Research Article

Survivorship and Spatial Patterns of an Urban Population of Texas Horned Lizards

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ABSTRACT Habitat fragmentation has negative consequences on threatened and endangered species by creating isolated populations. The Texas horned lizard (*Phrynosoma cornutum*) is experiencing population declines and localized extirpations throughout its range and has been classified as a species of greatest conservation need in Oklahoma, USA. Younger age classes have been poorly studied but may be vital to the stability of remaining populations. To address gaps in knowledge concerning subadult (hatchling and juvenile) morphometrics, survivorship, and home range sizes, we studied 2 cohorts of subadults, for 2 years each, covering their hatching and juvenile years (2016–2019). We used a combination of radio-telemetry and novel harmonic radar methodology to study a closed population of Texas horned lizards in 15 ha of native grassland at Tinker Air Force Base, Oklahoma. Population abundance for adults and juveniles was estimated as 56.5 ± 5.5 lizards and density as 7.96 lizards/ha. Our lowest estimates of survival indicated an average survival probability for the hatchling life stage of 0.285 (95% CI = 0.15–0.44), which is lower than for adults on the site. Average home range size increased from hatchling to adult life stages. Our results will have an immediate effect on the planning and assessment of ongoing headstart and management programs for Texas horned lizards. © 2021 The Authors. The *Journal of Wildlife Management* published by Wiley Periodicals LLC on behalf of The Wildlife Society.

KEY WORDS habitat fragmentation, harmonic radar, hatchling, home range, long-term monitoring, Oklahoma, telemetry, urbanization.

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, International Union for Conservation of Nature 2020). The United Nations reports 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 populations grow, the subsequent increase in urbanization continues to damage ecosystems through habitat loss, degradation, and fragmentation (Gibbons et al. 2000, Wiegand et al. 2005, Wilson et al. 2016), environmental pollution (Grimm et al. 2008), 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 (McKinney 2002, 2008; Dirzo and Raven 2003; 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).

Isolation caused by habitat fragmentation can have strong effects on the stability of wildlife populations, leading to 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

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movement between interacting populations, further increasing risk of genetic isolation and metapopulation extirpation (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 because 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 are generally less mobile than birds or mammals and have slower dispersal and recolonization rates (Craig et al. 2014, Larson 2014). Reptiles, especially species that are habitat specialists, are particularly sensitive to habitat fragmentation and modification (Mantyka-Pringle et al. 2012, Keinath et al. 2017, Doherty et al. 2020). For example, a comparative review of 35 turtle and squamate studies reported higher reptile extinction rates associated with habitat-specialist species compared with 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 for arid open areas where human development is likely (Pianka and Parker 1975, Munger 1984, Anderson et al. 2017). Historically, the range of this species extended throughout much of the Southwest from southern Colorado to northern Mexico and from western Missouri extending west through southern New Mexico and southeast Arizona (Sherbrooke 2003); however, during the past few decades, Texas horned lizards have experienced population declines and localized extirpations throughout parts of their range (Price 1990, Donaldson et al. 1994). In the United States, conservation status is described as imperiled in Missouri, Arkansas, and Oklahoma, vulnerable in Texas, Colorado, and Arizona, and secure in Kansas and New Mexico (Hammerson and Clausen 2020). In Oklahoma, the Texas horned lizard is listed as a Tier I species of greatest conservation need (Oklahoma Department of Wildlife Conservation 2015). Suspected reasons for the decline of horned lizard species, in general, are largely anthropogenic and include 1) introductions of the red imported fire ant (*Solenopsis invicta*); 2) loss of their preferred food source, harvester ants, resulting from widespread pesticide use; 3) over-collection for the exotic pet trade; 4) predation from domestic pets; 5) road mortality; and 6) loss, degradation, and fragmentation of the species' native habitat (Donaldson et al. 1994, Montgomery and Mackessy 2003, Endriss et al. 2007, Johnson Linam 2008, Barrows and Allen 2009, Brehme et al. 2018). Isolated populations of horned lizards in fragmented habitats persist; however, for many wildlife species, isolated populations are more susceptible to stochastic extirpation than larger contiguous populations (Burkey and Reed 2006, Clark et al. 2010, Walkup et al. 2017).

A population of Texas horned lizards in Oklahoma occurs on Tinker Air Force Base (TAFB) in Midwest City, Oklahoma (Endriss et al. 2007; Moody et al. 2007; Wolf et al. 2013, 2015; Ramakrishnan et al. 2018). Research on Texas horned lizards at TAFB has continued for the last 17 years, resulting in baseline understanding of this population's natural history and dynamics (Moody et al. 2007, Bogosian 2010, Bogosian et al. 2012, Wolf et al. 2014, Mook et al. 2017). Notably, a life-stage simulation analysis using demographic information for the TAFB population identified hatchling survival as having the strongest influence on population growth rate and emphasized the need to document hatchling survival more accurately (Wolf et al. 2014).

Survival of subadult reptiles (hatchling and juvenile) is often understudied and underestimated through traditional mark-recapture monitoring techniques because of 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 subadults' use of space has been documented for Texas horned lizards. Likewise, no published study has specifically focused on young age classes of Texas horned lizards; although, hatchling survivorship has been documented for the flat-tailed horned lizard (*Phynosoma mcalli*; Barrows and Allen 2009). Development of harmonic radar as a monitoring method 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).

Headstart programs, in which individuals of a threatened or endangered species are hatched 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 and captive breeding programs are now common practice in several Texas zoos, with hatchlings released just prior to brumation (i.e., period of below ground inactivity or torpor during the winter season), and no active monitoring after release (Cuthbert 2018, Scudder 2018). At the Oklahoma City Zoo and Botanical Gardens, a new headstart program began in summer 2019 from eggs obtained from TAFB. The objective of this Oklahoma-based project is to raise lizards for release in spring of each year, with cohorts being released after first brumation and others after second brumation. All individuals will be actively tracked post-release (S. J. Eliades, University of Oklahoma, personal communication). Although existing projects differ in the age at which lizards are released, increased understanding of subadult survivorship through tracking will help to optimize soft- and hard-release strategic plans for all headstart programs.

We addressed gaps in knowledge related to young age classes of Texas horned lizards using a combination of radio-telemetry and novel harmonic radar methodology. Our specific objectives were to characterize age-class specific body size, provide multi-year estimates of wild-born Texas horned lizard hatchling survivorship, test for and quantify home-range size changes from hatchling to adult life stages, and estimate population abundance and density in a small,

urban population of Texas horned lizards. We also compared population estimates incorporating harmonic radar technology to previous estimates for the study population based on radio-telemetry tracking and transect surveys alone. We predicted that body size measurements and home range area consistently would increase from hatchlings to juveniles to adults. Additionally, we predicted lower survivorship for subadults versus adults.

STUDY AREA

We conducted our study from April–October annually from 2016–2019, at TAFB, a large military installation in Midwest City (Oklahoma County), Oklahoma, USA (35.411755, −97.390797). This study site is in the southeastern portion of the greater Oklahoma City metropolitan area. Urban development covers roughly 75% of the base, leaving a fragmented arrangement of suitable horned lizard habitat. Current research activities are focused on Wildlife Reserve 3 (WR3), a 15-ha native prairie 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). The topography of WR3 is relatively flat with an elevation ranging from 370 m along the western edge to 384 m in the southeast corner (Fig. 1). The climate at TAFB is seasonal and classified officially as warm subhumid with pronounced day-to-day changes and more gradual changes across 4 seasons: spring (Mar–Jun),

Figure 1. Focal study site on Tinker Air Force Base, Oklahoma, USA, for a multiyear assessment of Texas horned lizards, 2016–2019. Wildlife Reserve 3 (WR3) is a native prairie grassland (~15 ha) surrounded by residential development and military buildings. Blue dashed outline indicates the full designated area of WR3; however, research was primarily restricted to the light blue shaded portion.

summer (Jun–Sep), fall (Sep–Dec), and winter (Dec–Mar; TAFB 2020). The average annual precipitation at TAFB is 92.8 cm, with average annual high and low temperatures of 22.2°C and 10.5°C, respectively. Over 330 native and exotic vertebrate species have been documented historically on TAFB property composed of 40 mammals, 212 birds, 35 reptiles, 12 amphibians, and 33 fish (TAFB 2020). Common larger vertebrates observed at TAFB include the fox squirrel (*Sciurus niger*), eastern cottontail rabbit (*Sylvilagus floridanus*), Virginia opossum (*Didelphis virginiana*), raccoon (*Procyon lotor*), bobcat (*Felis rufus*), coyote (*Canis latran*), American beaver (*Castor canadensis*), muskrat (*Ondatra zibethicus*), white-tailed deer (*Odocoileus virginianus*), and various small rodent species (e.g., woodrat [*Neotoma* spp.]; TAFB 2020). Dominant vegetation types are a mixture of native and non-native grassland species (little bluestem [*Schizachyrium scoparium*], big bluestem [*Andropogon gerardii*], indiangrass [*Sorghastrum nutans*], Maximilian sunflower [*Helianthus maximiliani*], and side oats grama [*Bouteloua curtipendula*]) interspersed with patches of eastern red cedar (*Juniperus virginiana*), 2 small ponds, and gravel paths (Moody et al. 2007). Harvester ants have not been documented to date at our study site (Ramakrishnan et al. 2018). Management activities are underway on and around WR3 specifically designed to connect Texas horned lizard habitat, such as prescribed burning and prairie restoration. During the time of this study, little to no immigration or emigration was expected because of a lack of connectivity to any other suitable areas.

METHODS

Animal Capture and Monitoring

We located, captured, and marked lizards for 4 consecutive years (2016–2019) during their active season each year (Apr–Oct) through structured visual searches and fortuitous encounters. We carried out field surveys of active lizards from 13 March to 3 November 2016, 22 March to 10 October 2017, 30 March to 5 November 2018, and 2 April to 18 October 2019. At our location, Texas horned lizards brumate underground from early November to late March (Wolf et al. 2013), and although we made a few observations of active lizards at the very end of March or the first few days of November, the majority of all lizard activity occurred between April and October each year. Visual searches consisted of groups of 1–6 researchers walking transects spaced approximately 3 m apart slowly and repeatedly throughout the study area. Person-hours varied but averaged 20 hours weekly. We conducted searches most actively from 0800–1300 to coincide with times of highest lizard activity (Moeller et al. 2005). We searched all areas of the reserve; however, we spent more time and effort in areas with bare ground because of an increased likelihood of detection, in contrast to areas where vegetation was so dense and high that visual observations were exceedingly rare (Wolf et al. 2014). When we found a lizard, 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 GeoExplorer Handheld Computer (Trimble GeoXT, Terrasync 2.3, Strategic Consulting International, Oklahoma City, OK, 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, we transported the lizard approximately 1.5 km to the TAFB Natural Resources Program lab for morphometric measurements and marking. Data collected for each individual included snout–vent length (SVL), mass, sex, and age class (juvenile or adult). To reduce travel-related stress on hatchlings, we did not transport them to the laboratory; instead, we measured and marked hatchlings at the site of capture with a portable field kit. We recorded mass for each lizard at each recapture event. We took measurements of SVL less frequently for recaptured animals to minimize stress and handling time.

The beginning of each field season (Apr–Jun) offered an opportunity to distinguish visually among age classes. We considered individuals to be hatchlings from the time of hatching until emergence from their first brumation at approximately 8 months of age, juveniles for 1 year beginning at emergence from the first brumation, and adults thereafter (Endriss et al. 2007). We determined age class based upon the size of the lizard at initial capture when the time of hatching was not known. Although juveniles are similar to hatchlings in weight (<5 g) immediately following emergence from the first brumation period, individuals grow to adult sizes and mass during the second half of the active season. During the field season, we classified individuals ≤10 g at initial capture as juveniles and those >10 g at initial capture as adults.

We individually tagged and marked all captured lizards before release. We marked each lizard weighing ≥5 g with a passive integrated transponder (PIT) tag (12.5 mm 134.2 kHz, Biomark, Boise, ID, USA) 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 (Hellgren et al. 2010). For lizards weighing <5 g, we clipped a unique combination of 2 toes as an alternative to a PIT tag until the individual grew large enough for safe implantation (Fig. S1, available online in Supporting Information). We saved all toe-clips for future genetic analysis. Lizards that obtained unique toe-clips at a younger age did not have toe IV removed when the PIT tag was implanted. Both toe-clipping and PIT tag insertion included the use of a topical anesthetic (Benzocaine gel, 200 mg; Patterson Dental, St. Paul, MN, USA). We sealed the PIT tag wound with Loctite super glue gel (Henkel Corporation, Düsseldorf, Germany) and we did not release the lizard until the glue had cured. We sterilized surgical tools between individuals in an iodine bath.

Following marking, we fit every captured individual with 1 of 2 monitoring devices, selected so as not to exceed 10% of the lizard's body mass: a very high frequency (VHF) radio-transmitter (BD-2, without temperature option; Holohil Systems, Carp, Ontario, Canada), or a small, flexible diode tag (0.03 g, on average) for detection via harmonic radar

(RECCO Rescue Systems, Lidingo, Sweden). We used VHF transmitters, emitting unique frequencies, with varying mass and battery life, to adjust for the size of the lizard: 1.8 g with battery life of 14 weeks, 1.4 g with life of 9 weeks, 1.0 g with life of 6 weeks, and 0.8 g with life of 4 weeks. We replaced transmitters as needed to maintain tracking through the entire active season. We attached the VHF transmitters with 100% non-toxic silicone adhesive on the dorsum of the lizard posterior to the head and added a braided elastic band to prevent loss during shedding (Endriss et al. 2007). Following marking and tagging, we released lizards within 2 hours at their original points of capture, which allowed silicone adhesive to fully dry. For smaller lizards, we attached the diode tag on the dorsum posterior to the head with 100% non-toxic silicone adhesive. We placed tags so that excess tag length extended beyond the tail and did not interfere with 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, because the diodes have no identifying markings or frequencies. All animal capture, handling methods, and minor surgeries, 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 from the Oklahoma Department of Wildlife Conservation (10014206) from 2016–2019.

Following release, we tracked tagged individuals using 1 of 2 receiver types: a handheld receiver attached to a 3-element Yagi antenna (for VHF transmitters) or a handheld RECCO model R8 receiver (for harmonic radar diode tags). When using the Yagi antenna, we homed in on the location of each lizard fitted with a VHF transmitter, then confirmed the location visually. When using the RECCO receiver, we slowly walked transects 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 1–5 times weekly during the active season (Apr–Oct), but tracking frequency varied as a result of local weather and lizard activity patterns. We did not track lizards during times of inclement weather, we increased frequency in July and August as hatchlings began to emerge from nest sites, and we decreased frequency toward the end of the active season as lizards decreased activity and began brumation. We re-captured individuals periodically as needed to re-attach or replace transmitters or diodes following shedding events, or to replace transmitters as battery life depleted.

Analysis of Survival and Home Range
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 2 different time periods. The first time period determined the probability of hatchling survival until the time of first brumation (roughly the first 3 months of life). The second time period extended until the following spring upon emergence from first brumation (roughly the first 8 months of life), which allowed us to determine any increased risk of death present during the brumation period from factors such as freezing. We considered the fate of a hatchling as survived if the individual was alive during the final week of the time period, or dead if we found its carcass. The fates of some hatchlings were unknown because of failure to relocate the individual (Table S2, available online in Supporting Information). Reasons for a failure to relocate individuals could include predators or scavengers removing hatchlings from the study area, diode failure, or location of a diode only (following a shedding event without subsequent recapture of the lizard). Because many individuals had unknown fates, we calculated an upper and lower estimate of survival for each cohort and time period. The upper estimate assumed lizards with unknown fates all survived to the end of the time period in question (i.e., start of brumation or emergence), whereas the lower estimate assumed all lizards with unknown fates were dead.

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). Preliminary analyses conducted separately for adult males and females showed no significant difference between the sexes; therefore, we calculated subsequent home range estimates on the pooled adult data set. We included only individuals that were located >5 times within 1 active season for analysis. Hatchling data included locations only from the 2016 and 2018 seasons; juvenile data included locations only from the 2017 and 2019 seasons. We pooled adult data 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. We conducted a Kruskal-Wallis test, followed by a Dunn's *post hoc* test, to compare home range area among age classes.

Mark-Recapture and Density Estimation
Mark-recapture techniques, although effective at estimating wildlife population abundance and density, require considerable investment of time and resources (Lettink and Armstrong 2003, Witmer 2005, Endriss 2006). When applied every few years, this method is effective to assess long-term population trends (Endriss 2006). To reassess population relative abundance and density of Texas horned lizards at TAFB, as compared to previous assessments onsite and using the same methodologies (Endriss et al. 2007,

Wolf et al. 2013), we selected 3 4–6-day periods during April–August 2019 to act as analogues of trapping occasions in mark-recapture terminology. The 3 mark-recapture sessions in 2019 were 22 and 24–26 April, 2–5 and 7 June, and 29 July–2 August. During these periods, groups of 1–6 researchers intensively searched the WR3 study area. We excluded the following from analysis: 1) hatchling captures, 2) repeat captures of the same individual within 1 trapping occasion, and 3) captures and recaptures outside designated occasions (Endriss et al. 2007, Wolf et al. 2013). We estimated population abundance of Texas horned lizards on the study area with R using package RMark (Laake 2013, Laake et al. 2013), with a closed population model that assumed constant capture and recapture probabilities over time. Similar to Endriss et al. (2007) and Wolf et al. (2013), our data set would not allow the fitting of more complex models.

We estimated the area of available Texas horned lizard habitat occupied by fitting a 100% MCP in ArcGIS (Esri, Redlands, CA, USA), using the convex hull method for all recorded lizard fixes in 2019. The MCP encompassed 2 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 horned lizards, we divided the abundance estimate by the area of usable habitat. Data sets and scripts used in analyses are deposited in Dryad (https://doi.org/10.5061/dryad.jwstqjq80).

RESULTS

Average SVL and mass increased across age classes and female adults were larger than male adults (Table 1). One-way analysis of variance (ANOVA) indicated that there was a significant effect of age class on SVL ($F_{3, 621} = 796.1$; $P < 0.001$; Fig. 2) and body mass ($F_{3, 1,447} = 1,224$; $P < 0.001$; Fig. 2); Tukey *post hoc* tests revealed statistical differences among all 4 groups for both SVL and mass (all $P < 0.001$). The SVL and body mass of Texas horned

lizards consistently increased during the active season for all age classes, reflecting growth; however, growth rates in adults were lower than rates observed in hatchlings and juveniles (Fig. 2).

To estimate the survival rate for hatchling horned lizards, we tracked the fates of hatchling lizards from 2 cohorts (2016 cohort: $n = 69$; 2018 cohort: $n = 83$; 152 individuals). We recorded 4,272 initial capture and recapture events (i.e., a fix) during the 4-year study period (Table S1, available online in Supporting Information). A low number of hatchling captures in 2017 ($n = 27$) resulted in insufficient sample size for analysis. Survival rates from time of hatching until beginning of first brumation ranged from 0.38–0.95 across years and unknown fate assumptions, and survival rates to emergence from first brumation ranged from 0.25–0.90 (Fig. 3; Table S3).

Preliminary analyses of home range sizes for individuals with >5, >10, and >20 recorded capture events showed no statistical difference in home range size estimation; therefore, we chose to be inclusive in range size estimation by including all individuals with >5 recorded capture events using 95% MCPs (Fig. 4; Miller et al. 2020). Average home range areas increased ontogenetically with body size. Hatchlings had the smallest average home range size ($\bar{x} = 0.005 \pm 0.011$ [SD] ha, range = <0.00–0.07 ha, $n = 52$), juveniles had an intermediate average home range size ($\bar{x} = 0.082 \pm 0.221$ ha, range = <0.00–1.51 ha, $n = 60$), and adults had the largest average home range size ($\bar{x} = 0.715 \pm 1.141$ ha, range = 0.00–5.43 ha, $n = 57$). There was a statistically significant difference between the 3 age classes (hatchlings, juveniles, adults [pooled]; $\chi_3^2 = 96.115$, $P < 0.001$), and pairwise comparisons between these groups were all significant ($P < 0.001$). Among adults, males tended to use a smaller home range (0.62 ha, $n = 30$) than females (0.82 ha, $n = 27$) on average; however, the sexes did not differ significantly ($P = 0.932$).

The unique and total captures resulting from the 3 mark-recapture sessions in 2019 were 28 unique and 59 total

Table 1. Snout–vent length (mm) and mass (g) for 3 age classes of Texas horned lizards at Tinker Air Force Base, Oklahoma, USA, 2016–2019. Hatchling data are averaged for the entire active season, the first month of life, and the final month prior to brumation. Juvenile data are averaged for the entire active season, the first month of active season, and the final month prior to brumation. Adult data represents the entire active season and are separated by sex.
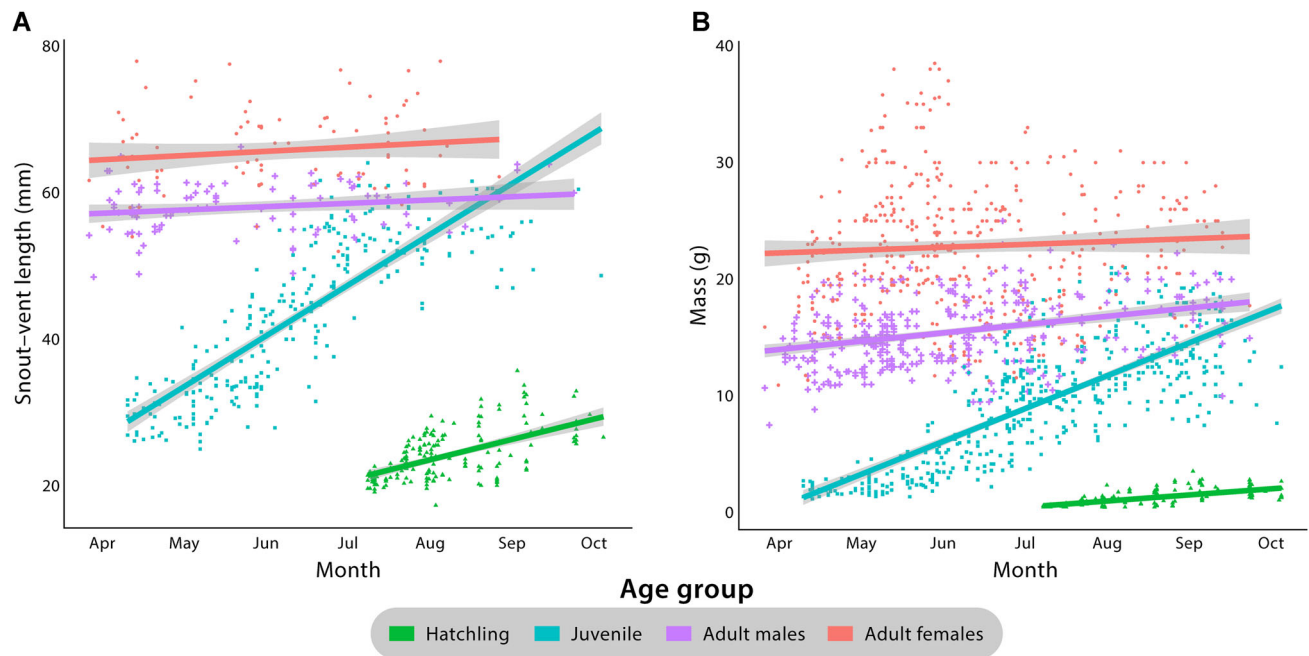
	Measurement							
	Snout–vent length (mm)				Mass (g)			
Age class	n	Range	$\bar{x}$	SD	n	Range	$\bar{x}$	SD
Hatchling[a]	180	17.3–33.7	24.0	3.3	163	0.5–2.8	1.2	0.7
Hatchling[b]	117	17.3–29.5	23.0	2.5	179	0.5–2.4	0.9	0.4
Hatchling[c]	22	22.1–32.9	27.4	3.1	122	1.0–2.8	1.8	0.5
Juvenile[a]	262	25.0–64.1	43.5	10.4	1515	1.2–21.0	9.3	4.9
Juvenile[d]	85	25.0–43.9	32.2	4.1	186	1.2–5.2	2.5	0.9
Juvenile[c]	4	48.7–60.5	53.7	5.6	136	7.5–20.5	13.4	3.3
Adult, all individuals	183	48.5–78.0	62.0	6.1	773	7.5–38.5	19.6	5.8
Adult, males only	90	48.5–66.3	58.0	3.6	341	7.5–25.0	15.5	2.9
Adult, females only	93	52.0–78.0	65.8	5.7	432	11.0–38.5	22.8	5.5

[a] Data pooled from entire active season (22 Mar–5 Nov).
[b] Data only from the first month after emergence from nest (Jul–Aug).
[c] Data only from the final month before brumation period (1 Oct–5 Nov).
[d] Data only from the first month out of brumation period (22 Mar–1 May).

Figure 2. Combined measurements of A) snout–vent length and B) mass during annual active seasons (~Apr–Oct) for hatchling, juvenile, adult male, and adult female Texas horned lizards at Tinker Air Force Base, Oklahoma, USA, 2016–2019. Data from all 4 years of study were pooled. 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; shaded areas surrounding trendlines represent 95% confidence intervals. Adult females are shown as salmon circles, adult males as purple plus signs, juveniles as turquoise squares, and hatchlings as green triangles. We recorded mass for each lizard at each recapture event (hatchling, $n = 163$; juvenile, $n = 515$; adult male, $n = 341$; adult female, $n = 432$); we measured snout–vent lengths (SVL) less frequently for recaptured animals to minimize stress, resulting in more records for mass than SVL (hatchling, $n = 180$; juvenile, $n = 262$; adult male, $n = 90$; adult female, $n = 93$).

(Apr session), 12 unique and 45 total (Jun session), and 14 unique and 32 total (Jul–Aug session). Two of the 3 mark-recapture sessions occurred in the first half of the active season before the emergence of hatchlings; therefore, we excluded hatchling captures in the third session from analysis; abundance and density estimates reflect the adult and juvenile populations only. Parameter estimates for the closed population model were 0.50 ± 0.10 for capture probability and 0.22 ± 0.05 for recapture probability. The population estimate for the reserve in 2019 was 56.5 ± 5.5 lizards (SE; 95% CI = 51.5–77.4). Based on an estimate of 7.10 ha for the area actively used, the population density was 7.96 lizards/ha. Both estimates were based on juvenile and adult age classes.

DISCUSSION

Texas horned lizard morphometrics, as measured by SVL (mm) and mass (g) increase linearly with ontogenetic shifts from hatchling to juvenile to adult, with juveniles exhibiting the highest rate of growth (Table 1; Fig. 2). Sexual dimorphism in Texas horned lizards is pronounced, with females always exhibiting larger SVL and mass than males and attaining sexual maturity at a large size (Montgomery et al. 2003), a pattern we also documented (Table 1; Fig. 2). Although values for hatchling morphometrics have not been widely reported in the literature, juvenile SVL and mass recorded at TAFB (43.5 ± 10.4 mm and 9.3 ± 4.9 g) are considerably smaller than those seen throughout Texas (54.0–58.9 mm and 9.8–17.4 g; Henke 2003). Previous researchers at TAFB reported that adult lizards have a smaller

SVL than Texas populations (TAFB females: 68.4 mm, males: 59.4 mm [Moody et al. 2007]; range for Texas adults, sexes pooled = 70.5–81.9 mm [Henke 2003]). These earlier data for the TAFB populations are consistent with results from our 2016–2019 study (Table 1; Fig. 2). From a survey of museum collections, Montgomery et al. (2003) reported a significant decrease in size for the species with increasing latitude, from Mexico to Colorado; however, adults from southeast Colorado were considerably larger than lizards from TAFB (females: 73.9 ± 0.8 mm, males: 67.9 ± 0.6 mm; Montgomery and Mackessy 2003). We do not know how the TAFB population compares with Texas horned lizards from other regions of Oklahoma because no statewide data exist. Smaller-than-average body size has been documented in urban settings in another lizard species (western fence lizard [*Sceloporus occidentalis*]; Putman et al. 2019); however, larger-than-average body sizes have also been documented in urban lizards (e.g., ornate tree lizard [*Urosaurus ornatus*], French et al. 2008; Puerto Rican crested anole [*Anolis cristatellus*] and brown anole [*A. sagrei*], Thawley et al. 2019).

Survival data of Texas horned lizards, particularly for young age classes, are often imprecise, problematic, or lacking from studies because the fate of many individuals is unknown (Hellgren et al. 2010). Therefore, field-based estimates of Texas horned lizard hatchling survival in other populations are currently not available. Contrary to our findings, for flat-tailed horned lizards in California, hatchling survivorship in their first year was >0.50 regardless of habitat characteristics, with a marked decline as animals progressed to juvenile and adult (Barrows and Allen 2009). For other species of lizard,
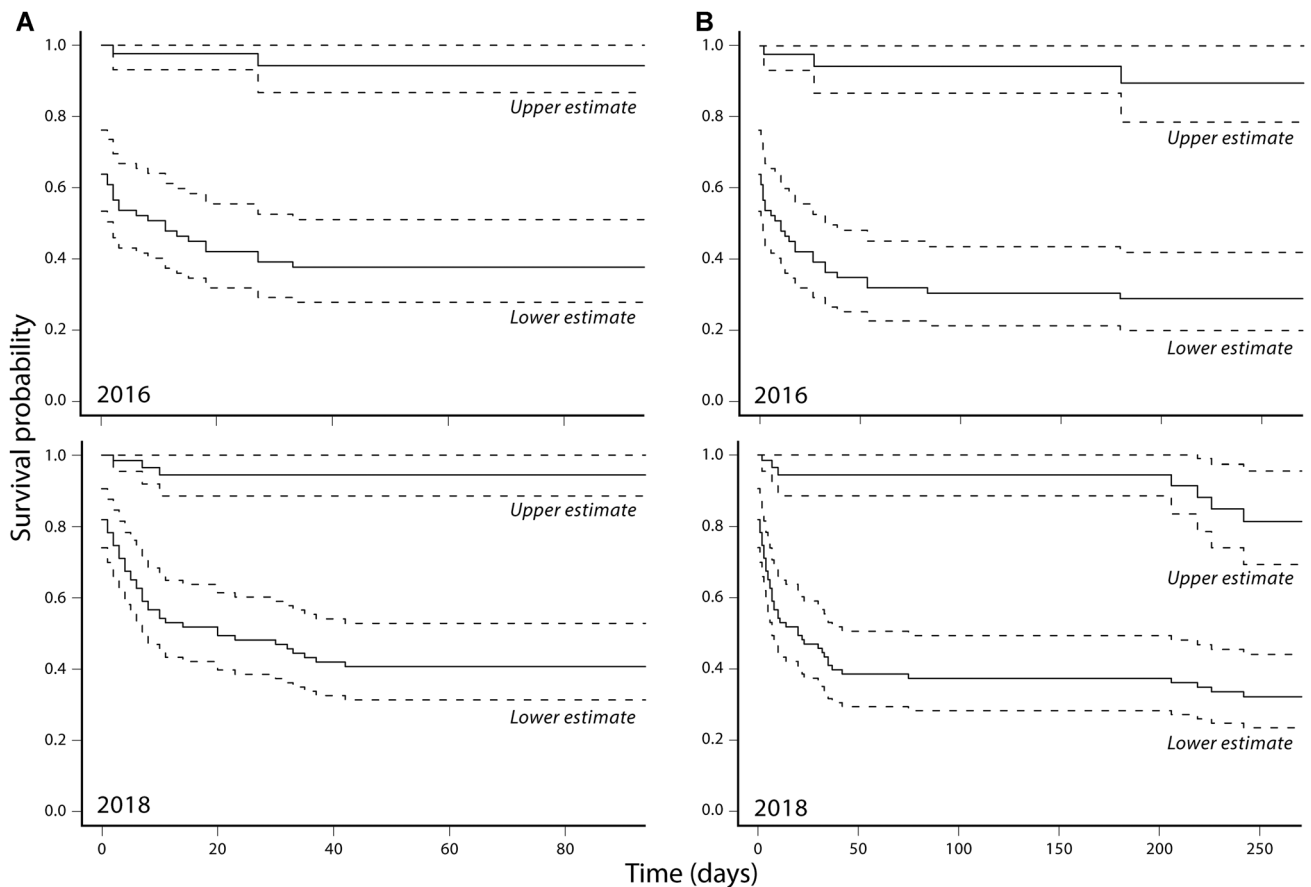
Figure 3. Kaplan-Meier survival curves of 2 cohorts of Texas horned lizards during the study period, 2016–2019, on Tinker Air Force Base, Oklahoma, USA ($n = 152$; 2016 cohort: $n = 69$; 2018 cohort: $n = 83$). Dashed lines represent 95% confidence intervals. Hatchling survival curves are estimated to A) first brumation and B) to first post-brumation spring. Upper estimates assumed lizards with undetermined fates survived to the end of the time period; lower estimates assumed lizards with undetermined fates were dead.

survival probability is considerably lower in early life stages compared to the adult life stage (Zúñiga-Vega et al. 2008, Massot et al. 2011, Kacoliris et al. 2013), and generally for reptiles, reported juvenile survival is approximately 13% lower than for conspecific adults, with average annual survival of juvenile lizards being 0.32 (Pike et al. 2008). Higher survival rates for adult Texas horned lizards, versus our documented rates for hatchlings, have been documented at various locations throughout the species' distribution: an adult survival rate of 0.59–0.70 at TAFB (Endriss et al. 2007), 0.01–0.47 for translocated lizards in north-central Texas (Miller et al. 2020), 0.09–0.54 for a wild population in southern Texas (Fair and Henke 1999), and 0.35–0.86 in southern Arizona (Munger 1986).

Two previous demographic studies of the TAFB population of Texas horned lizards used indirect, age-structure based, methodology to estimate hatchling survival rates. They used Euler's equation and known estimates of older age class survival and fecundity 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, field-based estimates (0.25–0.51) of hatchling survival, suggesting long-term stability of the TAFB population.

Our lower estimates of hatchling survivorship were based on the assumption that all lizards with unknown fates were dead. 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. Given the likelihood that some missing lizards survived without detection, this more conservative approach to calculating hatchling survivorship likely results in underestimated survivorship. Alternatively, our upper estimates of hatchling survivorship assumed that all lizards with unknown fates (e.g., lost or missing) survived. Given that hatchlings do not move far from their natal locations and that extensive searches uncovered no missing hatchlings, our upper estimates are likely too high. Therefore, the lower estimate may be more realistic and should be used in conservation planning.

A large number of the unknown fates for hatchling lizards resulted from loss of diodes via shedding (57.5% total, 48.8% in 2016 cohort, 65.2% in 2018 cohort), so improved attachment techniques warrant development. Nonetheless, unknown fates will continue to exist. The small and flexible
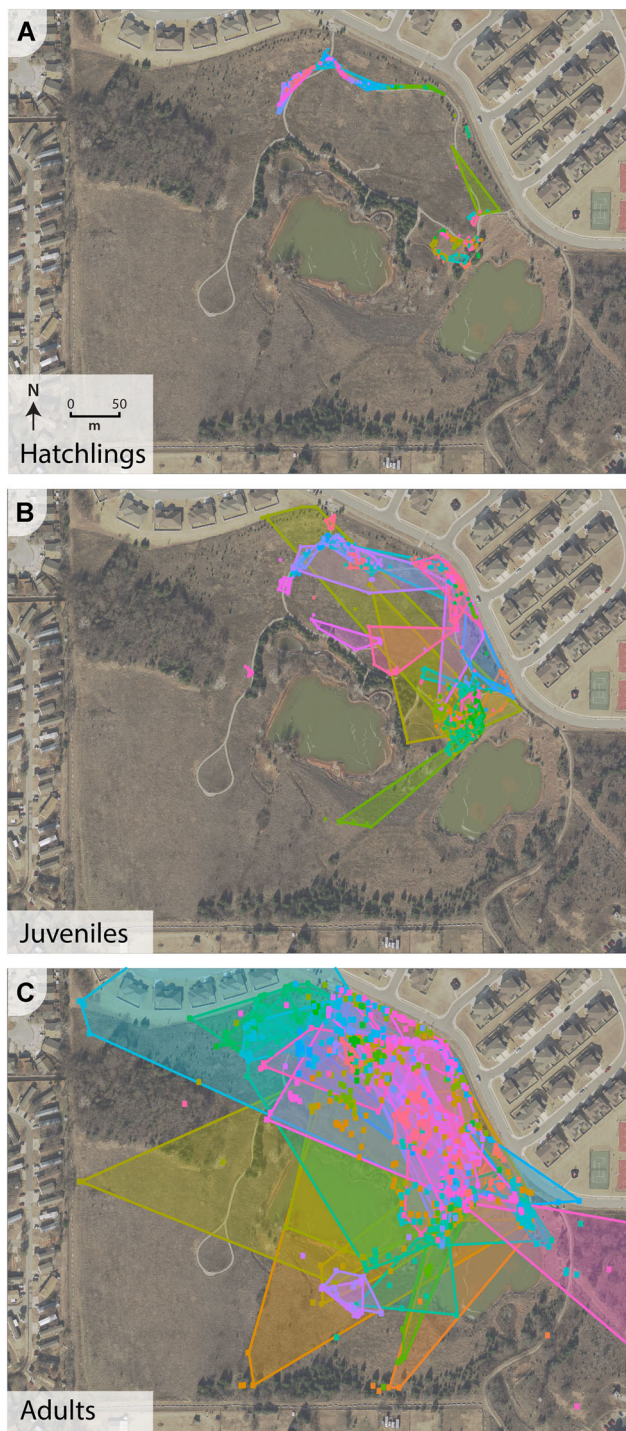
Figure 4. Visualization of estimated home ranges for pooled, multiyear data for 3 age classes of Texas horned lizards at Tinker Air Force Base, Oklahoma, USA, 2016–2019. Estimates are represented by 95% minimum convex polygons (MCPs) and are based on pooled data for both sexes across the multiyear study. All calculated MCPs are shown, with each colored polygon representing all data available for an individual lizard within each age class: A) hatchlings ($n = 52$), B) juveniles ($n = 60$), and C) adults ($n = 57$).

design of the diodes means they may be swallowed by a predator (e.g., snakes; Sherbrooke 2008). Horned lizards are often also moved long distances by humans or predators such as hawks, coyotes, or feral cats (Munger 1986, Giovanni et al. 2007). If lizards disperse or are removed

from the study area, the likelihood of lost diodes being found is low compared to radio-transmitters with extended ranges and individualized signals. The inability to assign unique frequencies to diodes precludes the search of specific individuals and requires direct encounters for identification.

Given the unique urban surroundings of our study site, predation pressure is likely lower than for more rural populations (Randa and Yunger 2006, Eötvös et al. 2018). Reduced abundance or absence of common natural predators of Texas horned lizards, such as diamondback rattlesnakes (*Crotalis atrux*), greater roadrunners (*Geococcyx californianus*), and coachwhips (*Masticophis flagellum*) were documented by earlier surveys (Wolf et al. 2013). Also notably absent from our study site is the invasive red imported fire ant, a predator of reptile eggs (Diffie et al. 2010, Thawley and Langkilde 2016) that has been linked to population declines in Texas horned lizards by displacing harvester ants, the lizard's preferred food source (Donaldson et al. 1994, Wojcik et al. 2001). Although typical urban settings can also lead to increased depredation from domestic cats (Woinarski et al. 2018), TAFB has regulations against free-roaming pets. Thus, the reduced abundance of predators at our study site may give our population higher survival rates than expected based on habitat quality.

The northern portion of WR3 on TAFB is bordered by an east–west road, driven nearly daily April–October by TAFB personnel and affiliated researchers and volunteers, and we expected it to be a source of mortality for horned lizards (Fig. 1). In the 16 years (2003–2019) that Texas horned lizard research has occurred on WR3, there have been only 2 documented cases of dead lizards found on the road. Although this could suggest that Texas horned lizards at TAFB avoid roads, it could also be that no habitat is available north of the road because of the housing development. Road avoidance 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). Road mortalities at our site could have gone undetected because of the removal of carcasses by avian scavengers (Santos et al. 2011, Hubbard and Chalfoun 2012). Vehicles have been reported to be a primary source of mortality for Texas horned lizards in Colorado, but this could be because road mortalities are easier to locate and identify than other deaths (Montgomery and Mackessy 2003). Although active roadways appear to be a minimal danger to Texas horned lizards on TAFB, they may restrict movement between habitat patches if actively avoided (Clark et al. 2010).

Our reported home range size averages for adult lizards fall within the 0.032–1.47-ha range estimated by Fair and Henke (1999) in southern Texas, who reported an average home range size of 0.73 ha. Miller et al. (2020) reported comparable values in north-central Texas with average home range areas for adult males and females of 1.34 ha and 1.72 ha, respectively. Previously at our study site, Endriss (2006) reported an average home range size of 0.43 ha for adult Texas horned lizards, which lies within the lower

end of the range documented currently at TAFB ($\bar{x} = 0.715 \pm 1.141$ ha, range $= 0.00–5.43$ ha). Conversely, research by Burrow et al. (2002) and Mitchell (2017) reported Texas horned lizard home ranges as high as 6.81 ha and 11.05 ha, respectively. Although the area of WR3 is small and isolated within an urban environment, the focal horned lizard population appears to be using the available habitat similar to populations in other parts of the species' range.

Our results show strong support for increased home range size with growth and development in Texas horned lizards. The small home range area used by hatchlings ($\bar{x} = 0.005 \pm 0.011$ ha, range $= <0.00–0.07$ ha) is likely due to mobility restrictions created by a small body size, which is only 6% of an adult's mass. Additionally, a small home range size could be a survival strategy for hatchling and juvenile lizards because large movements away from vegetative cover increase risk of predation for reptiles (Pietrek et al. 2009, Segura et al. 2020), and hatchling horned lizards are less protected than adults from predators by their body armor and occipital horns (Ballinger 1974, Sherbrooke 2003). Alternatively, hatchlings could have smaller home ranges because of more specific microhabitat preferences in the hatchling life stage than later life stages. Based on observations in 2016, we added location type (i.e., in vegetation or on path) to recapture data collection for the 2018 cohort. During 2018, we recorded hatchlings on man-made gravel paths (191 recapture events) and in prairie (189 recapture events) with nearly equal frequency.

Density and abundance appear stable for the TAFB population of horned lizards. Population abundance (56.5 ± 5 lizards) in 2019 was similar to most previous estimates at TAFB for the same site, 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, Southern Illinois University Carbondale, unpublished report). One notable exception is that our 2019 estimate was 72% higher than the estimate made by Wolf et al. (2013) of 32.9 ± 4.7 lizards in 2011. Construction of a housing development adjacent to WR3 in 2008–2011 resulted in a loss of 7.4 ha of lizard habitat, and 17 adult horned lizards were translocated in 2008 from the housing site to another, non-contiguous prairie at TAFB approximately 1.6 km away (Wolf et al. 2013, DeGregorio et al. 2020). The construction site and WR3 were separated by an existing gravel road; thus, WR3 itself remained constant in area with only the northern boundary area affected directly by land disturbance. The abundance estimates observed in 2019 likely represent natural variation in the population. Furthermore, the current density of horned lizards at TAFB reported here (7.96 lizards/ha) is higher than previous estimates from 2006 (5.00 lizards/ha) and 2011 (2.68 lizards/ha; Endriss et al. 2007, Wolf et al. 2013). The rebound in density highlights the resilience of these Texas horned lizards despite the small size and relative isolation of the population. A recent review of the effects of habitat fragmentation and modification on 367 squamate species showed that genera in Phrynosomatidae, including horned lizards (*Phrynosoma* spp.), spiny lizards (*Sceloporus* spp.), and side-blotched lizards (*Uta* spp.), are well-suited to patchily disturbed environments and may be somewhat resistant to habitat changes (Doherty et al. 2020).

Most reports regarding Texas horned lizards outside of TAFB, even at well-known sites like the Chaparral Wildlife Management Area, Texas (Hellgren et al. 2010), focus on occupancy within sites and allude to either population stability or decline, without estimation of abundance or density (Ballinger 1974, Donaldson et al. 1994, Busby and Parmelee 1996, Henke 2003). 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 2007, 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 are available to many researchers.

MANAGEMENT IMPLICATIONS

Long-term monitoring can document the persistence of small, urban populations of cryptic vertebrate species, and uncover the dynamics of critical life stages. Our results on hatchlings of the Texas horned lizard provide information on survival rates at different periods of development for consideration in the headstarting program. Small, soft-release enclosures could support headstarted Texas horned lizards until the end of the hatchling life stage. Given that brumation did not significantly reduce the probability of survival, releases made before first brumation should yield good success rates while helping reduce program costs. We encourage researchers to continue to monitor individuals after release with novel technologies, such as harmonic radar tracking.

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Associate Editor: Cynthia Paszkowski.

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