that increased efforts be undertaken to monitor population health in the state.

Texas Horned Lizards have been found in a wide range of semi-desert and grassland habitats. Often these contain sandy or loose, loamy soils that facilitate burrowing for nesting and hibernation (Burrow et al. 2001). They require a mosaic of micro-habitats to thermoregulate, and individuals move between open and shaded areas throughout the day and between seasons (Bogosian et al. 2012; Wolf et al. 2015). Home ranges can vary in size based on age, sex, and season, but range from $<100\ m^2 – 8400\ m^2$ (Fair and Henke 1999). These home ranges overlap with several harvester ant mounds, allowing horned lizards to maximize their food intake, while minimizing travel and ant over-harvesting (Whitford and Bryant, 1979). Because harvester ants often comprise the primary diet of *P. cornutum*, studies have suggested that increasing harvester ant populations via increasing their plant food sources could lead to rebounding lizard populations (McIntyre 2003). In contrast, the invasive red fire ant has been linked directly, and indirectly, to Texas Horned Lizard population declines, as they have been shown to outcompete native ants, to be unpalatable as a food source, and to depredate *P. cornutum* eggs, hatchlings, and even adults (Allen et al., 1994; Webb and Henke, 2003). Similar observations have been made for other horned lizard species, where population declines have been linked to the increased spread of another invasive Argentine ant, *Linepithema humile* (Suarez and Case 2002).

In Oklahoma, the most well-studied population of *P. cornutum* occurs at Tinker Air Force Base (TAFB), in Oklahoma Co., with published works and ongoing research covering population demographics, survival rates, habitat requirements, and general behavior (Endriss et al., 2007; Moody et al. 2007; Bogosian et al. 2012; Wolf et al. 2013). Since the initiation of the long-term horned lizard studies at TAFB in 2003, overall population size has declined and individual survival rates at all life stages have decreased. Small-scale habitat restoration studies on TAFB have shown little effect at reversing this trend (Endriss et al. 2007; Wolf et al. 2013). This research is based largely on tracking individual lizards via Very High Frequency (VHF) transmitters or harmonic radar diodes, which work well in the small wildlife reserve present on TAFB; however, the method is less feasible across larger areas of the state.

Even with the long-term study of the localized population of *P. cornutum* at TAFB, and a significant body of literature documenting the species' declining populations (Carpenter et al. 1993; Allen et al. 1994; Donaldson et al. 1994; Faire and Henke 1997; Burrow et al. 2001), a paucity of information exists about the current status of populations across large regions of the state, particularly in the shortgrass and mixed-grass prairie ecoregions of western Oklahoma. Historical museum records document a distribution for *P. cornutum* across most of the eastern ¾ of the state, but recent collection-based records are much more data deficient (Appendix I). In fact, large-scale surveys of western Oklahoma have not been conducted for several decades (Carpenter et al. 1993; Donaldson et al. 1994), but it is expected that population densities may be higher in the region due to lower-density human habitation. Furthermore, data regarding population-level genetic differences of horned lizards within the state of Oklahoma are non-existent, and only a few small-scale genetic studies have been conducted on populations in Texas (Guerra 1998; Sattler and Ries 1998; Williams et al. 2012; Wall 2014). Understanding the population genetic structure of *P. cornutum* in Oklahoma, particularly among fragmented populations, will allow researchers and wildlife managers to develop appropriate conservation strategies, particularly in light of the fact that declining populations often undergo genetic bottlenecks (Sattler and Ries 1998). Similarly, analyzing habitat preferences, primary food source availability, and the severity of conservation threat by invasive fire ants is of critical importance for long-term viability assessment of the species in the state.

This project worked to address these issues in collaboration with ODWC by conducting multi-month surveys across targeted public conservation lands in western Oklahoma to contribute to our understanding of several fundamental questions regarding Texas Horned Lizards. Our primary objectives were to identify their habitat requirements and determine the best methods for surveying and monitoring their populations. Secondarily, we collected qualitative data to examine potential *P. cornutum* insect prey.

A standardized methodology for Texas Horned Lizard population surveys is beneficial to conservation efforts in a variety of ways. First, any study seeking to monitor Texas Horned Lizard populations needs to employ defined and repeatable methodology, such that surveys are consistent not only over different timeframes, but also among regions and across a variety of researchers (Rich et al. 2017; Gibb et al. 2019; Fisher 2023). Information about Texas Horned Lizard populations across their range is limited currently by a dearth of quantitative surveys (IUCN 2007; ODWC 2016a). Secondly, in addition to being repeatable, a survey method should be effective at surveying lizards (Garden et al. 2007; Reid et al., 2013; Greene et al. 2016). Particularly in low-density populations, a survey method must be able to produce a substantial number of Texas Horned Lizard captures to allow for relevant data analyses (e.g. mark–recapture). Thirdly, a survey method should be efficient and not involve a large burden of time, personnel, or equipment (Field et al. 2005; Garden et al. 2007; Lukacs et al. 2011).

To address the need for standardized Texas Horned Lizard survey methods, we compared commonly used herpetological sampling methods: drift fence arrays, road cruising surveys, and both plot and transect searches. We also tracked fortuitous encounters outside of survey efforts. Scat analysis was not practical due to the large areas surveyed. This assessment of survey methods was conducted across three summers (2021–2023), each summer at a different ODWCowned wildlife management area in western Oklahoma, within the current range of Texas Horned Lizards. Our study aimed to elucidate the best methods at our field sites for capturing Texas Horned Lizards for population surveys to develop recommendations for future studies.

APPROACHES

Taxonomic Focus

During surveys, we noted the date and capture location (latitude and longitude) for all observed and captured lizards. To ensure data accuracy, we only included Texas Horned Lizards in our analyses that were physically captured. All captured horned lizards were marked using a unique toe clip combination (Vesy et al., 2021), taking two toes (no more than one toe per limb), and were released immediately after processing at the location of their capture.

Field Methodologies

Study Areas:

In 2021, we conducted our research on the western unit of the Beaver River WMA, located in Beaver County near the town of Beaver, OK in the Oklahoma Panhandle (Figures 2 and 3). The western unit of Beaver River WMA is 7,537 ha, and the survey sites within the WMA were a mosaic, composed of grasses interspersed with woody vegetation, especially Sand Sagebrush (*Artemisia filifolia*). The WMA straddles the boundary between two Level IV Ecoregions, the Canadian/Cimarron High Plains and the Canadian/Cimarron Breaks (U.S. Environmental Protection Agency, 2012). The survey sites within the Beaver River WMA fell into four vegetation classifications within the Oklahoma Ecological Systems Map: High Plains Shortgrass Prairie, High Plains Sand Prairie, High Plains Sandhills Shrubland, and Ruderal Plains Shrubland (Supplemental Table A; Diamond and Elliot 2015; ODWC 2016b).

In 2022, research was conducted in western Oklahoma at the Hal and Fern Cooper WMA (hereinafter "Cooper WMA"), spanning 6,507 ha in both Woodward and Harper counties and close to the city of Woodward, OK (Figures 3 and 4). Like Beaver River WMA, the vegetation community here is a mosaic dominated by grasses intermingled with Sand Sagebrush and other woody shrubs. Cooper WMA lies within the Pleistocene Sand Dunes Level IV Ecoregion (U.S. Environmental Protection Agency, 2012) and the survey sites fell into the following Oklahoma Ecological Systems Map classifications: High Plains Sandhill Shrubland, High Plains Sand Prairie, High Plains Riparian Deciduous Shrubland, Central Mixedgrass Prairie, and Ruderal Eastern Redcedar Shrubland (Supplemental Table A; Diamond and Elliot 2015; ODWC 2016b).

The study area for the 2023 field season was the Sandy Sanders WMA, which spans nearly 11,700 hectares in southwestern Oklahoma at the intersection between Beckham, Greer, and Harmon counites. Sandy Sanders WMA lies within the Southwest Tablelands Ecoregion and encompasses eroded canyons dominated by Redberry Juniper and Honey Mesquite shrublands. The primary vegetation communities on the WMA fell in the following Oklahoma Ecological Systems Map classifications: Canyon Grassland, Canyon Gyp Juniper Shrubland, and High Plains Mesquite Shrubland.

Survey Methods:

At Beaver River WMA (2021), our survey effort consisted of drift fence arrays (n = 10), transect searches on foot (n = 6), and road cruising transects (n = 2), and the field season ran from 3 June through 4 August 2021. The following year at Cooper WMA (2022), we continued using drift fence arrays at a lower level of effort (*n* = 4), road cruising surveys at a higher surveying frequency (*n* = 4), and transect searches (*n* = 8), plus we added plot searches (*n* = 9). Each method covered areas of different sizes, and the field season at Cooper WMA ran from 19 May through 4 August 2022. Our survey effort at Sandy Sanders WMA (2023) consisted of drift fence arrays (*n* = 4), transect searches on foot (*n* = 8), and road cruising transects (*n* = 3). We did not use the plot search technique at Sandy Sanders WMA due to its low efficiency. The 2023 field season at Sandy Sanders WMA was an abbreviated one and ran from only 14 June through 8 July 2023. The start of the season was delayed by plumbing repairs that were needed in our lodging facility and the season ended earlier than anticipated because of a university policy violation by the seasonal field crew. Because of the shorter season, the vegetation analyses were not completed, and we could not associate each Texas Horned Lizard observation with its corresponding habitat classification.

At each WMA, the survey site locations were selected based upon the site's perceived suitability for Texas Horned Lizards, including the presence of a mosaic of microhabitats, ant mounds, and/or prior knowledge of Texas Horned Lizard occurrence in the area by local personnel. In 2022, we also tracked the person-hours worked by each researcher for each survey method as a measure of efficiency (Rolfe and McKenzie 2000). Person-hours included all fieldwork time associated with each survey method but did not include time driving to and from survey sites.

For active survey methods (road cruising surveys and plot and foot searches), we employed standardized survey constraints to keep data comparable. Each active survey site was completed a maximum of one time per day, and observers did not complete two searches or two road cruising surveys in a row to avoid eye fatigue. Active surveys were completed between early June and early August and during the hours of highest Texas Horned Lizard activity: 0800–1200 h ("morning") and 1600–2030 h ("evening"). During the survey period, sunrise varied between 0621–0646 h and sunset was between 2048–2032 h. At the start and end of each active survey, the following data were collected: time, wind speed, cloud cover, and air temperature using the nearest Mesonet station (Beaver, Woodward, and Erick stations (Brock et al. 1995; McPherson et al. 2007). Active surveys were not carried out if the air temperature was below 21.1°C (70 °F), if it was raining, or if the ground was saturated from prior rain.

Drift Fence and Pitfall Trap Arrays

We utilized Y-array drift fences ("arrays"; Fair and Henke 1997; Crosswhite et al. 1999; Ribeiro-Júnior et al. 2008; Hutchens and Deperno 2009), comprised by three 8-m long sections ("wings") made of vinyl or galvanized steel flashing (58 cm tall) placed approximately 120° apart, and radiating from a center pitfall trap (18.9-L/5-gallon bucket). At the end of each of the three wings, we installed another 18.9-L/5-gallon bucket as a pitfall trap, bringing the total number of pitfall traps per array to four (Figure 1). Wings were buried approximately 5 cm deep into the ground, and each pitfall trap was embedded into the soil deep enough that the rim of the bucket was flush with the ground surface, or the soil was backfilled to create a small ramp. Where each wing met a pitfall trap, we allowed the wing to overhang the bucket (Crosswhite et al. 1999) by approximately 10 cm to facilitate pitfall captures. Each drift fence array also included six double-ended funnel traps (minnow traps or a similar design constructed from aluminum window screen mesh) that were placed two per wing, one on each side, approximately in the middle of the wings. Traps and buckets were shaded with either plywood squares or bucket lids. Arrays were checked twice a day, once in the morning and once in the afternoon or evening.

Road Cruising Surveys

Road cruising surveys consisted of driving a truck slowly at 8–12 mph (12.9–19.3 kph), with an average speed of 10.0 mph (16.1 kph), along predefined routes while actively searching the road and road-edge for Texas Horned Lizards and other herpetofauna. Road cruising surveys were completed with either one observer (driver only) or two observers (driver and one passenger). On Beaver River WMA, we established two road cruising routes mid-season. These routes were each 11.25 km in length and were adjacent to one another on the same one-lane dirt road that traversed the west side of the WMA. Each route was run twice. We originally did not intend to place much emphasis on the road cruising technique because we didn't believe that it would be readily applicable to detecting horned lizards; however, as the season progressed it became apparent from our fortuitous encounters that horned lizards routinely basked along road edges.

On Cooper WMA, we established four road cruising routes at the beginning of the season, and these had a mean length of 11.80 km (Route 1 = 11.24 km; Route 2 = 12.35 km; Route 3 = 11.76 km; Route 4 = 11.84 km; Figure 3). All stretches of road were only included in one route each, except for a 296 m stretch of road that was included in two survey routes (Routes 2 and 3). The average time spent driving a road cruising survey was 44 min and 7 s. During the 2022 field season, each route was surveyed at least five times in the morning with one observer and five times in the morning with two observers, along with at least five evening sessions with one observer and five evening sessions with two observers (Route 1, n = 20; Route 2, n = 22; Route 3, n = 22; Route 4, n = 21). We classified road sections into three categories: two-lane gravel roads, one-lane gravel/dirt roads, and two-track roads. Two-lane gravel roads were wider than the other road types, well-maintained, and topped with gravel. One-lane gravel/dirt roads consisted of gravel, dirt, or a combination of the two. Two-track roads had two bare ground strips, approximately tire-width, with vegetation growing in the middle. All four survey routes had sections of different road types. Route 1 consisted of one-lane gravel/dirt roads (58%) and two-track roads (42%). Route 2 was also made up of one-lane gravel/dirt roads (49%) and two-track roads (51%). Route 3 included two-lane gravel roads (21%), one-lane gravel/dirt roads (27%), and two-track roads (51%). Lastly, Route 4 was composed of two-lane gravel roads (56%), one-lane gravel/dirt roads (32%), and two-track roads (12%).

On Sandy Sanders WMA, we established two long and one short road cruising routes (Route 1 = 11.62 km, Route 2 = 12.69 km, Route 3 = 5.79 km); however, because of the abbreviated field season, each of these routes was completed only three times (twice in the morning and once in the evening) (Figure 5).

Plot and Transect Searches

Plot and transect searches were carried out by a single observer scanning the terrain ahead with a search goal of a 2-m wide visible field, though this was often reduced due to thick vegetation. A transect search consisted of two 500-m long parallel transects ("a" and "b"), marked by flagging tape, separated by 100 m. Every transect started along a road and extended perpendicularly away from the road. One transect-search included both transects "a" and "b", and total search time per transect search averaged 32 min and 7 s (range: 30 min and 0 s – 36 min and 32 s). Each plot search consisted of a 50x50 m square delineated using flagging tape.

We searched plots by walking 25 straight parallel lines through the plot, spaced approximately 2m apart. Mean search time per plot search was 32 minutes and 43 seconds (range: 30 min and 0 s – 39 min and 21 s). On Beaver River WMA, six transects were surveyed on foot four times (twice each in the morning and evening), but no plot surveys were established on this WMA. On Cooper WMA, eight transects and nine plots were surveyed 10 times over the field season (five each in the morning and evening). On Sandy Sanders WMA, eight transect were surveyed two times each (one morning and one evening), but no survey plots were established on this WMA because our experience at Cooper WMA indicated that the plot search technique had low efficiency (few observations per hour of search time).

Insect Pitfall Trapping:

We aimed to set three insect pitfall traps per drift fence array – randomly distributed within the array wings. We placed a light layer (1 cm deep) of propylene glycol in the bottom of each trap and left the traps in place for seven days at a time before replacing the trap with a new one for the next seven days. Insects would be strained, scooped, or pulled out with forceps from each trap and transferred to 50mL blue-cap VWR vials and covered with 70% ethanol. Each vial was labeled with a lab-grade marker, with writing etched over the top as a backup in case ethanol leaks removed the writing. Vial and vial caps were then wrapped together with a small square of parafilm to further seal each container before being placed into 16-place storage containers that were labeled by site and pitfall array.

Data Analysis

Road and Oklahoma Ecological Systems Analysis:

We digitized roads and lizard capture locations at Beaver River and Cooper WMAs using ArcGIS Pro (v3.0.4; ESRI). For Cooper WMA, roads and lizard captures along roads also were labeled by road classification type. We calculated the number of Texas Horned Lizard captures/km for fortuitous encounters along frequently traveled roads at both Beaver River WMA and Cooper WMA. For Cooper WMA, we calculated the number of Texas Horned Lizard captures/km for each road type classification, both for road cruising surveys and fortuitous encounters along road cruising survey routes.

To test whether Texas Horned Lizard captures along each road type classification deviated from the expected number of captures, we used a Chi-squared test in R (v4.2.2; R Core Team, 2022) to compare the proportion of captures/km for each road type classification at Cooper WMA during road cruising surveys with the averaged captures/km. We evaluated the association between Texas Horned Lizard capture locations and the Oklahoma Ecological System Map categories to indicate potential preferred habitats using ArcGIS Pro (ODWC, 2016b). Using all Texas Horned Lizard captures during 2021 and 2022, we determined the ecological system category associated with each capture based on the Oklahoma Ecological Systems Map, utilizing its fine-scale resolution (10 m; ODWC, 2016b). This mapping system uses remote sensing data and classifies Oklahoma into 165 land cover and vegetation types (ecological system categories; ODWC, 2016b).

Number of Observers Analysis:

To determine if there was a statistical difference in the number of Texas Horned Lizard captures between one- and two-observer road cruising surveys, we used a Bartlett's test in R to assess variance in captures between these two groups ($\chi 2 = 2.39$, $df = 1$, $p = 0.12$), followed by a *t*-test assuming equal variances.

Spatial Clustering Analysis:

We analyzed fortuitous Texas Horned Lizard encounters along frequently traveled roads (to and between drift fence arrays) at both Beaver River WMA and Cooper WMA. We also evaluated road cruising survey captures at Cooper WMA, which included captures occurring along one-lane gravel/dirt roads only and captures occurring along two-track roads only. For these analyses, we only used the first encounter for any lizards captured more than once. During data analysis (described below), each of the generated random point pattern replicates had the same number of lizard capture data points as the comparative field-generated data and were constrained along roads.

We evaluated Texas Horned Lizard spatial clustering along roads using two methods via the *spatstat* package (v3.0.6; Baddeley et al. 2015) in R. First, we used the *F*-function and simulation envelopes to compare observed Texas Horned Lizard point patterns to 9,999 randomly generated point patterns. The *F*-function measures the distribution of distances from an arbitrary reference point to all points within a point pattern (Anselin 2016), and the envelope simulation produces a visual comparison of clustering within the observed point pattern compared to the randomly generated simulations (envelope). We selected the *F*-function because it compares the distribution of nearest neighbor distances, regardless of the distance extent, with what would be expected in the null model (complete spatial randomness) rather than the *K*-function, which only considers the cumulative count of points within a designated radius around other points (Baddeley et al. 2015). If the *F*-function for observed point patterns (observed value of *F[r]*) falls within the simulated envelope, then the point pattern in question exists within the possibility of complete spatial randomness; if the function lies below the envelope, the observed point pattern is clustered; and if the function lies above the envelope, that indicates a tendency toward a non-random, evenly distributed spatial pattern (Anselin 2016).

Second, we evaluated Texas Horned Lizard clustering along roads with a Monte Carlo analysis using 9,999 simulations of randomly generated point patterns. This analysis tested the likelihood of observing a random mean nearest neighbor distance less than that of observed mean nearest neighbor distances. Our Monte Carlo analysis differs from the *F*-function above by calculating the mean nearest neighbor distance for each point and averaging this for every point pattern, whereas the *F*-function considers the entire point pattern to evaluate clustering. We calculated the mean nearest neighbor distance among observed capture patterns and randomly generated patterns using the nndist() function.

Occupancy Analysis:

To identify the influence of road cruising routes and other factors (habitat, time of day, weather, etc.) on the probability of Texas Horned Lizard occurrence, as well as detection probability, we modeled occupancy using confirmed observation data, based on whether or not a Texas Horned Lizard was captured along a stretch of road (MacKenzie and Royle 2005; Bailey et al. 2014). Observed sightings of Texas Horned Lizards reflect both the true occupancy and detection probability, and occupancy models separate these two elements and calculate estimates for occupancy and detection probability (uncertainty of detection given occupancy) individually. We utilized the occu() function (MacKenzie et al. 2002) from the *unmarked* package (v1.2.5; Fiske and Chandler 2011) in R. Initially, this involved analyzing occupancy for the four road cruising routes at Cooper WMA, with each route serving as a site. Due to the limited number of routes, there was little power to evaluate site-level covariates; the analyses focused instead on observation-level covariates because of repeated site visits. To complement this route-specific view, we evaluated how different road and habitat types may impact occupancy or detection by dividing road cruising routes into 1-km segments based on road classification type (two-lane gravel, one-lane gravel/dirt, two-track). This resulted in a total of 40 "sites". For this second analysis, we considered both site- and observation-level covariates. Analyses were limited to the first 20 times each route was surveyed for all models.

Observation-level covariates for occupancy modeling included air temperature (Mesonet), cloud cover (categorial), wind speed (categorial), Julian date, morning (0800–1200 h) or evening (1600–2030 h) survey (categorial), time of day (continuous), number of observers (one or two), observer identity (to control for differing observer abilities to capture Texas Horned Lizards), and average driving speed (onX; onXmaps, Inc.). Air temperature, cloud cover, wind speed, and time of day were calculated via the average of the start and end data for each road cruising survey. Numeric observation-level covariates were centered and standardized (i.e., zero mean and unit variance) using the scale() function in R.

Site-level covariates included road classification type, route, and composition (percentage) of three broad ecological system categories. Ecological system categories were assessed from the Oklahoma Ecological Systems Map, and we combined similar classifications along road cruising routes into broader categories: Central Mixedgrass Prairie, four High Plains categories combined, and two Ruderal Shrubland categories combined (Diamond and Elliot 2015). To determine the percentage of each road segment that fell into each ecological system category, we utilized ArcGIS Pro.

To better understand the effectiveness of drift fence arrays and the factors that may influence their success, we modeled occupancy for all drift fence arrays both at Beaver River (n = 10) and Cooper (n = 4) WMAs in a single model. Each week that a drift fence array was active was considered one observation period. For covariates, we used one observation-level (time in weeks) and three site-level covariates: WMA, EPA Level IV Ecoregion, and Oklahoma Ecological System Map (U.S. Environmental Protection Agency 2012; Diamond and Elliot 2015; ODWC 2016b).

Models were built and evaluated based upon *a priori* hypotheses including combinations of covariates. We considered 20 models for road cruising routes, 49 models for 1-km road segments, and 10 models for drift fences (models listed in Supplemental Tables C, D, and E). We utilized the vif() function in the *unmarked* package (v1.2.5; Fiske and Chandler 2011) in R to determine collinearity among covariates (Zurr et al. 2010). The only covariates that were collinear (had a variance inflation factor [VIF] >10; Montgomery and Peck 1992; Zurr et al. 2010) were the composition (percentage) of the three ecological system categories (High Plains, Central Mixedgrass, and Ruderal) for the 1-km road segments; therefore, only one of the three ecological system categories were included at a time in the models. We compared models for 1-km road segments using the Akaike information criterion (AIC), considering ΔAIC ≥ 2 and Akaike weight (w_i) to differentiate competitive models (Burnham and Anderson 2002). The relative support for each considered model is described by w_i (Burnham and Anderson 2002). We used AICc instead of AIC to compare models for road cruising routes and drift fences, as this provides a correction for the small sample sizes (road cruising route n = 80; drift fence n = 134). We again used ΔAICc and w_i to compare models. When there was more than one competitive model, the most parsimonious model (i.e., that with the fewest parameters) was retained (Arnold

2010). Any important site-level covariates were further analyzed for significant differences between groups using a single-factor ANOVA analysis performed in R, followed by a Tukey's honestly significant difference (HSD) test (Abdi and Williams 2010) (Supplemental Table B).

RESULTS AND DISCUSSION

Objective 1: Estimate the distribution, population density, and habitat requirements of *Phrynosoma cornutum* across three public conservation lands in western Oklahoma through intensive, three-month field surveys during the species' active season.

Texas Horned Lizard Occurrence Summary

We documented Texas Horned Lizards at all three of the western Oklahoma wildlife management areas that served as our study areas - Beaver River WMA in 2021, Cooper WMA in 2022, and Sandy Sanders WMA in 2023. On each area, Texas Horned Lizards were widespread and found in a wide range of locations and habitat conditions. Based on their distribution, they appeared to be relatively common in each area; however, their detection rates are relatively low and this may give the appearance that this species is uncommon and/or occurs in low density.

We had 31 Texas Horned Lizard captures on Beaver River WMA and none of these individuals were recaptured (Tables 1, 2, and 5). On Cooper WMA, we had 137 Texas Horned Lizard captures of 95 unique individuals (Tables 3 and 5). While the recapture rate appears high, especially compared to our data from Beaver River WMA, most of these recaptures represent a relatively small number of lizards that were found opportunistically multiple times along specific sections of frequently-traveled roads. When those individuals are removed, the number of lizards that were recaptured is only seven. On Sandy Sanders WMA, we had a short field season, however, in less than four weeks we had 65 captures of 63 unique individual Texas Horned Lizards (Tables 4 and 6).

We had hoped to find Texas Horned Lizards in sufficient densities on the WMAs to conduct a mark-recapture analysis over the course of each summer, in order to assess population size and density; however, several factors made that infeasible. Across all of the WMAs, most of the horned lizards were captured during road cruising surveys and these animals were widely spaced – often more than 1 km apart and well beyond what is viewed as a typical movement or dispersal distance for this species. The relatively large spatial distances between most of our marked individuals indicated that many of them were likely to represent different local populations. Additionally, we experienced a low number of recaptures on each WMA ($n = 0$, $n = 13$, $n = 2$), which made a mark–recapture analysis impossible on Beaver River and Sandy Sanders WMAs, and problematic on Cooper WMA because of the dispersed nature of the marked animals. Because of these complications, compounded with the low detection rates that we encountered, we were unable to estimate population densities on the three study areas.

Oklahoma Ecological Systems

We used the Oklahoma Ecological Systems Map to classify and define the habitat types on each of the WMAs and each of the Texas Horned Lizard capture sites. Horned lizard captures occurred across a wide range of habitat types on the three WMAs, and it appears that this species occupies most of the available plant communities in the three study areas. Because of the shortened field season on Sandy Sanders WMA, we were unable to complete our analysis and classification of the plant communities associated with each of the horned lizard capture sites, but qualitatively, we documented Texas Horned Lizards at multiple locations within the three most abundant ecological systems (habitat types) – Canyon Grassland, Canyon Gyp Juniper Shrubland, and High Plains Mesquite Shrubland (Supplemental Table A).

We were able to conduct a more comprehensive analysis of Texas Horned Lizard habitat associations on Beaver River and Cooper WMAs, and because the two areas share some of the same ecological systems, we pooled the data for these WMAs into one analysis. Texas Horned Lizard captures (n = 168) occurred in a total of seven ODWC Ecological System categories during our 2021 and 2022 field seasons (Table 8; Supplemental Table A; ODWC, 2016b). The most common ecological system category was High Plains Sandhill Shrubland, the second most common was High Plains Sand Prairie, and the third most common was High Plains Shortgrass Prairie (Diamond and Elliot, 2015; Table 8). These three ecological system categories yielded most of the Texas Horned Lizard captures (91%; Table 8). The remaining 9% of captures were distributed throughout the other four ecological system categories.

Objective 2: Develop and test standardized survey protocols for locating and monitoring *Phrynosoma cornutum* in the wild.

Field Data Summary

At Beaver River WMA, we had 31 Texas Horned Lizard captures: 23 fortuitous encounters, four road cruising captures, and four drift fence captures (Table 1). Of the drift fence captures, two occurred in pitfall traps and two occurred in funnel traps. The first summer field season provided substantial insight into the efficacies of the techniques that we considered for monitoring horned lizard populations and this informed our second and third summer surveys at Cooper and Sandy Sanders WMAs, respectively. Out of the four strategic survey methods, road cruising surveys provided the most captures and required the least amount of the field technicians' time. Although we installed and ran 10 Y-array drift fences (Figure 1) for the entire months of June and July, we had relatively few Texas horned lizard captures within the arrays compared to the effort required to install and monitor them. Interestingly, many Texas Horned Lizard captures were obtained either opportunistically by our team or the WMA staff when driving (n=23) or through a pilot road-cruising survey (Table 1). We observed a moderate diversity of reptiles and amphibians in our Y-array traps with a total of 27 species recorded and 256 individual captures (Table 2).

In 2022 at Cooper WMA, we had 137 Texas Horned Lizard captures: 95 fortuitous encounters, 33 road cruising survey captures, 7 drift fence captures, and 2 plot search captures (Table 5). Of the drift fence array captures, four occurred in pitfall traps and three occurred in funnel traps. Building upon the results of our 2021 summer fieldwork at Beaver River WMA, we revised our approach by reducing the effort placed into drift fence arrays, increasing our effort in road cruising surveys, and adding a plot-search component to our structured visual surveys on-foot. In total, the field team led by Ms. Alexandria Fulton and two full-time undergraduate research assistants captured 95 unique Texas horned lizards a total of 137 times. This was a substantial increase over the captures made during the previous year's surveys, with most observations being fortuitous encounters, followed by observations made while road cruising. Additional herpetofauna diversity observed by the survey team included a total of 22 species, composed of four frogs, ten snakes, five lizards, and three turtles (Table 3). At Cooper WMA, the average number of person-hours to capture one Texas Horned Lizard for each survey method was as follows: 3.5 person-hours/Texas Horned Lizard for road cruising surveys; 38.2

person-hours/Texas Horned Lizard for drift fence arrays; and 42.2 person-hours/Texas Horned Lizard for plot searches (Table 5).

We carried out a successful, but shortened (see significant deviations), third and final field season at Sandy Sanders WMA in 2023. Based on the results of our previous two years of summer fieldwork, we revised our approach to focus more effort on road cruising and walking transect surveys and less effort into drift fence arrays. In spite of the limitations of the short field season, in less than four weeks we had 65 captures of 63 unique individual Texas Horned Lizards. Of the 63 unique lizards, 13 were captured during fortuitous encounters (mostly along WMA roads), 27 were captured during road cruising surveys, one was captured in a drift fence array, and surprisingly 12 were captured during transect searches (Table 6). Ground-level, herbaceous vegetation is much sparser across much of Sandy Sanders WMA because of the different soil types, and we suspect that the lower vegetation density improved ground-level visibility and increased the detection rate for Texas Horned Lizards while conducting searches on foot relative to Beaver River and Cooper WMAs. In addition to the Texas Horned Lizards, 123 amphibians and reptiles of 18 other species were captured (Table 4).

Road Cruising Surveys

Texas Horned Lizards were captured on roads both during road cruising surveys and by fortuitous encounters (Table 7). Considering only road cruising surveys (Cooper WMA), the number of captures/km by road type classification significantly deviated from the expected proportion ($\chi 2 = 43.79$, $p < 0.0001$). One-lane gravel/dirt roads performed the best by number of Texas Horned Lizard captures/km for both road cruising surveys (0.92) and fortuitous encounters along road cruising survey routes (2.92; Table 7). Two-track roads performed the second best by Texas Horned Lizard captures/km (road cruising = 0.75; fortuitous = 1.18), followed by two-lane gravel roads (road cruising = 0.11; fortuitous = 0.11; Table 7). Along the roads we frequently traveled (to and between drift fence arrays), we fortuitously encountered more Texas Horned Lizards/km at Cooper WMA (11.48) compared to Beaver River WMA (3.35; Table 7).

Number of Observers

The number of Texas Horned Lizard captures did not differ between one- and two-observer road cruising surveys (t-statistic = -1.16, df = 75, $p = 0.25$).

Spatial Clustering

Texas Horned Lizard fortuitous encounters showed mixed evidence for spatial clustering. On Beaver River WMA, fortuitous encounters along frequently traveled roads ($n = 13$) did not show any evidence of spatial clustering and had a mean nearest neighbor distance of 159.71 m (Figure 6 A, B). The F-function showed strong support for the observed captures falling within the envelope of randomly generated point patterns (Figure 6 A), and our Monte Carlo analysis similarly showed no support for spatial clustering (mean nearest neighbor distance = 158.79 m, $p = 0.51$; Figure 6 B). In contrast, Cooper WMA fortuitous encounters along frequently traveled roads ($n = 45$) did have strong evidence for spatial clustering and had a mean nearest neighbor distance of 50.93 m (Figure 6 C, D). The F-function showed that observed captures fell below the envelope of randomly generated point patterns, indicating spatial clustering (Figure 6 C), and the Monte Carlo analysis similarly showed significant spatial clustering (mean nearest neighbor distance = 65.76 m, $p = 0.03$; Figure 6 D).

Road cruising survey captures at Cooper WMA, considering all roads (n = 29), did not show any evidence of spatial clustering and had a mean nearest neighbor distance of 577.68 m (Figure 6 E, F). The F-function showed support for the observed pattern falling within the envelope of randomly generated point patterns (Figure 6 E), and the Monte Carlo analysis produced similar results (mean nearest neighbor distance = 664.28 m, p = 0.21; Figure 6 F).

Evaluation of captures along one-lane gravel/dirt roads (n = 16) and captures along two-track roads (n = 12) during road cruising surveys at Cooper WMA resulted in moderate evidence for spatial clustering for each road type (Figure 6 G, J). Mean nearest neighbor distance for one-lane gravel/dirt road captures was 267.07 m (Figure 6 H) and 629.00 m for two-track road captures (Figure 6 J). The F-function for one-lane gravel/dirt roads and, separately, two-track roads showed observed capture patterns that fell within the envelopes of random point patterns, supporting lack of spatial clustering (Figure 6 G, I). Conversely, the Monte Carlo analysis for both scenarios suggested the observed point patterns were more clustered than expected through spatial randomness (one-lane gravel/dirt roads mean nearest neighbor distance = 669.65 m, $p < 0.001$; two-track roads mean nearest neighbor distance = 945.24 m, $p < 0.01$; Figure 6 H, J). Spatial clustering for two-lane gravel roads was not assessed due to too few captures (n = 1).

Occupancy Analysis

Texas Horned Lizards were captured along all four road cruising routes at Cooper WMA (route occupancy = 100%). Keeping occupancy constant, we evaluated the effect of observation-level covariates on detection probability. Based on AICc, the best model for road routes involved lizard detection with time of day and observer identity as covariates (Supplemental Tables C, D, and E). The null model estimated detection at 35.0% (95% CI = 25.4–46.0%); i.e., the estimated probability for detecting a Texas Horned Lizard along any road cruising route was 35.0% each time a survey was completed. Texas Horned Lizards were more likely to be detected earlier in the day ($\beta = -0.64$, $z = -2.22$, $p = 0.03$; Figure 7) than later in the day.

Considering single-observer efforts among the three observers, two observers performed similarly on the number of 1-km segments/Texas Horned Lizard (Observer 1 = 23.4 and Observer 2 = 23.8); Observer 3 performed less effectively with 65.5 1-km segments/Texas Horned Lizard. Two-observer efforts when Observer 3 was involved also resulted in fewer Texas Horned Lizard captures (47.0 1-km segments/Texas Horned Lizard with Observer 1 and 0 Texas Horned Lizards detected with Observer 2) compared to when Observers 1 and 2 were paired (15.1 1-km segments/Texas Horned Lizard). This suggests that observer bias (e.g., observer experience or visual acuity) may affect detection frequency.

Texas Horned Lizards were not captured along all 1-km road segments; therefore, we were able to consider occupancy probability with this method. When evaluating 1-km road segments (n = 40), no site-level covariates produced an occupancy model that was ≥2 ΔAIC superior to the null model. The null model with constant occupancy, estimated occupancy at 55.6% (95% CI = 32.8–76.3%) along each 1-km road segment across the field season (i.e., each road segment had a 55.6% probability of being occupied by at least one Texas Horned Lizard).

Considering detection probability for the 1-km road segments, a model using the road cruising route as the dependent variable was the most competitive (Supplemental Tables C, D and E). The null model estimated detection probability at 7.0% (95% CI = 4.4–11.0%); therefore, each time a 1-km stretch of road was surveyed, there was a 7.0% chance of detecting a Texas Horned Lizard if the site was occupied. Route 2 performed the best, with an average of 0.083 Texas Horned Lizards detected per 1-km segment, followed by Route 3 (0.036), Route 1

(0.035), and Route 4 (0.005). A single-factor ANOVA analysis comparing Texas Horned Lizard captures at the 1-km road segments by road cruising route found a significant difference in captures between routes ($F[3,36] = 3.13$; $p = 0.04$) but a Tukey's HSD test showed that there was a statistical difference between captures along Routes 2 and 4 only ($p = 0.02$; Supplemental Table B).

Drift fence occupancy modeling indicated a null model (i.e., constant occupancy and detection) was the best fit for our data. Occupancy was estimated at 43.2% (95% CI = 16.6–74.4%) and detection at 17.0% (95% CI = 7.9–32.8%) under this model. This indicates that the drift fence sites had a 43.2% probability of being occupied and, if the site was occupied, the drift fence array had a 17.0% chance of capturing a Texas Horned Lizard during each capture event (week).

<u>**RESULTING RESEARCH MANUSCRIPTS IN REVIEW**</u>

Fulton, A. M., E. A. Bergey, D. Becker, H. C. Lanier, J. L. Watters & C. D. Siler. Revised submission under revision. Comparative analysis of survey methodologies for population-level studies of Texas horned lizards (*Phrynosoma cornutum*). Ichthyology & Herpetology.

Objective 3: Evaluate the status of the SGCN species' primary food source (harvester ants) and monitor for the presence and prevalence of invasive species recognized as conservation threats (e.g., red fire ants) at each selected site.

We collected and sorted 21 boxes with up to 16 vials each of invertebrate pitfall trap bycatch. Each vial represents the contents of one pitfall trap and the invertebrates that were captured by that trap during a one-week period. The sorting of these samples consumed much more time than we anticipated, and that was due primarily to the difficulty of accurately identifying insect specimens, particularly ants, to the species level. Because our primary interests are potential ant prey species for horned lizards and invasive ant species, we sorted the ants in each vial into morpho-species and counted their abundance. On average, each sample vial contains 6.8 ant species or morpho-species (range 3 to 11). Ultimately, these sample vials will be made available to the Sam Noble Museum of Natural History for accession into their modern invertebrate collection and a database of the ant samples in the vials will be provided to ODWC and the USFWS.

Harvester ants (*Pogonomyrmex* species) are known to be important prey for horned lizards, and mounds of the red harvester ant (*Pogonomyrmex barbatus*) were common in all three study areas. Despite their widespread occurrence and apparent abundance, harvester ants made up a relatively small portion of the ants in our invertebrate traps. *Pogonomyrmex* ants were present in only 16% of the sample vials and were often represented by only 1 - 3 individuals per sample. It's likely that our sampling design has genus- or species-specific biases and may not accurately reflect the relative abundance of the entire ant community, and ants in the genus *Pogonomyrmex* may be under-sampled in our traps. In contrast to *Pogonomyrmex*, ants in the genus *Solenopsis* were frequently abundant in our traps and comprised nearly one third of the individual ants that were captured. We did not confirm the presence of the red imported fire ant (*Solenopsis invicta*) in any of the study areas, but we did find many individuals in the *Solenopsis geminata* group that could not be confirmed to the species level. This species group contains species that are native to Oklahoma, are very common, and form large super-colonies. Additionally, the similar-looking, native *Solenopsis molesta* was identified from several traps; this species is part of a different species complex and is not considered to be invasive.

Objective 4: Analyze population-level genetic diversity of the horned lizard to assess the long-term genetic viability of populations in western Oklahoma.

We did not fully address this objective within the grant. Between the 2021 and 2022 field seasons, we recruited a graduate student to work on this aspect of the grant. However, two things occurred during 2022 that caused us to re-evaluate the weight that we had placed on this objective. First, it became apparent during both of the first two field seasons that Texas Horned Lizards were widespread on Beaver River and Cooper WMAs. Despite the low detection rates during our surveys, it appeared that we were working with relatively large populations for which genetic concerns were unlikely to be a limiting factor for population size and persistence. Secondly, our graduate student was offered another research project by another lab at the University of Oklahoma that was a better fit for their research interests and decided to accept it. Rather than recruit another student, we decided to place additional effort into the field surveys and the analyses of the survey techniques, as well as occupancy modeling with the data for Cooper WMA. We began a collaboration with Dr. Dean Williams at Texas Christian University who has been looking at genetic differences across Texas Horned Lizard populations range wide. We have made our tissues samples from Beaver River and Cooper WMAs (primarily from toe clips) available to him for his work. Based on his genetic work to date, we believe that the Texas Horned Lizard populations in western Oklahoma belong to a much larger pool of populations that are considered the "northern populations" of Texas Horned Lizards. These genetically similar populations extend across northern Texas, Oklahoma, southeastern Colorado, northeastern New Mexico, and presumably western Kansas.

RECOMMENDATIONS

PRIORITY 1 – ESTABLISHING STANDARDIZED SURVEY PROTOCOLS

Based upon a comparison of captures, re-captures, and effort, we conclude that road cruising surveys were the best way to strategically survey for Texas Horned Lizards, particularly in areas such as Beaver River WMA and Cooper WMA where herbaceous ground cover is abundant. This corroborates the findings of previous research at sites in Texas (Fair and Henke 1997). Although fortuitous encounters produced the highest number of Texas Horned Lizard captures, such captures are of little use for estimating population size or density. Fortuitous encounters have long been used for Texas Horned Lizard research to find lizards for a variety of useful study aims (Wolf et al. 2013; Anderson et al. 2017), but the data must be quantifiable and comparable in order to estimate population size and density. For example, the data could be collected by using a standard unit of effort such as search time, number of observers, etc. (Fair and Henke 1997; Henke 2003). Although road cruising surveys provided the most captures per unit effort compared to other methods, they do have limitations. For example, they require the presence of drivable roads at the location of survey interest, which automatically excludes many small areas from road cruising surveys, although some areas with narrow trails may be appropriate for smaller, all-terrain vehicles (Hutchens and Deperno 2009; Godley et al. 2020).

At our field sites on western Oklahoma wildlife management areas, which have large areas and seemingly low Texas Horned Lizard densities, transect or plot searches were not suitable for population monitoring and produced few captures per unit effort. Because Texas Horned Lizards are cryptic and seem to occur at relatively low densities across much of their range (Whiting et al. 1993; Wolf et al. 2013), plot and transect searches may be of limited utility in most locations. However, at smaller sites with higher lizard densities, lower herbaceous vegetation density, and/or limited road access, plot and transect searches and scat collection has been shown to be successful (Ackel 2016; Huerta et al. 2023; Vesy et al. 2021). Given the slower speed of transect searches, they may not yield enough captures for population analysis when lizards are at low densities, even if the detectability of lizards during transect searches was similar to road cruising. For example, each transect search covered 1 km and was conducted 10 times at an average time of 32 minutes each. Assuming the same detection probability as our 1-km road cruising segments from the occupancy modeling and the site being occupied, there was still a 48.4% chance of not detecting any lizards in the 10 surveys (five hours of effort). If lizards are distributed at the same densities across both road routes and transect routes, we would predict a minimum of 5.6 detections over the 80 transect searches we conducted, but we observed none at Beaver River WMA and Cooper WMA, which suggests additional biological or ecological impediments to transect searches in these habitats. These may be explained by the lizards' cryptic nature (Pianka and Parker 1975; Sherbrooke 2008), the potential for lizards to move to cover as people approach, the thick vegetation obstructing visibility, or simply differences in the use of road edges versus other microhabitats in western Oklahoma. Roads provide a clear surface for detection, with ideal habitat features like threat visibility, edge cover, and ant prey (Montgomery and Mackessy 2003). Although we were not able to fully analyze our data from the abbreviated survey at Sandy Sanders WMA, the field crew there was able to detect 12 Texas Horned Lizards along 16 transect survey (eight transects surveyed twice each). Sandy Sanders WMA contains soils that are tighter (higher clay content) and support herbaceous vegetation that is much sparser on average. It's likely that the increased visibility where vegetation is sparse allowed for greater detection of horned lizards relatively to the sites on Beaver River WMA and Cooper WMA that contain sandy soils and denser vegetation.

Similarly, our results indicate that drift fence arrays are not effective for surveying Texas Horned Lizard populations at our study sites. The low population density and limited movement of these lizards result in drift fences rarely capturing individuals. This pattern was observed at Sandy Sanders WMA as well where only one Texas Horned Lizard was captured over a three-week period across three drift fence arrays. Texas Horned Lizards may be more adept at avoiding pitfall and funnel traps by circumventing their openings because of their relatively slow movements (AMF pers. obs.; Fair and Henke 1997). Their slow movement may cause them to avoid obstacles that would trap other lizards. Drift fences also involve other downsides, such as habitat disturbance, significant material costs and personnel time during installation, and frequent monitoring to prevent mortalities. Given the low capture success for Texas Horned Lizards at our sites and across their range, drift fences appear to be impractical for any standardized, range-wide monitoring effort.

PRIORITY 2 – CONSIDERATION OF ROAD AND ECOLOGICAL SYSTEMS IN SURVEY DESIGN

The three road-type classifications that made up our road cruising survey routes at Cooper WMA (two-lane gravel, one-lane gravel/dirt, two-track) differed in their ability to produce Texas Horned Lizard captures. This is an important consideration for other road cruising surveys in the future, as most study sites, including Cooper WMA, have limited road options available. Road-based encounters produced the highest number of overall lizard captures, with fortuitous encounters along roads producing around twice as many lizards as standardized road cruising surveys (although this was not corrected for time or miles). This in part is because some road segments at Cooper WMA were driven disproportionately frequently outside of road cruising survey efforts. At Cooper WMA, the performance rank of road types did not change when examining standardized road cruising surveys or fortuitous encounters along frequently driven roads, but the magnitude of the horned lizard numbers was notable. When considering only road cruising surveys, one-lane gravel/dirt roads were 0.17 Texas Horned Lizards/km better than two-track roads; however, when looking at fortuitous encounters along road cruising routes, one-lane gravel/dirt roads appeared to be 1.74 Texas Horned Lizards/km better than two-track roads. This is an example of the importance of using strategic survey efforts instead of relying on fortuitous encounters to understand Texas Horned Lizard populations and their distribution.

It is impossible to separate the true distribution of Texas Horned Lizards from their ability to be captured along roads at Cooper WMA. It could be that Texas Horned Lizards occurred in equal numbers along one-lane gravel/dirt and two-track roads and only that detection was highest along one-lane gravel/dirt roads. We hypothesize that Texas Horned Lizard population density along two-track roads may have been higher than what we detected due to the limited visibility along this road type; the narrow bare ground strips and ample vegetation allow fewer opportunities for spotting Texas Horned Lizards, compared to two-lane gravel and one-lane gravel/dirt roads. A more detailed population study would be needed to evaluate these hypotheses. Visibility along two-lane gravel roads is unobstructed, but it can be difficult to see across the entire two-lane-wide stretch of road (AMF pers. obs.). Two-lane gravel roads at Cooper WMA also had more traffic (AMF pers. obs.) that could have led to reduced use by Texas Horned Lizards.

Texas Horned Lizards can live in a variety of habitat types (Price, 1990). We found lizards in ten ecological system categories, but those should not be considered their only suitable habitat types. The ecological system categories where we captured lizards were limited by what was located within the WMA boundaries and biased by the areas we chose to survey. Even so, the ecological system categories of High Plains Sand Prairie, High Plains Sandhill Shrubland, and High Plains Shortgrass Prairie produced the greatest number of Texas Horned Lizard captures at the Beaver River WMA and Cooper WMA sites combined.

PRIORITY 3 – CONTINUED ASSESSMENTS OF SPATIAL DISTRIBUTION

There was moderate support for spatial clustering of Texas Horned Lizards along the equally sampled road cruising routes for both one-lane gravel/dirt roads and two-track roads, but we did not find spatial clustering when we considered the entire routes inclusive of all road types. Thus, spatial clustering may not significantly influence the lizard's distribution at Cooper WMA. Nevertheless, it is advisable to select routes covering a large area and to have multiple routes per study site to avoid density estimate errors due to potentially clustered captures. This approach should be applied to all survey methods, considering previous research showing clustered distributions around ant mounds and mosaic habitats (Whiting et al. 1993). Although fortuitous encounters along frequently driven roads at Cooper WMA showed spatial clustering of Texas Horned Lizards, this likely does not reflect their true distribution due to unequal sampling. Certain areas were driven more often than others, leading to biased results. The comparison between the minimal clustering observed in road cruising surveys and the stronger clustering in fortuitous encounters underscores the need to avoid relying solely on incidental sightings for understanding lizard distribution.

Our occupancy models indicated conditions that can optimize surveys. The top occupancy model for Texas Horned Lizard detection at Cooper WMA for road cruising routes included time (earlier in the day) and observer identity, while the top model for 1-km road segments included only route (n = 4). Predictions of increased detectability earlier in the day align with earlier research findings that observed higher detection rates in the morning (Fair and Henke 1997).

Controlling for the impact of an observer's ability to detect and capture lizards (i.e., observer identity) is a common problem for visual surveys (Crump and Forstner 2019; Lardner et al. 2019) and is a more challenging prospect. While ideally, a single observer would conduct all surveys, this is often impractical. To minimize bias, we recommend that all observers survey each route equally to balance strengths and weaknesses. For occupancy modeling, observer identity should be included as a detection covariate. Our findings align with studies that noted significant observer variation in horned lizard detection (Grant and Doherty 2007; Cooper and Sherbrooke 2012). We found no benefit in having two observers versus one during road cruising surveys and prior herpetofauna experience did not affect capture rates. At Cooper WMA, it was possible to drive slowly (8–12 mph; 12.9–19.3 kph) and focus on the road safely with one observer. This reduced costs and personnel needs, allowing for more thorough data collection by reallocating resources to additional surveys and sampling more locations. Similar approaches would likely be feasible for monitoring other wildlife management areas throughout the range of the Texas Horned Lizard.

The interpretation of route identity (routes 1 through 4) showing the strongest influence on detection probability at the 1-km road segment scale is perplexing. Each route included multiple road types and ecological systems, yet these variables did not rank within the top model covariates. This may reflect spatial clustering by the lizards, potentially in response to an unmeasured environmental characteristic such as predator density or prey availability. Future studies that incorporate these factors on a broader scale may be useful for evaluating the factors that drive Texas Horned Lizard distribution and abundance.

Given the low detectability of Texas Horned Lizards, especially by observers traveling on foot (at Beaver WMA, Cooper WMA, and likely other sites), repeated surveys are needed to determine lizard absences with confidence. For example, if our goal is to gather presence-absence data on Texas Horned Lizards without estimating population size, at Cooper WMA each road cruising route (mean length 11.80 km) would need to be surveyed seven times and each 1-km segment 42 times. This frequency ensures that, in the absence of any lizard encounters, there is >95% confidence in determining the site's unoccupied status, using the cumulative probability of non-detection. With enough encounters, road cruising surveys have the potential to estimate not only occupancy but also abundance and density by applying N-mixture models and considering daily movement distances (Veech and Cave 2021). Whether selecting survey sites or performing surveys, repeated visits are needed for accurately estimating occupancy and other population parameters.

VI. SIGNIFICANT DEVIATIONS

We encountered numerous challenges while carrying out this grant. During the initial year of the project, the Coronavirus pandemic developed two months prior to the initiation of the first field season. Because of the University of Oklahoma's restrictions on travel, student work, and on-campus research activities, all in-person research related to this project had to be put on hold starting on March 13, 2020 and continuing into the spring of 2021. We had to request an amendment to the grant to shift the field work timeline back a full year.

We experienced a personnel setback in 2022, when the graduate student that was selected to work on the population genetics component of the grant left the project unexpectedly and forced us to re-evaluate the need for and feasibility of completing Objective 4 of the grant. We chose to reduce the effort that we placed into the genetic component of the project and shifted those time and financial resources to additional analyses of the efficacies of our survey methods (Objective 2). We also encountered a second personnel setback during the 2023 field season when we had to delay the start of the season for two weeks due to serious maintenance issues with our lodging facility, and then had to end the season early (July 8) due to a non-injury vehicle accident that resulted in the university terminating the employment of our field technicians and restricting our access to university vehicles. This second personnel setback did not prevent us from implementing the grant's first three objectives, but it did reduce our ability to collect field data during the final season.

EQUIPMENT:

No equipment exceeding $5,000 in cost was purchased for this project.

Prepared by: Dr. Cameron D. Siler, Associate Curator for Herpetology, Sam Noble Museum; Associate Professor of Biology, School of Biological Sciences, University of Oklahoma

Date Prepared: September 27, 2024

Approved by: Scott Parry, Assistant Chief of Wildlife
Oklahoma Department of Wildlife Conservation

Andrea K. Crews, Chief of Administration
Oklahoma Department of Wildlife Conservation

LITERATURE CITED:

Abdi, H., and L. J. Williams. 2010. Tukey's honestly significant difference (HSD) test. Encyclopedia of Research Design 3(1):1–5.

Ackel, A. 2016. The devil in the details: population estimation for conservation management of Texas Horned Lizards (*Phrynosoma cornutum*). Unpubl. M.S. thesis, University of North Texas, Denton, Texas.

Anderson, W. M., D. B. Webster, C. J. Salice, and G. Perry. 2017. Habitat utilization by the Texas Horned Lizard (*Phrynosoma cornutum*) from two sites in central Texas. The Journal of North American Herpetology 1:28–33.

Anselin, L. 2016. Point Pattern Analysis: Nearest Neighbor Statistics. The Center for Spatial Data Science, The University of Chicago. https://spatial.uchicago.edu/sites/spatial.uchicago.edu/files/9_points_2_r.pdf (accessed 21 December 2022).

Arnold, T. W. 2010. Uninformative parameters and model selection using Akaike's information criterion. The Journal of Wildlife Management 74(6):1175–1178.

Baddeley, A., E. Rubak, and R. Turner. 2015. Spatial Point Patterns: Methodology and Applications with R. First edition. Chapman and Hall/CRC Press, Boca Raton, Florida.

Bailey, L. L., D. I. MacKenzie, and J. D. Nichols. 2014. Advances and applications of occupancy models. Methods in Ecology and Evolution 5(12):1269–1279.

Brock, F. V., K. C. Crawford, R. L. Elliott, G. W. Cuperus, S. J. Stadler, H. L. Johnson, and M. D. Eilts. 1995. The Oklahoma Mesonet: a technical overview. Journal of Atmospheric and Oceanic Technology 12:5–19.

Burnham, K. P., and D. R. Anderson. 2002. Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach. Second edition. Springer-Verlag, New York City, New York.

Burrow, A. L., R. T. Kazmaier, E. C. Hellgren, and D. C. Ruthven. 2001. Microhabitat selection by Texas Horned Lizards in southern Texas. The Journal of Wildlife Management 65(4):645–652.

Carpenter, C. C., R. St. Clair, and P. Gier. 1993. Determination of the distribution and Abundance of the Texas Horned Lizard (*Phrynosoma cornutum*) in Oklahoma. Final Report, Federal Aid Project E-18, Oklahoma Department of Wildlife Conservation.

Cooper Jr, W. E., and W. C. Sherbrooke. 2012. Choosing between a rock and a hard place: camouflage in the round-tailed horned lizard *Phrynosoma modestum*. Current Zoology 58(4):541–548.

Crosswhite, D. L., S. F. Fox, and R. E. Thill. 1999. Comparison of methods for monitoring reptiles and amphibians in upland forests of the Ouachita Mountains. Proceedings of the Oklahoma Academy of Science 79:45–50.

Crump, P. S., and M. R. Forstner. 2019. Bias and precision of lizard occupancy estimates vary among observers and between methods. Journal of Herpetology 53(1):13–21.

Demers, M. N. 1993. Roadside ditches as corridors for range expansion of the Western Harvester Ant (Pogonomyrmex occidentalis Cresson). Landscape Ecology 8(2):93–102.

Diamond, D. D., and L. F. Elliot. 2015. Oklahoma Ecological Systems Mapping Interpretive Booklet: Methods, Short Type Descriptions, and Summary Results.

Donaldson, W., A. H. Price, and J. Morse. 1994. The current status and future prospects of the Texas Horned Lizard (*Phrynosoma cornutum*) in Texas. The Texas Journal of Science 46:97–113.

Eifler, D. A., M. A. Eifler, and T. K. Brown. 2012. Habitat selection by foraging Texas Horned Lizards, *Phrynosoma cornutum*. The Southwestern Naturalist 57(1):39–43.

Endriss, D. A., E. C. Hellgren, S. F. Fox, and R. W. Moody. 2007. Demography of an urban population of the Texas Horned Lizard (*Phrynosoma cornutum*) in Central Oklahoma. Herpetologica 63(3):320–331.

Fair, W. S., and S. E. Henke. 1997. Efficacy of capture methods for a low density population of *Phrynosoma cornutum*. Herpetological Review 28(3):135–137.

Field, S. A., A. J. Tyre, and H. P. Possingham. 2005. Optimizing allocation of monitoring effort under economic and observational constraints. The Journal of Wildlife Management 69(2):473–482.

Fisher, J. T. 2023. Camera trapping in ecology: a new section for wildlife research. Ecology and Evolution 13(3):1–3.

Fiske, I. J., and R. B. Chandler. 2011. unmarked: an R package for fitting hierarchical models of wildlife occurrence and abundance. Journal of Statistical Software 43(10):1–23.

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(3):218–227.

Gibb, R., E. Browning, P. Glover-Kapfer, and K. E. Jones. 2019. Emerging opportunities and challenges for passive acoustics in ecological assessment and monitoring. Methods in Ecology and Evolution 10(2):169–185.

Godley, J. S., J. L. Hofkes, and C. M. Reilly. 2020. Minimum density estimates of terrestrial snakes in the Munson Sandhills adjoining Apalachicola National Forest, Florida. Herpetological Review 51(2):221–226.

Grant, T. J., and P. F. Doherty Jr. 2007. Monitoring of the Flat-Tailed Horned Lizard with methods incorporating detection probability. The Journal of Wildlife Management 71(4):1050–1056.

Greene, D. U., R. A. McCleery, L. M. Wagner, and E. P. Garrison. 2016. A comparison of four survey methods for detecting fox squirrels in the southeastern United States. Journal of Fish and Wildlife Management 7(1):99–106.

Hellgren, E. C., A. L. Burrow, R. T. Kazmaier, and D. C. Ruthven. 2010. The effects of winter burning and grazing on resources and survival of Texas Horned Lizards in a thornscrub ecosystem. The Journal of Wildlife Management 74(2):300–309.

Henke, S. E. 2003. Baseline Survey of Texas Horned Lizards, *Phrynosoma cornutum*, in Texas. The Southwestern Naturalist 48(2):278–282.

Henke, S., and W. Fair. 1998. Management of Texas Horned Lizards. Wildlife Management Bulletin of the Caesar Kleberg Wildlife Research Institute 2:1–7.

Huerta, J. O., S. E. Henke, D. B. Wester, C. B. Eversole, S. L. Webb, and F. Hernandez. 2023. Feasibility and application of using Texas Horned Lizard scat to predict lizard size and age class. Wildlife Society Bulletin 47(e1146):1–14.

Hutchens, S. J., and C. S. Deperno. 2009. Efficacy of sampling techniques for determining species richness estimates of reptiles and amphibians. Wildlife Biology 15(2):113–122.

IUCN. 2007. The IUCN Red List of Threatened Species: *Phrynosoma cornutum*. https://www.iucnredlist.org/species/64072/12741535 (accessed 29 December 2021).

Lardner, B., A. A. Y. Adams., A. J. Knox, J. A. Savidge, and R. N. Reed. 2019. Do observer fatigue and taxon bias compromise visual encounter surveys for small vertebrates? Wildlife Research 46(2):127–135.

Lukacs, P. M., J. A. Gude, R. E. Russell, and B. B. Ackerman. 2011. Evaluating cost-efficiency and accuracy of hunter harvest survey designs. Wildlife Society Bulletin 35(4):430–437.

MacKenzie, D. I., J. D. Nichols, G. B. Lachman, S. Droege, A. A. Royle, and C. A. Langtimm. 2002. Estimating site occupancy rates when detection probabilities are less than one. Ecology 83(8):2248–2255.

MacKenzie, D. I., and J. A. Royle. 2005. Designing occupancy studies: general advice and allocating survey effort. Journal of Applied Ecology 42(6):1105–1114.

McPherson, R. A., C. A. Fiebrich, K. C. Crawford, J. R. Kilby, D. L. Grimsley, J. E. Martinez, J. B. Basara, B. G. Illston, D. A. Morris, K. A. Kloesel, A. D. Melvin, H. Shrivastava, J. M. Wolfinbarger, J. P. Bostic … A. J. Sutherland. 2007. Statewide monitoring of the mesoscale environment: a technical update on the Oklahoma Mesonet. Journal of Atmospheric and Oceanic Technology 24:301–321.

Mirkin, S., M. R. Tucker, and D. A. Williams. 2021. Predation release of Texas Horned Lizards (*Phrynosoma cornutum*) living in small towns. Ecology and Evolution 11(10):5355–5363.

Montgomery, C. E., and S. P. Mackessy. 2003. Natural history of the Texas Horned Lizard, *Phrynosoma cornutum* (Phrynosomatidae), in southeastern Colorado. The Southwestern Naturalist 48(1):111–118.

Montgomery, D. C., and E. A. Peck. 1992. Introduction to Linear Regression Analysis. Second edition. Wiley, Hoboken, New Jersey.

Moody, R. W., D. A. Endriss, E. C. Hellgren, and S. F. Fox. 2007. Studying a population of Texas Horned Lizards (*Phrynosoma cornutum*) in an urban/military environment. Iguana: Conservation, Natural History, and Husbandry of Reptiles 14(1):9–17.

Oklahoma Department of Wildlife Conservation (ODWC). 2016a. Oklahoma Comprehensive Wildlife Conservation Strategy: A Strategic Conservation Plan for Oklahoma's Rare and Declining Wildlife.

Oklahoma Department of Wildlife Conservation (ODWC). 2016b. Oklahoma Ecological Systems Map.

Pianka, E. R., and W. S. Parker. 1975. Ecology of horned lizards: a review with special reference to *Phrynosoma platyrhinos*. American Society of Ichthyologists and Herpetologists 1975(1):141–162.

Price, A. H. 1990. *Phrynosoma cornutum* (Harlan): Texas Horned Lizard, p. 469.1–469.7. In: Catalogue of American Amphibians and Reptiles.

R Core Team. 2022. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/.

Ramakrishnan, S., A. J. Wolf, E. C. Hellgren, R. W. Moody, and V. Bogosian III. 2018. Diet selection by a lizard ant-specialist in an urban system bereft of preferred prey. Journal of Herpetology 52(1):79–85.

Reid, N., M. G. Lundy, B. Hayden, D. Lynn, F. Marnell, R. A. McDonald, and W. I. Montgomery. 2013. Detecting detectability: identifying and correcting bias in binary wildlife surveys demonstrates their potential impact on conservation assessments. European Journal of Wildlife Research 59:869–879.

Ribeiro-Júnior, M. A., R. A. Gardner, and T. C. S. Ávila-Pires. 2008. Evaluating the effectiveness of herpetofaunal sampling techniques across a gradient of habitat change in a tropical forest landscape. Journal of Herpetology 42(4):733–749.

Rich, L. N., C. L. Davis, Z. J. Farris, D. A. W. Miller, J. M. Tucker, S. Hamel, M. S. Farhadinia, R. Steenweg, M. S. Di Bitetti, K. Thapa, M. D. Kane, S. Sunarto, N. P. Robinson, A. Paviolo … M. J. Kelly. 2017. Assessing global patterns in mammalian carnivore occupancy and richness by integrating local camera trap surveys. Global Ecology and Biogeography 26(8):918–929.

Rolfe, J. K., and N. L. McKenzie. 2000. Comparison of methods used to capture herpetofauna: an example from the Carnarvon basin. Records of the Western Australian Museum, Supplement 61:361–370.

Sherbrooke, W. C. 2002. Seasonally skewed sex-ratios of road-collected Texas Horned Lizards (*Phrynosoma cornutum*). Herpetological Review 33(1):21–24.

Sherbrooke, W. C. 2008. Antipredator responses by Texas Horned Lizards to two snake taxa with different foraging and subjugation strategies. Journal of Herpetology 42(1):145–152.

Sherbrooke, W. C. 2020. Current names: a guide to recent name changes of horned lizard species. Sonoran Herpetologist 33(1):4–10.

Stark, R. C., S. F. Fox, and M. L. David. 2005. Male Texas Horned Lizards increase daily movements and area covered in spring: a mate searching strategy? Journal of Herpetology 39(1):169–173.

U.S. Environmental Protection Agency. 2012. Level IV Ecoregions of Oklahoma. U.S. EPA Office of Research and Development (ORD) and National Health and Environmental Effects Research Laboratory (NHEERL).

Veech, J. A., and T. Cave. 2021. Using road surveys and N-mixture models to estimate the abundance of a cryptic lizard species. Journal of Herpetology 55(1):46–54.

Vesy, M. N., J. L. Watters, R. W. Moody, E. M. Schauber, J. M. Mook, and C. D. Siler. 2021. Survivorship and spatial patterns of an urban population of Texas Horned Lizards. The Journal of Wildlife Management 86(6):1267–1279.

Wall, A. E. 2014. Home range and genetics of Texas Horned Lizards (*Phrynosoma cornutum*) in two small towns in South Texas. Unpubl. M.S. thesis, Texas Christian University, Fort Worth, Texas.

Whiting, M. J., J. R. Dixon, and C. R. Murray. 1993. Spatial distribution of a population of Texas Horned Lizards (*Phrynosoma cornutum*: Phrynosomatidae) relative to habitat and prey. The Southwestern Naturalist 38(2):150–154.

Williams, D. A., N. D. Rains, and A. M. Hale. 2019. Population genetic structure of Texas Horned Lizards: implications for reintroduction and captive breeding. PeerJ 2019(10):1–28.

Wolf, A. J., E. C. Hellgren, V. Bogosian, and R. W. Moody. 2013. Effects of habitat disturbance on Texas Horned Lizards: an urban case study. Herpetologica 69(3):265–281.

Zuur, A. F., E. N. Ieno, and C. S. Elphick. 2010. A protocol for data exploration to avoid common statistical problems. Methods in Ecology and Evolution 1(1):3–14.

Figure 1. Y-array drift fence array structures deployed at all three study areas - Beaver River Wildlife Management Area (2021), Cooper WMA (2022), Sandy Sanders WMA (2023). Above is a diagram of one Y-array drift fence.

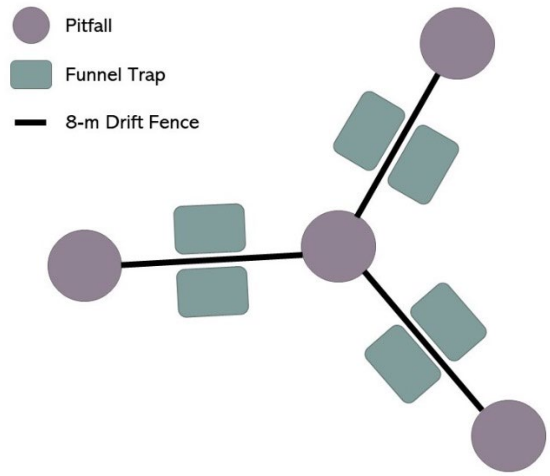


Figure 2. Driving routes (adjacent and highlighted in yellow) used for road cruising surveys at Beaver River Wildlife Management Area in Summer 2021.

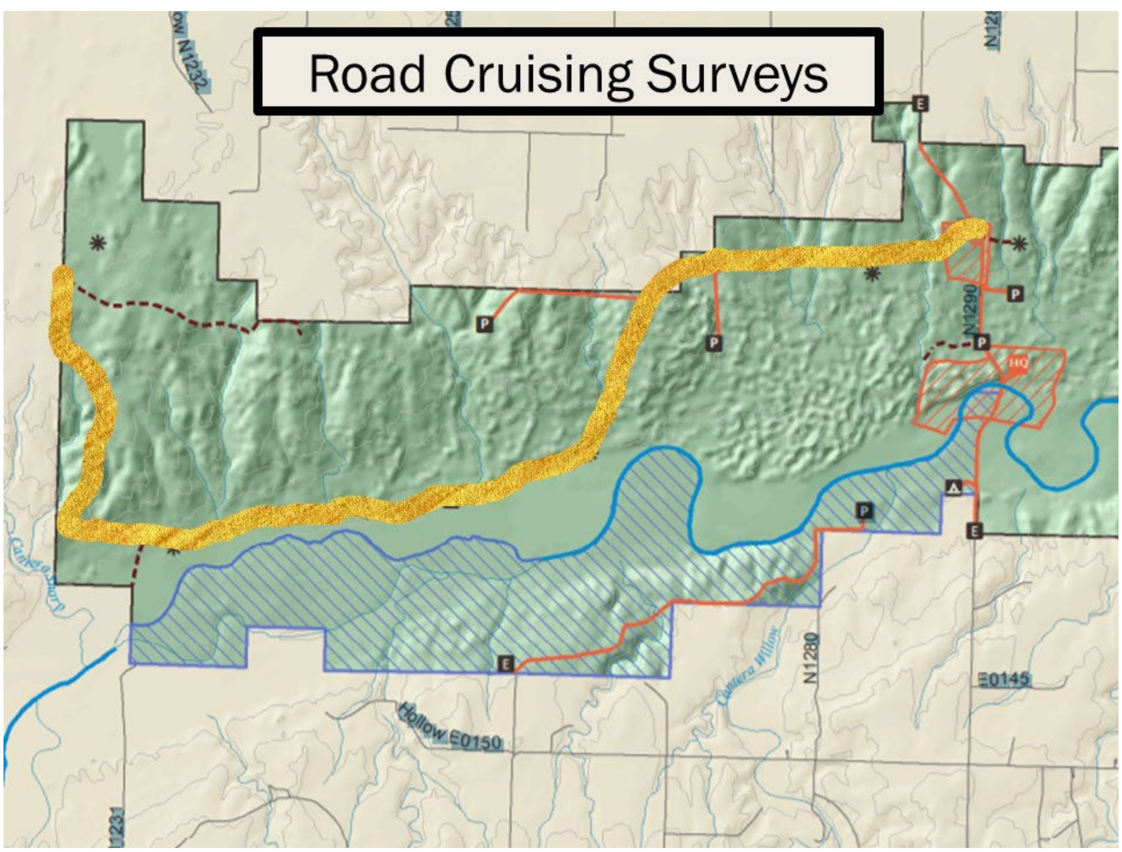


Figure 3. Road cruising survey routes at Cooper Wildlife Management Area (WMA). Inset shows the location of both survey locations: Beaver River WMA (2021) and Cooper WMA (2022). Scale bar in the lower left of the figure indicates 5 km.

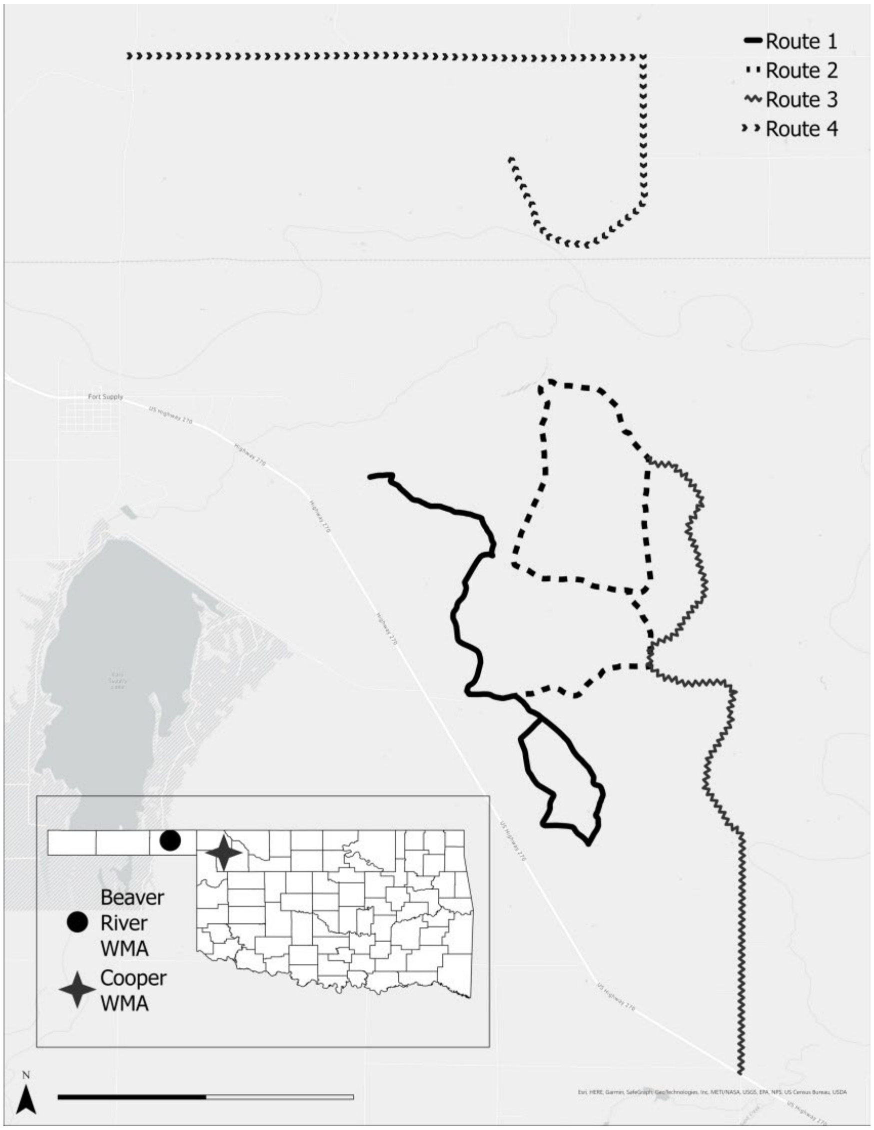


Figure 4: Map showing distribution of Texas horned lizard captures during the Summer 2022 survey effort at Cooper Wildlife Management Area. A total of 137 capture events were recorded between 19 May–3 August 2022. Each capture event is shown on the map along road cruising paths (black lines). Individual capture event locations are indicated by color-coded circles that correspond with survey methodology as follows: drift fence (n = 7 capture events); fortuitous encounters (n = 93); plot foot surveys (n = 2); and road cruising (n = 36).

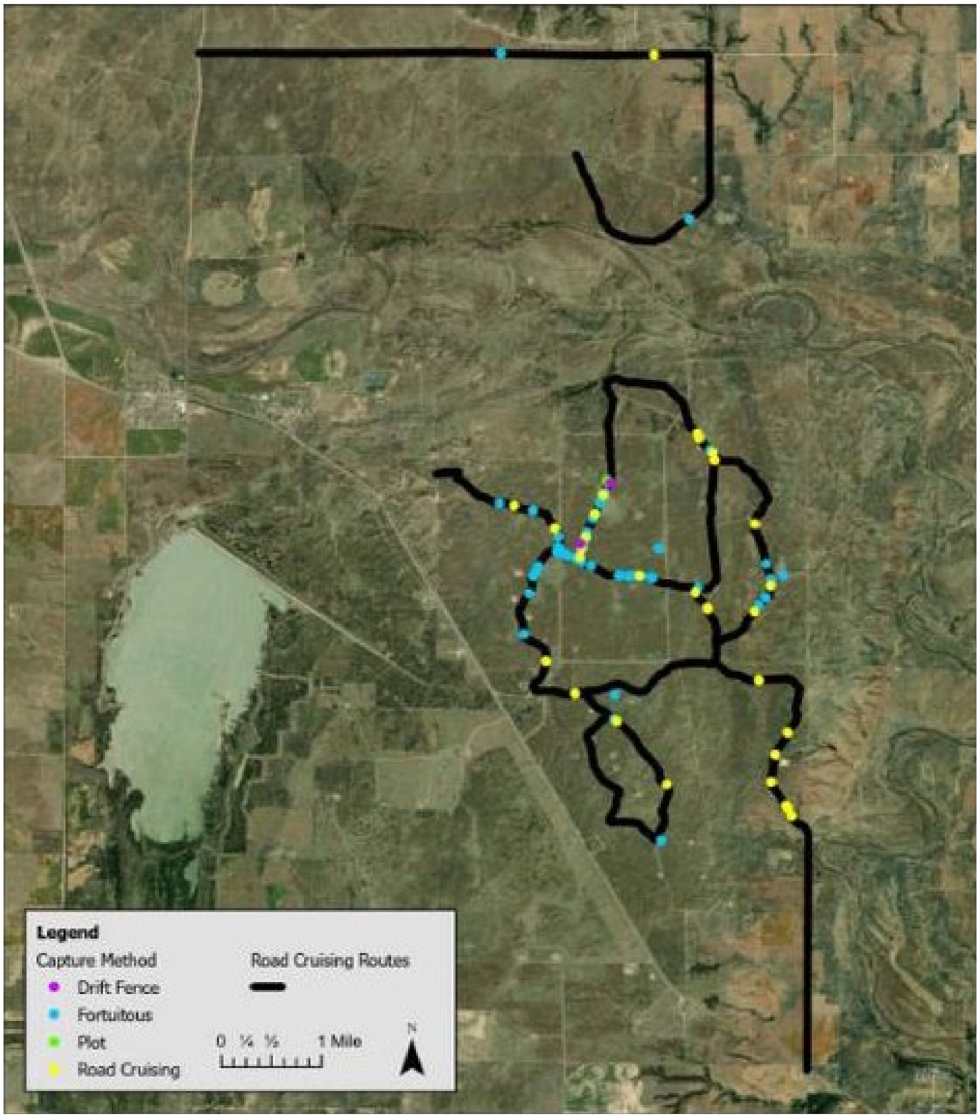


Figure 5. Visual depiction of drift fence arrays (two each at the large black and white squares), driving routes (solid lines), and walking routes (yellow fuzzy lines) for 2023.

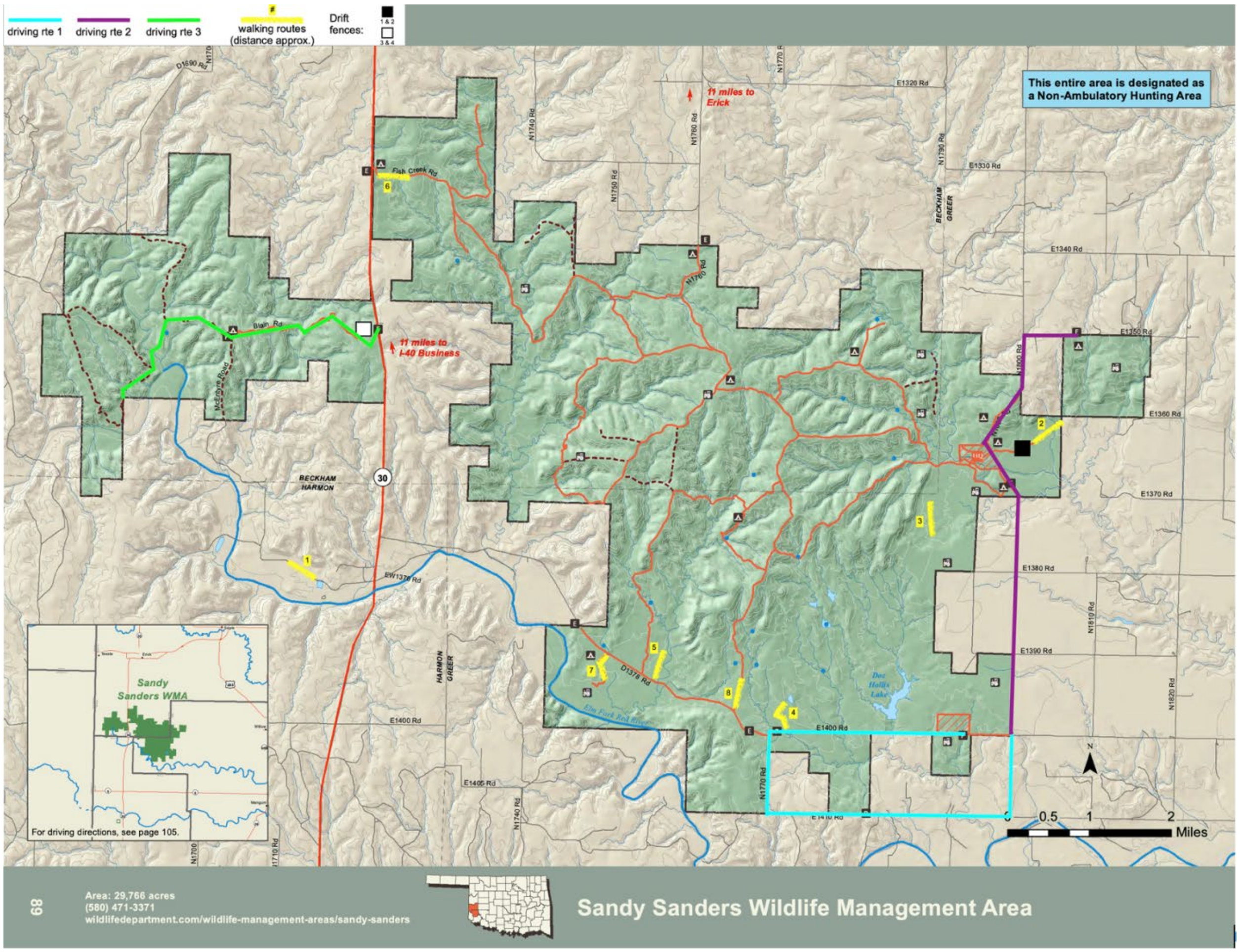
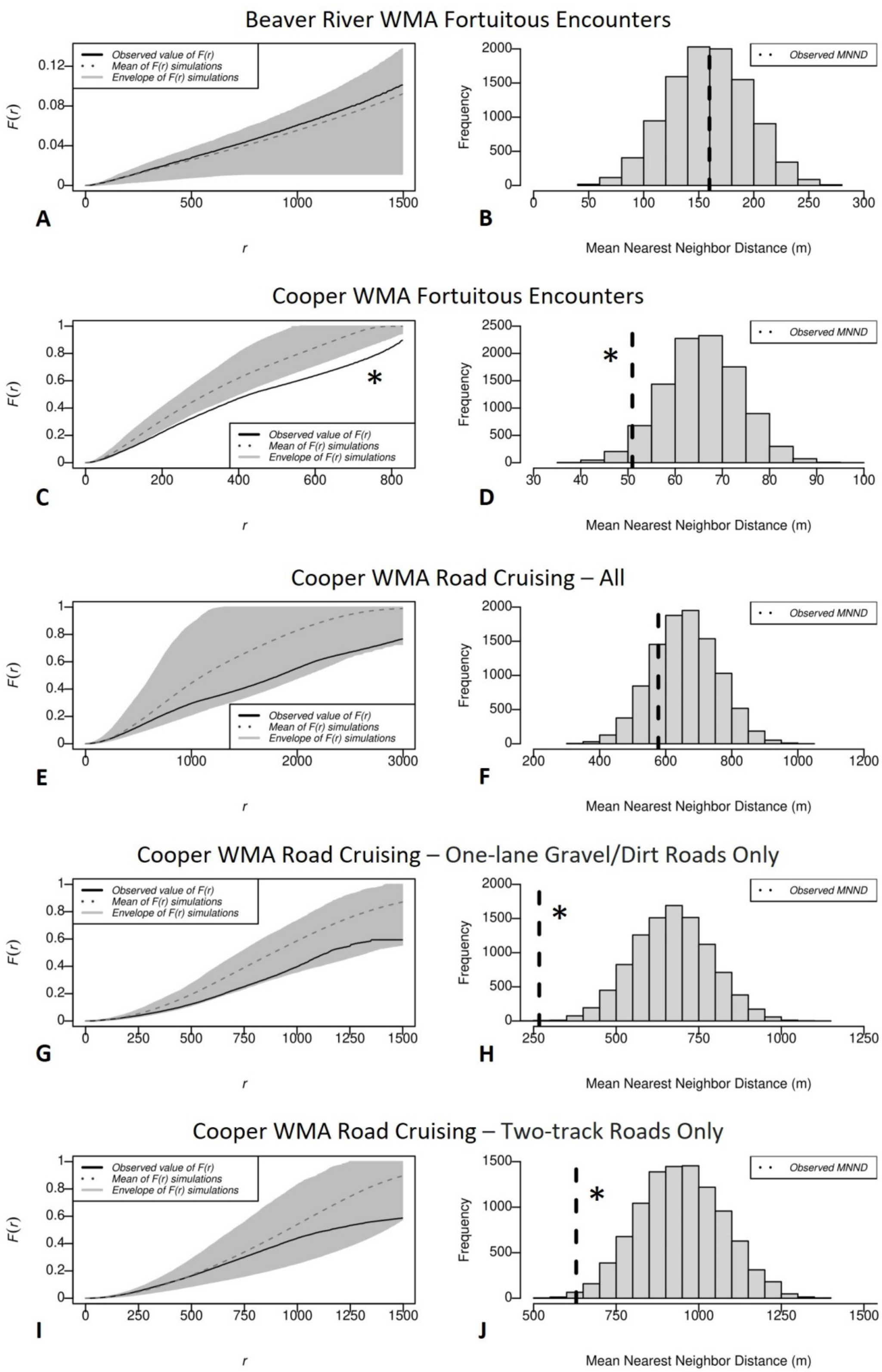


Figure 6 (next page). Spatial clustering of Texas Horned Lizards (*Phrynosoma cornutum*) along roads at Beaver River Wildlife Management Area (2021) and Cooper Wildlife Management Area (2022) in western Oklahoma. This figure evaluates the observed Texas Horned Lizard locations compared to 9,999 randomly generated point pattern simulations by two methods: envelope analysis (left) and Monte Carlo analysis (right). A, C, E, G, I: The solid black line is the observed capture pattern, and the gray envelope comprises the randomly generated point patterns. F(r) is the proportion of distances in each point pattern that is less than the distance in m (r). B, D, F, H, J: The dashed black line is the mean nearest neighbor distance of the observed capture pattern, and the gray bars illustrate the mean nearest neighbor distance of the randomly generated point patterns.



* = observed capture pattern is significantly different from spatial randomness

Figure 7. Occupancy model detection predictions for Texas Horned Lizards (*Phrynosoma cornutum*) at road cruising survey routes (n = 4) at Cooper Wildlife Management Area in 2022, located in western Oklahoma. Detection is estimated to be higher earlier in the day. The black line represents the predicted mean, and the gray envelope shows the 95% confidence interval.

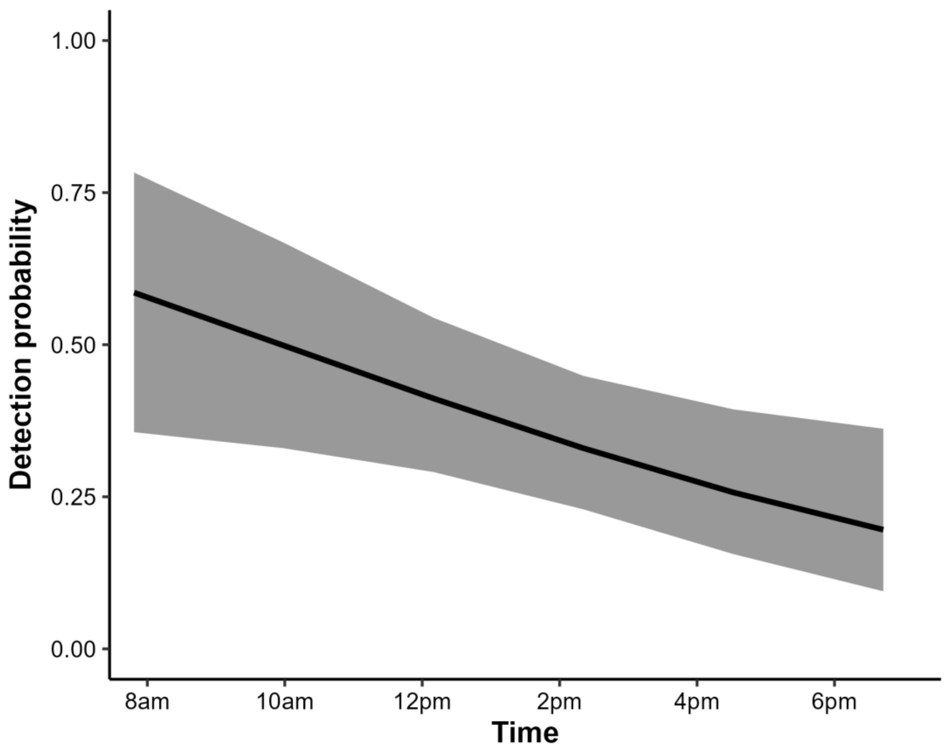


Table 1. Summary of Texas horned lizard captures at Beaver River Wildlife Management Area during summer 2021. No Texas horned lizards were recaptured. Data collection and summary led by A. Fulton (Project GRA at the time).

Survey Method	Total Number Texas Horned Lizards	Approximate Person-Hours
Y-Array Drift Fence	4	500+
Road Cruising	4	4
Visual Encounter On-Foot Searches	0	12
Opportunistic Road Cruising	23	N/A

Table 2. Summary of reptile and amphibian captures at Beaver River WMA (and vicinity) in the summer of 2021 by any capture method (funnel trap, pitfall trap, road cruising, dead-on-road, and hand captures combined). Data collection and summary led by A. Fulton (Project GRA at the time).

SPECIES	**TOTAL NUMBER**
AMPHIBIANS	
Ambystoma mavortium	5
Anaxyrus americanus	1
Anaxyrus cognatus	21
Anaxyrus woodhousii	1
Spea bombifrons	52
Spea multiplicata	1
REPTILES	
Arizona elegans	3
Aspidoscelis sexlineatus	47
Crotalus viridis	3
Crotaphytus collaris	1
Diadophis punctatus	1
Heterodon nasicus	5
Heterodon platirhinos	6
Lampropeltis calligaster	2
Lampropeltis holbrooki	6
Masticophis flagellum	3
Pantherophis emoryi	2
Phrynosoma cornutum	31
Pituophis catenifer	6
Plestiodon obsoletus	33
Rena dissecta	2
Rhinocheilus lecontei	4
Sceloporus consobrinus	10
Sonora semiannulata	2
Tantilla nigriceps	4
Terrapene ornata	2
Thamnophis radix	2

Table 3. Summary of species observed as part of summer-long sampling via drift fences and road cruising at Cooper WMA.

Group	**Genus**	**Species**	**Number**
Frogs	*Anaxyrus*	*woodhousii*	1
	Acris	*blanchardi*	1
	Lithobates	*blairi*	2
	Spea	*bombifrons*	3
Snakes	*Arizona*	*elegans*	7
	Coluber	*constrictor*	26
	Lampropeltis	*calligaster*	4
	Lampropeltis	*holbrooki*	1
	Masticophis	*flagellum*	3
	Pituophis	*catenifer*	11
	Sistrurus	*catenatus*	4
	Tantilla	*nigriceps*	3
	Thamnophis	*proximus*	1
	Thamnophis	*sirtalis*	1
Lizards	*Aspidoscelis*	*sexlineata*	7
	Plestiodon	*septentrionalis*	3
	Phrynosoma	*cornutum*	95
	Sceloporus	*consobrinus*	8
	Scincella	*lateralis*	1
Turtles	*Kinosternon*	*flavescens*	2
	Terrapene	*ornata*	25
	Trachemys	*scripta*	1
Total			210

Table 4. Summary results of herpetological captures from Sandy Sanders WMA.

Group	Genus	Species	Number captured
Anura (frogs)	*Anaxyrus*	*debilis*	3
	Anaxyrus	*punctatus*	8
	Acris	*blanchardi*	8
	Gastrophyne	*olivacea*	2
	Lithobates	*catesbeianus*	1
Serpentes (snakes)	*Coluber*	*constrictor*	2
	Lampropeltis	*calligaster*	1
	Lampropeltis	*holbrooki*	1
	Masticophis	*flagellum*	2
	Pituophis	*catenifer*	1
	Rhinocheilus	*lecontei*	1
	Thamnophis	*marcianus*	1
	Diadophis	*punctatus*	1
	Crotalus	*atrox*	1
Squamata (lizards)	*Crotaphytus*	*collaris*	2
	Phrynosoma	*cornutum*	53
	Sceloporus	*consobrinus*	2
	Aspidoscelis	*gularis*	29
Testudines (turtles)	*Terrapene*	*ornata*	4
TOTAL			**123**

Table 5. Summary of Texas Horned Lizard (*Phrynosoma cornutum*) survey effort and captures at Beaver River and Cooper Wildlife Management Areas in western Oklahoma. Each day a drift fence array was active is considered one trap day. The total number of unique individuals describes all captures through the entire field season, while the unique number of individuals by sample type describes within that sample type only (*).

Beaver River WMA (2021)

Sample type	Dates	Number of sites	Person-hours	Trap days	Number captures	Number unique individuals
Drift fence	3 Jun–4 Aug	10	–	846	4	4
Road Cruise	12 July – 30 July	2	–	–	4	4
Fortuitous	6 Jun–3 Aug	–	–	–	23	23
Total	**3 Jun–4 Aug**	**10**	**–**	**–**	**31**	**31**

Cooper WMA (2022)

Sample type	Dates	Number of sites	Person-hours	Trap days	Number captures	Number unique individuals
Drift fence	20 May–4 Aug	4	267.6	296	7	7
Road cruising	30 May–4 Aug	4	114.6	–	33	29
Plot search	7 Jun–4 Aug	9	84.3	–	2	1
Transect search	25 Jun–4 Aug	8	130.3	–	0	0
Fortuitous	19 May–3 Aug	–	–	–	95	68
Total	**19 May–4 Aug**	**25**	**596.8**	**–**	**137**	**95***

Table 6. Summary results of Texas Horned Lizard data from 2023 on Sandy Sanders WMA. Note: two individuals were excluded for the "by county" and "by location/method" summaries as the recorded GPS were inaccurate.

Captures by sex:	**Male**	**Female**	**Unknown/ juvenile**	
	7	26	22	
Captures by county:	**Beckham**	**Greer**	**Harmon**	
	9	37	7	
Captures by location/method:	**Driving routes**	**Walking routes/foot surveys**	**Drift fence**	**Fortuitous encounter (includes roads not part of driving routes)**
	27	12	1	13

Table 7. Summary of Texas Horned Lizard (*Phrynosoma cornutum*) captures along roads at Beaver River and Cooper Wildlife Management Areas in western Oklahoma. "Frequently traveled" roads are routes to and between drift fence arrays that were driven at least two times per day and included road cruising survey routes outside of designated surveys. Fortuitous captures occurred outside of survey efforts.

Beaver River WMA (2021)

Road description	Road length (km)	Capture type	Number captures	Captures/km (season total)
Frequently traveled	3.88	Fortuitous	13	3.35

Cooper WMA (2022)

Road description	Road length (km)	Capture type	Number captures	Captures/km (season total)
Frequently traveled	6.01	Fortuitous	69	11.48
Road cruising routes–				
Two-lane gravel	9.10	–	–	–
	–	Surveys	1	0.11
	–	Fortuitous	1	0.11
One-lane gravel/dirt	19.51	–	–	–
	–	Surveys	18	0.92
	–	Fortuitous	57	2.92
Two-track	18.58	–	–	–
	–	Surveys	14	0.75
	–	Fortuitous	22	1.18

Table 8. Oklahoma Department of Wildlife Conservation Ecological System assignment based on capture location for 168 Texas Horned Lizard (*Phrynosoma cornutum*) captures occurring at Cooper and Beaver River Wildlife Management Areas in western Oklahoma during the summers of 2021 and 2022. Additional descriptions of habitat types are available in Supplemental Table A.

Ecological System Categories	Number captures	Percent captures
Central Mixedgrass: Prairie/Pasture	7	4.2%
High Plains: Riparian Deciduous Shrubland	1	0.6%
High Plains: Sand Prairie	54	32.1%
High Plains: Sandhill Shrubland	77	45.8%
High Plains: Shortgrass Prairie	22	13.1%
Ruderal Eastern Redcedar Woodland and Shrubland	1	0.6%
Ruderal Plains Shrubland	6	3.6%
Total captures	**168**	**100%**

Supplemental Table A. Habitat description for all Oklahoma Ecological Systems in which Texas Horned Lizard (*Phrynosoma cornutum*) captures occurred at Beaver River, Cooper, and Sandy Sanders Wildlife Management Areas in western Oklahoma during the summers of 2021, 2022, and 2023.

Central Mixedgrass: Prairie/Pasture	Common species: Field Brome (*Bromus arvensis*), Cheatgrass (*Bromus tectorum*), Prairie Broomweed (*Amphiachyris dracunculoides*), Three-awn (*Aristida*) species, Hairy Grama (*Bouteloua hirsuta*), Buffalograss (*Bouteloua dactyloides*), Sideoats Grama (*Bouteloua curtipendula*), Grama (*Bouteloua*) species, Little Bluestem (*Schizachyrium scoparium*), Silver Bluestem (*Bothriochloa laguroide*s), Western Ragweed (*Ambrosia psilostachya*), Mesquite (*Prosopis* spp.), Eastern Redcedar (*Juniperus virginiana*), Osage Orange (*Maclura pomifera*), Honeylocust (*Gleditsia triacanthos*) Additional details: This category includes a wide range of grasslands that vary in precipitation and temperature.
High Plains: Riparian Deciduous Shrubland	Common species: Willow (*Salix*) species , Winged Elm (*Ulmus alata*), Elm (*Ulmus*) species, Honeylocust (*Gleditsia triacanthos*), Western Soapberry (*Sapindus saponaria*), Sugar Hackberry (*Celtis laevigata*), Ash (*Fraxinus*) species Additional details: This category is found along first- and second-order streams, with varying water levels and human activities. It is generally wetter than neighboring uplands.
High Plains: Sand Prairie	Common species: Little Bluestem (*Schizachyrium scoparium*), Sand Bluestem (*Andropogon hallii*), Switchgrass (*Panicum virgatum*), Sand Dropseed (*Sporobolus cryptandrus*), Sand Lovegrass (*Eragrostis trichodes*), Sandburs (*Cenchrus spp.*), Western Ragweed (*Ambrosia psilostachya*), Field Brome (*Bromus arvensis*), Cheatgrass (*Bromus tectorum*), Bermudagrass (*Cynodon dactylon*), Giant Sandreed (*Calamovilfa gigantea*), Sand Sagebrush (*Artemisia filifolia*), Chickasaw Plum (*Prunus angustifolia*), Havard Shin Oak (*Quercus havardii*), Soapweed Yucca (*Yucca glauca*) Additional details: The soil types for this category are aeolian or alluvial deep sands.
High Plains: Sandhill Shrubland	Common species: Sand Sagebrush (*Artemisia filifolia*), Fragrant Sumac (*Rhus aromatica*), Chickasaw Plum (*Prunus angustifolia*), Sand Bluestem *(Andropogon hallii*), Sand Dropseed (*Sporobolus cryptandrus*), Cheatgrass (*Bromus tectorum*), Western Ragweed (*Ambrosia psilostachya*), Soapweed Yucca (*Yucca glauca*), Grama (*Bouteloua*) species, Schweinitz Flatsedge (*Cyperus schweinitzii*), Yellow Sundrops (*Oenothera serrulata*), Annual Buckwheat (*Eriogonum annuum*), Havard Shin Oak (*Quercus havardii*) Additional details: This category commonly co-occurs with grassland habitats. The soil types for this category are aeolian or alluvial deep sands.

High Plains: Shortgrass Prairie	Common species: Blue Grama (*Bouteloua gracilis*), Buffalograss (*Bouteloua dactyloides*), Sideoats Grama (*Bouteloua curtipendula*), Silver Bluestem (*Bothriochloa laguroides*), Little Bluestem (*Schizachyrium scoparium*), Sand Dropseed (*Sporobolus cryptandrus*), Broom Snakeweed (*Gutierrezia sarothrae*), Soapweed Yucca (*Yucca glauca*), Prickly Pear (*Opuntia* spp.), Plains Blackfoot (*Melampodium leucanthum*), Rocky Mountain Zinnia (*Zinnia grandiflora*), Sand Sagebrush (*Artemisia filifolia*), White Sagebrush (*Artemisia ludoviciana*) Additional details: This category is distributed over a wide range of typically medium-textured soils.
Ruderal Eastern Redcedar Woodland and Shrubland	Common species: Hackberry (*Celtis*) species, Winged Elm (*Ulmus alata*), Elm (*Ulmus*) species, Ash (*Fraxinus*) species, Post Oak (*Quercus stellata*), Honeylocust (*Gleditsia triacanthos*), Black Locust (*Robinia pseudoacacia*), Western Soapberry (*Sapindus saponaria*), Lotebush (*Ziziphus obtusifolia*), Osage Orange (*Maclura pomifera*) Additional details: This category is generally underlaid by prairie soils.
Ruderal Plains Shrubland	Common species: Soapweed Yucca (*Yucca glauca*), Sand Sagebrush (*Artemisia filifolia*), White Sagebrush (*Artemisia ludoviciana*), Tree Cholla (*Cylindropuntia imbricata*), Chickasaw Plum (*Prunus angustifolia*), Siberian Elm (*Ulmus pumila*), Sugar Hackberry (*Celtis laevigata*), Soapberry (*Sapindus saponaria*), Broom Snakeweed (*Gutierrezia sarothrae*), Plains Broomweed (*Gutierrezia texana*), Grama (*Bouteloua*) species, Sand Dropseed (*Sporobolus cryptandrus*), and Brome (*Bromus*) species Additional details: This category is generally underlaid by prairie soils.
Canyon Grassland	Common Species: Hairy Gramma (*Bouteloua hirsuta*) Silver Bluestem (*Bothriochloa laguroides*), Little Bluestem (*Schizachyrium scoparium*), Stiff Greenthread (*Thelesperma fillifolium*), Broom Snakeweed (*Gutierrezia sarothrae*), White Sage (*Artemesia ludoviciana*), Additional details: This category is usually associated with weathering sedimentary rocks.
Canyon Gyp Juniper Shrubland	Common Species: Redberry Juniper (*Juniperus pinchottii*), Mesquite (*Prosopis glandulosa*), Silver Bluestem (*Bothriochloa laguroides*), Little Bluestem (*Schizachyrium scoparium* Additional details: Found on weathering sedimentary rock where gypsum is common.
High Plains Mesquite Shrubland	Common Species: Mesquite (*Prosopis glandulosa*), Plains Pricklypear (*Opuntia humifusa*), Prairie Broomweed (*Gutierrezia texana*), Silver Bluestem (*Bothriochloa laguroides*), Little Bluestem (*Schizachyrium scoparium,* Soapweed Yucca (*Yucca glauca*), Additional details: Occurs on relatively level, deep clay soils.

Supplemental Table B. Full Tukey's HSD test results for Texas Horned Lizard (*Phrynosoma cornutum*) captures along 1-km road segments at Cooper Wildlife Management Area in western Oklahoma by route (one–four) from occupancy modeling.

Road routes	Difference between means	Lower 95% CI	Upper 95% CI	*p*-value
one-two	0.97	-0.42	2.35	0.26
one-three	0.03	-1.29	1.35	>0.99
one-four	0.60	-0.75	1.95	0.63
two-three	0.94	-0.42	2.30	0.26
two-four	1.57	0.18	2.95	0.02
three-four	0.63	-0.69	1.95	0.58

Supplemental Table C. Full model selection results for occupancy analysis of Texas Horned Lizards (*Phrynosoma cornutum*) road cruising surveys at Cooper Wildlife Management Area in western Oklahoma in 2022. Table summarizing analyses by road cruising route (n sites=4; n samples=40). Variables listed include: Ψ=occupancy probability; p=detection probability; "." denotes a null (constant) model component; *k*=number of parameters; and *wi*=AIC weight. **Observation-level covariates**: am.pm=morning or evening survey; cloud=cloud cover; date=Julian date; num.obs=number of observers; obs.name=observer name(s); speed=average driving speed; temp=air temperature; time=time of day; wind=wind speed.

Model	***k***	**ΔAICc**	w_i
Ψ(.), *p*(time+obs.name)	11	0.00	0.460
Ψ(.), *p*(time+date)	4	3.27	0.107
Ψ(.), *p*(time)	3	5.96	0.052
Ψ(.), *p*(date+am.pm)	4	6.42	0.043
Ψ(.), *p*(date)	3	6.96	0.036
Ψ(.), *p*(obs.name+am.pm)	11	7.26	0.027
Ψ(.), *p*(obs.name)	10	7.81	0.022
Ψ(.), *p*(time+temp)	4	8.11	0.018
Ψ(.), *p*(date+temp)	4	8.14	0.018
Ψ(.), *p*(am.pm)	3	8.73	0.014
Ψ(.), *p*(date+num.obs)	4	8.81	0.013
Ψ(.), *p*(.)	2	9.05	0.010
Ψ(.), *p*(num.obs+obs.name)	11	9.89	0.007
Ψ(.), *p*(temp)	3	9.92	0.007
Ψ(.), *p*(speed)	3	10.43	0.004
Ψ(.), *p*(speed+temp)	4	10.84	0.003
Ψ(.), *p*(num.obs)	3	11.04	0.002
Ψ(.), *p*(wind)	3	11.11	0.002
Ψ(.), *p*(cloud)	6	14.86	0.000
Ψ(.), *p*(cloud+temp+wind)	8	17.49	0.000

Supplemental Table D. Full model selection results for occupancy analysis of Texas Horned Lizards (*Phrynosoma cornutum*) road cruising surveys at Cooper Wildlife Management Area in western Oklahoma in 2022. Table summarizing analyses by road cruising route 1-km segments (n sites=40; n samples=800). Variables listed include: Ψ=occupancy probability; p=detection probability; "." denotes a null (constant) model component; *k*=number of parameters; and *wi*=AIC weight. **Site-level covariates**: route=road cruising route (one–four); class=road classification type (two-lane gravel, one-lane gravel/dirt, two-track); central=percentage of site composed of Central Mixedgrass habitat*; plains=percentage of site composed of High Plains habitat*; ruderal=percentage of site composed of Ruderal habitat*; *Combined classifications from Oklahoma Department of Wildlife Conservation's Ecological Systems Map. **Observation-level covariates:** am.pm=morning or evening survey; cloud=cloud cover; date=Julian date; num.obs=number of observers; obs.name=observer name(s); speed=average driving speed; temp=air temperature; time=time of day; wind=wind speed.

Model	***k***	**ΔAIC**	w_i
***Ψ*(.), *p*(route)**	5	0.00	6.7e-01
***Ψ*(.), *p*(route+class)**	7	3.51	1.2e-01
***Ψ*(.), *p*(class)**	4	5.69	3.9e-02
***Ψ*(route), *p*(time+obs.name)**	14	6.97	2.1e-02
***Ψ*(.), *p*(obs.name)**	10	7.10	1.9e-02
***Ψ*(class), *p*(time+obs.name)**	13	7.69	1.4e-02
***Ψ*(plains), *p*(time+obs.name)**	12	8.18	1.1e-02
***Ψ*(route), *p*(.)**	5	8.30	1.1e-02
***Ψ*(.), *p*(date)**	3	8.32	1.0e-02
***Ψ*(class), *p*(.)**	4	8.81	8.2e-03
***Ψ*(central), *p*(.)**	3	8.93	7.7e-03
***Ψ*(.), *p*(.)**	2	8.97	7.6e-03
***Ψ*(plains), *p*(.)**	3	9.78	5.0e-03
***Ψ*(.), *p*(wind)**	3	9.84	4.9e-03
***Ψ*(route), *p*(obs.name+num.obs)**	14	9.96	4.6e-03
***Ψ*(class), *p*(obs.name+num.obs)**	13	10.08	4.3e-03
***Ψ*(.), *p*(time)**	3	10.22	4.1e-03
***Ψ*(plains), *p*(am.pm+obs.name)**	12	10.48	3.6e-03
***Ψ*(plains), *p*(obs.name+num.obs)**	12	10.65	3.3e-03
***Ψ*(.), *p*(plains)**	3	10.71	3.2e-03
***Ψ*(class), *p*(am.pm+date)**	6	10.89	2.9e-03
***Ψ*(route), *p*(am.pm+date)**	7	11.03	2.7e-03
***Ψ*(class), *p*(time+date)**	6	11.24	2.4e-03
***Ψ*(route), *p*(time+date)**	7	11.28	2.4e-03
***Ψ*(plains), *p*(date+num.obs)**	5	11.38	2.3e-03
***Ψ*(route), *p*(time+temp)**	7	11.41	2.2e-03
***Ψ*(plains), *p*(am.pm+date)**	5	11.48	2.2e-03
***Ψ*(plains), *p*(time+date)**	5	11.85	1.8e-03
***Ψ*(route+class), *p*(.)**	7	11.89	1.8e-03
***Ψ*(route), *p*(time+speed)**	7	12.05	1.6e-03
***Ψ*(class), *p*(time+temp)**	6	12.06	1.6e-03
***Ψ*(class), *p*(time+speed)**	6	12.20	1.5e-03
***Ψ*(ruderal), *p*(.)**	3	12.64	1.2e-03

Ψ(plains), *p*(time+temp)	5	13.02	1.0e-03
Ψ(plains), *p*(time+speed)	5	13.12	9.5e-04
Ψ(.), *p*(speed)	3	15.85	2.4e-04
Ψ(.), *p*(central)	3	15.85	2.4e-04
Ψ(.), *p*(ruderal)	3	17.23	1.2e-04
Ψ(.), *p*(num.obs)	3	17.46	1.1e-04
Ψ(.), *p*(am.pm)	3	17.61	1.0e-04
Ψ(route), *p*(cloud+temp+wind)	11	17.74	9.4e-05
Ψ(.), *p*(temp)	3	17.93	8.6e-05
Ψ(class), *p*(cloud+temp+wind)	10	18.64	6.0e-05
Ψ(class), *p*(am.pm+obs.name)	13	18.74	5.7e-05
Ψ(class), *p*(date+num.obs)	6	18.89	5.3e-05
Ψ(plains), *p*(cloud+temp+wind)	9	19.54	3.8e-05
Ψ(route), *p*(am.pm+obs.name)	14	20.74	2.1e-05
Ψ(route), *p*(date+num.obs)	7	20.89	2.0e-05
Ψ(.), *p*(cloud)	6	23.01	6.8e-06

Supplemental Table E. Full model selection results for occupancy analysis of Texas Horned Lizards (*Phrynosoma cornutum*) road cruising surveys at Cooper Wildlife Management Area in western Oklahoma in 2022. Table summarizing analyses by drift fence (n sites=14; n samples=134). Variables listed include: Ψ=occupancy probability; p=detection probability; "." denotes a null (constant) model component; *k*=number of parameters; and *wi*=AIC weight. **Site-level covariates:** epa.habitat=EPA Level IV Ecoregion; odwc.habitat=Oklahoma Department of Wildlife Conservation Ecological System; site=Cooper or Beaver River WMA. **Observation-level covariates:** week=time in week.

Model	*k*	ΔAICc	AICc Weight
***Ψ*(.), *p*(site)**	3	0.00	0.280
***Ψ*(.), *p*(.)**	2	0.34	0.201
***Ψ*(.), *p*(epa.habitat)**	4	1.56	0.127
***Ψ*(.), *p*(week)**	3	1.87	0.102
***Ψ*(site), *p*(.)**	3	1.92	0.099
***Ψ*(.), *p*(odwc.habitat)**	6	2.44	0.068
***Ψ*(site), *p*(week)**	4	3.43	0.040
***Ψ*(odwc.habitat), *p*(.)**	6	3.76	0.033
***Ψ*(epa.habitat), *p*(.)**	4	4.08	0.028
***Ψ*(odwc.habitat), *p*(week)**	7	5.33	0.015

Appendix I.—Summary of historical and modern voucher specimen records for Oklahoma populations of *Phrynosoma cornutum*, organized by county and collection year. Data summarized from SNM specimen holdings and a search of specimen availability on VertNet. Counties of highest conservation priority within the Oklahoma Comprehensive Wildlife Conservation Plan for biological surveys and monitoring for the Texas Horned Lizard are shown in bold, with counties targeted in this study highlighted in gray.

	No. Specimens			
County	**1890–1930**	**1931–1960**	**1961–1990**	**1991–2020**
Alfalfa	11	1	0	0
Beaver	0	4	1	0
Beckham	0	6	1	3
Bryan	0	3	0	0
Caddo	0	1	0	0
Canadian	0	0	0	2
Choctaw	0	2	0	0
Cimarron	10	1	6	2
Cleveland	25	46	8	2
Comanche	7	11	1	0
Creek	1	3	0	0
Custer	16	1	0	0
Dewey	0	16	0	0
Ellis	0	0	2	7
Garfield	0	6	8	0
Garvin	0	4	0	0
Grant	0	0	1	0
Greer	2	7	5	7
Harmon	24	4	3	3
Harper	1	2	3	3
Jackson	0	7	0	0
Jefferson	0	0	2	0
Kay	2	0	0	0
Kingfisher	1	2	0	0
Latimer	0	1	0	0
Logan	0	9	0	0
Love	0	1	0	0
Major	4	1	2	0
Marshall	0	7	1	0
Mayes	0	1	0	0
McClain	1	0	1	0
Noble	0	1	0	0
Nowata	0	2	0	0
Oklahoma	2	0	7	2
Okmulgee	1	3	0	0
Osage	0	1	0	0
Pawnee	7	0	2	0
Payne	1	5	0	0
Pottawatomie	0	37	0	0

Roger Mills	4	2	0	2
Rogers	0	1	0	0
Seminole	0	2	0	0
Stephens	1	0	0	0
Texas	5	0	1	0
Tillman	0	1	0	0
Tulsa	17	25	0	0
Washington	1	2	0	0
Washita	1	0	0	0
Woods	10	0	0	1
Woodward	4	1	0	0
TOTAL	159	230	55	34

Appendix II.—Map of current known Texas Horned Lizard populations in western Oklahoma (based on vouchered museum specimen GPS coordinates obtained from VertNet), showing locations of identified public conservation lands of highest priority.