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SURVIVORSHIP AND SPATIAL ECOLOGY OF TEXAS HORNED LIZARDS AT TINKER
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ABSTRACT Habitat fragmentation has negative consequences on threatened and endangered species by creating isolated populations within urban settings. The Texas horned lizard (*Phrynosoma cornutum*) is experiencing population declines and localized extirpations throughout its range and is now considered a species of greatest conservation need in Oklahoma, USA. While adults of this species have been extensively studied, subadults remain understudied, yet may be vital to the stability of remaining populations. To address the gaps in knowledge, we used a combination of traditional radio telemetry and novel harmonic radar methodology to assess the survivorship and movement of two cohorts of subadult Texas horned lizards within a closed population at Tinker Air Force Base, a large military installation in central Oklahoma. Each cohort was monitored across a two-year period, resulting in a study that spanned four years in total (2016–2019). We provide the first robust, baseline estimate of wild-born hatchling survivorship in this species. Our lowest estimates of survival indicate an average survival probability for the hatchling life stage (0.285; 95% CI 0.15–0.44), within the range or slightly higher than previously predicted for the population. Average home range size was calculated with 95% minimum convex polygons, with results supporting ontogenetic increases in home range area required for Texas horned lizards from hatchling to adult life stages. We also provide age-class specific morphometric averages and updated population abundance and density estimates for this small, urban population. Our results inform the planning and assessment of future headstart and management programs for Texas horned lizards.

KEY WORDS habitat fragmentation, harmonic radar, hatchling, home range, Oklahoma, telemetry, urbanization.

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INTRODUCTION

Urban expansion and development persist worldwide (Seto et al. 2011, McDonnell and MacGregor-Fors 2016) and are recognized as contributing factors to the decline of over 3,000 threatened and near-threatened species on our planet (Maxwell et al. 2016, IUCN 2020). The United Nations report that the world's urban population grew from an estimated 0.8 billion in 1950 to 4.2 billion in 2018; growth is expected to continue, with the number of people living in urban locations reaching 5 billion by 2028 and 6 billion by 2041 (United Nations 2018). As human population numbers grow, the subsequent increase in urbanization continues to cause damages to ecosystems in a number of ways, including habitat loss, degradation, and fragmentation (Gibbons et al. 2000, Wiegand et al. 2005, Wilson et al. 2016), environmental pollution (Grimm et al. 2008, Hien et al. 2020), and the introduction of invasive species and infectious diseases (Riley et al. 2005, Bradley and Altizer 2007, Bombin and Reed 2016). It is now widely accepted that species richness declines with increasing urbanization, and that habitat loss is the greatest threat to biodiversity (Wilcove et al. 1998, McKinney 2002, Dirzo and Raven 2003, Gardner et al. 2007, McKinney 2008, Haddad et al. 2015, Leclerc et al. 2020, Piano et al. 2020). One of the most pressing threats of urbanization to wildlife is habitat fragmentation, the process by which a large contiguous habitat becomes divided into smaller isolated patches (Liu et al. 2016, de Andrade et al. 2019).

Population isolation from habitat fragmentation can have strong effects on the stability of wildlife populations, leading to population declines (Wiegand et al. 2005, Berry et al. 2010, Wilson et al. 2016). Furthermore, encroaching urbanization can isolate populations from each other (Dixo et al. 2009, Amaral et al. 2016). For example, city infrastructures may become insurmountable barriers that impede important movement between interacting populations,

further increasing risk of genetic isolation and metapopulation extinction (Burkey and Reed 2006, Traill et al. 2010, Benson et al. 2016, Ceia-Hasse et al. 2018). As urbanization and anthropogenic habitat changes continue to increase, species with low vagility may be more vulnerable than species with high dispersal capabilities, as fragmentation can affect their movement within and among habitat patches (Henle et al. 2004, Kokko and López-Sepulcre 2006, Della Rocca and Milanesi 2020). Among major vertebrate groups, amphibians and reptiles generally are less mobile than birds or mammals and have slower dispersal and recolonization rates (Craig et al. 2014, Larson 2014). Reptiles, and especially habitat-specialist species, are particularly sensitive to habitat fragmentation (Mantyka-Pringle et al. 2012, Keinath et al. 2017). For example, a comparative review of 35 turtle and squamate studies found higher reptile extinction rates associated with habitat specialist species compared wtih habitat generalists (Foufopoulos and Ives 1999).

Among reptiles, the Texas horned lizard (*Phrynosoma cornutum*) is an iconic species of the American Southwest with many natural history traits that put it at increased risk of population declines and localized extirpations from urbanization (Ballinger 1974). Some of these traits include low vagility, a specialized diet consisting predominantly of harvester ants (*Pogonomyrnex* spp.), and specific habitat preferences towards arid open areas where human development is likely (Pianka and Parker 1975, Munger 1984, Anderson et al. 2017). Historically, the species' range extended throughout much of the American Southwest from southern Colorado to northern Mexico and from western Missouri to eastern New Mexico (Sherbrooke 2003); however, Texas horned lizards have experienced continued population declines and localized extirpations during the past few decades (Price 1990, Donaldson et al. 1994). Currently, the Texas horned lizard is listed as a threatened species in Texas, USA

(Donaldson et al. 1994, Henke 2003, TPWD 2020), and a Tier I species of greatest conservation

need in Oklahoma, USA (ODWC 2015). Suspected reasons for the decline of horned lizards are

largely anthropogenic and include: introductions of the red imported fire ant (*Solenopsis invicta*),

loss of preferred food source (*Pogonomyrnex* spp.) resulting from widespread pesticide use,

over-collection for the exotic pet trade, predation from domestic pets, and loss, degradation, and

fragmentation of the species' native habitat (Donaldson et al. 1994, Endriss et al. 2007, Johnson

Linam 2008). Edge effects of fragmentation, in this case between suitable horned lizard habitat

and human development, also put horned lizards at increased risk of mortality from motor

vehicles (Brehme et al. 2018). Isolated populations of horned lizards in fragmented habitats

persist; however, these populations are more susceptible to stochastic extirpation than larger

contiguous populations (Gotelli 2008).

A long-studied population of Texas horned lizards in Oklahoma occurs on Tinker Air Force

Base (TAFB) in Midwest City, Oklahoma, USA (Endriss et al. 2007, Moody et al. 2007,

Bogosian III 2010, Bogosian III et al. 2012, Wolf et al. 2013, 2014, 2015, Mook et al. 2017,

Ramakrishnan et al. 2018). This study site is in the southeastern portion of the greater Oklahoma

City metropolitan area, which is home to over 1.3 million people (U.S. Census Bureau, 2015).

Research on this population of Texas horned lizards has continued for the last 16 years, resulting

in a baseline understanding of the natural history of *Phrynosoma cornutum* and population

dynamics specific to the TAFB population (Endriss et al. 2007, Moody et al. 2007, Bogosian III

2010, Bogosian III et al. 2012, Wolf et al. 2013, 2014, 2015, Mook et al. 2017, Ramakrishnan et

al. 2018). Notably, a life-stage simulation analysis using population demographic information for

the TAFB population identified hatchling survival as having the strongest influence on

population growth rate and emphasized the need to more accurately estimate hatchling survival

(Wolf et al. 2014).

Survival of subadult reptiles is often both understudied and underestimated through traditional mark-recapture monitoring techniques due to the small size and secretive nature of individuals during early life stages (Pike et al. 2008, Ballouard et al. 2013). To date, no field-based estimate of hatchling survival or subadult space use of Texas horned lizards has been documented, and no peer-reviewed study specifically focused on young age classes of *P. cornutum* has been published. However, improved development of a monitoring method called harmonic radar has made tracking of small wildlife species possible and is now widely used for a variety of vertebrates (Engelstoft et al. 1999, Alford and Rowley 2007, Gourret et al. 2011) and invertebrates (Milanesio et al. 2017, Makinson et al. 2019). Such a methodology presents a promising avenue for more effectively studying and monitoring all age classes of wild Texas horned lizard populations.

In this study, we implement harmonic radar methodology, along with traditional radio telemetry tracking, on TAFB to address gaps in knowledge related to young age classes of *P. cornutum*. Specifically, we aim to provide the first estimate of wild-born hatchling survivorship by tracking two cohorts of Texas horned lizard hatchlings, each across a two-year period. Additionally, we evaluate whether ontogenetic increases in home range size area occur from hatchling to adult life stages. Finally, we evaluate age-class specific morphometric averages and estimate population abundance and density specific to this small, urban population of Texas horned lizards. The results of this study will aid in assessing the success of future headstart programs and other range-wide management decisions for this declining species by land managers and conservation agencies.

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STUDY SITE

Our study site is located on Tinker Air Force Base (TAFB), a large military installation in Midwest City (Oklahoma Co.), Oklahoma (35.411755 N, -97.390797 E; datum = NAD83). Urban development covers roughly 75% of the base, leaving a highly fragmented arrangement of suitable Texas horned lizard habitat. Current research activities are focused on Wildlife Reserve 3 (WR3), a 15-ha native prairie grassland managed by the Natural Resources Program of TAFB for recreational activities such as hiking, jogging, and fishing, and surrounded by residential development and military buildings (Moody et al. 2007; Fig. 1). Dominant vegetation types are a mixture of native and non-native grasslands interspersed with patches of eastern red cedar, two small ponds, and gravel paths. Management activities on and around WR3 specifically designed to connect and defragment horned lizard habitat, such as prescribed burning and prairie restoration, are underway; however, during the time of this study, little to no immigration or emigration was expected for the population of Texas horned on WR3 due to a lack of connectivity to any neighboring suitable habitat.

METHODS

Animal Capture and Marking

We located and captured lizards for 4 consecutive years (2016–2019) from April–October, hereafter referred to as the active season, through structured visual searches and fortuitous encounters. Texas horned lizards brumate underground from roughly November to April (Sherbrooke 2003); no searches or tracking efforts were made during this period of inactivity. Visual searches consisted of groups of 1–6 researchers walking transects slowly and repeatedly throughout the study area while looking for lizards. Searches were conducted most actively from 0800–1300 h to coincide with times of highest lizard activity (Moeller et al. 2005). We searched all areas of the reserve; however, more time and effort were given to areas with bare ground, while less time and effort were given to areas where vegetation was so dense and high that visual observations of horned lizards would be exceedingly rare (Wolf et al. 2014). When a lizard was found, we captured it by hand and recorded the location of capture in Universal Transverse Mercator (UTM) coordinates using the North American Datum 1983 (NAD83) with a handheld Trimble GPS Pathfinder Pocket Receiver (Trimble GeoXT, Terrasync 2.3, Strategic Consulting International, Oklahoma City, Oklahoma, USA). We stored all data in a geodatabase maintained by the United States Air Force.

Following the visual encounter and capture of a new adult or juvenile individual in the field, the lizard was transported approximately 1 mile to the TAFB Natural Resources Program lab for morphometric measurements and marking. To reduce travel-related stress on young lizards, individuals identified as hatchlings were not transported to a lab space; instead, morphometric measurements and marking were done at the site of capture with a portable field kit. We recorded basic morphometric information for each individual, including snout–vent length

(SVL), mass, sex, and age class (hatchling, juvenile, or adult). Individuals were considered hatchlings from the time of hatching until emergence from their first brumation at approximately eight months of age, juveniles for one year beginning at emergence from the first brumation (approximately 8–20 months of age), and adults beginning in their third year (Endriss et al. 2007). We used SVL and mass to distinguish between age classes; the beginning of the field season (April–June) offered an opportunity to visually distinguish between age classes due to the small size of juveniles and the absence of hatchlings.

All captured horned lizards were individually marked and tagged before release. We marked each lizard weighing more than 5.0 g with a passive integrated transponder (PIT) tag (12.5mm 134.2 kHz, Biomark Inc., Boise, ID) sub-dermally implanted on the lower abdomen and clipped the fourth toe of the front right foot (Toe IV) as a secondary mark to more easily distinguish PIT-tagged individuals from new captures in the field (Hellgren et al. 2010). For lizards weighing less than 5.0 g, we clipped a unique combination of two toes as an alternative to a PIT tag until the individual's body size and weight were large enough for the safe surgical implantation of a PIT tag (Fig. 2). All toe-clips were retained and saved for future genetic analysis. Lizards who obtained unique toe-clips at a younger age did not have Toe IV removed when the PIT tag was implanted. Following marking, we fit every captured individual with one of two monitoring devices: (1) a very high frequency (VHF) radio transmitter (BD-2, Holohil Systems Ltd., Carp, Ontario, Canada) or (2) a small, flexible diode tag for detection via harmonic radar (RECCO Rescue Systems, Lidingo, Sweden; www.recco.com). We used VHF transmitters, emitting unique frequencies, with varying weights and battery life, to adjust for the size of the lizard: (1) 1.8 g with battery life of 14 weeks, (2) 1.4 g with battery life of 9 weeks, (3) 1.0 g with battery life of 6 weeks, and (4) 0.8 g with battery life of 4 weeks. Transmitters were replaced as often as

needed to maintain tracking through the entire active season. If the mass of a transmitter did not exceed 10% of the lizards' body mass, we attached the transmitter with 100% non-toxic silicone adhesive on the dorsum of the lizard posterior to the head and secured with a braided elastic band to prevent the loss of transmitters during shedding events (Endriss et al. 2007). For smaller lizards that transmitters would have exceeded 10% of their body weight, we attached a diode tag on the dorsum posterior to the head with 100% non-toxic silicone adhesive. Placement was made so that excess tag length extended beyond the tail and did not interfere with lizard locomotion and natural behaviors. We painted diode tags with non-toxic paint closely matching ground color to mimic natural crypsis and labeled each tag with the corresponding lizard's unique identification number (assigned sequentially since the start of the project), as the diodes themselves have no identifying markings or frequencies. Following marking and tagging, lizards were released within the same day at their original points of capture. All animal capture and handling methods followed procedures approved by Southern Illinois University Carbondale Institutional Animal Care and Use Committee (14-059 & 18-015), the University of Oklahoma Institutional Animal Care and Use- Committee (R18-012 & R18-024), and permits issued to R. W. Moody by the Oklahoma Department of Wildlife Conservation (#10014206) from 2016–2019.

Monitoring

Following release, we tracked tagged individuals using 1 of 2 receiver types: (1) a handheld receiver attached to a 3-element Yagi antenna (for VHF transmitters) or (2) a handheld RECCO model R8 receiver (for harmonic radar diode tags). When using the Yagi antenna, we homed in on the exact location of each lizard fitted with a VHF transmitter. When using the RECCO receiver, we slowly walked in straight lines throughout the study area while listening for audible

pings emitted from the device indicating the presence of a diode tag, then visually located the lizard to determine its identifying number. Texas horned lizards are predominantly diurnal (Pianka and Parker 1975) so we limited tracking efforts to daylight hours. We attempted to track each individual lizard 1 to 5 times weekly during the active season (April–October), but tracking frequency varied as a result of local weather and lizard activity patterns. For example, tracking was not done during times of inclement weather, increased in frequency in July and August as hatchlings began to emerge from nest sites, and decreased in frequency toward the end of the active season as lizards decreased daily activity and began to enter brumation. Individuals were re-captured periodically as needed to re-attach or replace transmitters or diodes following shedding events, or to replace transmitters as battery life depleted. We recorded SVL and mass for each lizard during these recapture events. A total of 4,272 capture and recapture events were recorded during the 4-year study period (Table 1).

Analysis of Survival

We estimated survivorship for 2 cohorts of Texas horned lizard hatchlings with the Kaplan-Meier estimator for staggered entry (survival package in R, Therneau 2020) to account for a high number of censored animals (Pollock et al. 1989). We estimated hatchling survival rates for two different time periods: the first time period determined the probability of hatchling survival until the time of first brumation (roughly the first three months of life; labeled Period A). The second time period extended until the following Spring upon emergence from first brumation (roughly the first eight months of life; labeled Period B). The fate of a hatchling was considered "survived" if the individual was known to be alive during the final week of the time period, or "dead" if a horned lizard carcass was found. The fates of some hatchlings were undetermined due to failure to relocate the individual. Reasons for a failure to locate could include predators

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removing hatchlings from the study area, diode failure, or discovering a diode without a lizard following a shedding event without subsequent recapture of the lizard. Due to a high number of individuals with unknown fates, we calculated an upper and lower estimate of survival for each cohort and time period. The upper estimate assumed lizards with undetermined fates survived to the end of the time period in question (i.e. Period A or Period B), while the lower estimate assumed lizards with undetermined fates were dead.

Analysis of Home Range

We measured the yearly home range size (ha) for each lizard using 95% minimum convex polygons (MCPs; in the R package adehabitatHR, Calenge 2006), and estimated the mean home range size used by each age class (Kernohan et al. 2001). We included only individuals that were located >5 times within one active season for analysis (hatchlings: $n = 52$, juveniles: $n = 60$, adults: $n = 57$). Hatchling data included locations only from the 2016 and 2018 seasons; juvenile data included locations only from the 2017 and 2019 seasons. Adult data were pooled from all 4 years. Though single wayward movements can skew polygon size upwards, MCPs are simple and can estimate home range size without a reliance on an underlying statistical distribution (Row et al. 2012). Additionally, MCPs are a commonly used method for home range analysis of reptiles (Buchanan et al. 2017, Miller et al. 2020) allowing useful comparisons among studies. A Kruskall-Wallis test, followed by a Dunn's post hoc test, was conducted to compare home range area among age classes.

Mark-Recapture and Density Estimation

Mark-recapture techniques are effective to estimate wildlife population abundance and density; however, mark-recapture requires considerable investment of both time and resources (Lettink and Armstrong 2003, Witmer 2005, Endriss 2006). When applied every few years, this method is

effective to assess long-term trends in population abundance and density (Endriss 2006). To reassess population relative abundance and density of Texas horned lizards at TAFB, we selected three 4–6-day periods during April–August 2019 to be considered analogous to trapping occasions in mark-recapture terminology. During these periods, groups of 1–6 researchers intensively searched the WR3 study area for Texas horned lizards. In following with methodological standards previously used at this study site, all hatchling captures, repeat captures of the same individual within one trapping occasion, as well as captures and recaptures outside of these occasions, were not included in analysis (Endriss et al. 2007, Wolf et al. 2013). Population abundance of Texas horned lizards on the study area was estimated in R (R Core Team, 2019) with package RMark (Laake 2013, Laake et al. 2013) using a closed population model. Similar to Endriss (2007) and Wolf (2013), our data set would not allow the fitting of complex models, therefore we used the simplest model that assumed constant rates of capture (0.50 ± 0.10) and recapture probability (0.22 ± 0.05) across time, as they suggested.

We estimated the total Texas horned lizard habitat area by fitting a 100% Minimum Convex Polygon (MCP) in ArcGIS using the Convex Hull method for all recorded lizard fixes in 2019. The MCP encompassed two large ponds on WR3 and part of a developed area adjacent to the site, therefore we subtracted the area of the ponds and developed area from the MCP. To calculate the density of Texas horned lizards, we divided the abundance estimate by the total area used.

RESULTS

Morphometrics Among Age Classes

Average SVL and weight (respectively) were 24.0 ± 3.3 mm and 1.2 ± 0.7 g for hatchlings, 43.5 ± 10.4 mm and 9.3 ± 4.9 g for juveniles, 62.0 ± 6.1 mm and 19.6 ± 5.8 g for adults (Table 2). A One-Way ANOVA concluded there was a significant effect of age on SVL between the three age classes ($F_{2, 620}$ = 1075; $P < 0.001$; Fig. 2), and a Tukey post hoc test revealed SVL was significantly smaller for hatchlings than both juveniles ($P < 0.001$) and adults ($P < 0.001$), and that juveniles were significantly smaller than adults ($P < 0.001$). One-Way ANOVA also concluded age had a significant effect on mass between the three age classes ($F_{2, 1446}$ = 1152; $P < 0.001$; Fig. 2), and a Tukey post hoc test revealed mass was significantly smaller for hatchlings than both juveniles ($P < 0.001$) and adults ($P < 0.001$), and that juvenile mass was significantly smaller than adult mass ($P < 0.001$). The SVL and body mass of Texas horned lizards consistently increased during the active season for all age classes, reflecting growth, but was much less substantial for adults than for juveniles or hatchlings (Fig. 3).

Survival of Hatchling Horned Lizards

To estimate the survival rate for hatchling horned lizards, we tracked the fates of hatchling lizards from 2 cohorts (2016 cohort: $n = 84$; 2018 cohort: $n = 101$), totaling 185 individuals. A low number ($n = 27$) of hatchling captures in 2017 resulted in insufficient sample size for analysis. For the 2016 cohort, we documented 69 individuals captured during the hatchling life stage. For the 2018 cohort, 83 lizards were captured during the hatchling life stage. Survival rates through Period A (from time of hatchling until beginning of first brumation) ranged from 0.38–0.96, and through Period B (until emergence from first brumation) ranged from 0.25–0.90 (Table 3, Fig. 4).

Analysis of Home Range

We estimated home range size of all individuals with more than five recorded capture events using 95% MCPs (Fig. 5). Average home range areas increased with ontogenetic growth (Table 4). Age class had a significant effect on home range size for individual lizards ($P < 0.001$). Home range size was smaller for hatchlings than both adults ($P < 0.001$) and juveniles ($P < 0.001$). Home range size was also smaller for juveniles than adults ($P < 0.001$).

Mark-Recapture and Density Estimate

During the 3 monthly trapping occasions in 2019, 50 lizards were captured 54 times, which includes only the first capture of an individual within a trapping occasion (Table 5). Two of 3 mark-recapture trapping occasions occurred in the first half of the active season before the emergence of hatchlings, therefore hatchling captures in the third session were excluded from analysis; abundance and density estimation reflect the population size of only adult and juvenile horned lizards. The population estimate in 2019 was 56.5 ± 5.5 lizards (SE; 95% CI: 51.5–77.4). Based on an estimated size for the study area of 7.10 ha, the density of Texas horned lizards was estimated at 7.96 lizards/ha.

DISCUSSION

Population abundance (56.5 ± 5 lizards) on the study site in 2019 was similar to most previous estimates at TAFB, including an estimate of 53 ± 11 lizards in 2005 by Endriss et al. (2007) and an estimate of 54.5 ± 21.5 lizards in 2016 (J. W. Mook and E. M. Schauber, Southern Illinois University Carbondale, unpublished report). One notable exception is that our 2019 estimate is 72% higher than the estimate of 32.9 ± 4.7 lizards for 2011 made by Wolf et al (2014). Variance in population demographic rates over the course of any long-term study could be explained by natural fluctuations in vital rates relating to long-term climatic shifts (Miller et al. 2020). However, fluctuations in population abundance and density at TAFB also coincide with anthropogenic habitat disturbance at the study site. Construction of a housing development adjacent to WR3 in 2008–2011 resulted in a loss of 7.4 ha of suitable Texas horned lizard habitat. This loss of nearly 40% of available habitat might explain the coinciding 38% decrease in Texas horned lizard abundance reported at that time at the site (Wolf et al. 2013). The rebound in population abundance back to estimates reported before the habitat loss occurred suggest the ability for Texas horned lizards to recover despite the small size and relative isolation of the population. Similar rebounds in population size among reptiles have been observed in other reptile communities, such as in Australia where Davis et al. (2015) reported a variety of reptile species showed rapid recovery (within 5 years) following a large disturbance event. Alternatively, it is possible that the 2011 estimates of population abundance and density were underestimated, and the population has remained stable throughout the long-term continuous study at TAFB.

Most reports regarding Texas horned lizards outside of TAFB focus on occupancy within sites and allude to either population stability or decline, without estimation of abundance or

density (Ballinger 1974, Donaldson 1994, Busby and Parmelee 1996, Henke 2003). For example, Chaparral Wildlife Management Area in Texas has a well-studied population of Texas horned lizards (Burrow 2000, Hellgren et al. 2010), yet to our knowledge, population abundance and density at the site remain undocumented. Given the natural crypsis and secretive nature of horned lizard species, mark-recapture studies often fail to yield adequate lizard captures for statistical analysis (Grant and Doherty 2010, Dibner et al. 2017). Furthermore, because of the time-consuming nature of mark-recapture methodology, plots of land exceeding more than a few hectares may require more tracking hours and resources than is possible for most research programs. Although estimates of density for this species are not common, Whiting et al. (1993) reported a density of slightly less than three Texas horned lizards per hectare. Our density estimation (7.96 lizards/ha) more closely matches the l0 lizards/ha estimate reported in populations of horned lizards in New Mexico (Whitford and Creuser 1977).

Similar to abundance and density estimation, survival data of Texas horned lizards are also often imprecise, problematic, or lacking from studies due to many censored (missing with unknown fates) individuals (Hellgren et al. 2010). This problem is exacerbated when focusing specifically upon young age classes that are more difficult to locate and monitor; therefore, field-based estimates of hatchling survival in other populations for direct comparisons are currently not available. For other species of lizard, survival probability is considerably lower in early life stages when compared to the adult life stage (Zúñiga-Vega et al. 2008, Massot et al. 2011, Kacoliris et al. 2013). For example, the reported survival probability estimates of hatchling, juvenile, and adult *Sceloporus grammicus* in central Mexico were 0.418, 0.522, and 0.685, respectively (Zúñiga-Vega et al. 2008). Broadly stated, juvenile survival for most reptile species

is approximately 13% lower than conspecific adults, with average annual survival of juvenile lizards being 0.32 (Pike et al. 2008).

This study documents the first time that Texas horned lizard hatchling survivorship has been estimated using direct, field-based monitoring methodology. Two previous demographic studies of the TAFB population of *P. cornutum* used indirect, age-structure based, methodology; Euler's equation and known estimates of older age class survival and fecundity were used to estimate the hatchling survival rate threshold necessary for population stability (Hellgren et al. 2000, Endriss et al. 2007, Wolf et al. 2014). This critical value of hatchling survival was estimated to be 0.19–0.25 in 2007 (Endriss et al. 2007), and 0.33 in 2014 (Wolf et al. 2014). These critical values are slightly lower than or within the range of our lower estimates (0.25–0.51) of hatchling survival found with field-based monitoring methodology, further suggesting long-term population stability of TAFB.

Our lower estimates of hatchling survivorship were based on the assumption that all lizards with unknown fates were dead; however, we found an average of 25 (8 adult; 17 juvenile) new (i.e. initial capture) individuals each study year, indicating that some lizards escape detection for long periods of time and it is likely that some missing lizards had actually survived and that our lower estimates are underestimated. Alternatively, our upper estimates of hatchling survivorship assumed that all lizards with unknown fates (e.g. "lost" or "missing") survived; however, extensive person-hours (from 20–40 per week) in the field did not result in the subsequent recapture of missing lizards. Given that our results indicate that hatchlings do not move far from their natal locations, we feel it is unlikely all missing lizards survived to subsequent seasons and that upper estimates are likely too high. Therefore, the lower estimate may be the more

conservative approach to take, but the actual survival probability is likely somewhere in between the lower and upper estimates.

Most lizards with unknown fates were lost from the study following the shedding of their diode, so improved attachment techniques for diodes should help reduce the number of lost individuals. One potential improvement would be to add a collar or harness to prevent the loss of diodes following shedding events. Unfortunately, even with improved attachment methods preventing the shedding of diodes, unknown fates will continue to exist. For example, the small and flexible design of the diodes means they may be consumed by a predator, such as a snake, that swallows its prey whole (Sherbrooke 2008). Horned lizards are often also moved long distances by predators such as hawks, coyotes, feral cats, or humans (Munger 1986, Giovanni et al. 2007). If lizards disperse or are removed from the study area by predators, the likelihood of lost diodes being found is low compared to radio transmitters with extended ranges and the ability to assign unique frequencies to individuals. The inability to assign unique frequencies to diodes also does not allow for the search of specific individuals, instead researchers must rely upon visual encounters along transects for marked individuals, after being alerted to the presence of a lizard by the diode and receiver.

Given the unique urban surroundings of our study site, predation pressure is likely lower than for more rural populations (Radzio and O'Connor 2017, Eötvös et al. 2018). We expect a reduced abundance of common Texas horned lizard natural predators, such as coyotes (*Canis latrans*), greater roadrunners (*Geococcyx californianus*), and coachwhips (*Masticophis flagellum*) (Wolf et al. 2013). The invasive red imported fire ant (*Solenopsis invicta*) is a known predator of reptile eggs (Diffie et al. 2010, Thawley and Langkilde 2016), and has been linked to population declines in *P. cornutum* by displacing harvester ants (*Pogonomyrmex*), their preferred food

source (Donaldson et al. 1994, Wojcik et al. 2001). Our population of horned lizards is currently unaffected by *S. invicta*, as none have been observed to-date at the study site. While a typical urban setting can also lead to increased depredation from domestic cats (Woinarski et al. 2018), TAFB has regulations against free-roaming house pets (J. Krupovage, United States Air Force, personal communication). We understand that the reduced abundance of predators at our study site may give our population higher survival rates than those seen in more rural or natural populations. Future research studies documenting hatchling survival in rural or secluded settings should consider this difference when making comparisons to our results. As urbanization further fragments suitable habitats, more populations of Texas horned lizards will likely find themselves isolated inside of urban areas. We stress the importance of using location-specific vital rates in analyses of population viability; vital rates measured at the population described here may not match those found within another population (Frederiksen et al. 2014).

The northern portion of WR3 on TAFB is bordered by an east–west road that we expected to serve as an additional source of mortality in horned lizards (Fig. 1); however, only 1 known road mortality was recorded during the study period of 2016–2019. After the addition of all previous years (2003–2015) of recorded data at TAFB, a total of only 2 road mortalities were recorded over 16 years (2003–2019) of continuous monitoring, suggesting that Texas horned lizards at TAFB avoid roads. This behavior has been documented in other reptile species, such as Blanding's turtles (*Emydoidea blandingii*), eastern massasaugas (*Sistrurus catenatus*) and prairie kingsnakes (*Lampropeltis calligaster calligaster*) (Richardson et al. 2006, Paterson et al. 2019), but has not been documented in horned lizard species to our knowledge. Contrary to our findings, vehicles have been reported to be a primary source of mortality for Texas horned lizards in other studies, but this could be misleading considering road mortalities are easier to

locate and identify than other mortality events (Montgomery and Mackessy 2003). While active

roadways may not be a direct danger to Texas horned lizards, they can restrict movement

between habitat patches if actively avoided (Clark et al. 2010).

Our results show strong support for increased home range size with lizard growth and

development in *P. cornutum*. The small home range area used by hatchlings is likely due to

mobility restrictions based on small hatchling body size, as the mean body mass within the

hatchling life stage is only 6% that of the adult life stage. Additionally, a small home range size

could be a survival strategy for hatchling and juvenile lizards, as large movements away from

vegetative cover increase risk of predation for reptiles (Pietrek et al. 2009, Segura et al. 2020).

Hatchling horned lizards are not as well protected from predators as are adults, due to small body

size and underdeveloped body armor, such as occipital horns (Ballinger 1974, Sherbrooke 2003).

By minimizing movements, hatchling horned lizards may therefore increase their survival

probability, as seen and documented in other reptile species (Radzio and O'Connor 2017).

Alternatively, hatchlings could be using less home range area because of more specific

microhabitat preferences in the hatchling life stage than older life stages. For example, after

repeated instances of locating hatchling lizards of the 2016 cohort on man-made gravel paths

within the reserve, we added additional information of microhabitat type (i.e. "in vegetation" or

"on path") to relocation data for the 2018 cohort. During 2018, we recorded hatchling locations

on man-made gravel paths (191 location instances) and natural prairie habitat (189 location

instances) in almost equal amounts, which could show a preference towards areas with bare

ground for easier mobility. We recognize that this 50/50 split in habitat preference could be

exaggerated due to detection bias, as horned lizards are more exposed to the researchers when on

gravel paths than in vegetation patches, and therefore more easily located. Detection probability

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likely also increases with age class, as seen in other lizard species (Molina-Zuluaga et al. 2013).

Further research into hatchling microhabitat use, including substrate preference and prey

availability, could provide a more complete understanding of the spatial use difference seen

among the age classes.

MANAGEMENT IMPLICATIONS

Headstart programs, in which individuals of a threatened or endangered species are hatched and/or raised in captivity (Burke 2015) are used as a management strategy for a variety of lizard species (Pérez-Buitrago et al. 2008, Santos et al. 2009). Texas horned lizard headstart programs are now common practice in Texas (Cuthbert 2018, Scudder 2018) and are in the beginning stages in Oklahoma (S. J. Eliades, University of Oklahoma, personal communication). The information gathered in this study regarding survival, home range, and movements will help to better plan these programs, and serve as a baseline for evaluating program efficacy for the TAFB population. Given the small home range area used by hatchlings, we believe small, soft-release enclosures with an appropriate supply of native ants and vegetative cover would support headstarted Texas horned lizards if individuals are released during the end of the hatchling life stage. Given that brumation did not significantly reduce the probability of survival, we believe releases made before first brumation will help to reduce costs affiliated with headstart programs, without significantly reducing an individual lizard's chance of survival. We encourage researchers to continue to monitor individuals both while in captivity and post-release and to compare results of survival with those provided here.

LITERATURE CITED

Alford, R., and J. Rowley. 2007. Techniques for tracking amphibians: the effects of tag attachment, and harmonic direction finding versus radio telemetry. Amphibia-Reptilia 28:367–376.

Amaral, K. E., M. Palace, K. M. O'Brien, L. E. Fenderson, and A. I. Kovach. 2016. Anthropogenic habitats facilitate dispersal of an early successional obligate: implications for restoration of an endangered ecosystem. PLOS ONE 11:e0148842.

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

Ballinger, R. E. 1974. Reproduction of the Texas horned lizard, *Phrynosoma cornutum*. Herpetologica 30:321–327.

Ballouard, J. M., S. Caron, T. Lafon, L. Servant, B. Devaux, and X. Bonnet. 2013. Fibrocement slabs as useful tools to monitor juvenile reptiles: a study in a tortoise species. Amphibia–Reptilia 34:1–10.

Benson, J. F., P. J. Mahoney, J. A.Sikich, L. E. Serieys, J. P. Pollinger, H. B. Ernest, and S. P. Riley. 2016. Interactions between demography, genetics, and landscape connectivity increase extinction probability for a small population of large carnivores in a major metropolitan area. Proceedings. Biological Sciences, 283(1837):20160957.

Berry, R. B., C. W. Benkman, A. Muela, Y. Seminario, and M. Curti. 2010. Isolation and decline of a population of the Orange-breasted Falcon. The Condor 112:479-489.

Bogosian III, V. 2010. Habitat niche modeling in the Texas horned lizard (*Phrynosoma cornutum*): applications to planned translocation. Disseration, Southern Illinois University at Carbondale, Carbondale, USA.

Bogosian III, V., E. C. Hellgren, M. W. Sears, and R. W. Moody. 2012. High-resolution niche models via a correlative approach: comparing and combining correlative and process-based information. Ecological Modelling 237:63–73.

Bombin, A., and L. K. Reed. 2016. The changing biodiversity of Alabama *Drosophila*: important impacts of seasonal variation, urbanization, and invasive species. Ecology and Evolution 6:7057–7069.

Bradley, C. A., and S. Altizer. 2007. Urbanization and the ecology of wildlife diseases. Trends in Ecology and Evolution 22:95–102.

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

Buchanan, S. W., B. C. Timm, R. P. Cook, R. Couse, and L. C. Hazard. 2017. Spatial ecology and habitat selection of eastern hognose snakes. The Journal of Wildlife Management 81:509–520.

Burke, R. L. 2015. Head-starting turtles: learning from experience. Herpetological Conservation and Biology 10:299–308.

Burkey, T. V., and D. H. Reed. 2006. The effects of habitat fragmentation on extinction risk: mechanisms and synthesis. Songklanakarin Journal of Science and Technology 28:9–37.

Busby, W. H., and J. R. Parmelee. 1996. Historical changes in a herpetofaunal assemblage in the Flint Hills of Kansas. The American Midland Naturalist 135:81–91.

Calenge, C. 2006. The package "adehabitat" for the R software: a tool for the analysis of space

    and habitat use by animals. Ecological Modelling 197:516–519.

Ceia-Hasse, A., L. M. Navarro, L. B. de Agua, and H. M. Pereira. 2018. Population persistence

    in landscapes fragmented by roads: Disentangling isolation, mortality, and the effect of

    dispersal. Ecological Modelling 375:45–53.

Clark, R. W., W. S. Brown, R. Stechert, and K. R. Zamudio. 2010. Roads, interrupted dispersal,

    and genetic diversity in timber rattlesnakes. Conservation Biology 24:1059–1069.

Craig, M. D., A. H. Grigg, R. J. Hobbs, and G. E. St J. Hardy. 2014. Does coarse woody debris

    density and volume influence the terrestrial vertebrate community in restored bauxite mines?

    Forest Ecology and Management 318:142–150.

Cuthbert, L. 2018. Texas horned lizard, once common, now must be captive bred. National

    Geographic. <https://www.nationalgeographic.com/animals/2018/10/horned-lizard-texas- -

    threatened-species-video-news/>. Accessed 5 May 2020.

Davis, R. A., T. S. Doherty, and G. Moreno-Rueda. 2015. Rapid recovery of an urban remnant

    reptile community following summer wildfire. PLOS ONE 10:e0127925.

de Andrade, A. C., L. D. Franzini, and D. O. Mesquita. 2019. Assesssing the effect of

    urbanization on tropical forest dwelling teiid lizards. Ecological Indicators 99:225–259.

Della Rocca, F., and P. Milanesi. 2020. Combining climate, land use change and dispersal to

    predict the distribution of endangered species with limited vagility. Journal of Biogeography

    47:1427–1438.

Dibner, R. R., D. F. Doak, and M. Murphy. 2017. Discrepancies in occupancy and abundance

    approaches to identifying and protecting habitat for an at-risk species. Ecology and evolution

    7:5692–5702.

Diffie, S., J. Miller, and K. Murray. 2010. Laboratory observations of red imported fire ant (Hymenoptera: Formicidae) predation on reptilian and avian eggs. Journal of Herpetology 44:294–296.

Dirzo, R., and P. H. Raven. 2003. Global state of biodiversity and loss. Annual review of Environment and Resources 28:137–167.

Dixo, M., J. P. Metzger, J. S. Morgante, and K. R. Zamudio. 2009. Habitat fragmentation reduces genetic diversity and connectivity among toad populations in the Brazilian Atlantic Coastal Forest. Biological Conservation 142:1560–1569.

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

Endriss, D.A. 2006. Ecology of an urban population of the Texas horned lizard (*Phrynosoma cornutum*) in central Oklahoma. Thesis, Oklahoma State University, Stillwater, USA.

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

Engelstoft, C., K. Ovaska, and N. Honkanen. 1999. The harmonic direction finder: a new method for tracking movements of small snakes. Herpetological Review 30:84.

Eötvös, C. B., T. Magura, and G. L. Lövei. 2018. A meta-analysis indicates reduced predation pressure with increasing urbanization. Landscape and Urban Planning 180:54–59.

Frederiksen, M., J. D. Lebreton, R. Pradel, R. Choquet, and O. Gimenez. 2014. Identifying links between vital rates and environment: a toolbox for the applied ecologist. Journal of Applied Ecology 51:71–81.

Foufopoulos, J., and A. R. Ives. 1999. Reptile extinctions on land-bridges: life-history attributes
and vulnerabilty to extinction. The American Naturalist 153:1–25.

Gardner, T. A., J. Barlow, and C. A. Peres. 2007. Paradox, presumption and pitfalls in
conservation biology: the importance of habitat change for amphibians and reptiles.
Biological Conservation 138:166–179.

Gibbons, J. W., D. E. Scott, T. J. Ryan, K. A. Buhlmann, T. D. Tuberville, B. S. Metts, J. L.
Greene, T. Mills, Y. Leiden, and S. Poppy. 2000. The global decline of reptiles, déjà vu
amphibians: reptile species are declining on a global scale. Six significant threats to reptile
populations are habitat loss and degradation, introduced invasive species, environmental
pollution, disease, unsustainable use, and global climate change. BioScience 50:653–666.

Giovanni, M. D., C. W. Boal, and H. A. Whitlaw. 2007. Prey use and provisioning rates of
breeding Ferruginous and Swainson's hawks on the southern Great Plains, USA. The Wilson
Journal of Ornithology 119:558–569.

Gotelli, N. J. 2008. A primer of ecology. Sinauer Associates, Sunderland, Massachusetts, USA.

Gourret, A., R. Alford, and L. Schwarzkopf. 2011. Very small, light dipole harmonic tags for
tracking small animals. Herpetological Review 42:522–525.

Grant, T. J., and P. F. Doherty Jr. 2007. Monitoring of the flat-tailed horned lizard with methods
incorporating detection probability. The Journal of Wildlife Management 71:1050–1056.

Grimm, N. B., D. Foster, P. Groffman, J. M. Grove, C. S. Hopkinson, K. J. Nadelhoffer, D. E.
Pataki, and D. P. Peters. 2008. The changing landscape: ecosystem responses to urbanization
and pollution across climatic and societal gradients. Frontiers in Ecology and the
Environment 6:264–272.

Haddad, N. M., L. A. Brudvig, J. Clobert, K. F. Davies, A. Gonzalez, R. D. Holt, T. E. Lovejoy, J. O. Sexton, M. P. Austin, and C. D. Collins. 2015. Habitat fragmentation and its lasting impact on Earth's ecosystems. Science Advances 1:e1500052.

Hellgren, E. C., R. T. Kazmaier, D. C. Ruthven III, and D. R. Synatzske. 2000. Variation in tortoise life history: demography of *Gopherus berlandieri*. Ecology 81:1297–1310.

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

Henke, S. E. 2003. Baseline survey of Texas horned lizards, *Phrynosoma cornutum*, in Texas. The Southwestern Naturalist 48:278–282.

Henle, K., K. F. Davies, M. Kleyer, C. Margules, and J. Settele. 2004. Predictors of species sensitivity to fragmentation. Biodiversity and Conservation 13:207–251.

IUCN. 2020. The IUCN Red List of Threatened Species. Version 2020-1. <https://www.iucnredlist.org>. Accessed 17 May 2020.

Johnson Linam, L. A. 2008. Texas horned lizard watch, 10-year summary report, 1997–2006. Texas Parks and Wildlife Division, USA. <https://tpwd.texas.gov/publications/pwdpubs/pwd_rp_w7000_1442/index.phtml>. Accessed 20 July 2020.

Kacoliris, F. P., I. Berkunsky, and M. A. Velasco. 2013. Sex and size affect annual survival in a threatened sand lizard. The Herpetological Journal 23:59–62.

Keinath, D. A., D. F. Doak, K. E. Hodges, L. R. Prugh, W. Fagan, C. H. Sekercioglu, S. H. Buchart, and M. Kauffman. 2017. A global analysis of traits predicting species sensitivity to habitat fragmentation. Global Ecology and Biogeography 26:115–127.

Kernohan, B. J., R. A. Gitzen, and J. J. Millspaugh. 2001. Analysis of animal space use and movements. Pages 125–166 *in* J. J. Millspaugh and J. M. Marzluff, editors. Radio tracking and animal populations. Academic Press, San Diego, California, USA.

Kokko, H., and A. López-Sepulcre. 2006. From individual dispersal to species ranges: perspectives for a changing world. Science 313:789–791.

Laake, J. L. 2013. RMark: An R Interface for analysis of capture-recapture data with MARK. AFSC Processed Rep. 2013-01, 25 p. Alaska Fisheries Science Center, NOAA, National Marine Fisheries Service, 7600 Sand Point Way NE, Seattle, WA 98115.

Laake, J. L., D. S. Johnson, and P. B. Conn. 2013. marked: an R package for maximum likelihood and M arkov C hain M onte C arlo analysis of capture–recapture data. Methods in Ecology and Evolution 4(9):885–890.

Larson, D. M. 2014. Grassland fire and cattle grazing regulate reptile and amphibian assembly among patches. Environmental Management 54:1434–1444.

Leclerc, C., S. Villeger, C. Marino, and C. Bellar. 2020. Global changes threaten functional and taxonomic diversity in insular species worldwide. Diversity and Distributions 26:402–414.

Lettink, M., and D. P. Armstrong. 2003. An introduction to using mark-recapture analysis for monitoring threatened species. Department of Conservation Technical Series A 28:5–32.

Liu, Z., C. He, and J. Wu. 2016. The relationship between habitat loss and fragmentation during urbanization: an empirical evaluation from 16 world cities. PLOS ONE 11:e0154613

Makinson, J. C., J. L. Woodgate, A. Reynolds, E. A. Capaldi, C. J. Perry, and L. Chittka. 2019. Harmonic radar tracking reveals random dispersal pattern of bumblebee (*Bombus terrestris*) queens after brumation. Scientific Reports 9:1–11.

Massot, M., J. Clobert, L. Montes-Poloni, C. Haussy, J. Cubo, and S. Meylan. 2011. An

    integrative study of ageing in a wild population of common lizards. Functional Ecology

    25:848–858.

Mantyka-Pringle, C. S., T. G. Martin, and J. R. Rhodes. 2012. Interactions between climate and

    habitat loss effects on biodiversity: a systematic review and meta-analysis. Global Change

    Biology 18:1239–1252.

Maxwell, S. L., R. A. Fuller, T. M. Brooks, and J. E. Watson. 2016. Biodiversity: the ravages of

    guns, nets and bulldozers. Nature News 536:143.

McDonnell, M. J., and I. MacGregor-Fors. 2016. The ecological future of cites. Science 352:

    936–938.

McKinney, M. L. 2002. Urbanization, biodiversity, and conservation: the impacts of

    urbanization on native species are poorly studied, but educating a highly urbanized human

    population about these impacts can greatly improve species conservation in all ecosystems.

    BioScience 52:883–890.

McKinney, M. L. 2008. Effects of urbanization on species richness: a review of plants and

    animals. Urban Ecosystems 11:161–176.

Milanesio, D., M. Saccani, R. Maggiora, D. Laurino, and M. Porporato. 2017. Recent upgrades

    of the harmonic radar for the tracking of the Asian yellow-legged hornet. Ecology and

    Evolution 7:4599–4606.

Miller, K. J., D. R. Erxleben, N. D. Rains, J. C. Martin, H. A. Mathewson, and J. M. Meik. 2020.

    Spatial use and survivorship of translocated wild-caught Texas horned lizards. The Journal of

    Wildlife Management 84:118–126.

Moeller, B. A., E. C. Hellgren, D. C. Ruthven III, R. T. Kazmaier, and D. R. Synatzske. 2005. Temporal differences in activity patterns of male and female Texas horned lizards (*Phrynosoma cornutum*) in southern Texas. Journal of Herpetology 39:336–339.118.

Molina-Zuluaga, C., P. F. Doherty Jr., J. Jaime Zúñiga-Vega, and J. Gastón Zamora-Abrego. 2013. Survivorship, growth, and detection of a knob-scaled lizard in Queretaro, Mexico. Journal of Herpetology 47:156–161.

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

Moody, R. W., D. A. Endriss, E. C. Hellgren, and S. F. Fox. 2007. Studying a population of Texas horned lizards (*Phrynosoma cornutum*) in an urban/military environment. Iguana 14:9–17.

Mook, J., E. M. Schauber, M. Vesy, R. W. Moody, and D. Nolan. 2017. *Phrynosoma cornutum* (Texas horned lizard) Behavior. Herpetological Review 48:197–198.

Munger, J. C. 1984. Home ranges of horned lizards (*Phrynosoma*): circumscribed and exclusive? Oecologia 62:351–360.

Munger, J.C. 1986. Rate of death due to predation for two species of horned lizard, *Phrynosoma cornutum* and *P. modestum*. Copeia 1986:820–824.

Oklahoma Department of Wildlife Conservation (ODWC). 2015. Oklahoma comprehensive wildlife conservation strategy: a strategic conservation plan for Oklahoma's Rare and declining wildlife. <https://www.wildlifedepartment.com/sites/default/files/Oklahoma%20Comprehensive%20Wildlife%20Conservation%20Strategy.pdf>. Accessed 16 May 2020.

Paterson, J. E., J. Baxter-Gilbert, F. Beaudry, S. Carstairs, P. Chow-Fraser, C. B. Edge, A. M. Lentini, J. D. Litzgus, C. E. Markle, K. McKeown, and J. A. Moore. 2019. Road avoidance and its energetic consequences for reptiles. Ecology and Evolution 9:9794–9803.

Pérez-Buitrago, N., M. A. García, A. Sabat, J. Delgado, A. Álvarez, O. McMillan, and S. M. Funk. 2008. Do headstart programs work? Survival and body condition in headstarted Mona Island iguanas *Cyclura cornuta stejnegeri*. Endangered Species Research 6:55–65.

Pianka, E. R., and W. S. Parker. 1975. Ecology of homed lizards: a review with special reference to *Phrynosoma platyrhinos*. Copeia 1975:141–162.

Piano, E., C. Souffreau, T. Merckx, L. F. Baardsen, T. Backeljau, D. Bonte, K. I. Brans, M. Cours, M. Dahirel, N. Debortoli, E. Decaestecker, K. De Wolf, J. M. T. Engelen, D. Fontaneto, A. T. Gianuca, L. Govaert, F. T. T. Hanashiro, J. Higuti, L. Lens, K. Martens, H. Matheve, E. Matthysen, E. Pinseel, R. Sablon, I. Schon, R. Stoks, K. Van Doninck, H. Van Dyck, P. Vanormelingen, J. Van Wichelen, W. Vyverman, L. De Meester, F. Hendrickx. 2020. Urbanization drives cross-taxon declines in abundance and diversity at multiple spatial scales. Global Change Biology 26:1196–1211.

Pietrek, A. G., R. S. Walker, and A. J. Novaro. 2009. Susceptibility of lizards to predation under two levels of vegetative cover. Journal of Arid Environments 73:574–577.

Pike, D. A., L. Pizzatto, B. A. Pike, and R. Shine. 2008. Estimating survival rates of uncatchable animals: the myth of high juvenile mortality in reptiles. Ecology 89:607–611.

Pollock, K. H., S. R. Winterstein, C. M. Bunck, and P. D. Curtis. 1989. Survival analysis in telemetry studies: the staggered entry design. The Journal of Wildlife Management 53:7–15.

Price, A. H. 1990. *Phrynosoma cornutum*. Catalogue of American Amphibians and Reptiles 469:1–7.

Radzio, T. A., and O'Connor, M. P. 2017. Behavior and temperature modulate a
thermoregulation–predation risk trade-off in juvenile gopher tortoises. Ethology 123:957–
965.

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

Richardson, M. L., P. J. Weatherhead, and J. D. Brawn. 2006. Habitat use and activity of prairie
kingsnakes (*Lampropeltis calligaster calligaster*) in Illinois. Journal of Herpetology 40:423–
428.

Riley, S. P., G. T. Busteed, L. B. Kats, T. L. Vandergon, L. F. Lee, R. G. Dagit, J. L. Kerby, R.
N. Fisher, and R. M. Sauvajot. 2005. Effects of urbanization on the distribution and
abundance of amphibians and invasive species in southern California streams. Conservation
Biology 19:1894–1907.

Row, J. R., G. Blouin-Demers, and S. C. Lougheed. 2012. Movements and habitat use of eastern
foxsnakes (*Pantherophis gloydi*) in two areas varying in size and fragmentation. Journal of
Herpetology 46:94–99.

Santos, T., J. Pérez-Tris, R. Carbonell, J. L. Tellería, and J. A. Díaz. 2009. Monitoring the
performance of wild-born and introduced lizards in a fragmented landscape: implications for
ex situ conservation programmes. Biological Conservation 142:2923–2930.

Segura, A., J. Jimenez, and P. Acevedo. 2020. Predation of young tortoises by ravens: the effect
of habitat structure on tortoise detectability and abundance. Scientific Reports 10:1–9.

Seto, K. C., M. Fragkias, B. Güneralp, and M. K. Reilly. 2011. A meta-analysis of global urban
land expansion. PLOS ONE 6:e23777.

Scudder, C. 2018. Dallas Zoo sets 46 horned lizards loose with its first-ever wildlife release. The

    Dallas Morning News. <https://www.dallasnews.com/news/texana/2018/09/18/dallas-zoo-

    sets-46-horned-lizards-loose-with-its-first-ever-wildlife-release/>. Accessed 5 May 2020.

Sherbrooke, W. C. 2002. Seasonally skewed sex-ratios of road-collected Texas horned lizards

    (*Phrynosoma cornutum*). Herpetological Review 33:21.

Sherbrooke, W. C. 2003. Introduction to horned lizards of North America No. 65. University of

    California Press, Los Angeles, California, USA.

Sherbrooke, W. C. 2008. Antipredator responses by Texas horned lizards to two snake taxa with

    different foraging and subjugation strategies. Journal of Herpetology 42:145–152.

Texas Parks and Wildlife Department (TPWD). 2020. Nongame and Rare Species Program:

    Federal and State Listed Amphibians and Reptiles in Texas.

    <http://tpwd.texas.gov/huntwild/wild/wildlife_diversity/nongame/listedspecies/amphibians-

    reptiles.phtml>. Accessed 18 May 2020.

Thawley, C. J., and T. Langkilde. 2016. Invasive fire ant (*Solenopsis invicta*) predation of

    Eastern Fence Lizard (*Sceloperus undulatus*) eggs. Journal of Herpetology 50(2):284–288.

Therneau, T. M. 2020. A package for survival analysis in R. R package version 3.2-3.

    https://CRAN.R-project.org/package=survival. Accessed 1 April, 2020.

Traill, L. W., B. W. Brook, R. Frankham, and C. J. A. Bradshaw. 2010. Pragmatic population

    viability targets in a rapidly changing world. Biological Conservation 143(1):28–34.

United Nations (2018). The World Urbanization Prospects: The 2018 Revision. The United

    Nations New York. <https://www.un.org/development/desa/publications/2018-revision-of-

    world-urbanization-prospects.html>. Accessed 5 May, 2020.

Whiting, M. J., J. R. Dixon, and R. C. Murray. 1993. Spatial distribution of a population of

   Texas horned lizards (*Phrynosoma cornutum*: Phrynosomatidae) relative to habitat and prey.

   The Southwestern Naturalist 38:150–154.

Whitford, W. G., and F. M. Creusere. 1977. Seasonal and yearly fluctuations in Chihuahuan

   Desert lizard communities. Herpetologica 33:54–65

Wiegand, T., E. Revilla, and K. A. Moloney. 2005. Effects of habitat loss and fragmentation on

   population dynamics. Conservation Biology 19:108–121.

Wilcove, D. S., D. Rothstein, J. Dubow, A. Phillips, and E. Losos. 1998. Quantifying threats to

   imperiled species in the United States. BioScience 48:607–615.

Wilson, M. C., X.-Y. Chen, R. T. Corlett, R. K. Didham, P. Ding, R. D. Holt, M. Holyoak, G.

   Hu, A. C. Hughes, and L. Jiang. 2016. Habitat fragmentation and biodiversity conservation:

   key findings and future challenges. Landscape Ecology 31:219–227.

Witmer, G. W. 2005. Wildlife population monitoring: some practical considerations. Wildlife

   Research 32:259–263.

Woinarski, J. C. Z., B. P. Murphy, R. Palmer, S. M. Legge, C. R. Dickman, T. S. Doherty, G.

   Edwards, A. Nankivell, J. L. Read, and D. Stokeld. 2018. How many reptiles are killed by

   cats in Australia? Wildlife Research 45: 247–266.

Wojcik, D. P., C. R. Allen, R. J. Brenner, E. A. Forys, D. P. Jouvenaz, and R. S. Lutz. 2001. Red

   imported fire ants: impact on biodiversity. American Entomologist 47:16–23.

Wolf, A. J., E. C. Hellgren, V. Bogosian, and R. W. Moody. 2013. Effects of habitat disturbance

   on Texas horned lizards: an urban case study. Herpetologica 69:265–281.

Wolf, A. J., E. C. Hellgren, E. M. Schauber, V. Bogosian III, R. T. Kazmaier, D. C. Ruthven III, and R. W. Moody. 2014. Variation in vital-rate sensitivity between populations of Texas horned lizards. Population Ecology 56:619–631.

Wolf, A. J., J. Mook, M. Vesy, R. W. Moody, and D. Nolan. 2015. *Phrynosoma cornutum* (Texas horned lizard) habitat use. Herpetological Review 46:633–634.

Zúñiga-Vega, J. J., F. R. Méndez-de La Cruz, and O. Cuellar. 2008. Demography of the lizard *Sceloporus grammicus*: exploring temporal variation in population dynamics. Canadian Journal of Zoology 86:1397–1409.

Figure 1. Map of study site on Tinker Air Force base (TAFB), Oklahoma, USA. Wildlife

Reserve 3 (WR3) is a native prairie grassland (~15 ha) surrounded by residential development

and military buildings. Blue outline indicates the full designated area of WR3; however, research

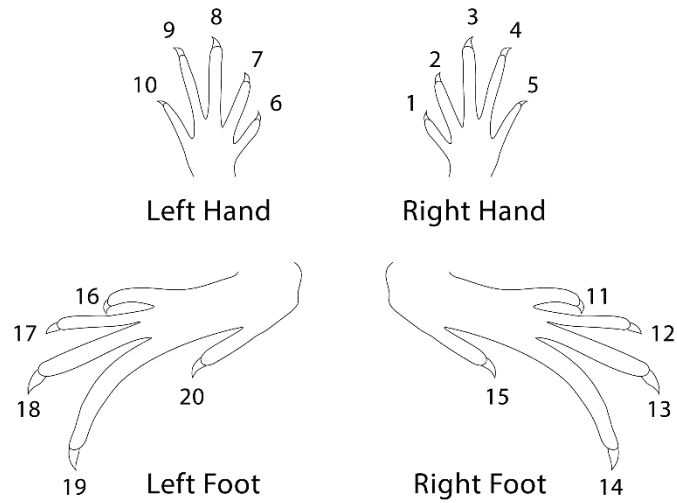was primarily restricted to the light blue shaded portion.

Figure 2. Toe numbering system for identification of hatchling and juvenile Texas horned lizards. Each individual lizard had a unique combination of two toes clipped. Only one toe was removed from an individual foot (e.g. 1-9 is a valid combination, but 1-5 is not a valid combination).

Table 1: Number of recorded fixes by year of study.

Year	New captures	Recaptures	Other[a]	Total fixes
2016	98	1,046	49	1,193
2017	57	1,036	46	1,139
2018	99	743	102	944
2019	33	898	65	996
Total	287	3,723	262	4,272

[a] Non-lizard fix: diode tag, radio transmitter, or fecal sample only.

Table 2. Morphometric measurements of snout–vent length (mm) and mass (g) for the three age classes of *Phrynosoma cornutum* during study period of 2016–2019 at Tinker Air Force base (TAFB), Oklahoma, USA.

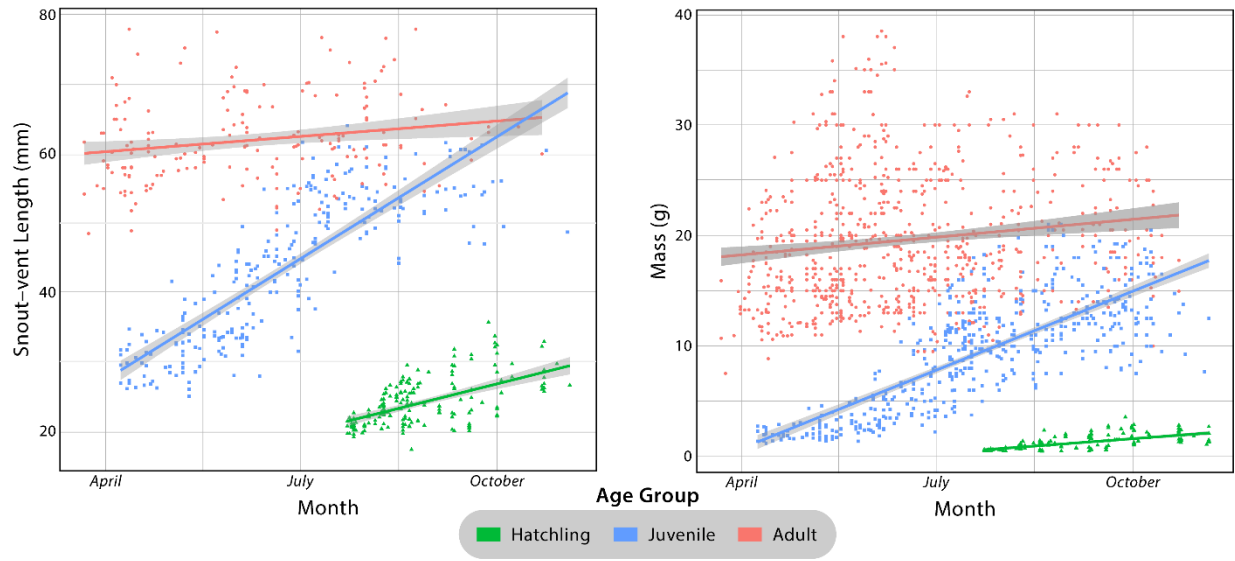| | Measurement | | | | | |
| | Snout–vent length (mm) | | | Mass (g) | | |
Age class	Range	x̄	SD	Range	x̄	SD
Hatchling	17.3–33.7	24.0	3.3	0.5–2.8	1.2	0.7
Juvenile	25.0–64.1	43.5	10.4	1.2–21.0	9.3	4.9
Adult	48.5–78.0	62.0	6.1	7.5–38.5	19.6	5.8

Figure 3. Morphometric measurements over time for three age classes of *Phrynosoma cornutum* at Tinker Air Force base (TAFB), Oklahoma, USA, during 2016–2019. Data from all four years of study were pooled together. Each point represents a single measurement in time for an individual lizard. Trendlines represent the average expected measurement for the age class at a given date. Adults are shown as red circles, juveniles as blue squares, and hatchlings as green triangles.

Table 3. Kaplan-Meier survival probability of two cohorts of *Phrynosoma cornutum* during study period of 2016–2019 on Tinker Air Force base (TAFB), Oklahoma, USA. Survival probabilities shown followed by 95% confidence intervals in parentheses. Upper estimates assumed all individuals with unknown fates were alive at the end of the time period in question; lower estimates assumed all individuals with unknown fates died.

Cohort	n[a]	Period A *to first brumation*		Period B *to first spring post-brumation*	
		Survival (95% CI) Lower estimate	Survival (95% CI) Upper estimate	Survival (95% CI) Lower estimate	Survival (95% CI) Upper estimate
2016	69	0.38 (0.28–0.51)	0.94 (0.87–1.00)	0.25 (0.15–0.40)	0.90 (0.79–1.00)
2018	83	0.41 (0.31–0.53)	0.95 (0.89–1.00)	0.32 (0.24–0.44)	0.81 (0.69–0.96)

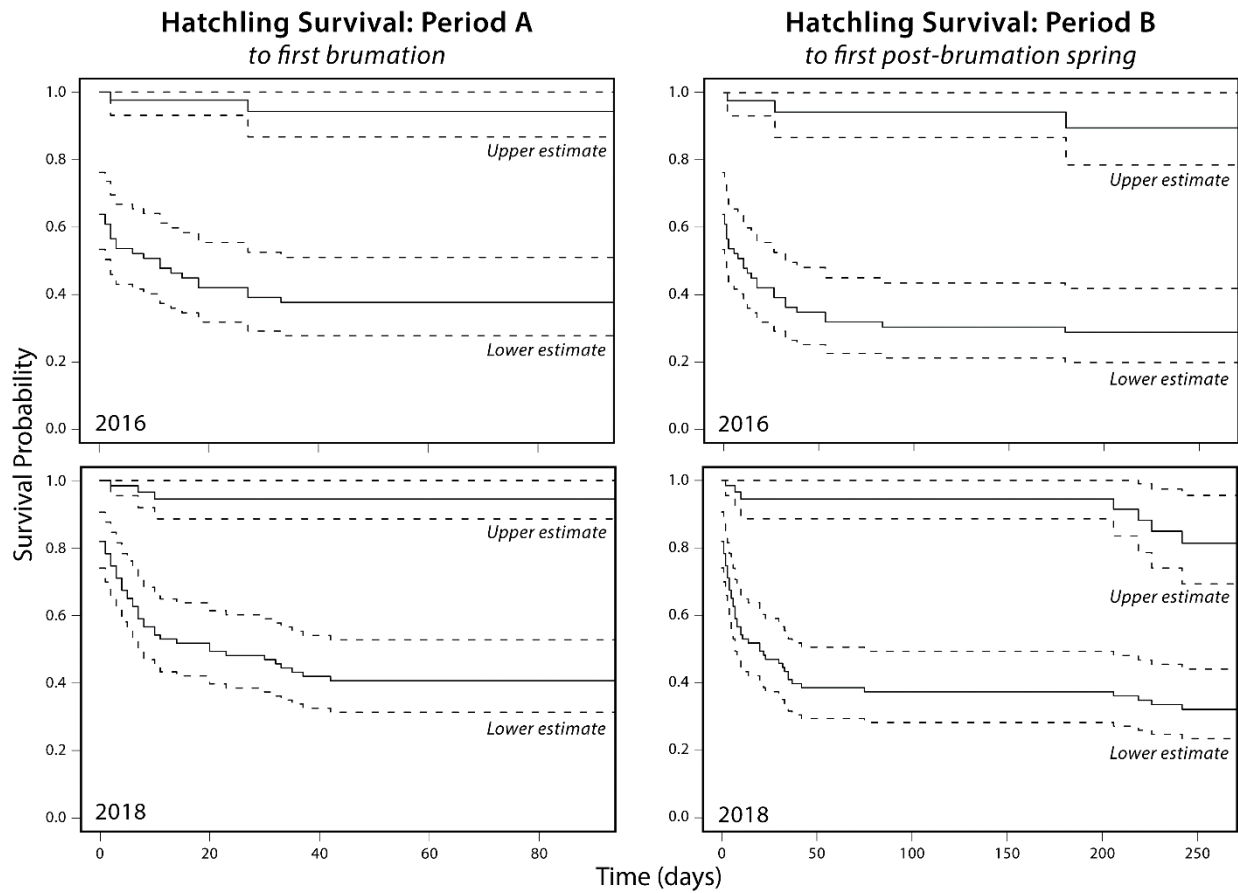[a] No. of animals contributing to the estimate.

Figure 4. Kaplan-Meier survival curves of two cohorts of *Phrynosoma cornutum* during the study period of 2016–2019 on Tinker Air Force base (TAFB), Oklahoma, USA. Upper estimates assumed lizards with undetermined fates survived to the end of the time period; lower estimates assumed lizards with undetermined fates were dead.
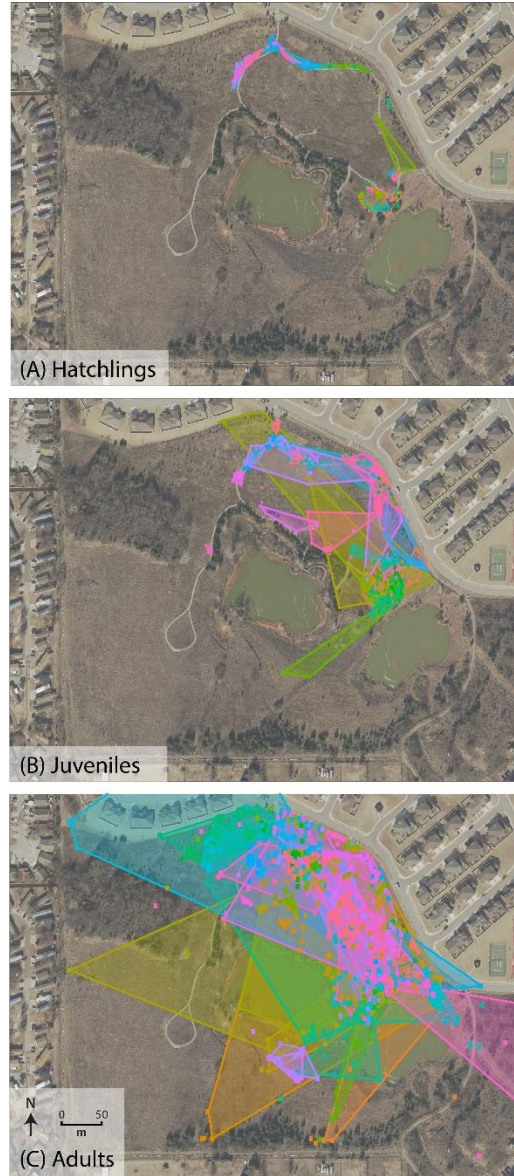
Figure 5. Estimated home ranges for three distinct age classes of Texas horned lizards at Tinker Air Force base (TAFB), Oklahoma, USA, represented by 95% minimum convex polygons. Each colored polygon represents one individual's area used over one active season. (A) Hatchlings had the smallest average home range size (<0.01 ha, $n = 53$). (B) Juveniles had a medium average home range size (0.082 ha, $n = 60$). (C) Adults had the largest average home range size (0.715 ha, $n = 57$)

Table 4. Home range size (in hectares; ha) measured by 95% minimum-convex polygons (MCPs) of individual Texas horned lizards during study period of 2016–2019 at Tinker Air Force base, Oklahoma, USA. Area used was calculated with 95% minimum-convex polygons for all individuals with more than 5 recorded localities within one active-season period.

Age class	min (ha)	max (ha)	x̄ (ha)	SD
Hatchling	<0.001	0.071	0.005	0.011
Juvenile	<0.001	1.510	0.082	0.221
Adult	0.002	5.428	0.715	1.141

Table 5. Summary of mark-recapture sessions for Texas horned lizards at Tinker Air Force Base,

Oklahoma County, Oklahoma, USA in 2019.

Capture Occasion	Capture Dates	Unique Captures	Total Captures
1	April 22, 24–26	28	59
2	June 2–5, 7	12	45
3	July 29–31, August 1, 2	14	32