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COMPARATIVE ANALYSIS OF SURVEY METHODOLOGIES FOR POPULATION-LEVEL STUDIES OF TEXAS HORNED LIZARDS (*PHRYNOSOMA CORNUTUM*)

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COMPARATIVE ANALYSIS OF SURVEY METHODOLOGIES FOR POPULATION-LEVEL STUDIES OF TEXAS HORNED LIZARDS (*PHRYNOSOMA CORNUTUM*)

A THESIS APPROVED FOR THE
SCHOOL OF BIOLOGICAL SCIENCES

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ABSTRACT

Texas horned lizards (*Phrynosoma cornutum*) are classified by the Oklahoma Department of Wildlife Conservation as a Tier 1 Species of Greatest Conservation Need and have similar designations throughout their range. Updated population assessments are needed range-wide to understand the current state of Texas horned lizard populations. However, most Texas horned lizard studies have relied upon fortuitous encounters and the lack of a standardized approach for population monitoring has significantly hampered our understanding of population trends. I carried out, with the assistance of field technicians, two summers of Texas horned lizard field research in western Oklahoma. I performed a comparative assessment of strategic survey methods: road cruising, drift fence arrays, and foot searches using transects and plots. Effort (person-hours) was logged for all methodologies. Road cruising surveys performed the best, with an average of 3.5 person-hours/Texas horned lizard followed by drift fence arrays (38.2 person-hours/Texas horned lizard) and plot foot searches (42.2 person hours/Texas horned lizard). Not all road types performed equally; one-lane gravel/dirt roads had the highest number of Texas horned lizards/km. Occupancy analyses using road cruising survey data indicated that the number of observers (one vs. two) did not significantly impact detection, whereas observer identity did affect detection, regardless of prior experience. Occupancy analyses indicated that time of day and time of year were important detection factors, with earlier in the day and in the spring/early summer showing higher detection probability. The number of recaptured lizards was inadequate to generate reliable population estimates using mark-recapture methodologies, and obtaining enough recaptures for these methods may be problematic. When comparing all methods, road cruising surveys are the most efficient and effective way to strategically survey

Texas horned lizards, and care should be taken to plan surveys in a way that optimizes detection, limits bias, and ensures datasets are comparable across the range.

INTRODUCTION

There are currently 17 recognized species of horned lizards, belonging to the genus *Phrynosoma* (Family: Phrynosomatidae), with distributions ranging from Mexico to Canada (Sherbrooke 2020). The Texas horned lizard (*Phrynosoma cornutum*) is an iconic and beloved species of the American Southwest and northern Mexico. Historically, horned lizard research has focused on Texas horned lizards due to their broad range. The Texas horned lizard range covers, at least in part, Arizona, Arkansas, Colorado, Kansas, Missouri, New Mexico, Oklahoma, Texas, and northern Mexico owing to their ability to live in relatively diverse desert and grassland habitats, with a variety of soils, and at elevations of up to 1830 m (Price 1990).

In much of their range, Texas horned lizards have suffered severe population declines for decades. This includes in Texas, Kansas, and Oklahoma: all states where Texas horned lizards were once found statewide (Carpenter et al. 1993; IUCN 2007; Miller et al. 2020). The decline of this ant-specialist species has been caused by a myriad of factors, including habitat loss and alteration, over-collection for the pet trade, pesticide use reducing available prey, and red imported fire ants (*Solenopsis invicta*) outcompeting their native ant prey (Carpenter et al. 1993; Donaldson et al. 1994; Henke & Fair 1998). In Oklahoma, Texas horned lizards were once encountered commonly, but today, they are classified by the Oklahoma Department of Wildlife Conservation as a Tier I Species of Greatest Conservation Need (Oklahoma Department of Wildlife Conservation 2016a). This designation is due to both their decline and need for updated range and population data, with the last comprehensive surveys and population assessments completed over 30 years ago (Carpenter et al. 1993; Oklahoma Department of Wildlife Conservation 2016a). In addition, Texas horned lizards are currently under petition for listing as a State Endangered Species to the Oklahoma Department of Wildlife Conservation by the Center for Biological Diversity (Center for Biological Diversity et al. 2014). To understand the condition of Texas horned lizard populations in Oklahoma and beyond requires updated and optimized surveys.

Studying Texas horned lizards in their natural environment comes with a unique set of challenges. As with most reptile species in temperate climates, they are not active year-round. In Oklahoma, the Texas horned lizard active season runs approximately April–October, with precise times dependent upon weather (Vesy et al. 2021). Where they are present, Texas horned lizards are often found in low densities that fluctuate over time (Endriss et al. 2007; Wolf et al. 2013; Williams et al. 2019; Vesy et al. 2021). Horned lizards are characterized by a dorsoventrally flattened body shape (“pancake-shaped”), short legs, and spiky body armor, particularly on the head (Pianka & Parker 1975). Relative to other lizards, they move slowly, with an awkward-appearing gait and a reliance on camouflage that makes them hesitant to run when approached (Pianka & Parker 1975). Low population density and the cryptic nature (reliance upon camouflage) of Texas horned lizards makes mark-recapture studies challenging; it is difficult both to initially encounter, and then later recapture, enough individuals (Pianka & Parker 1975; Hellgren et al. 2010). Hatchlings are even more difficult to detect and are subject to high mortality, further complicating the understanding of Texas horned lizard populations (Wolf et al. 2014; Vesy et al. 2021).

A wide variety of methods have been used to monitor Texas horned lizard populations including foot searches, drift fence trapping, road cruising surveys, and, recently, scat surveys and DNA analysis (Fair & Henke 1997; Burrow et al. 2001; Hellgren et al. 2010; Trinh 2016; Veech & Cave 2021; Huerta et al. 2023). All these survey methods have challenges with detecting Texas horned lizards and have been deployed ad hoc, with little comparison of their relative merits, and variable success rates based upon landscape features (Fair & Henke 1997; Hellgren et al. 2010). Most Texas horned lizard studies have relied upon “fortuitous encounters” (i.e., opportunistically finding lizards by walking or driving outside of constrained survey efforts) to detect lizards (Henke 2003; Moody et al. 2007; Hellgren et al. 2010; Wolf et al. 2013; Anderson et al. 2017). Fortuitous encounters work well for some needs, such as sourcing lizards for attaching radiotelemetry transmitters, but this method is not appropriate for population surveys due to the inability to compare lizard captures among sites by expended capture effort or area. With the difficulty of surveying for the cryptic and sometimes elusive Texas horned lizard, there is a substantial need for standardized survey methodologies that can be employed for population monitoring.

A standardized methodology for Texas horned lizard population surveys would be beneficial to conservation efforts in a variety of ways. Firstly, any study seeking to learn about Texas horned lizard populations, including size and density, needs to employ defined and repeatable methodology. There is currently a lack of information about Texas horned lizard populations across their range, including in Oklahoma, due to a dearth of surveys from which population information can be estimated (IUCN 2007; Oklahoma Department of Wildlife Conservation 2016a). It is paramount that surveys are not only repeatable over short time frames to get reliable current population estimates, but also can be repeated over longer time frames (for future monitoring), greater regions (i.e., other field sites and portions of their range), and across a variety of researchers. This would allow data to be directly comparable and enable not only quantifiable baseline surveys but continued, meaningful monitoring of populations. Secondly, a survey method needs to not only be repeatable, but also effective. Texas horned lizards have proven a great challenge to detect. Particularly in low-density populations, a survey method must be able to produce a substantial number of Texas horned lizard captures to allow for data analysis. Thirdly, a survey method should be efficient. Budget and personnel constraints are a constant in conservation research; an efficient survey method that does not involve a large burden of time, personnel, or equipment would allow more researchers to conduct broader scale Texas horned lizard research.

To address the need for standardized Texas horned lizard survey methods, we compared three commonly used methods: drift fence arrays, road cruising surveys, and foot searches. This comparative assessment of survey methods was conducted across two summers (2021–2022) at two Wildlife Management Areas (WMAs) in western Oklahoma, within the current range of Texas horned lizards. Our study aimed to elucidate the best methods for capturing Texas horned lizards for population surveys and arrive at recommendations for future survey and monitoring efforts. Furthermore, our objective was to identify population analyses compatible with the data obtained from successful survey efforts in order to learn more about the Texas horned lizard populations at these field sites. Texas horned lizard populations have suffered declines for decades, but there is no power behind anecdotal evidence of this decline; to assess viability and ensure appropriate protections of this species, updated state- and range-wide surveys are needed to understand current population dynamics and to serve as future comparisons.

FIELD METHODS

Texas Horned Lizard Biology–

Texas horned lizards are ant-specialists, preferring the sizeable harvester ants (*Pogonomyrmex* spp.), with ants composing up to >99% of their diet (Pianka & Parker 1975; Eifler et al. 2012). Ant mounds are commonly located on bare patches of ground, including unpaved roads (Demers 1993). Texas horned lizards can be found in a variety of arid and semiarid habitat types and thrive in mosaic habitat with mixed herbaceous vegetation, woody vegetation, and bare ground (Whiting et al. 1993; Henke & Fair 1998; Burrow et al. 2001). Mosaic habitat provides not only supports for their ant prey, but also a provides a clear view for spotting predators, vegetative cover from predators, and opportunities to thermoregulate (Henke & Fair 1998; Eifler et al. 2012). Texas horned lizards are a relatively slow lizard species with their short legs and round, dorsoventrally flattened bodies (Pianka & Parker 1975; Sherbrooke 2008). The pattern and roughness of their skin provides camouflage, which is their main defense from predators (Pianka & Parker 1975; Sherbrooke 2008). If a Texas horned lizard is not moving, it can be almost impossible to spot by the human eye. Texas horned lizards are frequently found on roads (Sherbrooke 2002). The bare ground and adjacent vegetation of unpaved roads meets their habitat needs, and the gravel and/or dirt composition of the roads provides an almost perfect match for the lizards' camouflage.

Study Areas–

Fieldwork occurred within two different WMAs in western Oklahoma, utilizing a different WMA each year. In 2021, we carried out Texas horned lizard research at Beaver River WMA located in Beaver County near the town of Beaver, OK in the Oklahoma Panhandle (Figure 1).

Beaver River WMA is 18,624 acres in size and is managed by the Oklahoma Department of Wildlife Conservation. Our survey sites at Beaver River WMA fall into the Level IV Ecoregions of Canadian/Cimarron High Plains and Canadian/Cimarron Breaks (U.S. Environmental Protection Agency 2012). The survey locations are composed of primarily High Plains: Shortgrass Prairie, underlaid with medium-textured soils, and to a lesser extent Ruderal Plains Shrubland that is underlaid with prairie soils (Diamond & Elliot 2015; Oklahoma Department of Wildlife Conservation 2016b). Consistent with these ecological system categories, the vegetation community across the survey sites is a mosaic comprised of mostly grasses interspersed with woody vegetation. The most prevalent vegetation species (from most to least abundant) were: western ragweed (*Ambrosia psilostachya*), sideoats grama (*Bouteloua curtipendula*), hairy grama (*Bouteloua hirsuta*), sand sagebrush (*Artemisia filifolia*), silver bluestem (*Bothriochloa laguroides*), buffalo grass (*Bouteloua dactyloides*), and the invasive species Japanese brome (*Bromus japonicus*; Diamond & Elliot 2015).

In 2022, our research was conducted in western Oklahoma at the Hal and Fern Cooper WMA (hereinafter “Cooper WMA”) spanning both Woodward and Harper counties and close to the city of Woodward, OK (Figure 1). Cooper WMA is 16,080 acres in size and is managed by the Oklahoma Department of Wildlife Conservation. Our survey areas within Cooper WMA are entirely located in the Pleistocene Sand Dunes Ecoregion (Level IV Ecoregion; U.S. Environmental Protection Agency 2012). Cooper WMA is primarily composed of High Plains: Sandhill Scrubland with, less commonly, interspersed High Plains: Sand Prairie and High Plains: Sandy Deciduous Shrubland (Diamond & Elliot 2015; Oklahoma Department of Wildlife Conservation 2016b). Sandy soils underlie Cooper WMA (Diamond & Elliot 2015). The vegetation community here is also a mosaic dominated by grasses with intermingled woody vegetation. Common vegetation species across these ecological system categories and the most dominant at our study sites include sand sagebrush (*Artemisia filifolia*), little bluestem (*Schizachyrium scoparium*), and western ragweed (*Ambrosia psilostachya*; Diamond & Elliot 2015). The invasive species Japanese brome (*Bromus japonicus*) is also present.

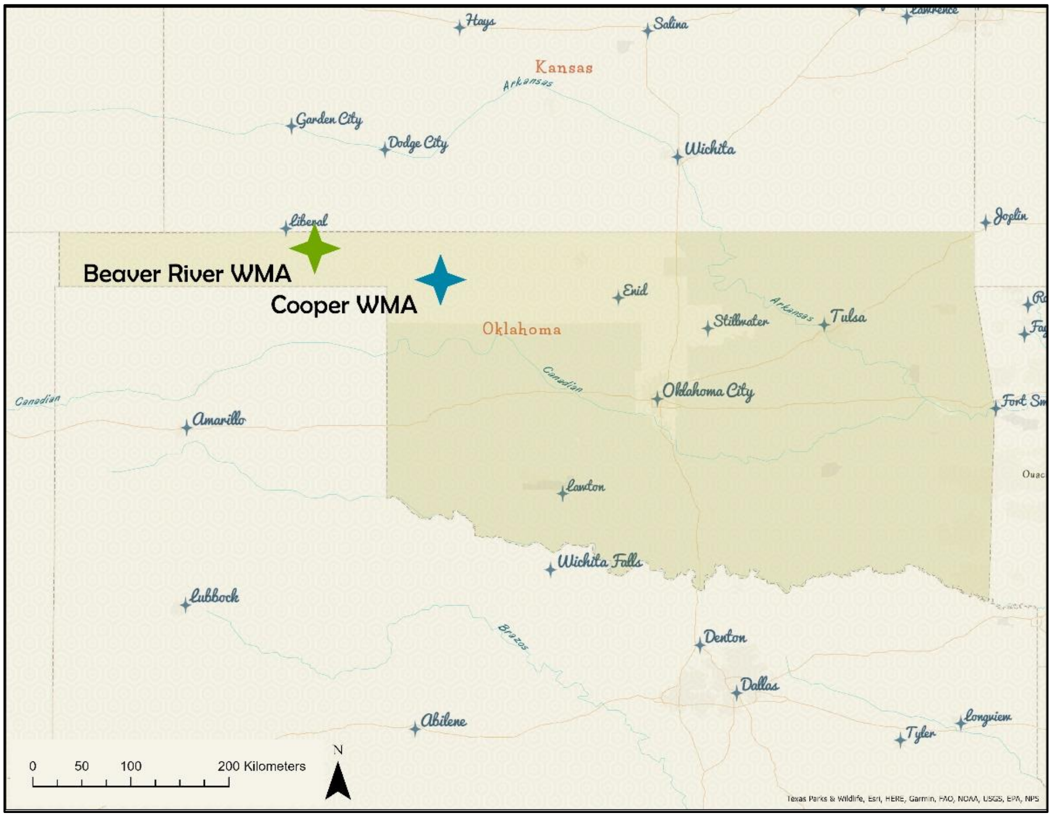


FIGURE 1. Locations of our Texas horned lizard (*Phrynosoma cornutum*) field sites in 2021 (Beaver River WMA) and 2022 (Cooper WMA).

General–

At Beaver River WMA (2021), our survey effort consisted of drift fence trapping. The following year at Cooper WMA (2022), we continued drift fence trapping, but included road cruising surveys, plot foot searches, and transect foot searches due to low drift fence captures in

2021 (see Table 1 for summary of survey methods and effort). Survey site locations were selected based upon perceived suitability for Texas horned lizards including presence of mosaic habitat, ant mounds, and/or prior knowledge of Texas horned lizard occurrence in the area.

In 2022, we tracked the person-hours (Rolfe & McKenzie 2000) worked by each researcher for each survey method as a measure of efficiency. Person-hours included carrying out surveys; installation, repair, and material removal needed for survey methods; processing all herpetofauna captured during surveys; and recording data in the field. We did *not* include in person-hours the commute time between our housing and survey locations, travel between or to survey locations, herpetofauna processing time for encounters outside of formal surveys, survey site location scouting, or computer data entry.

For active survey methods (road cruising surveys, plot foot searches, and transect foot searches), we employed standardized survey constraints to keep data comparable and recorded environmental conditions. Each active survey site was completed a maximum of one time per day, and observers did not complete two foot searches or two road cruising surveys in a row to avoid eye fatigue. Active surveys were completed entirely during the hours of most Texas horned lizard activity: 8:00 am–12:00 pm (“morning”) and 4:00 pm–8:30 pm (“evening”). At the start and end of each active survey, the following data were collected: time, wind speed, cloud cover, and air temperature using the Mesonet Woodward station (WOOD, #107; Brock et al. 1995; McPherson et al. 2007). At the end of each survey, we also recorded total time spent searching for Texas horned lizards. 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 wet from prior rain.

TABLE 1. Summary of Texas horned lizard (*Phrynosoma cornutum*) survey effort and captures at Beaver River and Cooper WMAs. Each day a drift fence array was active is considered one trap day. *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
Fortuitous	6 Jun–3 Aug	–	–	–	27	27
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 foot search	7 Jun–4 Aug	9	84.3	–	2	1
Transect foot 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***

Drift Fence Arrays–

We utilized Y-array drift fences ("arrays"; Fair & Henke 1997; Crosswhite et al. 1999; Ribeiro-Júnior et al. 2008; Hutchens & Deperno 2009) with each composed of three 8-m long sections ("wings") made of vinyl or galvanized steel flashing (58 cm tall) placed approximately 120° apart, 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. Wings were buried approximately 10 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. 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 that were placed two per wing, one on each side, approximately in the middle of the wings. Dirt ramps were used on each funnel trap to prevent animals from going behind the traps and to smooth the transition from the ground into the trap. Funnel and pitfall traps were shaded from the intense Oklahoma sun by angled plywood boards or elevated 18.9-L/5-gallon bucket lids. In 2021, the funnel traps we used were black vinyl-coated minnow traps (42 cm long, 22 cm center diameter, 2.5 cm openings). In 2022, we used handmade funnel traps constructed of aluminum window screen mesh and office staples (76 cm long, 23 cm diameter, 4 cm openings; Fair & Henke 1997; pers. Comm. Jeff LeClere). All arrays were located near roads (3–65 m). In 2021, we paired our 10 arrays into five groups of two, placing each array a mean distance of 68 m (27–123 m) from its nearby counterpart. In 2022, we dispersed arrays and did not pair them. 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 12.9–19.3 kph (8–12 mph), with an average speed of 16.1 kph (10.0 mph), along predefined routes at Cooper WMA while actively searching the road for Texas horned lizards. When a Texas horned lizard was spotted, the vehicle was stopped, and the observer(s) quickly exited the vehicle to attempt a capture. Road cruising surveys were completed with either one or two observers. There were four road cruising routes with 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). 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 minutes and 7 seconds. Over the field season, all routes were completed at least five times in the morning with one observer, five times in the evening with one observer, five times in the morning with two observers, and five times in the evening with two observers (Route 1 *n*=20; Route 2 *n*=22; Route 3 *n*=22; Route 4 *n*=21).

We classified roads into three categories: two-lane gravel roads, one-lane gravel/dirt roads, and two-track roads. One-lane gravel/dirt roads consisted entirely of gravel, entirely of dirt, or a combination of the two. Two-track roads are defined as roads where there are two bare ground, approximately tire-width, strips with vegetation growing in the middle. 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 was comprised of 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%).

Foot Searches–

During foot searches at Cooper WMA, we walked, looking ahead of our feet, with as wide and far of a visual range as possible depending upon the surrounding vegetation and habitat composition, with a goal of a 2-m wide visual range (though this was often reduced due to thick vegetation). One observer at a time was used for foot searches and each site was completed 10 times over the season, five in the morning and five in the evening.

Each plot foot search consisted of a 50x50 m square delineated using flagging tape. We searched plots by walking 25 straight lines through the plot, spaced approximately two m apart, back and forth between two parallel sides of the plot. Mean search time per plot foot search was 32 minutes and 43 seconds (30 minutes and 0 seconds–39 minutes and 21 seconds). Plots had a mean distance from the nearest major road of 145 m (7–490 m).

A transect foot search was comprised 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 away from the road with the far side of each transect at least 500 m from any main road in the WMA. To complete one transect foot search required the completion of both transects “a” and “b”, and total search time per transect foot search was on average (mean) 32 minutes and 7 seconds (range: 30 minutes and 0 seconds–36 minutes and 32 seconds).

Herpetofauna Data Collection–

We collected data on all Texas horned lizard captures, including date and capture location (latitude/longitude; GPS), both during survey efforts and for fortuitous encounters in 2021 and 2022. For all Texas horned lizard captures in 2022, we also recorded time, wind speed, cloud cover, and air temperature using the Mesonet Woodward station (WOOD, #107; Brock et al. 1995; McPherson et al. 2007). The following biological data were collected on all Texas horned lizards: mass (g; Pesola scale); body measurements (mm; digital calipers; snout-vent length, tail-vent length, right and left occipital spike length); sex; cloacal swab for microbiome; photograph of ventral and dorsal surfaces; and any physical abnormalities. All captured Texas horned lizards were also marked using a unique toe clip (Vesy et al. 2021), taking two toes with no more than one toe per limb. All Texas horned lizards were released immediately after processing at the location of their capture, except for two lizards (one from Beaver River WMA and one from

Cooper WMA) that were vouchered into the Sam Noble Museum of Natural History Herpetological Collection, University of Oklahoma, Norman, OK.

ANALYTICAL METHODS

Roads and Counting Captures–

Digitization of roads and Texas horned lizard capture locations was completed using ArcGIS Pro (ESRI; v3.0.4). I digitized and measured the roads that we drove frequently (to and between drift fence arrays) at both WMAs and road cruising routes by road type classification at Cooper WMA.

I determined the road type classification associated with each Texas horned lizard capture along road cruising survey routes at Cooper WMA. I calculated the number of Texas horned lizard captures/km for fortuitous encounters along frequently travelled roads at both WMAs. For Cooper WMA, I 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, I considered road cruising survey captures at Cooper WMA and 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 with the averaged captures/km.

I evaluated the association of Texas horned lizard capture sites to ecological system categories to indicate potential preferred habitats. Using all 168 Texas horned lizard captures during 2021 and 2022 and ArcGIS Pro (ESRI; v3.0.4), I determined the ecological system category associated with each capture based on the Oklahoma Ecological Systems Map, utilizing its fine-scale resolution (10 m; Oklahoma Department of Wildlife Conservation 2016b). This mapping system uses remote sensing data and classifies Oklahoma into 165 land cover and vegetation types (ecological system categories). I used the ‘Spatial Join’ function to join the capture points with the ecological system categories. I excluded the “Urban Low Intensity” category, which includes “most non-industrial areas within cities and towns” (Diamond & Elliot 2015), because it does not accurately describe any of the areas at the WMAs we surveyed, although some road segments were classified in this category. This resulted in 30 ecological system categories in the WMAs. If a capture location fell within Urban Low Intensity, the next closest ecological system category was selected for its designation using the “closest” spatial join match option.

Spatial Clustering–

I analyzed all fortuitous Texas horned lizard encounters along frequently travelled roads (to and between drift fence arrays) both at Beaver River WMA (*n* captures=13; Figure 5a–b) and Cooper WMA (*n* captures=69; Figure 5c–d). I also considered road cruising survey captures at Cooper WMA by evaluating all captures during road cruising surveys (*n* captures=33; Figure 6a–b), captures occurring along one-lane gravel/dirt roads only (*n* captures=18; Figure 6c–d), and captures occurring along two-track roads only (*n* captures=14; Figure 6e–f). During data analysis (described below), each generated replicate random point pattern had the same number of lizard-capture data points as the comparative field-generated data and were constrained along roads.

I evaluated Texas horned lizard spatial clustering along roads by two methods using *R* packages (v4.2.2; *R* Core Team 2022). First, I used the *F*-function and simulation envelopes in the ‘spatstat’ package (v3.0.6; Baddeley et al. 2015) 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 (the envelope; Figures 5a, 5c, 6a, 6c, and 6e). I 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, that 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 non-random, evenly distributed pattern (Anselin 2016). The figure produced by this 'envelope' simulation plots distance in m (*r*) against *F*(*r*), the proportion of distances in a point pattern that are less than the distance (m) when measured from an arbitrary reference point.

In the second method, I evaluated Texas horned lizard clustering along roads with a Monte Carlo analysis using 9,999 simulations of randomly generated point patterns to test the likelihood of observing a random mean nearest neighbor distance less than that of observed mean nearest neighbor distances (Figures 5b, 5d, 6b, 6d, and 6f). This 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 (instead of calculating for each point and then averaging). I calculated the mean nearest neighbor distance among observed capture patterns and randomly generated patterns using the 'nndist' function from the 'spatstat' package in *R* (v3.0.6; Baddeley et al. 2015).

Occupancy Analysis–

To understand the influence of road cruising routes and other factors on the probability of Texas horned lizard occurrence and detection, I modeled occupancy using detection/non-detection data. Observed sightings of Texas horned lizards reflect both the true occupancy and detection probability, while occupancy analysis separates these two elements and calculates estimates for occupancy and detection probability individually. I utilized the ‘occu’ function (MacKenzie et al. 2002) from the ‘unmarked’ package (v1.2.5; Fiske & Chandler 2011) in *R* (v4.2.2; *R* Core Team 2022). Initially, this involved analyzing occupancy for the four road cruising routes at Cooper WMA. Due to the limited number of sites (routes; *n*=4), there was little power to evaluate site-level covariates; analyses focused instead on observation-level covariates. To complement this route-specific view and evaluate how different road and habitat types may impact occupancy or detection, I modeled occupancy by dividing road cruising routes into one-km segments by road classification types (two-lane gravel, one-lane gravel/dirt, two-track). This resulted in a total of 40 “sites”. Due to these constraints, some sections of the road cruising routes were not included in this analysis (7.2 km and two Texas horned lizard captures). To avoid biasing segment selection, I digitized all segments starting from the northern extent of each road classification type stretch. For this second analysis, I considered both site-level 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, cloud cover, wind speed, Julian date, morning (8:00am–12:00pm) or evening (4:00pm–8:30pm) survey (categorical), time of day (continuous), number of observers (one or two), observer identity (to account for possible inter-observer differences), and average driving speed. Air temperature, cloud cover, wind speed, and time of day covariates were calculated by using 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 base *R* (v4.2.2; *R* Core Team 2022).

Site-level covariates for occupancy modeling of road cruising surveys included: road classification type, route, and composition (percentage) of three ecological system categories. Ecological system categories were assessed from the Oklahoma Department of Wildlife Conservation's Ecological Systems Map and combining similar classifications along road cruising routes into broader categories: Central Mixedgrass, High Plains, and Ruderal (Diamond & Elliot 2015; Oklahoma Department of Wildlife Conservation 2016b). To determine the amount of each road segment that fell into each ecological system category, I utilized ArcGIS Pro (ESRI; v3.0.4) and started with the 'Densify' tool to add vertices every 10 m along the route polylines. Next, I converted these vertices to points with the 'Feature Vertices to Points' tool. Then, I performed a 'Spatial Join' where I assigned each point an ecological system category. I excluded the ecological system category of "Urban Low Intensity", as Cooper WMA is not an urban area, although some roads were classified as such. If a point occurred in "Urban Low Intensity", the next closest ecological system category was specified as the match. I excluded any points in ecological system categories describing planted crops, due to low sample size.

To better understand the effectiveness of drift fence trapping and factors that may influence its success, I 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, I used one observation-level (time in weeks) and three site-levels (WMA, EPA Level IV Ecoregion, and Oklahoma Department of Wildlife

Conservation Ecological System; U.S. Environmental Protection Agency 2012; Diamond & Elliot 2015; Oklahoma Department of Wildlife Conservation 2016b).

I started with single-covariate models using each covariate to compare against the null models to identify important factors for either occupancy or detection probability, and then continued to combine significant covariates to form multi-covariate models. I evaluated 11 models for road cruising routes, 23 models for one-km road segments, and nine models for drift fences. I compared models for one-km road segments and drift fences using the Akaike information criterion ("AIC"; Table 4), considering ΔAIC $\geq$2 and AIC weight to differentiate strongly supported models (Burnham & Anderson 2002). AIC weight provides the relative support for all considered models (Burnham & Anderson 2002). I used AICc, to compare models for road cruising routes, as this provides a correction for the small sample sizes (*n*=80) used in this analysis. Again, here I focused on comparing ΔAICc and AICc weight to determine what models were most supported. When there was more than one model within two ΔAIC/ ΔAICc of each other, the model with the lowest number of parameters was retained (Burnham & Anderson 2002). I used the 'modavgPred' function in the 'AICcmodavg' package (v2.3.2; Mazerolle 2023) to visualize model-averaging predictions of detection for important covariates (Figure 7). Important site-level covariates were further analyzed for significant differences between groups using a single-factor ANOVA analysis performed with Analysis Tools in Microsoft® Excel® (v2305).

Number of Observers–

To determine if there is a statistical difference in the number of Texas horned lizard captures between one-observer and two-observer road cruising surveys, I analyzed data using Analysis

Tools in Microsoft® Excel® (v2305). I used an *F*-test to assess variance in Texas horned lizard captures between these two groups, followed by a *t*-test assuming equal variances.

Mark-recapture–

Because population size is a key parameter needed for conservation and monitoring, I attempted to estimate Texas horned lizard survival, capture probability, and population size at Cooper WMA using a POPAN model in Program MARK for live captures (v10; White & Burnham 1999; Cooch & White 2014). As no Texas horned lizards were recaptured at Beaver River WMA mark-recapture analysis was not possible for this field site. I aggregated each week of the Cooper WMA (2022) field season into one capture event, starting at the beginning of the survey efforts (20 May 2022) and ending with the last day of the field season (4 August 2022) for a total of eleven capture events (i.e., weeks). Capture events had a time interval of one between events, as they were consecutive weeks. I used one attribute group for analysis, combining all lizards regardless of sex or age (no hatchlings were captured). This reflected the uncertainties in sexing and aging lizards, but resulted in a larger dataset. For this analysis, all captures during the field season were included regardless of the survey method associated with the capture. If a lizard was captured at least once during a survey event, it was assigned a value of “1”; and if a known individual was not detected during a capture event it was assigned a value of “0”. See Supplemental Materials 1.1 for the complete capture history.

The POPAN model uses the Jolly-Seber framework, and as is typical of this sort of analysis, some core assumptions were broken; this should be considered when interpreting the results (Olsen 2006). Jolly-Seber assumptions are relevant for POPAN modeling (Cooch & White 2014). Firstly, both the assumptions that all marked lizards had an equal probability of being recaptured and that the study area never changed were not met (Cooch & White 2014). We did not visit all study areas within Cooper WMA every week and the time spent at survey areas varied by week. Although not a perfect solution, having each capture event as one week (instead of one day) helps to even out survey effort, allowing coverage of more study areas during each capture event. Also, individual Texas horned lizard behavior and home range selection can impact the recapture probability; for example, a lizard that spends most of its time on a road is more likely to be captured than one that spends time in a vegetated area. In addition, some lizards may have resided in different areas of their home range over the survey times, and not all their home range may have been included in our study areas. Secondly, it is uncertain whether the assumption that all marked lizards had equal survival probability between capture events and that no lizards exited the population were met (Cooch & White 2014). Individual lizard behavior and home range can also impact survivorship, and that was beyond the control of our research efforts. For example, if a lizard spends more time on roads than in vegetated areas, that may expose the lizard to more risk of predators and vehicle strikes. Furthermore, the age of a lizard may impact their survival probability and for this modeling, all lizard age groups were included without separation. Additionally, our study took place over eleven weeks, and there could have been undiscovered mortality of marked lizards during this period. The next two assumptions were met: marked lizards were accurately identified, and all captured lizards were immediately released (Cooch & White 2014). We always processed lizards in the location of capture and released them immediately after we finished. The toe clip marks that the lizards were given were easy to spot when examined carefully and are non-reversible. POPAN models also have an assumption in addition to the core Jolly-Seber mark-recapture assumptions: marked and unmarked lizards are equally likely to be captured (Cooch & White 2014). Our research meets this assumption, as the marks we gave were discreet and unable to be ascertained until a lizard was captured. There also was no evidence of Texas horned lizards developing an increased aversion to capture.

In the POPAN model, survival probability (ϕ) estimates the chance that an individual will survive from one capture event to the next capture event (Cooch & White 2014). A survival probability is generated for each interval between capture events with ϕ_1 reflecting the survival probability between capture events one and two, ϕ_2 reflecting the survival probability between capture events two and three, and so on (Cooch & White 2014). All survival probability estimates are viable in POPAN except for the final survival probability, which is confounded (in this case, ϕ_{10} is unusable and has not been reported; Cooch & White 2014). The estimates for capture probabilities (p) in POPAN describe the chance that a lizard will be captured during each capture event (catchability; Cooch & White 2014). Capture probability is estimated for every capture event (here, $p1$–$p11$), though the estimates for the first and last capture events will always be confounded and have not been reported (here, $p1$ and $p11$; Cooch & White 2014). The *PENT* (probability of entrance) estimates the probability that new individuals are entering the surveyed population (Cooch & White 2014). *PENT* is estimated for every capture event after the initial, but the first and last generated *PENT* will always be confounded and the estimates have not been reported (in this case, *PENT1* and *PENT10*; *PENT0* is not calculated and relates to the first capture event; Cooch & White 2014). $N*$ is the gross population, the total estimated size of the studied population (Cooch & White 2014). This number ($N*$) is a single number that is generated and covers the entire study area during the survey period accounting for the inability of studies to reach all target individuals (Cooch & White 2014). In addition to estimating $N*$, POPAN also estimates N. This N is the population estimate as it relates to each capture event considering only the mark-recapture data (Cooch & White 2014). *N* is generated for each capture event, and the first and last *N* estimates cannot be used due to confounding (here, *N1* and *N11* are not reported; Cooch & White 2014). Lastly, POPAN produces estimates for new individuals entering the population (Cooch & White 2014). This includes gross births and immigration (*B**), which considers the total number of new births and newly immigrated individuals (Cooch & White 2014). Another measure POPAN estimates is net births and immigration (*B*); this considers births and immigration, in addition to deaths, to give an estimate of actual population growth (Cooch & White 2014). For both *B** and *B*, estimates are generated for the time periods between each capture event (Cooch & White 2014). *B*1* and *B1* refer to the population change between capture events one and two, *B*2* and *B2* refer to the population change between capture events two and three, and so on (Cooch & White 2014). Due to confounding, the first and last iterations of *B** and *B* are not usable (here, *B*1* and *B1*; *B*10* and *B10*; Cooch & White 2014).

When running the POPAN model, I selected parameter-specific link functions and specified "Sin" for both survival probability (ϕ) and capture probability (p; Cooch & White 2014). I chose the link function "MLogit(1)" for *PENT* (probability of entrance into the population) as all Texas horned lizards are put into one group for this analysis (Cooch & White 2014). And *N* was specified as "Log" (Cooch & White 2014).

RESULTS

Field Data Summary–

In 2021 at Beaver River WMA, we had a total of 31 Texas horned lizard captures: 27 fortuitous encounters and four drift fence captures (Table 1). Of the drift fence captures in 2021, two occurred in pitfall traps and two occurred in funnel traps. In 2022 at Cooper WMA, we had a total of 137 Texas horned lizard captures: 95 fortuitous encounters, 33 road cruising survey captures, seven drift fence captures, and two plot foot search captures (Table 1). Of the drift fence array captures in 2022, four occurred in pitfall traps and three occurred in funnel traps.

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 foot searches.

Roads and Counting Captures–

Texas horned lizards were captured on roads both during road cruising surveys and by fortuitous encounter (Table 2). Considering only road cruising surveys (Cooper WMA), the number of captures/km by road type classification showed a significant deviation from the expected proportion ($\chi^2=43.79$; p-value<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 2; Figure 2). Two-track roads performed the second best (road cruising=0.75; fortuitous=1.18), followed by two-lane gravel roads (road cruising=0.11; fortuitous=0.11; Table 2; Figure 2). Along the roads we frequently travelled (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 2).

TABLE 2. Summary of Texas horned lizard (*Phrynosoma cornutum*) captures along roads at Beaver River and Cooper WMAs. Frequently travelled roads are routes to and between drift fence arrays that were driven at least two times per day. 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 travelled	3.88	Fortuitous	13	3.35

Cooper WMA (2022)

Road description	**Road length (km)**	**Capture type**	**Number captures**	**Captures/km (season total)**
Frequently travelled	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

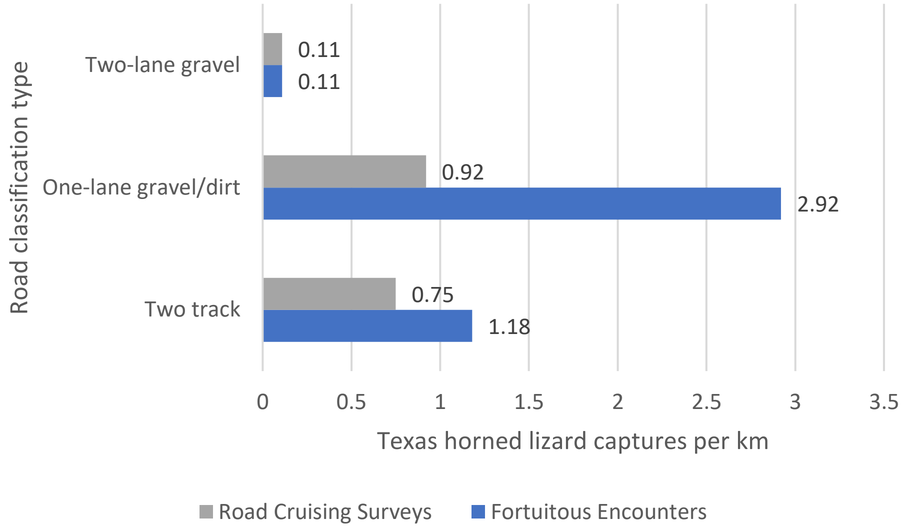
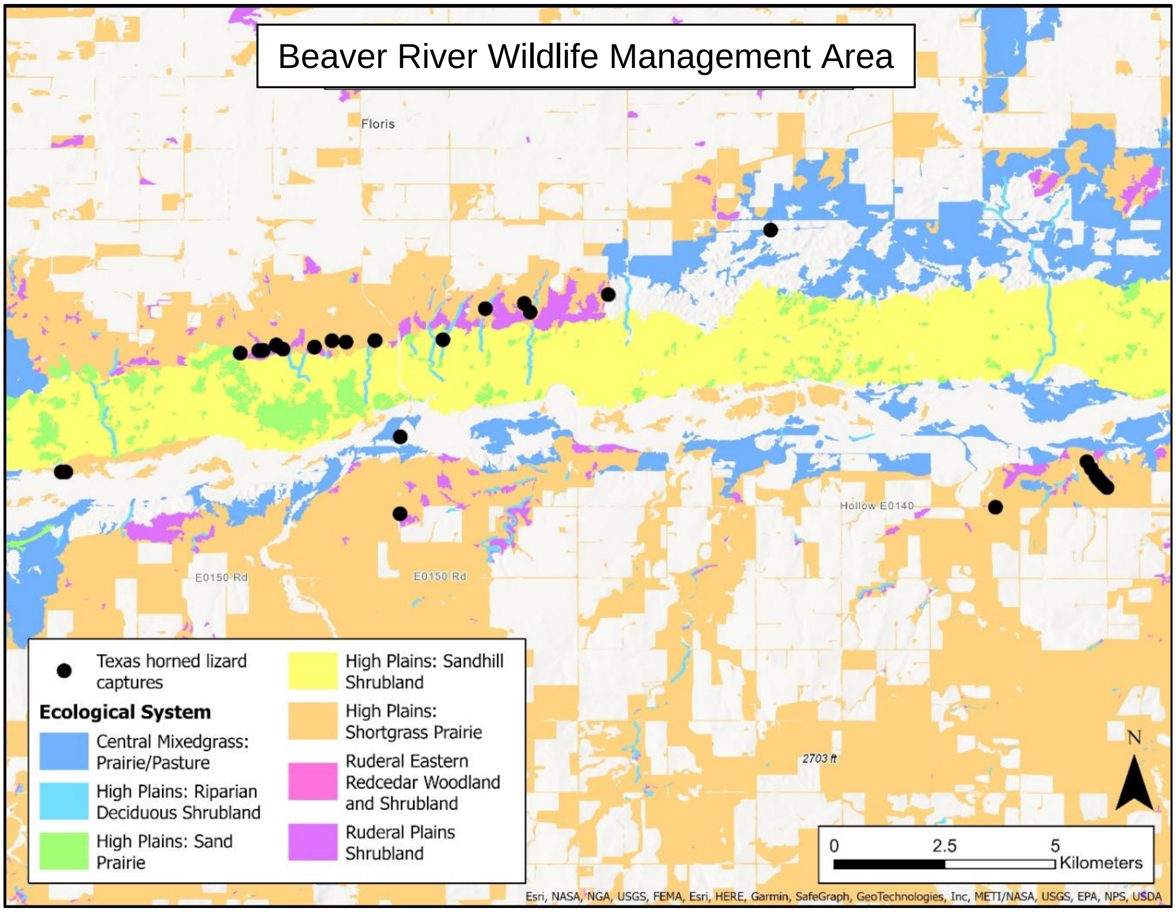


FIGURE 2. Number of Texas horned lizard captures (*Phrynosoma cornutum*) per km along road cruising survey routes at Cooper WMA in 2022 across the entire field season.

Texas horned lizard captures (*n*=168) occurred in a total of seven Oklahoma Department of Wildlife Conservation Ecological System categories during our 2021 and 2022 field seasons (Figures 3 and 4; Table 3; Oklahoma Department of Wildlife Conservation 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 & Elliot 2015; Table 3; Figures 3 and 4). These three ecological systems categories yielded the majority of Texas horned lizard captures (91%; Table 3). The remaining 9% of captures were distributed throughout the other four ecological system categories (Table 3; Figures 3 and 4).

TABLE 3. Oklahoma Department of Wildlife Conservation Ecological System assignment based on capture location for 168 Texas horned lizard (*Phrynosoma cortunum*) captures occurring at Cooper WMA and Beaver River WMA during the summers of 2021 and 2022.

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%



Esri, NASA, NGA, USGS, FEMA, Esri, HERE, Garmin, SafeGraph, GeoTechnologies, Inc, METI/NASA, USGS, EPA, NPS, USDA

FIGURE 3. Texas horned lizard (*Phrynosoma cornutum*) capture locations from Beaver River WMA in 2021 and their associated ecological system categories from Oklahoma Department of Wildlife Conservation's Oklahoma Ecological Systems Map.

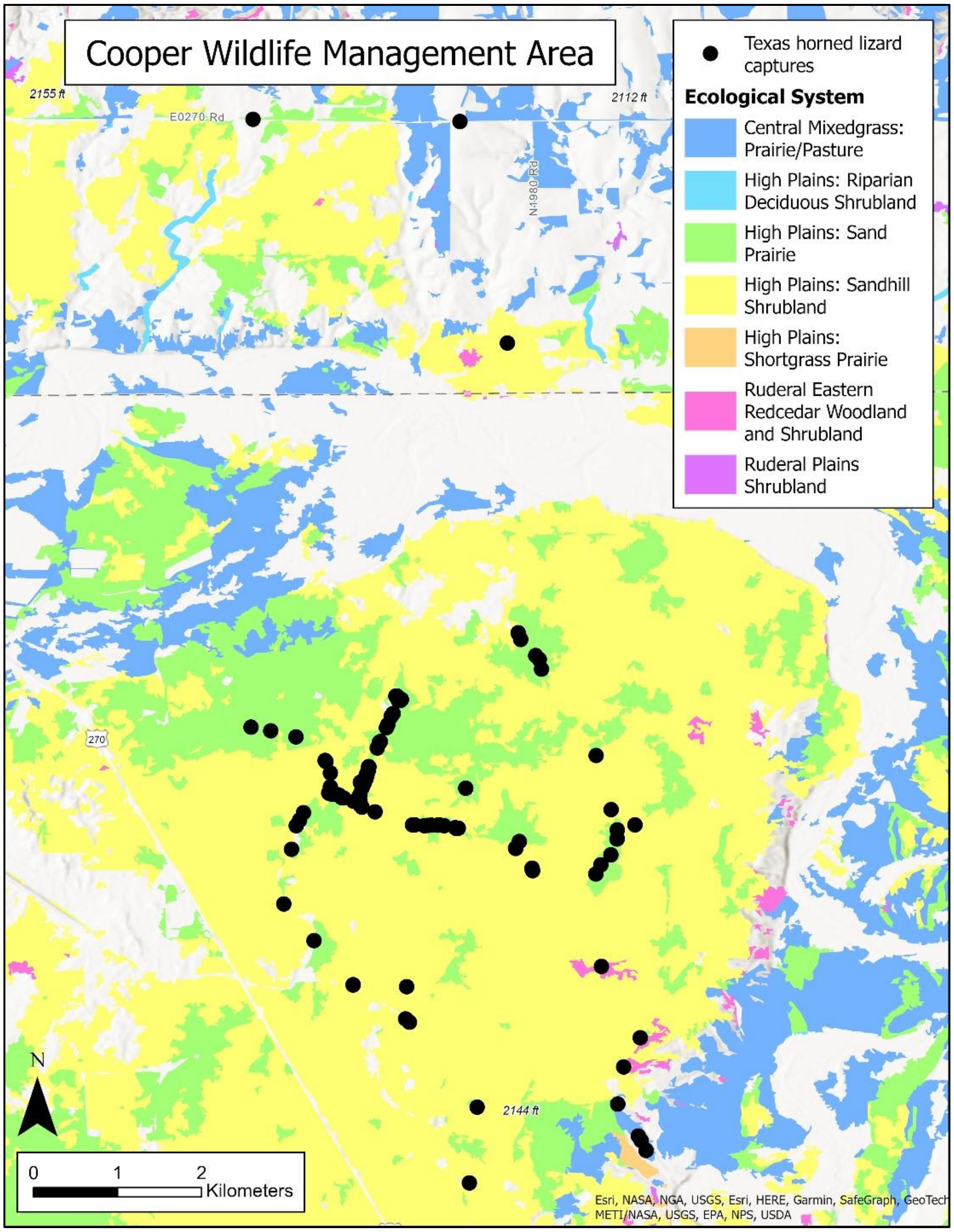


FIGURE 4. Texas horned lizard (*Phrynosoma cornutum*) capture locations from Cooper WMA in 2022 and their associated ecological system categories from Oklahoma Department of Wildlife Conservation's Oklahoma Ecological Systems Map.

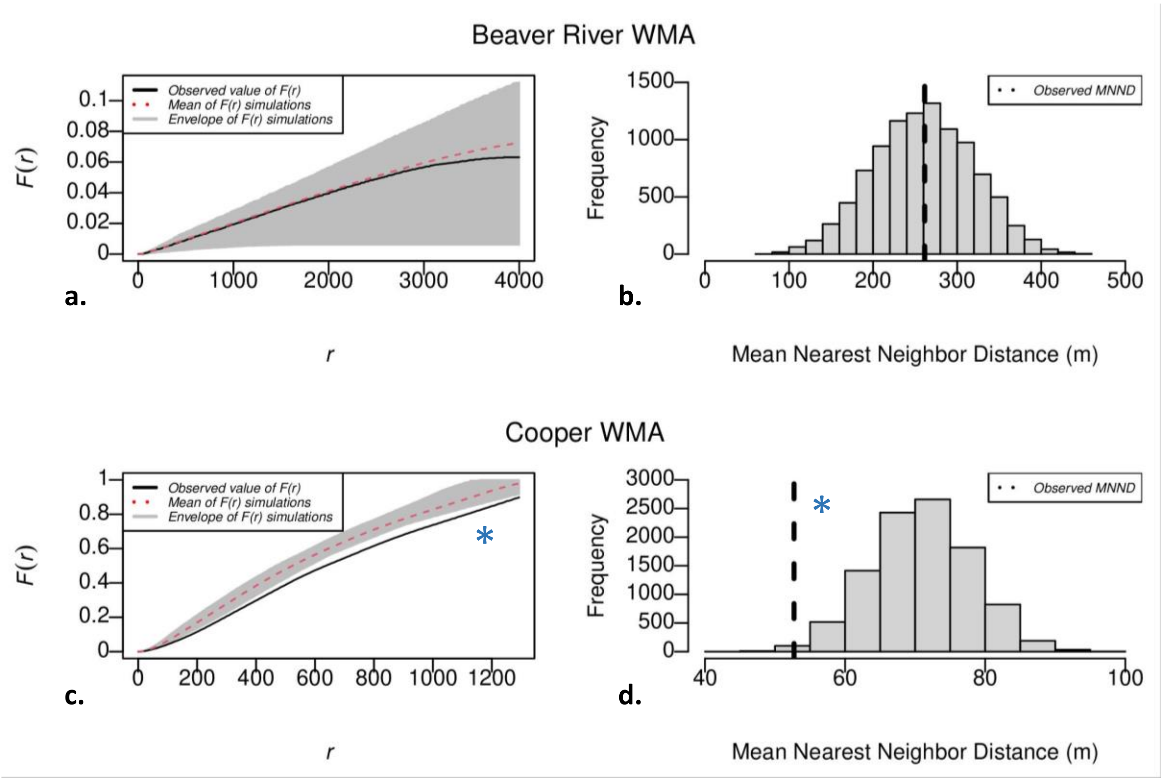
Spatial Clustering–

Texas horned lizard fortuitous encounters showed mixed evidence for spatial clustering. Beaver River WMA fortuitous encounters along frequently traveled roads did not show any evidence of spatial clustering and had a mean nearest neighbor distance of 261.34 m (Figure 5a–b). The envelope analysis shows strong support for the observed captures falling within the envelope of randomly generated point patterns (Figure 5a), and the Monte Carlo analysis showed no support for spatial clustering (mean nearest neighbor distance=259.85 m; *p*-value=0.5071; Figure 5b). In contrast, Cooper WMA fortuitous encounters along frequently traveled roads did have strong evidence for spatial clustering and had a mean nearest neighbor distance of 52.71 m (Figure 5c–d). The envelope analysis showed that the observed captures fell well below the envelope of randomly generated point patterns, indicating spatial clustering (Figure 5c) and the Monte Carlo analysis produced a *p*-value of 0.0042 (mean nearest neighbor distance=76.05 m) providing further evidence for a spatially clustered pattern (Figure 5d).

Road cruising survey captures at Cooper WMA considering all roads did not show any evidence of spatial clustering and had a mean nearest neighbor distance of 794.77 m (Figure 6a–b). The envelope analysis showed support for the observed pattern falling within the envelope of randomly generated point patterns (Figure 6a) and the Monte Carlo analysis produced an insignificant *p*-value (0.0979) (mean nearest neighbor distance=1,105.76 m), showing that points were not more clustered than could be randomly expected (Figure 6b).

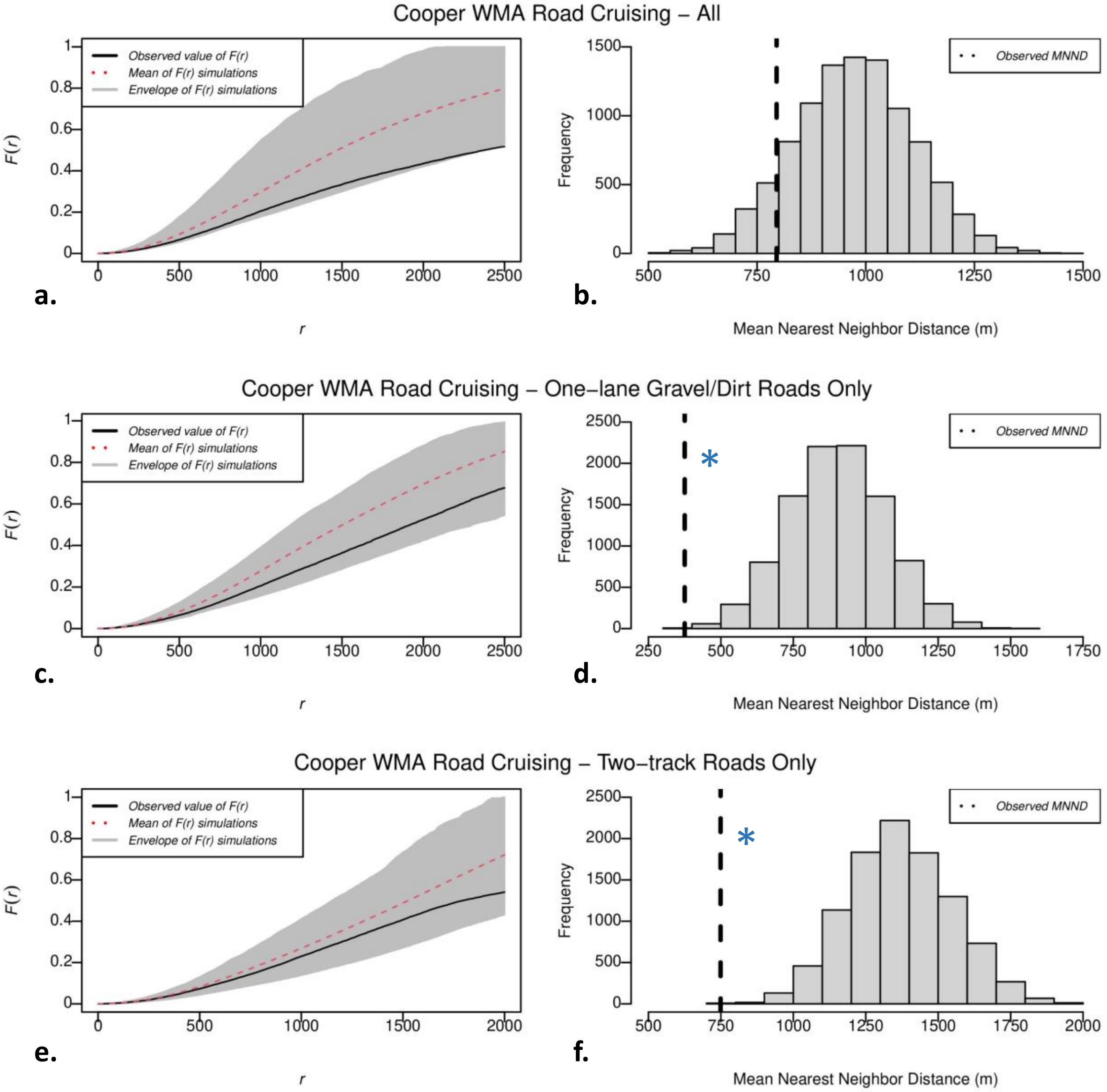
Evaluation of captures along one-lane gravel/dirt roads and captures along two-track roads during road cruising surveys at Cooper WMA resulted in moderate evidence for spatial clustering for each road type (Figure 6c–f). Mean nearest neighbor distance for one-lane gravel/dirt road captures was 375.02 m (Figure 6d) and 748.85 m for two-track road captures

(Figure 6f). The envelope analysis for evaluations of both one-lane gravel/dirt roads and, separately, two-track roads showed observed capture patterns that fell within the envelopes of random point patterns supporting non-clustering (Figure 6c and 6e). Conversely, the Monte Carlo analysis for both scenarios provides evidence that the observed point patterns were more clustered than expected through spatial randomness (one-lane gravel/dirt roads mean nearest neighbor distance=902.28 m and *p*-value=0.0004; two-track roads mean nearest neighbor distance=1,369.89 m and *p*-value=0.0001; Figure 6d and 6f). Spatial clustering for two-lane gravel roads was not analyzed due to a small sample size (*n*=1).



* = observed capture pattern is significantly different from spatial randomness

FIGURE 5. Spatial clustering of fortuitously encountered Texas horned lizards (*Phrynosoma cornutum*) along the roads we frequently traveled (to and between drift fence arrays) at Beaver River WMA in 2021 and Cooper WMA in 2022. 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**: The solid black line is the observed capture pattern, and the grey 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**: The dashed black line is the mean nearest neighbor distance of the observed capture pattern, and the grey bars illustrate the mean nearest neighbor distance of the randomly generated point patterns.



∗ = observed capture pattern is significantly different from spatial randomness

FIGURE 6. Spatial clustering of Texas horned lizards (*Phrynosoma cornutum*) captured during road cruising surveys at Cooper WMA in 2022. 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**: The solid black line is the observed capture pattern, and the grey 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**: The dashed black line is the mean nearest neighbor distance of the observed capture pattern, and the grey bars illustrate the mean nearest neighbor distance of the randomly generated point patterns.

Occupancy Analysis–

Texas horned lizards were captured at all four road cruising routes at Cooper WMA (occupancy=100%). Keeping occupancy constant, I evaluated the effect of all observation-level covariates on detection probability. Based on AICc, the best model for road routes involved lizard detection with time of day and observer name as covariates (Table 4). Julian date also proved to be a significant covariate in explaining detection (Table 4). 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 (slope=-0.64; *z*=-2.22; *p*-value=0.0262) and earlier in the field season (slope=-0.58; *z*=-2.04; *p*-value=0.0415; Figure 7). As depicted in Figure 7, the available data were able to provide model-averaging detection predictions between 7:48am–6:42pm and 9 Jun–22 Jul.

Considering single observer efforts by the three observers, two observers performed similarly on the number of one-km segments/Texas horned lizard (Observer 1=23.4 and Observer 2=23.8); Observer 3 performed less effectively with 65.5 one-km segments/Texas horned lizard. Two-observer efforts when Observer 3 was involved also resulted in fewer Texas horned lizard captures (47.0 one-km segments/Texas horned lizard with Observer 1 and zero Texas horned lizards detected with Observer 2) compared to when Observers 1 and 2 were paired (15.1 one-km segments/Texas horned lizard).

Texas horned lizards were not captured at all one-km road segments; therefore, I was able to consider occupancy probability with this method. In the analysis evaluating each one-km road segment separately (*n*=40), none of the site-level covariates produced an occupancy model that was $\geq$2 ΔAIC superior to the null model. The null model with constant occupancy estimated 55.6% occupancy (95% CI=32.8–76.3%); that is, each one-km road segment had a 55.6% probability of being occupied by at least one Texas horned lizard across the field season.

Considering detection probability for the one-km road segments, two site-level covariates, route and road classification type, showed a significant impact ($\geq$2 ΔAIC superior to the null model). None of the nine observation-level covariates showed a significant effect on detection (no models produced an AIC that was $\geq$2 ΔAIC better than the null model). The top detection probability model included only road cruising route (Table 4). The null model estimated detection probability at 7.0% (95% CI=4.4–11.0); that is, each time a one-km stretch of road was surveyed, there was a 7.0% chance of detecting a Texas horned lizard if the site was occupied. On average, it took 25.8 surveys of one-km road segments to capture one Texas horned lizard. Route 2 performed the best, with an average of 0.083 Texas horned lizards detected per one-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 one-km road segments by road cruising route determined there was a significant difference in captures between routes (*F*-statistic=3.13; *df*=3; *p*-value=0.0374). In contrast, a single-factor ANOVA analysis comparing Texas horned lizard captures at the one-km road segments by road classification type indicated no statistically significant difference (*F*-statistic=1.92; *df*=2; *p*-value=0.1613).

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).

TABLE 4. Detection probability model selection using AIC and AICc for Texas horned lizards (*Phrynosoma cornutum*) occupancy analysis of road cruising surveys at Cooper WMA in 2022. Ψ=occupancy probability, p=detection probability, and a "." denotes a null (constant) model component. Date=Julian date; time=time of day; obs.name=observer name(s), route=road cruising route (one–four), and road.class=road classification type (two-lane gravel, one-lane gravel/dirt, two-track).

By road cruising route (n=4)

	ΔAICc	**AICc Weight**	**AICc**	**Number of Parameters**
Ψ(.), *p*(time+obs.name)	0.00	0.9987	98.42	11
Ψ(.), *p*(time+date)	3.51	0.0012	101.94	4
Ψ(.), *p*(time)	6.23	0.0000	104.66	3
Ψ(.), *p*(date)	7.13	0.0000	105.56	3
Ψ(.), *p*(.)	9.49	0.0000	107.91	2

By road cruising route one-km segments (n=40)

	ΔAIC	**AIC Weight**	**AIC**	**Number of Parameters**
Ψ(.), *p*(route)	0.00	0.8047	250.23	5
Ψ(.), *p*(route+road.class)	3.51	0.1393	253.74	7
Ψ(.), *p*(road.class)	5.69	0.0468	255.92	4
Ψ(.), *p*(.)	8.97	0.0091	259.20	2

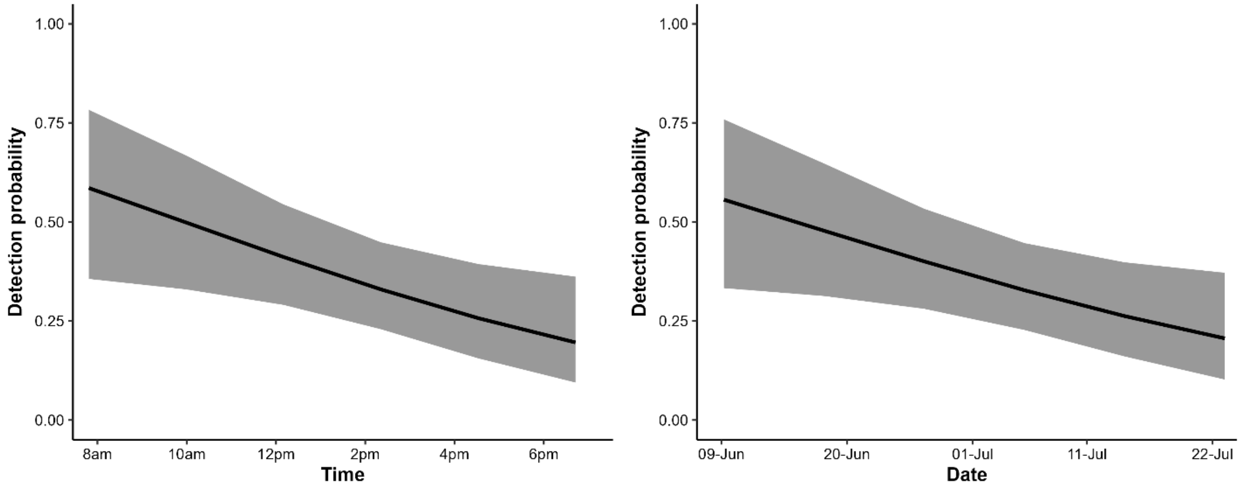


FIGURE 7. Occupancy model-averaging detection predictions for Texas horned lizards (*Phrynosoma cornutum)* at road cruising survey routes (*n*=4) at Cooper WMA in 2022. Detection is estimated to be higher earlier in the day and earlier in the summer.

Number of Observers–

Comparing differences in the number of Texas horned lizard captures from one- vs. two-observer road cruising surveys resulted in a *p*-value of 0.25 (*t*-statistic=-1.16; *df*=75). This demonstrates that there is no statistical significance in the number of Texas horned lizard captures whether there were one or two observers involved in the survey.

Mark-recapture–

The irregular results produced by the POPAN mark-recapture analysis indicate that this particular analysis was not well-suited to the data we gathered. Thus, the following results should not be interpreted literally, but used as an example. While POPAN mark-recapture analysis produces estimates for most parameters by each capture event (or between capture events), I believe it is most productive to focus on the averages (means) for the purposes of this example. In the POPAN model, some estimates are based on real parameters, and some are estimated from derived parameters. Real estimates are values that have been calculated directly from the presented data, whereas derived parameter estimates have been projected from the real estimate values (Cooch & White 2014). Full model results can be found in Table 5 (real estimates) and Table 6 (derived parameter estimates). Gross population size (N^*) is estimated by both real and derived parameter estimates and describes the population size of the entire area. N^* is broad and considers detection/non-detection of known individuals, as well as individuals that were not able to be encountered due to the site selection and survey methods, and thus helps to remediate for the imperfection of studies (Cooch & White 2014). The estimated gross population size (N^*) for the entire Cooper WMA in 2022 is estimated as 440.6 (95% CI=177.9–1525.7; real) or 465.0 (95% CI=2.1–103,011.0; derived parameter; Tables 5 and 6).

Survival probability (ϕ), capture probability (p), and *PENT* (probability of entrance into the population) are all reported as real estimates (Table 5). Mean survival probability (ϕ) is estimated as 0.75 (95% CI=0.48–0.96); this would suggest that in this population, a Texas horned lizard is estimated to have a 75% chance of survival from week-to-week (Table 5). Mean capture probability (p) is estimated as 0.17 (95% CI=0.08–0.37); this estimates that in this population, there is a 17% chance that a Texas horned lizard will be caught during each capture event, assuming it is present in the survey area (Table 5). Mean *PENT* (probability of entrance into the population) is estimated as 0.12 (95% CI=0.10–0.26); meaning that there is a 12% chance that new Texas horned lizard individuals enter the surveyed population between capture events (consecutive weeks; Table 5). There is an outlier found in the estimate of *PENT*2 (0.77); if mean *PENT* is calculated without this outlier, the average *PENT* is 0.02 (2%).

Gross births and immigration (*B**), net births and immigration (*B*), and population estimates by capture event (*N*) are all found by using derived parameter estimates (Table 6). Mean gross birth and immigration (*B**) is estimated as 52.9 (95% CI=43.7–126.5); this means that from week to week, it is estimated that there are 52.9 individuals entering the surveyed population through either birth or immigration (Table 6). The first *B** estimate (*B*2*) is an outlier (337.4), and if mean *B** is calculated without the outlier included, the average *B** is 12.3. Mean net births and immigration (*B*) is estimated as 51.6 (95% CI=43.5–114.3); this estimates that from week to week, considering births, immigration, and deaths, there are 51.6 individuals entering the population (Table 6). The first *B* estimate (*B2*) is also an outlier (337.4); if mean *B* is calculated without *B2*, the average is 10.7. As both *B** and *B* are very similar in estimates, that provides evidence that mortality is low in this population of Texas horned lizards. Mean population estimates by capture event (*N*) are 123.2 (95% CI=50.2–393.1); this estimates that on average across each capture event, the Texas horned lizard population in only the surveyed area was 123.2 individuals during each week (Table 6). On a weekly basis, lizard populations should not dramatically fluctuate, which indicates that the *N3* estimate (364.4) is an overestimation. Calculating mean *N* without *N3* provides an average of 93.0 individuals. *N* considers only detection/non-detection and doesn’t account for individuals that were outside of the surveyed locations, therefore this estimate is narrow in scope when compared to *N**.

TABLE 5. Estimates of Texas horned lizard (*Phrynosoma cornutum*) survival probability (ϕ), capture probability (*p*), *PENT* (probability of entrance into the population), and *N** (gross population size) at Cooper WMA during the 2022 field season as estimated through a POPAN mark-recapture model. The irregular results indicate that this analysis was not well-suited to the data we gathered, and the following results should not be interpreted literally. Each capture event is one week. Survival probability (ϕ) describes the chance a Texas horned lizard will survive from one capture event to the next capture event (e.g., ϕ_1 is the survival probability between capture events one and two). Capture probability (*p*) is estimated by capture event (e.g., *p2* is the second capture event). *PENT* is also estimated by capture event (e.g., *PENT2* is the estimate for capture event two). *N** is the total population size of the studied population (gross population). Parentheses indicate an outlier. See text for further details.

			95% Confidence Intervals	
Index	**Estimate**	**SE**	**Lower**	**Upper**
ϕ_1	0.48	598.68	0.00	1.00
ϕ_2	1.00	0.00	1.00	1.00
ϕ_3	0.31	0.24	0.05	0.81
ϕ_4	0.66	0.24	0.20	0.94
ϕ_5	1.00	0.00	1.00	1.00
ϕ_6	1.00	0.00	1.00	1.00
ϕ_7	0.91	0.48	0.00	1.00
ϕ_8	0.42	0.27	0.08	0.86
ϕ_9	1.00	0.00	1.00	1.00
mean ϕ	**0.75**	**66.66**	**0.48**	**0.96**
p2	0.41	0.00	0.41	0.41
p3	0.01	0.01	0.00	0.07
p4	0.23	0.25	0.02	0.83
p5	0.07	0.03	0.03	0.15
p6	0.10	0.03	0.05	0.19
p7	0.11	0.04	0.06	0.21
p8	0.13	0.07	0.04	0.35
p9	0.34	0.18	0.10	0.71
p10	0.17	0.09	0.06	0.40
mean *p*	**0.17**	**0.08**	**0.08**	**0.37**

PENT2	(0.77)	(0.00)	(0.77)	(0.77)
PENT3	0.00	0.00	0.00	0.00
PENT4	0.11	0.23	0.00	0.92
PENT5	0.00	0.00	0.00	0.00
PENT6	0.00	0.00	0.00	0.00
PENT7	0.00	0.00	0.00	0.00
PENT8	0.00	0.00	0.00	0.00
PENT9	0.06	0.06	0.01	0.39
mean *PENT*	**0.12**	**0.04**	**0.10**	**0.26**
without outlier	**0.02**	**0.04**	**0.00**	**0.19**
N*	**440.6**	**287.6**	**177.9**	**1525.7**

TABLE 6. Derived parameter estimates of Texas horned lizard (*Phrynosoma cornutum*) gross births and immigration (*B**), net births and immigration (*B*), population estimates by capture event (*N*), and gross population estimate (*N**) at Cooper WMA during the 2022 field season as estimated through a POPAN mark-recapture model. The irregular results indicate that this analysis was not well-suited to the data we gathered, and the following results should not be interpreted literally. Each capture event is one week. Gross births and immigration (*B**) considers births and immigration, and net births and immigration (*B*) considers births and immigration, in addition to deaths, to give an estimate of actual population growth. For both *B** and *B*, estimates are generated between capture events (e.g., *B*2* and *B2* are the population changes between capture events one and two). *N** is the gross population, the total population size of the studied population. *N* is a population estimate as it relates to each capture event considering only the mark-recapture data (e.g., *N2* is the estimate for capture event two). See text for further details. Parentheses indicate an outlier.

			95% Confidence Interval	
Parameter	**Estimate**	**SE**	**Lower**	**Upper**
Gross Birth + Immigration Estimates				
*B*2*	(337.4)	(0.0)	(337.4)	(337.4)
*B*3*	0.0	0.0	0.0	0.0
*B*4*	60.9	96.8	6.7	549.7
*B*5*	0.0	0.0	0.0	0.0
*B*6*	0.0	0.0	0.0	0.0
*B*7*	0.0	0.0	0.0	0.0
*B*8*	0.0	0.0	0.0	0.0
*B*9*	25.2	24.5	5.1	124.8
mean *B**	**52.9**	**15.2**	**43.7**	**126.5**
without outlier	**12.3**	**17.3**	**1.7**	**9.6**
Net Birth + Immigration Estimates				
B2	(337.4)	(0.0)	(337.4)	(337.4)
B3	0.0	0.0	0.0	0.0
B4	49.9	79.6	5.5	452.1

B5	0.0	0.0	0.0	0.0
B6	0.0	0.0	0.0	0.0
B7	0.0	0.0	0.0	0.0
B8	0.0	0.0	0.0	0.0
B9	25.2	24.5	5.1	124.8
mean *B*	**51.6**	**13.0**	**43.5**	**114.3**
without outlier	**10.7**	**14.9**	**1.5**	**82.4**
Population Estimates				
N2	27.0	0.0	27.0	27.0
N3	(364.4)	(337.8)	(77.8)	(1705.6)
N4	111.9	121.4	19.9	630.3
N5	124.2	30.2	77.7	198.7
N6	124.2	30.2	77.7	198.7
N7	124.2	30.2	77.7	198.7
N8	112.9	57.1	44.3	287.7
N9	47.3	23.8	18.7	119.8
N10	72.6	33.3	30.8	171.1
mean *N*	**123.2**	**73.8**	**50.2**	**393.1**
without outlier	**93.1**	**40.8**	**46.7**	**229.0**
Gross Population Estimate				
N*	**465.0**	**20698.8**	**2.1**	**103011.0**

DISCUSSION

General Summary–

Road cruising surveys yielded the most Texas horned lizards per person-hour out of all strategic survey methods, with the majority of captures occurring along one-lane gravel/dirt roads and two-track roads. Most Texas horned lizard captures, by all methods combined, occurred between three ecological system categories: High Plains: Sand Prairie, High Plains: Sandhill Shrubland, and High Plains: Shortgrass Prairie (Diamond & Elliot 2015). There was mixed support for spatial clustering of Texas horned lizard captures during both road cruising surveys and by fortuitous encounters. Texas horned lizard detection during road cruising surveys was not impacted by the number of observers (one vs. two), but there was evidence it was affected by observer identity regardless of prior experience. There is also evidence that Texas horned lizards were more likely to be detected earlier in the day and earlier in the field season, and that the particular road cruising route being surveyed greatly impacted detection probability. Despite performing each road cruising survey 20–22 times each, there was insufficient recapture data to obtain reliable mark-recapture estimates.

Field Data Summary–

Based upon a comparision of captures, re-captures, and effort, I recommend that road cruising surveys be utilized as the primary method for Texas horned lizard population surveys where possible. Road cruising surveys performed drastically better than the other trialed survey methods (>10 times more captures per unit effort). Although fortuitous encounters produced the highest number of Texas horned lizard captures, such captures are of little use for estimating populations. 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; Vesy et al. 2021), but data must be quantifiable and comparable for estimating population size and density; for example, by using unit effort (e.g., trap effort, search time, number of observers, etc.). In 2022, at Cooper WMA, we found that road cruising surveys produced the highest number of Texas horned lizard captures out of the strategic survey methods we tested (3.5 person-hours/Texas horned lizard). Road cruising surveys require the presence of drivable roads at the location of survey interest. This automatically excludes many small areas from road cruising survey efforts, although some areas with narrow trails may be appropriate for smaller, all-terrain vehicles (Hutchens & Deperno 2009; Godley et al. 2020).

In large areas with low Texas horned lizard density, such as our WMA field sites in western Oklahoma, I do not recommend using foot searches, either based on pre-defined plots or transects, for population assessment and monitoring as these searches produced few lizard captures per unit effort. However, foot searches may be useful under other conditions. With the human population ever-growing and Texas horned lizard habitat continuing to be encroached upon by development, it is likely that Texas horned lizards will increasingly rely upon fragmented habitat patches as time progresses (Endriss et al. 2007; Wolf et al. 2013). Furthermore, fragmented habitat patches can and do support robust populations of Texas horned lizards (Wall 2014; Vesy et al. 2021; Mirkin et al. 2021). There is evidence that fragmented habitat patches can support higher population densities of Texas horned lizards than unfragmented habitats when there is suitable vegetation structure and prey availability (Ackel 2016 reported up to ~233 Texas horned lizards/hectare using mark-recapture estimates) compared to uninterrupted, expansive habitat (e.g., Whiting et al. 1993 reported ~3 Texas horned lizards/hectare using mark-recapture estimates). A higher Texas horned lizard population density combined with less area to survey provides a better chance for fruitful foot searches. Studies with smaller survey areas have shown success with foot searches in addition to working with alternative methods such as scat collection (Ackel 2016; Huerta et al. 2023). But in most of their range, Texas horned lizards occur at such a low density (Whiting et al. 1993; Wolf et al. 2013; Vesy et al. 2021) that it is difficult to cover enough ground on foot to encounter lizards. Additionally, visually detecting Texas horned lizards in vegetated habitat, even with bare ground patches, is incredibly difficult. They are cryptic, blending into the soil and rocks perfectly, and opportunities to spot Texas horned lizards only occur if the lizards are moving. Vegetated cover not only obstructs the view for spotting Texas horned lizards, but also provides cover for lizards to go beneath. They are experts at hiding in place and make ready use of low-lying vegetation and litter cover to slip beneath to evade detection.

Similarly, the results of this study suggest drift fence arrays are not a useful approach for surveying or monitoring Texas horned lizard populations. The low density of Texas horned lizards in these habitats means that most drift fences are unlikely to capture many individuals, due the low overlap with lizard home ranges. In addition, I have personally observed Texas horned lizards expertly evading both pitfall and funnel traps. Texas horned lizards move much more slowly than most other lizard species, which may lead them to avoid unknown obstacles that would capture other lizard species. Other considerations against drift fence arrays for this type of monitoring are the habitat destruction that occurs during their installation (i.e., digging trenches for wings and holes for pitfall traps), the purchase of materials to construct them, and the frequent checking to avoid mortalities. When these are contrasted with the low success of the arrays in capturing Texas horned lizards, implementing this approach in most habitats may not be worthwhile.

Roads and Counting Captures–

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) did not perform equally well in producing Texas horned lizard captures. This will provide a challenge for selecting road cruising survey routes, as most study sites, including Cooper WMA, have limited options available for roads. By considering only the 33 Texas horned lizard captures that occurred during road cruising surveys, we can see a meaningful distribution of captures, as each segment of road was driven approximately the same number of times (20–22). When fortuitous encounters along frequently driven roads at Cooper WMA are considered, the number of Texas horned lizard captures is larger (*n*=69), but the relevance is reduced. This is because some road segments at Cooper WMA were driven disproportionately frequently, as they were on the way to other survey sites, at a main intersection, or required to enter or exit the WMA. At Cooper WMA, the performance rank of road type classification did not change whether considering only road cruising surveys or fortuitous encounters along frequently driven roads, but the magnitude of the difference was different. When considering only road cruising surveys, one-lane gravel/dirt roads are 0.17 Texas horned lizards/km better than two-track roads; but when looking at fortuitous encounters along road cruising routes, one-lane gravel/dirt roads are 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 occurrence of Texas horned lizards from their detection along roads; it could be that Texas horned lizards occur in equal numbers along one-lane gravel/dirt and two-track roads and only that detection is highest along one-lane gravel/dirt roads.

Regardless of the driving factor of Texas horned lizard captures along roads, the impact remains the same: Texas horned lizards are more likely to be found along one-lane gravel/dirt roads, followed shortly behind by two-track roads. Two-lane gravel roads performed the poorest, 6.8–8.4x worse than the other road types. I believe it is reasonable to expect that Texas horned lizard populations along two-track roads may be higher than 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. Visibility along two-lane gravel roads is unobstructed, but it can be difficult to see across the entire two-lane-wide stretch of road. Two-lane gravel roads at Cooper WMA also had more traffic that could have led to reduced use by Texas horned lizards. When possible, in future research, I recommend road cruising surveys prioritize one-lane gravel/dirt roads when available, two-track roads as a second choice, and avoid two-lane gravel roads.

The majority (91%) of all Texas horned lizard captures during 2021 and 2022 occurred in three ecological system categories: High Plains: Sand Prairie, High Plains: Sandhill Shrubland, and High Plains: Shortgrass Prairie (Diamond & Elliot 2015). Texas horned lizards can live in a variety of habitat types (Price 1990); we found lizards in seven ecological system categories, but those should not be considered their only suitable ecological system categories. The ecological system categories that we captured lizards in were limited by what was found at the WMAs 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 do clearly support viable populations of Texas horned lizards and when deciding upon field sites to sample, or survey locations within a field site, one could consider the presence of these ecological system categories.

Spatial Clustering–

There was moderate support of 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 no spatial clustering considering the entire routes inclusive of all road types (Figure 6). Based on these findings, spatial clustering is possible but does not appear to be a large driving factor behind Texas horned lizard distribution at Cooper WMA. Nonetheless, when selecting road cruising routes, it would be prudent to select roads covering as large of an area as possible, and where feasible, have multiple routes per study site. By covering more area, surveys can avoid mistaking density estimates from clustered Texas horned lizard captures as being reflective of an entire site. It is advisable to also extend this reasoning to all survey methods. If a survey location provides many or few Texas horned lizard captures, these captures may not be representative over a broader area due to spatial clustering.

Although spatial clustering analysis of fortuitous encounters along frequently driven roads at Cooper WMA did show spatial clustering of Texas horned lizards (Figure 5), this is not reflective of the true spatial distribution. These areas were driven multiple times daily, but not all stretches were traversed the same number of times. Certain areas were driven disproportionately often, such as a main intersection on the way to and from study locations, which results in unequal sampling. Comparing the little evidence of spatial clustering from road cruising surveys at Cooper WMA to the strong evidence among fortuitous encounters provides another cautionary example of the importance of not relying upon fortuitous encounters to provide an understanding of Texas horned lizard distribution.

Occupancy Analysis & Number of Observers–

Results of occupancy modeling indicated conditions that can optimize surveys. The top occupancy model for Texas horned lizard detection at Cooper WMA for road cruising routes included the covariates of time and observer name; and the top model for one-km road segments included only route. Model-averaging predictions of time for the road cruising routes demonstrate that Texas horned lizards are more likely to be detected earlier in the day. If one is planning road cruising surveys, it would be beneficial to allocate more effort to surveys earlier in the day to maximize detection. Although Julian date was not included in the top model, there was sufficient evidence supporting its effect on Texas horned lizard captures along road cruising routes. Model-averaging predictions for detection by road cruising routes indicate that earlier in the field season was better for detecting Texas horned lizards. Our study, as is common, was limited to the summer break between academic semesters. Although we do not have road cruising data prior to 30 May, it would be beneficial to start sampling earlier in the spring, as moving into the hot summer months detection probability was reduced. The higher detectability of Texas horned lizards in the spring is likely influenced by their mating season, where males have increased movement searching for females, especially in May (Stark et al. 2005). Controlling the impact on lizard detection of the identity of the observers is a more challenging prospect. In our study, prior herpetofauna surveying or fieldwork experience did not impact the detection rates of observers. Ideally, all surveys would be completed by a single observer, but that is not feasible in most scenarios. To minimize the impact of varying observer detection probability, I recommend that all observers survey each route an equal number of times, whereby any observer strengths or weaknesses would be evenly applied to all routes. Furthermore, if occupancy modeling is the goal, I recommend including observer identity as a detection covariate.

The interpretation of route (one–four) showing the strongest impact on detection probability at the one-km road segments is perplexing, as the best ways to describe what may impact our ability to find Texas horned lizards along the routes are through road classification types and ecological system categories, and these did not rank as the top model covariates. Although road classification type was not included in the top model, there was significant support for it impacting detection probability at the one-km road segments. This is also difficult to interpret, because an ANOVA test did not provide any support for a difference in Texas horned lizard captures by road classification type. While the driving factors behind route and road classification type impacting detection probability are unclear, this brings further evidence to the usefulness of surveying a variety of available roads.

The results of both occupancy modeling and the t-test indicate that there is no benefit to Texas horned lizard detection by having two observers (vs. one observer) when performing road cruising surveys. We surveyed an equal number of times with one and two observers. When considering occupancy modeling for detection with the four road cruising routes, the number of observers was not significant as a covariate (z=0.31; p-value>0.05); when analyzing by one-km road segments, it was significant as a covariate (z=0.79; p-value$\leq$0.05) but did not rank in the top models by AIC. The t-test showed that there was not a significant difference (t-statistic=-1.16; df=75; p-value>0.05) in Texas horned lizard captures based on one or two observers. At Cooper WMA, the roads we drove were not heavily trafficked, and we were able to safely drive slowly (12.9–19.3 kph; 8–12 mph) and focus on the road, even with just one observer in the vehicle. At other field sites where it would be safe to do so, I recommend using one observer. Using one observer not only reduces the needed budget and personnel for performing road cruising surveys but may open opportunities to get more thorough data by allocating extra resources into driving road cruising routes additional times or dividing up field crews to sample additional locations.

Detection probability was estimated at 35.0% for the road cruising routes (11.24–12.35 km) and 7.0% for one-km road segments. This means that each time a road cruising route was surveyed, there was a 35.0% chance of detecting at least one Texas horned lizard if they were present; and that each time a one-km stretch of road was surveyed, there was a 7.0% chance of detecting a Texas horned lizard if the site was occupied. If one was not concerned with estimating population size and was focusing on obtaining presence/absence of Texas horned lizards, each road cruising route would need to be completed seven times and each one-km segment 41 times if Texas horned lizards were not encountered to ascertain if the site was unoccupied with >95% confidence, using the cumulative probability of non-detection. This underscores the importance of repeated sampling. Our road cruising routes had a mean length of 11.80 km and although this is a substantial distance, there was still a 65.0% chance that no lizards were detected each time we surveyed. Whether selecting survey sites or performing surveys, not encountering Texas horned lizards on the initial visits does not mean the site isn't occupied; repeated visits are needed.

Mark-recapture–

Despite the four road cruising survey routes at Cooper WMA having been completed 20–22 times each, there was just not enough recapture data to complete mark-recapture analysis with this alone (33 captures, four recaptures; Table 1). The POPAN mark-recapture model in Program MARK (White & Burnham 1999) was completed using all captures, regardless of capture method, which broke some of the core assumptions of this model (see Analytical Methods: Mark-recapture) and produced unreliable estimates. Because of this, it is important to recognize that the estimates provided by the model cannot be used to fully describe the Texas horned lizard population at Cooper WMA. As shown in Tables 5 and 6, some of the standard errors associated with this analysis were overly large, and some of the 95% confidence intervals did not show an appropriate range (too narrow or too broad).

The mean estimate of survival probability (ϕ=75%) is very low. If this were accurate, that would mean that every week 25% of the Texas horned lizard population at Cooper WMA was removed, which would very quickly leave no lizards. We did not witness any sort of substantial decline during the field season. A survival probability estimate at the upper end of the mean 95% confidence interval would be more reasonable (ϕ=96%). The average *PENT* (with outlier removed) is a 2% chance every week of Texas horned lizards entering the surveyed population. This is likely an overestimation, especially since our surveying took place outside of hatchling season and therefore there were no new births in our population, but it could also describe the movement of Texas horned lizards around the WMA from outside to inside of our surveyed locations. The estimates of B^* (gross births and immigration) and B (births and immigration), even with the outlier removed, showed high mean estimates of new individuals entering the surveyed population weekly (B^*=12.3 individuals and B=10.7 individuals). I believe that these estimates are high because throughout the field season, we migrated around to different survey locations which led to us exploring areas we had not previously spent time in, and thus discovering new Texas horned lizard individuals. A core assumption of the model is that all individuals have an equal chance of detection each capture event; this was impossible to meet with our study locations changing throughout the field season. Capture probability (p) was estimated at a 17% chance that an individual would be caught during each capture event, which seems reasonable based upon the road cruising detection probability and gives further evidence to why repeated sampling is important. A short visit at a field site is unlikely to gather a representative sample of lizard data.

The gross population estimates (N^*) were 440.6 (real estimate) and 465.0 (derived parameter estimate), and both came with very large 95% confidence intervals. Despite the uncertainty with the confidence intervals and the issues with the model assumptions, these estimates seem to be a reasonable description of what the population at Cooper WMA may look like. The mean estimate of N (weekly population size considering only the mark-recapture data), with the outlier removed, was 93 individuals. I know this to be an underestimate, because in the model there were 94 unique individuals (live captures).

There is a lot of power in using mark-recapture modeling for population estimates, but based on this study, to gather enough recaptures to perform a solid analysis requires a great amount of repeated surveying; ~20 sampling repeats per road cruising route is not enough. Using broadly defined survey periods (weeks) over a variety of survey methods and fortuitous encounters provided unreliable mark-recapture estimates and caution is advised to use only constrained and comparable survey efforts. For future research aiming to perform mark-recapture analysis, I recommend limiting the number of road cruising survey routes to whatever will be feasible to complete a large number of times. As a starting point, we surveyed our four road cruising routes 20–22 times each (83 surveys total), but garnered only four Texas horned lizard recaptures. If these results were extrapolated to ten recaptures, one would be looking at driving 11.80 km (average) long routes approximately 207 times to get ten recaptures, although this is a very rough estimate and would highly vary by site. This should be taken into consideration if it is within the scope of a project before setting upon the goal of mark-recapture analysis using road cruising surveys. Care should also be taken to not oversample, which can lead to eye fatigue for technicians, reduced captures, and added expense.

CONCLUSION

For population-level surveys of Texas horned lizards, standardized survey methods are needed, and my results indicate that road-cruising surveys are the most efficient and effective method. Road cruising surveys need to be completed many times to generate enough recapture data to perform mark-recapture analysis (a realistic starting point would be 200+ times, though this will vary by site and captures) and may be beyond the scope of many projects. If looking for only presence/absence of Texas horned lizards, our road cruising survey results indicate that seven site visits would be the minimum needed to determine if a site was unoccupied (>95% confidence). I recommend surveying multiple routes that cover large areas, to reduce sampling bias from potential spatial clustering. Texas horned lizard detection can vary across survey routes and road classification types, and a survey strategy covering a broad area would be advantageous to best understand the local population (and not accidentally mistake an abundance or lack thereof in a certain area as being representative over the broader area). Road cruising surveys have the best chance of detecting Texas horned lizards in the spring, before the summer heat in Oklahoma and elsewhere, and earlier in the day (morning preferred to afternoon/evening). Where possible, the most productive road type to select for road cruising surveys are one-lane gravel/dirt roads, followed by two track roads, and avoiding the busier two-lane gravel roads. There is no need to include two observers during road cruising surveys; one observer performs just as well if roads have minimal traffic. The identity of the observer can make a difference. Ensure that all observers survey each site an equal number of times or have the same observer perform all surveys. Employing 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.

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SUPPLEMENTAL MATERIALS

1.1 Capture history for Texas horned lizards at Cooper WMA during the 2022 field season. Each column denotes one capture event (one week) beginning 20 May and ending 4 August, and each row is a unique individual. A “1” indicates a positive detection (regardless of how many times an individual was captured), and an “0” indicates non-detection.

	Week										
Individuals	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**
1	0	1	0	0	0	0	0	0	0	0	0
2	0	1	0	1	0	0	1	0	0	0	0
3	0	1	0	0	0	0	0	0	0	0	0
4	0	1	0	0	0	0	0	0	0	0	0
5	0	1	0	0	0	0	0	0	0	0	0
6	0	1	0	0	0	0	0	0	0	0	0
7	0	1	0	0	0	0	0	1	0	0	0
8	0	1	0	0	0	0	0	0	0	0	0
9	0	1	0	0	0	0	0	0	0	0	0
10	0	0	0	1	0	0	0	0	0	0	0
11	0	0	0	0	0	0	0	0	1	1	0
12	0	0	0	0	0	0	0	0	1	0	0
13	0	1	0	0	0	0	0	0	0	0	0
14	0	1	0	0	0	0	0	0	0	0	0
15	0	0	1	0	0	0	0	0	0	0	0
16	0	0	1	0	0	0	0	0	0	0	0
17	0	0	1	0	0	0	0	0	0	0	0
18	0	0	0	1	0	0	1	0	1	0	0
19	0	0	0	1	0	0	0	0	0	0	0
20	0	0	0	1	0	0	0	0	0	0	0
21	0	0	0	1	0	0	0	0	0	0	0
22	0	0	0	1	0	0	0	0	0	0	0
23	0	0	0	1	0	0	0	0	0	0	0
24	0	0	0	1	0	0	0	0	0	0	0
25	0	0	0	1	0	1	0	0	0	1	0
26	0	0	0	1	1	1	0	1	1	1	0
27	0	0	0	1	0	0	0	0	0	0	0
28	0	0	0	1	0	0	0	0	0	0	0
29	0	0	0	1	0	0	0	0	0	0	0
30	0	0	0	1	0	0	1	0	0	0	0
31	0	0	0	1	0	0	0	0	1	0	0

32	0	0	0	1	0	0	0	0	0	0	0
33	0	0	0	1	0	0	0	0	0	0	0
34	0	0	0	1	0	0	0	0	0	0	0
35	0	0	0	1	0	0	0	0	0	0	0
36	0	0	0	1	0	0	0	0	0	0	0
37	0	0	0	1	0	0	0	0	1	1	0
38	0	0	0	1	0	0	0	0	0	0	0
39	0	0	0	1	0	0	0	0	0	0	0
40	0	0	0	1	0	0	0	0	0	0	0
41	0	0	0	1	0	0	1	0	0	0	0
42	0	0	0	0	1	0	0	0	0	0	0
43	0	0	0	0	1	1	0	1	0	0	0
44	0	0	0	0	1	0	0	0	0	0	0
45	0	0	0	0	1	0	0	0	0	0	0
46	0	0	0	0	1	0	0	0	0	0	0
47	0	0	0	0	1	0	0	0	0	0	0
48	0	0	0	0	1	0	0	0	1	0	1
49	0	0	0	0	1	0	0	0	1	0	0
50	0	0	0	0	0	1	0	0	0	0	0
51	0	0	0	0	0	1	0	0	0	0	0
52	0	0	0	0	0	1	0	0	1	0	0
53	0	0	0	0	0	1	0	0	0	0	0
54	0	0	0	0	0	1	0	0	1	0	0
55	0	0	0	0	0	1	0	0	0	0	0
56	0	0	0	0	0	1	0	0	0	0	0
57	0	0	0	0	0	1	0	0	0	0	0
58	0	0	0	0	0	1	0	0	0	0	0
59	0	0	0	0	0	0	1	0	0	0	0
60	0	0	0	0	0	0	1	1	0	0	0
61	0	0	0	0	0	0	1	0	0	0	0
62	0	0	0	0	0	0	1	0	0	0	0
63	0	0	0	0	0	0	1	0	0	0	0
64	0	0	0	0	0	0	1	0	0	0	0
65	0	0	0	0	0	0	1	0	0	0	0
66	0	0	0	0	0	0	1	0	0	0	0
67	0	0	0	0	0	0	1	0	0	0	0
68	0	0	0	0	0	0	1	0	1	0	0
69	0	0	0	0	0	0	0	1	0	0	0
70	0	0	0	0	0	0	0	1	0	0	0
71	0	0	0	0	0	0	0	1	0	0	0
72	0	0	0	0	0	0	0	1	0	0	0
73	0	0	0	0	0	0	0	1	0	0	0
74	0	0	0	0	0	0	0	1	0	1	0
75	0	0	0	0	0	0	0	1	0	0	0
76	0	0	0	0	0	0	0	1	0	0	0

77	0	0	0	0	0	0	0	1	0	0	1
78	0	0	0	0	0	0	0	1	0	0	0
79	0	0	0	0	0	0	0	1	0	0	0
80	0	0	0	0	0	0	0	0	1	0	0
81	0	0	0	0	0	0	0	0	1	0	0
82	0	0	0	0	0	0	0	0	1	0	0
83	0	0	0	0	0	0	0	0	1	0	0
84	0	0	0	0	0	0	0	0	1	0	0
85	0	0	0	0	0	0	0	0	0	1	0
86	0	0	0	0	0	0	0	0	0	1	0
87	0	0	0	0	0	0	0	0	0	1	0
88	0	0	0	0	0	0	0	0	0	1	0
89	0	0	0	0	0	0	0	0	0	1	0
90	0	0	0	0	0	0	0	0	0	1	0
91	0	0	0	0	0	0	0	0	0	1	0
92	0	0	0	0	0	0	0	0	0	0	1
93	0	0	0	0	0	0	0	0	0	0	1
94	0	0	0	0	0	0	0	0	0	0	1