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EFFECT OF AGE-CLASS ON THE SURVIVORSHIP AND SPATIAL MOVEMENT PATTERNS OF HEADSTARTED TEXAS HORNED LIZARDS SOFT-RELEASED INTO AN URBAN POPULATION

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EFFECT OF AGE-CLASS ON THE SURVIVORSHIP AND SPATIAL MOVEMENT PATTERNS OF HEADSTARTED TEXAS HORNED LIZARDS SOFT-RELEASED INTO AN URBAN POPULATION

A THESIS APPROVED FOR THE

SCHOOL OF BIOLOGICAL SCIENCES

BY THE COMMITTEE CONSISTING OF

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ABSTRACT

Texas horned lizards (*Phrynosoma cornutum*) have experienced population declines and localized extirpations throughout their historic range, largely due to anthropogenic habitat loss. Consequently, there is broad interest in reinforcing persisting natural and urban populations, as well as reintroducing the species into previously occupied environments. To this end several headstart programs have been established that temporarily rear young wild-sourced or captive-bred hatchlings in captivity before their release into the wild. To understand how the age of headstarted lizards affects reintroduction success, we implemented a 2-year radio-telemetry study (April 2023 – October 2024) at an urban wildlife reserve on Tinker Air Force Base, Oklahoma. We compared the spatial movement patterns and survivorship of 2 soft-released cohorts of headstarted lizards, raised either to juvenile or adult age, to resident lizards of the corresponding age class.

The headstarted adult cohort (n = 16) was smaller on average and exhibited significantly lower daily movement distances, smaller home range sizes, and lower survivorship compared to resident adults (n = 19). However, despite these differences, they successfully underwent brumation, attempted reproduction, and maintained body weight post-release. In contrast, we did not observe significant differences in spatial movement metrics between the headstarted juvenile cohort (n = 8), and the resident juveniles (n = 9). Although we did not detect a difference in survivorship between the headstarted and resident juveniles, the statistical power of our survival analysis was limited by small sample size. The headstarted juveniles were initially much larger than the resident juveniles due to accelerated growth during headstarting, though this difference diminished by the end of the season. Low survivorship was observed across both headstarted and resident age classes, with nearly all recorded mortalities being attributed to predation. Notably,

nearly one-third involved unusual decapitations, indicating that nearby domestic cats may be responsible.

Our findings highlight the necessity of post-release monitoring, and suggest that headstarting Texas horned lizards to juvenile age before reintroduction may serve as a worthwhile supplement to the current method of releasing headstarted hatchlings before brumation. For threatened urban populations, future reintroduction efforts should be coupled with predator management strategies to mitigate mortality risk.

INTRODUCTION

Texas horned lizards (*Phrynosoma cornutum*) are a species of North American reptile distinguished by unique morphological characteristics and specialized behaviors adapted for survival in arid environments (Sherbrooke 2003). They have dorsoventrally compressed body forms, color patterns, and scale structures that aid in rapid thermoregulation, camouflage, and water acquisition (Sherbrooke 2003). Furthermore, large amounts of mucus in their pharynx and esophagus, as well as a toxicity-reducing blood plasma factor, enable them to prey almost entirely on ants, including venomous harvester ants (genus *Pogonomyrmex*) (Pianka and Parker 1975, Ramakrishnan et al. 2018, Fertschai et al. 2021). However, their physical attributes, combined with their sit-and-wait foraging strategy and crypsis-based defense behaviors, result in a generally sedentary lifestyle, with poor locomotor ability compared to other lizard species (Pianka and Parker 1975, Sherbrooke 2003). As such, they prefer heterogenous habitats that contain a mosaic of bare ground, herbaceous plants, and woody vegetation to meet their energetic and thermoregulatory needs, avoid predation, and navigate effectively (Fair and Henke 1998, Burrow et al. 2001, Tucker et al. 2023).

Unfortunately, by the early 1970s, localized extinctions and population declines were observed for this species throughout large portions of their historic range in Oklahoma and Texas, eventually leading to their listing as a Tier I Species of Greatest Conservation Need by the Oklahoma Department of Wildlife Conservation (Price 1990, Donaldson et al. 1994, Oklahoma Department of Wildlife Conservation 2015). Anthropogenic habitat degradation and fragmentation, widespread pesticide use poisoning native ant populations, the introduction of invasive red fire ants (*Solenopsis invicta*), and overcollection for the pet trade are among the proposed drivers behind the population declines (Price 1990, Donaldson et al. 1994, Henke

2003). Compounding the problem, the very morphological and ecological traits that make Texas horned lizards well adapted to their environments are also expected to limit their ability to disperse between habitat patches or exploit alternative prey (Sherbrooke 2003, Wall et al. 2024). Habitat and dietary specialists are typically less capable of responding to growing environmental stressors than generalists, which elevates their risk of extirpation (Prieto-Ramirez et al. 2020, Simpson et al. 2023). Given the recorded declines in populations of Texas horned lizards, numerous wildlife management actions have been undertaken over the last several decades (Howery 1996, Linam 2008, Miller et al. 2019, Williams et al. 2019); however, there exists a critical need for programmatic evaluation in order to optimize goals across the varied conservation initiatives.

Among the wildlife management actions taken with populations of Texas horned lizards is headstarting, a last resort strategy often used in the field of conservation to prevent extirpation of threatened species by supplementing or establishing wild populations with additional individuals that may survive and reproduce (Haskell et al. 1996). Unlike other approaches to bolster declining populations through direct translocation (transfer) of animals captured from other wild populations to the population of concern, headstart programs use captive-bred or wild-sourced hatchlings (or neonates) that are raised temporarily in captivity (Escobar et al. 2010, Nguyen et al. 2023). While in captivity, individuals are protected from the elevated mortality risk often experienced during young life stages in the wild, allowing them to grow to larger body sizes and/or older age classes. In doing so, the headstarted cohort is expected to experience higher survivorship upon release to the wild than they would have otherwise, thereby increasing recruitment into the target population (Haskell et al. 1996, Alberts 2007). Consequently, these programs are best suited for species whose population growth rate is most influenced by

subadult, rather than adult, vital rates (e.g., survival or recruitment per unit time) (Alberts 2007, Enneson and Litzgus 2008). As this is the case for Texas horned lizards (Wolf et al. 2014), several zoos in Texas and Oklahoma have established headstart programs for the species, operating primarily by hard-releasing captive-bred hatchlings right before their winter brumation period (Williams et al. 2019, Vesy et al. 2021).

Post-release assessments that have been conducted on other reptile translocation or headstarting programs have shown these initiatives to have mixed success in their primary aims (Dodd and Seigel 1991, Pérez-Buitrago et al. 2008, Germano and Bishop 2009, Choquette et al. 2023). Unsurprisingly, long-term goals are unlikely to be realized if the necessary short-term objectives are not met first. For example, translocated animals may fail to increase recruitment rates or establish populations if post-release survivorship is low or they exhibit poor site fidelity, which can arise for a myriad of reasons. Predators may be more likely to detect the newly released animals as they familiarize themselves with the new environment, especially if they disperse over long distances or move erratically while attempting to leave the target site (Reinert and Rupert 1999, Butler et al. 2005, Berger-TAL and Saltz 2014). Ontogenetic differences between life stages, as well as the conditions of the natural or captive pre-release environment, may also influence translocated animals' post-release behavior or morphological development (Aubret and Shine 2008, Roe et al. 2010, DeGregorio et al. 2017, Kraus et al. 2017, Mullin et al. 2023, Nguyen et al. 2023). Furthermore, characteristics of the target site, such as habitat composition, predator abundance, or distance from the previous site, can contribute to translocation response (Germano and Bishop 2009, Corbit et al. 2022). The need to identify the factors that lead to short-term success is particularly evident for horned lizards, as previous wild-to-wild translocation studies have reported variable post-release survivorship (Rosen and

McCabe 2012, Miller et al. 2019, DeGregorio et al. 2020). To date, no post-release studies have been published that examine how Texas horned lizards respond to current headstarting practices or explore alternative methods that may prove pivotal in increasing the efficacy of future releases.

Over two decades of research on an urban population of Texas horned lizards on Tinker Air Force Base (TAFB), located in Oklahoma County, Oklahoma, USA (35.4161° N, 97.4114° W) has provided significant insight into their demography, ecology, genetics, and natural history (Endriss et al. 2007, Moody et al. 2007, Ramakrishnan et al. 2018, Williams et al. 2019). Pertinent to current management efforts for this population, adults at TAFB are smaller and have lower reproductive output compared to populations in lower latitudes (Endriss et al. 2007). While adult survival rates are higher than those of juveniles, hatchling survival appears to be the most influential vital rate affecting population growth (Endriss et al. 2007, Wolf et al. 2014). Additionally, in response to habitat modification on base, several spatial ecology, survivorship, and translocation studies have also been conducted (Bogosian 2010, Wolf et al. 2013, DeGregorio et al. 2020). For example, from 2008–2010, the construction of housing and military infrastructure reduced the suitable habitat for the lizards, and attempts to reduce mortality by translocating the lizards from construction sites directly to another site on base proved ineffective, as the lizards had significantly lower survival rates (Bogosian 2010). Although some reptile species respond well to this method of direct translocation (a so-called “hard release”) (Bertolero et al. 2007, Westaway et al. 2024), stress from transport and unfamiliarity with a new environment can cause abnormal spatial behaviors or modified activity budgets, leading to low survivorship (Plummer and Mills 2000, Butler et al. 2005, Berger-Tal et al. 2020).

In contrast to hard release translocation, “soft release” methodologies are believed to benefit reintroduced animals by employing various techniques that allow them to acclimate to their new environment, practice natural behaviors, and prevent immediate predation (Resende et al. 2021). This approach typically involves temporarily confining the individuals to an outdoor pen at the reintroduction site to minimize predation risk while they adjust to local conditions, hopefully leading to positive resultant vital rates after full release (Knox et al. 2017, Resende et al. 2021). To explore the utility of this approach for the horned lizards at TAFB, beginning in 2016, researchers again translocated individuals from areas of anthropogenic disturbance, this time keeping them in pens at the release site for 2 weeks (DeGregorio et al. 2020). Once fully released, the soft-released juveniles moved greater distances per day than the residents of the same age class but demonstrated similar annual survival rates. However, interestingly, soft-released adults exhibited reduced movement and lower survivorship compared to the resident adults (DeGregorio et al. 2020). Although the sample size for the translocated adults was small, these results underscore the need for further investigation to better understand the factors contributing to successful translocation of threatened Texas horned lizards.

To ensure that headstarting programs meet conservation objectives, released individuals must remain healthy and demonstrate survivorship and natural spatial use patterns similar to those of wild residents of the same age classes (Kleiman 1989). To evaluate this expectation, we carried out a 2-year study to compare the survivorship, daily movement rates, and home range sizes between headstarted and wild lizards from two life stages (juvenile and adult) and investigated whether conservation headstarting initiatives are effective for populations living in urban environments. Specifically, we explored the effect of age class on Texas horned lizard reintroduction to optimize existing, and identify alternative, methodologies to conservation

headstarting initiatives for this species. Soft release approaches were employed with two groups of headstarted lizards, raised to either juvenile or adult age classes, back into the urban TAFB population from which they were collected as hatchlings. Lizards released as adults are guaranteed to have survived to reproductive age and are expected to benefit from the associated survival advantage of larger body size (Tetzlaff et al. 2019*b*, Mullin et al. 2023); however, additional time spent in captivity can adversely affect animals' ability to perform natural behaviors or survive post-release (Roe et al. 2010, Degregorio et al. 2013, DeGregorio et al. 2017). Conversely, lizards released as juveniles are expected to benefit from the shorter captivity duration while still avoiding predation at their most vulnerable hatchling body sizes and experience accelerated growth compared to wild individuals (Haskell et al. 1996, Sacerdote-Velat et al. 2014). Releasing headstarted animals at a juvenile life stage, however, means they must first survive to sexual maturity before they may contribute to the growth of the target population (Dodd and Seigel 1991). Finally, we also documented any potential reproductive behaviors in the headstarted adult cohort and tracked the seasonal growth of juveniles.

The results of this study improve our understanding of how the structure of headstarting programs impacts post-release spatial movement patterns and survivorship for animals in conservation programs. Furthermore, this comparative dataset establishes a baseline for evaluating factors critical for optimizing headstarting approaches for horned lizards, including considerations of how time in captivity may influence post-release survival, spatial use, growth rate, and reproductive behavior.

METHODS

Study Area

Tinker Air Force Base is a 2,000-ha urban military installation located in Midwest City, Oklahoma, USA. Within the base lies our study site, Wildlife Reserve 3 (WR3), a multi-use 15-ha grassland composed of mixed native and non-native plant species, intersected with a loop walking trail, 2 man-made fishing ponds, and a small wood stand in the northwest quadrant. Further description of plant species and climate of WR3 can be found in Vesy et al. (2021). The reserve is flanked by residential housing to the north and west and military infrastructure to the south and east. Due to these surroundings, the residing population of Texas horned lizards is expected to be highly insular, with minimal immigration or emigration (Wolf et al. 2013, Wall et al. 2024). Numerous native species capable of depredating horned lizards also inhabit the reserve, including western rat snakes (*Pantherophis obsoletus*), speckled king snakes (*Lampropeltis holbrooki*), prairie king snakes (*Lampropeltis calligaster*), raccoons (*Procyon lotor*), striped skunks (*Mephitis mephitis*), coyotes (*Canis latrans*), bobcats (*Lynx rufus*), opossums (*Didelphis virgiana*), and numerous birds of prey (Bogosian et al. 2012).

Headstarting, Soft-Release and Tracking Protocols

Our study aimed to release both age classes of headstarted lizards simultaneously for comparison with the resident population, however due to a lack of available hatchlings in 2022 to captive-raise to juvenile age, the study was staggered into 2 releases: adults in 2023 and juveniles in 2024. At TAFB, individuals are considered to be hatchlings until they emerge from their first brumation at approximately 8 months of age, then as juveniles until they emerge from their second brumation as adults at roughly 20 months (Endriss et al. 2007). The first release consisted of 18 wild individuals previously captured from WR3 in August 2021, either as hatchlings or eggs, and transported to the Oklahoma City Zoo and Botanical Gardens (OKC Zoo) to be

captive-raised until adulthood as part of their newly established pilot headstart program. While at the OKC zoo, we housed lizards separately in ~75 L glass terrariums (~76.20 × 33.02 × 33.02 cm) containing refugia of cholla wood, basking rocks, artificial plants and shallow water dishes, all placed atop a substrate mixture of sand, mulch, decomposed granite, and soil. Each tank maintained a temperature gradient using an overhead 100 W basking bulb (Fluker's, Port Allen, LA, USA) for 8:16 hour on/off cycles on one side. Ultraviolet light was provided by a 10.0 UVB bulb (T5 HO ReptiSun, Zoo Med Laboratories Inc., San Luis Obispo, CA, USA) spanning the length of the tank for 11:13 hour on/off cycles. We supplied water twice a day by misting the enclosure walls and artificial plants using a reverse osmosis and deionization filtered water setup with a misting system (MistKing, Jungle Hobbies Ltd., Emeryville, ON, Canada). Ambient temperature of the room remained at 28.6 °C and environmental conditions were not adjusted to replicate natural seasonal shifts that trigger brumation in wild Texas horned lizards. Due to the difficulty of acquiring harvester ants, horned lizards' preferred prey, we fed the lizards a diet of fruit flies and pinhead crickets every other day, until they reached larger sizes in which their diet was supplemented with larger crickets and meal worms. Before prey items were presented to the lizards, they were dusted with Formic-Cal Plus Ant Eater supplement (Repashy Ventures, Oceanside, CA, USA). Nearly all the headstarted lizards survived in captivity until adulthood, although 2 individuals that became sick had to be euthanized by the OKC Veterinary staff.

On May 5th, 2023, we released 16 adult headstarted lizards (9 males and 7 females) after ensuring there would not be any inclement weather during their first 3 consecutive days in the soft release pen. The construction of the pen took place over the preceding 3 days after we first identified suitable habitat within the area occupied by the resident lizard population that was also far enough away from the loop trail to prevent anthropomorphic disturbance. We then buried tan

36 cm vinyl flashing approximately 13 cm into the soil to form an 8 m by 9 m rectangle. The walls of the pen were reinforced by screwing the flashing to 60 cm garden stakes buried at 1 m intervals along the perimeter, and holes were drilled into the flashing to allow invertebrates to enter the pen. Additionally, we installed 10, 1.5 m T-posts within the pen that were connected with bailing wire to support a canopy of deer fencing attached to the buried garden stakes to prevent predator access. We weighed the lizards weekly to ensure there was an adequate supply of prey available. After 3 weeks, the animals were fully released to the rest of the reserve after we removed the flashing from the corner of the pen. The timing of the release, along with the soft-release duration time, was chosen to avoid drawbacks from a previous iteration of the pilot program which was characterized by high mortality rates during a 5-week soft-release in the month of June.

The wild, resident adult lizards were found in early April of the 2023 active season, by relocating 13 lizards that had been previously marked and tracked at TAFB. We captured 6 additional adults either through opportunistic encounters while tracking the tagged individuals, or during one of 3 inventory surveys that took place throughout the active season. These inventory surveys took place once a month from June to August, during which groups of researchers spent 4 days walking transects spaced 3 m apart throughout the reserve looking for new lizards. Upon capture, or within the week prior to soft release for the headstarted individuals, we implanted unmarked animals with an 8 mm passive integrated transponder (PIT) tag (Biomark, Boise, ID, USA) and marked them a secondary toe-clip on the fourth toe following procedures previously used at TAFB (Vesy et al. 2021). This allowed us to identify recovered individuals whose tag may have shed or failed. To relocate the lizards, we used 100% non-toxic silicon adhesive to attach 0.95 – 1.1 g very high frequency (VHF) radio transmitters (BD-2

series, Holohil Systems, Carp, Ontario, Canada) to the upper dorsum of the lizards. The transmitters were further secured to the lizards with collars made from 3 mm elastic bands. Towards the end of the season, some resident lizards were instead outfitted with digital radio tags 1.0 g (HybridTag, Cellular Tracking Technology, Rio Grande, NJ, USA), which included a brown-painted, flexible diode (0.03 g, on average), glued on to the underside of the tag. To ensure the transmitters weighed less than 10% of each individual's body mass, we weighed and measured snout-vent length of each lizard before attaching it. VHF radio transmitters were replaced as needed before battery failure, and the digital radio transmitters were similarly replaced if they stopped functioning.

Once radiomarked, we used telemetry to home to the lizards' locations 3 to 6 times a week until the end of the active season in October, using either a TR-8 handheld receiver with Yagi antenna (Telonics Inc., Mesa, AZ, USA) or the CTT Locator (Cellular Tracking Technology) for VHF and CTT tags, respectively. If a lizard's tag appeared to be malfunctioning, we attempted to locate the animal for tag replacement by walking transects around its last known location while waving a harmonic radar receiver (Handheld model R9, RECCO Rescue Systems, Lidingo, Sweden), which emitted an audible ping when near a diode or VHF tag. Upon visual relocation, we recorded the lizard's Universal Transverse Mercator (UTM) coordinates (North American Datum 1983) using a handheld Trimble GeoExplorer computer (Trimble GeoXT, Terrasync 2.3, Strategic Consulting International, Oklahoma City, OK, USA), along with their survival status, whether they were active or burrowed, and any observed reproductive behavior. To minimize stress for the animals, we limited handling time by taking morphometric measurements during tag changes, with additional field measurements taken only periodically to monitor the lizards' growth and health.

For the second release, we collected 9 hatchlings opportunistically from August to September 2023 and brought them to the OKC Zoo to be headstarted until their release as juveniles in May 2024. From this cohort, 8 survived to be headstarted and soft-released using the same methodology as the adult cohort; however, they were fully released from the pen after 2 weeks (May 5^{th} – 20^{th}) when we noticed a slight decline in mass in a few individuals. Resident juveniles were captured between mid-May and mid-June in 2024 by opportunistic encounters while researchers continued tracking surviving adult lizards. Due to the juveniles' small stature (< 5 g), we opted to forgo using PIT tag to reduce potential stress on the animals and instead marked them with a unique combination of two toe-clips (Vesy et al. 2021). All juveniles were tagged with either a thin, flexible, diode if their weight was < 5 g, a 0.45 g VHF transmitter (BD-2x series, Holohil Systems) if they weighed between 5 and 10 g, or 0.95 – 1.1 g BD-2 VHF transmitters if they exceeded 10 g. Tag changes, morphometric measurements, and population tracking methods remained the same for the juveniles, and the surviving adult lizards, until the end of the study in October 2024.

Analysis of Movement and Home Range

To compare movement between headstarted and resident groups within each age-class, we estimated daily movement rates using the *calculate motion statistics* tool in ArcGIS Pro (Esri, Redlands, CA, USA) to measure the geodetic distance between individuals' consecutive fixes, then we divided that value by the number of days that had elapsed. Since this method likely underestimates the actual distances moved, we minimized this bias by only including fixes where no more than 2 days had elapsed since the previous one (i.e. 1 day in between fixes where the lizard was not located). For accurate group comparisons, we calculated daily movement rates for residents by only using relocations collected after the release of the headstarted group. We also

only used data collected during the 2023 active season to analyze adult movement and home range due to sample size limitations by the 2024 season.

To account for the repeated measures per individual, the varying intervals in which different individuals remained in the study, and the right skew of the data, we analyzed natural log-transformed daily movement rates using linear mixed models (LMMs). To do this we used the *lme4* package (Bates et al. 2015), and all subsequent statistical analysis where conducted in R v4.2.2 (R Core Team 2022). We fit models with the predictor variables *origin* (whether the lizard belonged to the headstarted or resident group) and *days* (number of days elapsed since the headstarted lizards' release until the end of the active season) as fixed effects, while *individual lizard ID* was treated as a random effect. The *days* variable was first centered and scaled (total # of days per season ~ 120, mean = 0, SD = 1) before inclusion in the models for model stability and computational efficiency. We used Akaike Information Criterion (AIC) model selection to compare a series of models fitted using restricted maximum likelihood (REML), all of which included an interaction between variables (*origin* * *days*), but varied in their random effect structure: random intercept-only, random slope-only, or random intercept-and-slope. After ensuring the model with the lowest AIC met model assumptions, we included its random effect structure in a set of models fitted using maximum likelihood that varied in their fixed effects: null, *origin* only, *days* only, additive effects (*origin* + *days*), and a full interaction (*origin* * *days*). Finally, the most parsimonious model was refit using REML to estimate parameters and we used the *MuMIN* package to calculate the conditional and marginal coefficient of determination values (Bartoń 2024). The conditional R^2 measures the variance explained by both the random and fixed effects, while the marginal R^2 measures the variance explained by the fixed effects only. We also

measured the furthest distance each headstarted individual moved away from the soft release pen and summarized this dispersal information for both the age-classes.

Following the framework put forth by Signer et al. (2021), we compared the home ranges between headstarted and resident groups within each age-class using multiple estimators, despite our expectation that the relative comparison between groups would be robust to estimator choice. Limitations in our tracking methodology and subsequent data did not allow for the use of modern estimation techniques that incorporate animal movement into model design; however, our movement data is available on Movebank to facilitate inter-study comparisons (Crane et al. 2021, Silva et al. 2022). For individuals with greater than 10 relocations, we estimated their home range area in hectares derived by 95% minimum convex polygons, or hulls formed by the 95% isopleths generated by kernel density estimation (KDE) using the *amt* package (Signer et al. 2019). The KDEs derived using the reference bandwidth selection method (h_{ref}) were over-smoothed, leading to area overestimates, while the least-squares cross-validation (*lscv*) method often failed to converge. Instead, we present estimates obtained using plug-in bandwidth selection with a spatial resolution of 2 m, though we acknowledge this method resulted in under-smoothed utilization distributions for some individuals (Pagano et al. 2021). We also note that increasing the spatial resolution did not meaningfully change the relative differences between headstarted and resident groups. Since home range estimates can be underestimated for animals with few relocations, we performed preliminary Spearman's correlation tests to evaluate if area estimates correlated with the number of relocations for each estimator. Statistically significant results were not observed for any of the tests at an alpha level of 0.05. We performed Student's t-tests to compare the mean area use between the headstarted and resident groups for both estimators, after first applying a natural logarithm transformation to meet test assumptions.

Analysis of Survival and Body Condition

We used the *survival* package to compare lizard survivorship between headstarted and resident groups within age classes (Therneau 2024). Survival rates were obtained using the Kaplan-Meier estimator, as this method allows for right censoring and delayed entry of individuals (Pollock et al. 1989). Since resident lizards could enter the study a few weeks before or after the headstarted lizard release, we applied a risk set adjustment to include an individual in the risk set at each mortality event only if they had been previously located. This method prevents bias in survival probabilities that can arise from left truncation, but relies on the assumption of "independent delayed entry", that is, an individual's hazard risk is independent of entry time (Backenroth et al. 2022).

An animal was considered deceased if we found their carcass, their transmitter visibly damaged or with no sign of shedding, or if we located the snake that had consumed them. Nearly all the transmitters or remains were recovered within 5 days of the animal's last relocation. Mortality was dated as the day an individual's tag or remains were found if their last fix was the day prior, or if multiple days had passed, as a date approximately in the middle of the time interval between their last fix and recovery of their body or tag. Alternatively, an animal was coded as right-censored on the date their transmitter failed to produce a traceable signal, their shed tag was recovered, or the day they left the reserve and could no longer be tracked.

Survival analysis spanned from April 2023 to October 2024 for the adult age class and throughout the 2024 active season for the juveniles (May to October). Unfortunately, one headstarted juvenile had to be euthanized due to a broken jaw and we were unable to determine if the injury occurred during predation escape or if they were accidentally injured the day prior by volunteers or wildlife reserve visitors. Thus, we report a high estimate of survival for the headstarted juvenile cohort by treating that individual as censored, and a low estimate

considering them to be predated. To be conservative in our survival comparison we treated that individual as deceased.

For both age classes, we constructed Cox proportional hazards models containing the predictor variable *origin* to obtain the hazard ratio between headstarted and resident groups. A second model included *entry date* (the number of days after the start of the survival analysis that an individual was included in the study) as an additional covariate (Cox 1972). To test the independent delayed entry assumption, a likelihood ratio test was used to compare the goodness of fit of both models. If the null hypothesis is not rejected there is evidence that the assumption was met (Backenroth et al. 2022). Before exploring outputs from all constructed Cox proportional hazard models, we first ensured that the proportional hazards assumption was met (Therneau 2024). Given the small sample of juveniles, in addition to the construction of a Cox proportional hazards model, we further evaluated the differences in survival rates by calculating 95% confidence intervals around the mean difference in survival between the 2 groups on the 130^{th} day since the start of the survival analysis, which corresponded with the final day of the study, using 10,000 bootstrap resamples.

We used the lizards' mass as an indicator of their body condition to determine if they were adequately foraging and maintaining weight in the wild. Before summarizing mean mass measurements for the different age classes and groups, we subtracted the average weight of the transmitter if an individual was wearing it during measurement. We pooled both sexes of headstarted adults that had 2 or more mass measurements, spaced at least a month apart, and performed a two-sided paired t-test between their pre-release weight and their last active season measurement. When calculating the mean mass for residents we used their maximum measurement and if the individual was female, we did not include their measurements if they

were likely gravid (Endriss et al. 2007). Juveniles were expected to have substantial increases in body size throughout the season, so both headstarted and resident lizards' weights were summarized from June through August by averaging individuals' measurements across the month. There were too few resident juveniles in May, so for comparative purposes, measurements taken after May 26th were binned together with June measurements for both groups.

RESULTS

Movement and Home Range

Both age classes demonstrated relatively sedentary movement patterns expected of this species (Table 1). We removed 1 headstarted adult and 1 resident juvenile as outliers from the spatial analysis for abnormally low movement rates compared to all other adult lizards and insufficient tracking data, respectively. AIC model selection for the random effects component (*individual lizard ID*) of our candidate log-transformed daily movement rate LMMs indicated that the model including random intercept & slope effects was the best fit for both age classes. However, the two age classes differed in the AIC selected fixed effects. The top model for adult movement included 1,066 observations and the additive fixed effects of *origin* and *days* (scaled). It accounted for 84% of the cumulative model weight, with a ΔAIC 3.5 units lower than the next best model. Both parameter estimates were statistically significant, providing evidence for higher movement rates in the resident adults ($\beta_{resident}$ = 0.978, CI = 0.779 – 1.373), and gradually declining movement throughout the season (β_{days}= -0.328, CI = -0.487 – -0.172). After accounting for individual and seasonal variation, a three-fold difference in daily movement rates between origin groups was detected on the linear scale. The fixed effects accounted for 55% of the conditional variance (R^2 = 0.294).

In contrast, model selection for juveniles' movement supported the null model as the most parsimonious. It included 586 observations and accounted for 55% of the cumulative model weight, with a ΔAIC 2.2 units lower than the next competing model. Therefore, we found no evidence that juveniles' daily movement was influenced by their *origin* or the date of observation. Maximum dispersal distances from the release site for the adult headstarted cohort ranged from 29.78 – 142.02 m, with a median of 71.9 m (IQR = 53.43 – 114.04). The headstarted juveniles' maximum dispersal ranged from 13.87 – 292.93 m, with a median of 96.45 m (IQR = 56.09 – 199.64).

Home range estimates coincide with the movement trends observed for both age classes (Table 2; Fig. 1). Headstarted adults had lower area estimates on average than residents for both 95% MCP (t_{28} = -3.925, $P < 0.001$) and 95% KDE methods (t_{28} = -3.769, $P < 0.001$), and there was no evidence supporting a difference in area use between headstarted and resident juveniles for either the MCP (t_{14} = -0.356, $P = 0.727$), or KDE method (t_{14} = 0.0646, $P = 0.949$).

Survival and Body Condition

All individuals from both cohorts of headstarted animals survived the soft-release period; however, they had lower survival rates than wild lizards by the conclusion of the study (Table 3; Fig. 2). For the adult age class, individuals that survived to enter brumation also survived throughout the wintering period, which ended within 10 days before or after April 1, 2024. Therefore, we consider survival to that date to be an approximate representation of each origin group's annual survival rate. We used the cox proportional hazards models without the entry date covariate, as the likelihood ratio test was insignificant (χ^2 = 1.021, $P = 0.312$). This model detected a nearly four-fold greater hazard risk for the headstarted lizards compared to the resident adults for the entire study period (HR = 3.63, CI = 1.38 – 9.59, $z = 2.606$, $P = 0.009$). In

contrast, the Cox proportional hazards model for juvenile survival, which treated the ambiguous headstart death as a predation, did not detect a difference in hazard risk between the origin groups (HR = 3.165, CI = 0.850 – 11.80, z = 1.303, P = 0.086). Neither did the bootstrap analysis, as the confidence interval around the mean difference between the 2 groups' end of season survival rates (day 130) after 10,000 resamples included 0 ($\overline{x}$ = 0.327, CI = -0.193 – 0.778). However, we acknowledge that uncertainty around the HR is likely a reflection of our small sample sizes.

Before being released from the soft release pen, the 5 headstarted adult females had a mean weight of 13.44 g (± 1.05 SD), which increased to 15.44 g (± 1.78) for their end measurements. The 7 headstarted males, whose pre-release weight averaged 11.45 g (± 0.76), remained constant, ending with a mean of 11.40 g (± 0.78). We did not detect a statistically significant difference between average pre-release and post-release weights after pooling the sexes (t_{11} = -1.937, p = 0.079). Resident adult females reached larger body sizes than their headstarted counterparts on average ($\overline{x}$ = 18.35 ± 2.32 g, n = 8), as did the resident males ($\overline{x}$ = 15.21 ± 1.38 g, n = 8). The headstarted juvenile cohort's average mass for the pooled sexes increased from June ($\overline{x}$ = 11.18 ± 2.48 g, n = 8) to August ($\overline{x}$ = 13.37 ± 0.70 g, n = 3); resident juveniles, although much smaller on average in June ($\overline{x}$ = 6.07 ± 2.05 g, n = 9), reached similar sizes by August (13.07 ± 2.26 g, n = 6) (Fig. 3). Note the discrepancy in sample size between juvenile groups in August.

Mortality and Reproduction

Among both age classes, predation accounted for nearly all mortalities, however, we were only able to clearly identify specked and prairie kingsnakes as predators (Table S1; Fig. S1, available online in Supporting Information). Interestingly, at least 9 of the headstarted adults survived 83 days post-release before a mass predation event by a small mammalian predator killed 5

individuals within 48 hours. These individuals, along with another lizard whose tag was recovered similarly damaged, were residing within 75 m of each other along the northern fence corridor separating the reserve from the mowed residential turf grass (Fig. 1). Throughout 2024, we found the bodies of 2 headstarted and 3 resident adults, as well as 3 headstarted and 2 resident juveniles, all with their head, or portions of them, removed. We also observed 2 cotton rats (*Sigmodon hispidus)* that died in a similar manner. An avian predator may have been responsible for these unusual deaths; however, a previous study on predation of Texas horned lizards by Swainson's hawks (*Buteo swainsoni*) found 33 intact lizard heads in nests without their bodies, suggesting that either the heads were left over from dismemberment of the lizard, or the heads were removed at the nest to avoid injury (Lazcano et al. 2017). Given their small head size, sharp occipital and temporal horns, and tough dermal scales, it seems unlikely the heads were being preferentially targeted and consumed. The nature of these deaths, combined with multiple sightings on the reserve, points to cats (*Felis catus*) from the surrounding residential areas as the potential culprits.

In 2024, we observed reproductive behaviors in 2 of the surviving headstarted adults. In May, the male was observed attempting to copulate with an headstarted juvenile female, who had reached adult sizes due to headstarting. Then, in mid-June a female dropped approximately 7 g and had been digging a nest evidenced by the mud caked on her claws. The timing and amount of weight dropped, along with the nest digging behavior, coincided with the wild nesting females; however, we were unable to locate the exact nest location for confirmation.

DISCUSSION

This study examined the variable ways different age-classes of Texas horned lizards respond to headstarting and subsequent soft release back into an existing urban population. Our results

indicate that the headstarted adults were sufficiently thermoregulating and foraging since they all survived the soft release period, most survived approximately 3 months, and nearly all mortalities were caused by predation rather than desiccation, overheating, or starvation (Table S1; Figure S1, available online in Supporting Information). Additionally, surviving adults underwent brumation, and two individuals performed natural reproductive behaviors the year following their wild release in 2024. However, compared to the resident population, the headstarted adults were characterized by smaller body sizes, reduced spatial movement patterns, and lower survivorship.

Survival of reintroduced animals depends largely on maintaining energy reserves necessary for homeostasis and growth (Kleiman 1989). In our study, headstarted adults never experienced extensive weight loss; however, individuals of neither sex reached the body sizes of the corresponding sexes in the resident group. While 6 lizards experienced moderate gains, 5 individuals remained within ± 0.5 g of their starting weight, and the individual excluded from spatial analysis, identified as ID_1083, lost nearly 2 g by the time it reached brumation. However, we note that during the 2023 active season we aimed to reduce handling stress by recording morphometrics primarily during tag changes, which prevented the collection of fine-scale growth trends.

Another desired outcome of a translocation project is for relocated animals to perform the natural movement behaviors necessary to forage, naturally interact with conspecifics, and avoid predation in the wild (Kleiman 1989, Berger-TAL and Saltz 2014). Usually, researchers are concerned with increased mortality risk if the translocated animals released into unfamiliar territory make erratic movements or exhibit low site fidelity by dispersing far away from the release site (Reinert and Rupert 1999, Plummer and Mills 2000, Germano and Bishop 2009).

This was not observed in our study, in fact, our findings align with previous research at TAFB in which translocated wild adults moved less distance per day than residents and did not make large homing movements (DeGregorio et al. 2020). Most of the headstarted adults exhibited reluctance to explore much of the available reserve habitat evidenced by the clustering of their home ranges near the release site (Fig. 1).

The headstarted group experienced a marked decline in survivorship due to mass predation in August, during which 6 lizards were predated (5 within just 2 tracking days) along the fence line delineating the northern boundary of the reserve, 50 m from the release pen (Figure S1, available online in Supporting Information). The fence perimeter did not function as a physical barrier to animal movement, as the horizontal beams connecting the posts were 90 cm above the ground. It did, however, separate the tall prairie vegetation on the reserve side from the mowed neighborhood turf grass on the other side, creating a habitat edge. On the rare occasions when a lizard moved beyond this border, we would transfer them back to the reserve side to prevent human-induced mortality. Based on the small dentition marks found on the recovered transmitters, we believe that striped skunks, possibly a single individual that repeatedly traveled along the fence, may be responsible for the predation events. Additional transmitters from 2 headstarted individuals were also recovered along this stretch of fence; however, we could not reliably determine the individuals' fate, as the tags did not show signs of damage and may have simply been shed.

The results from the release of headstarted adults are likely the culmination of husbandry conditions experienced before reintroduction and characteristics of the urban release site. While in captivity the headstarted adult lizards were confined for nearly 1.5 years in ~75 L enclosures that contained refugia in the form of cholla wood, artificial plants, and sandstone rocks. Although

the physical features were used by the lizards, they were not particularly similar to refugia they would encounter at the release site, and the enclosure space limited their possible environmental interactions. As animals develop, they may modify their behaviors to better suit their current habitat, which in turn can drive future habitat selection preferences and locomotion performance (Aubret and Shine 2008). This behavioral plasticity might have conditioned the headstarted adults to utilize less of the available habitat post-release. Husbandry conditions, such as simplistic enclosures or longer duration in captivity, can also reduce captive animal competency in performing fitness-related activities (Almli and Burghardt 2006, Degregorio et al. 2013). Abnormal spatial movement patterns or maladaptive behaviors can hinder proper habitat selection, inhibit resource acquisition, and increase predator exposure, potentially leading to poor body condition or death for translocated animals (Roe et al. 2010, DeGregorio et al. 2017). Additionally, although precautions were made regarding the headstarted animals' welfare, stress from long-term confinement in captivity and/or subsequent tracking post-release may still impact the health and subsequent growth of released individuals (Teixeira et al. 2007, Breed et al. 2019).

In our study, we could not confidently identify any clear association between the spatial movement metrics measured and the headstarted adults' body condition. Interestingly, in 2024, ID_1083 regained the weight lost before brumation and made further gains totaling ~5 g. It also attempted to mate and demonstrated spatial movement patterns similar to those of the resident adults. Similarly, before being predated in 2023, 3 of the 5 individuals whose final weight was similar to their initial weight were in the process of regaining mass after post-release losses. Since most of the headstarted lizards did not experience dramatic weight loss and resident adults were also using the habitat near the release pen, the environment evidently provided necessary thermal refugia and sufficient prey. Thus, we tentatively presume that despite some atypical

movement patterns and lower average body sizes among headstarted adult lizards, they remained competent foragers. However, their lower daily movement rates likely limited encounters with residents during the mating season (May – June), as the latter were typically located farther into the reserve. The headstarted adults' window to mate with residents was already shortened, as we could not transport them to TAFB until May 5th due to poor weather conditions and they required several weeks in the soft release pen to acclimate. Unfortunately, this nullified one of the main benefits of releasing sexually mature animals: the potential to reproduce in their first year of reintroduction.

The primary pitfall associated with our release of headstarted adult Texas horned lizards, as with many headstart programs, was lower post-release survivorship resulting from a high number of predation events. Despite their morphological adaptations for crypsis, wild *P. cornutum* do still face significant predation pressure, with survivorship estimates varying across its range: 0.59 – 0.70 & 0.57 (CI = 0.32 – 0.93) at TAFB (Endriss et al. 2007, DeGregorio et al. 2020); 0.09 – 0.54 in southern Texas (Fair and Henke 1999); and 0.35 – 0.86 in southern Arizona (Munger 1986). Our survival rate estimate for the headstarted adult cohort in 2023 was lower than that of the resident lizards at TAFB, but within the ranges reported in other studies. Unfortunately, by the end of the 2024 field season, there were no known survivors: one headstarted adult had to be immediately euthanized post-brumation due to a cloacal infection, two others were found decapitated, and one was censored due to signal loss.

Surprisingly, despite having access to the entire reserve, during August 2023 nearly one-half of the headstarted adult lizards were residing alongside the northern fence boundary of the reserve, of which 6 were predated. This dispersal towards the perimeter may have been stochastically driven due to the location of the release pen, or through selection for habitat

structures contained within the habitat edge by the lizards. Regardless of the reason, such man-made linear features can increase mortality risk for prey species by increasing the perimeter-to-area ratio of habitat patches or serving as corridors that facilitate animal movement, thereby amplifying their exposure to predators (Barrows et al. 2006, Wolf et al. 2013, Hansen et al. 2019, Dickie et al. 2020).

In the wild, horned lizards rely not only on crypsis to avoid predators but will also initiate flight behaviors to escape imminent threats to their survival (Cooper and Sherbrooke 2010*a*, *b*). Prey naïveté, or the inability to recognize predators, can reduce survivorship by altering prey species' antipredator behaviors, such as shortening their flight initiation distances (FIDs), and has been observed in populations isolated on islands, individuals living in predator-removed environments, and domesticated populations (Brokordt et al. 2006, Cooper et al. 2014, Ross et al. 2022). Consequently, there are concerns that headstarting animals in complete isolation from predators during critical periods of their ontogenetic development may negatively impact their post-release survivorship (Tetzlaff et al. 2019*a*). Most headstarted adult lizards in our study survived for several months post-release and were likely exposed to predators during that time; however, they did not receive predator recognition training while in captivity.

Perhaps more important for urban lizard populations is their perception of humans as predators. While many species can habituate to human disturbance, those that cannot may suffer negative impacts to fitness-related activities due to heightened fear responses (McGowan et al. 2014, Pellitteri-Rosa et al. 2017, Putman et al. 2024). For these species, fear can manifest in earlier escape attempts (greater FIDs), staying closer to refuges, or increased hiding, which can lead to poor body condition (Garrido and Pérez-Mellado 2015, Putman et al. 2024). Anecdotally, we observed that some headstarted adults appeared to respond to researcher approach by fleeing

early rather than relying on crypsis. Premature fleeing can increase the likelihood of a predator visually detecting prey, and while this poses a cost to any prey species, it stands to reason it would be worse for a species whose morphological adaptations are for camouflage, not high-speed escapes (Cooper and Sherbrooke 2010*b*). Since crypsis would not have prevented human capture during captivity (or when necessary post-release), it is possible some individuals shifted towards initiating escape behavior earlier when threatened, though we did not test this hypothesis. We are uncertain whether the high mortality rate of the adult headstarts was due to phenotypic shifts in their antipredator behavior in either direction (e.g. shorter or greater FIDs), the reserve edge acting as an ecological trap, unfortunate circumstance, or some other unknown factor. Regardless, personnel involved in headstarting programs must consider core reintroduction objectives and minimize unnecessary physical interactions that could increase stress in the captive animals or disrupt natural behaviors during subsequent post-release field monitoring (Teixeira et al. 2007, Berger-Tal et al. 2020).

In contrast to the headstarted adult cohort, the headstarted juveniles demonstrated positive responses to the post-release metrics used in this study, with some caveats owing to our small sample size. Our results indicate that the headstarted juveniles' spatial movement patterns were comparable to those of the residents, despite being nearly twice as large as their wild counterparts at the start of the 2024 season. The most parsimonious LMM for the log-transformed daily movement rates was the null model, revealing that not only was there no effect of *origin*, but that the *days* variable was also an uninformative predictor. Therefore, even though the resident juveniles were growing larger as the season progressed, movement rates were not dependent on body size; thus, we conclude that the headstarted juveniles demonstrated natural movement patterns typical of this urban population (Table 2). Similarly, we did not detect a

significant difference in home range sizes between the two groups, regardless of the estimator used in our analysis.

Interestingly, the juvenile cohort moved away from the release site to occupy the core range utilized by residents more readily than the adult cohort. During the 2024 season, researchers decided not to immediately relocate individuals attempting large dispersal movements away from the reserve, opting instead to continue tracking to see if they could successfully emigrate to other potential habitat fragments at TAFB. 3 juveniles attempted these dispersals, including 1 headstart and 1 resident, both of which occurred in early August after spending weeks in their small, separate home ranges. We rescued the headstarted disperser from a storm drain and relocated the individual back to their home range, believing a human had transported him. In actuality, this was likely a voluntary movement, as the next day the lizard again dispersed outside the reserve, albeit in a slightly different direction. Unfortunately, we lost signal from this individual and 1 of the 2 resident dispersers, though this suggests that ontogenetically influenced dispersal behavior in Texas horned lizards is retained even if an individual is kept temporarily in captivity. Typically, overdispersion is considered a negative outcome in translocation projects (Berger-TAL and Saltz 2014). In this case, however, the lizards from both groups were well-established in their home ranges before making these exploratory excursions. Although there is inherent risk for animals traveling long distances, especially through urban matrices (e.g. falling in storm drains), some subadult dispersals may benefit fragmented populations through colonization of new habitat patches or gene flow with geographically proximate subpopulations.

A striking difference between the headstarted and wild juveniles was the discrepancy in their masses at the time of soft release. Hatchlings at TAFB reach an average weight of 0.9 ± 0.4 g before entering brumation, which increases to 1.8 ± 0.5 g the month after they emerge from their

burrows as juveniles (Vesy et al. 2021). Despite having constant environmental conditions and feeding opportunities throughout the overwintering period in captivity, the headstarted individuals decreased their activity from December through February and experienced only modest weight gains (2.87 ± 0.64 g to 3.36 ± 0.81 g). However, from late March to May, their weight nearly doubled (5.45 ± 1.29 g to 10.31 ± 1.82 g), making them far larger than the 2 approximately 2.5 g residents we were tracking at that time. The headstarted juveniles' larger body sizes, and associated increases in horn and spine lengths, ultimately did not protect them from larger predators, as four were predated within the 35 days post-release. Still, the increased mass during subadult ages may provide advantages by enabling predation on larger, more nutritious prey species, promoting faster growth rates at later life stages, and enhancing resistance to translocation-related stressors and stochastic environmental conditions deadly to smaller individuals (Madsen and Shine 2000, Alberts 2007).

Conservative estimates of Texas horned lizard hatchling survivorship from previous research at TAFB ranged from 0.25 – 0.51, though true survival rates were likely higher, as individuals with unknown fates were assumed deceased for this estimate (Vesy et al. 2021). Eight out of the nine hatchlings collected for this phase of the study survived captivity, confirming that headstarting effectively reduced their mortality risk during this age class. By the conclusion of this study, we did not detect a difference in survivorship between headstarted and resident juveniles, though both groups had lower seasonal survival than the wild adults. While these results are consistent with previous demographic and translocation research at our study site, they should be interpreted with some caution (Wolf et al. 2013, DeGregorio et al. 2020). Our sample size for the juvenile age class was limited, and we only tracked a single headstarted lizard to brumation, compared to 4 resident juveniles. The leading cause of mortality for headstarted

juveniles was the unusual decapitations observed throughout the 2024 field season. However, we found no evidence to suggest maladaptive antipredator behaviors to have contributed to this outcome, as the decapitations were distributed across life stages and origin groups.

As urbanization continues to fragment and degrade wildlife habitats, conservation efforts will increasingly need to focus on habitat patches within urban matrices that can support declining populations (Brown et al. 2024). A meta-analysis of squamate responses to human-mediated habitat modification suggests that members of the family Phrynosomatidae may be better equipped to persist in these disturbed areas compared to other species (Doherty et al. 2020). Indeed, our study population of Texas horned lizards was able to persist on the reserve despite a reduction in their available habitat caused by the construction of residential housing (Wolf et al. 2013). Numerous small towns in Texas also support resident populations; however, compared to those living in natural areas, these urban populations (including WR3's) are more isolated, have reduced genetic diversity, and have lower effective population sizes (Wall et al. 2024). The lack of gene flow between populations or sub-populations is largely due to the lizards' limited dispersal ability, which is further restricted by incompatible anthropogenic surroundings (Sherbrooke 2003, Wall et al. 2024). Lower genetic diversity can lead to a loss of adaptability, with important ramifications for the long-term survival of these populations in future environments (Williams et al. 2019). Additionally, these urban populations are highly dependent on thermal refugia provided by heterogeneous vegetation, and if removed, can experience population declines with lower likelihoods of recolonization (Tucker et al. 2023).

Interestingly, population estimates of Texas horned lizards residing in small urban areas have revealed they can occur at much greater densities than in the wild, possibly due to reduced predation pressure (Ackel 2015). To better understand this hypothesis, research comparing

predation attempts on foam Texas horned lizard models placed in two Texas towns and a nearby rural ranch found significantly more attacks on the ranch, namely by avian and unknown predators (Mirkin et al. 2021). However, the immobile models were not well-suited for capturing attempts made by snakes, and cats were recorded ignoring the models, despite being known predators of reptiles in urban areas (Loss and Marra 2017).

Previous research on our study population also suggested that, given the urban surroundings and TAFB's regulations against free-roaming pets, predation pressure was likely lower than in rural populations (Vesy et al. 2021). Unfortunately, this was not the case during our study. In the fall of 2024, the TAFB Natural Resource Office responded to the numerous lizard decapitations by setting small mammal traps along the northern perimeter of WR3 to remove any cats dwelling nearby. The traps captured multiple native mesocarnivore species known to inhabit the base, including opossums, raccoons, and skunks. Cats were also successfully trapped, confirming that either the pet policy was being ignored by residents of the adjacent neighborhood or stray cats were entering from outside the base.

If cats were indeed responsible for decapitating lizards, they would have accounted for approximately one-third of the total deaths documented in this study. Introduced cats are known to have detrimental impacts on reptile populations globally, so we find it unlikely that Texas horned lizards' antipredator behaviors and morphological adaptations provide the same level of protection against cats compared to native predators (Loss and Marra 2017). In addition to the mortalities, 5 resident adults were censored in May and June 2024 due to signal loss, which represented an unusually high number of transmitter failures. This period coincides with the lizards' breeding season, so it is possible they moved outside the range of our receiver in search of mates, despite our extensive searches of WR3 and the adjacent neighborhood. However, it is

also possible that signal loss occurred via predators removing lizards from the reserve. Given the lack of immigration into this isolated population, its stability will largely depend on maintaining sufficient annual survival rates.

The field of conservation increasingly relies on the translocation of wild-sourced or captive-bred individuals to slow declines in threatened populations or reestablish lost populations. Translocation can be a versatile tool to meet these conservation objectives across taxa. Unfortunately, it is often applied without the necessary post-release monitoring (Escobar et al. 2010), which, when it has been performed, has revealed mixed programmatic success (Germano and Bishop 2009). Even if short-term translocation aims are met (e.g. satisfactory survivorship, performance of natural behaviors, or reproductive success), the realization of long-term population-level goals is not guaranteed (Germano and Bishop 2009). In this study, we identify factors likely to contribute to desired Texas horned lizard reintroduction outcomes and highlight several key considerations essential for future headstarting initiatives. Our soft release methods proved suitable for both cohorts of headstarted lizards. However, it is likely the post-release behavior of headstarted adults was influenced negatively by the length of time they spent in captivity. It is possible that under different husbandry conditions these abnormal behaviors may not have been present or as pronounced. We suspect that natural spatial movement behaviors are more likely to be retained if headstarted lizards are housed in more spacious outdoor enclosures during early development to more closely emulate their release site environment and climate. Physical structures that closely mimic natural substrate and vegetation, along with the stimulus from nearby conspecifics, may assist in the recognition of refugia and microclimates, and encourage appropriate intraspecific interactions post-release (Stamps and Swaisgood 2007).

Although there is little research on predator avoidance training for reptiles, young, semi-captive El Hierro giant lizards (*Gallotia simonyi*) shifted their basking and locomotion behaviors after undergoing repeated training trials using kestrel and cat models, presumably to reduce predator exposure (Burunat-Pérez et al. 2018). We are not confident that abnormal antipredator behaviors resulted in decreased survivorship among headstarted lizards in our study, but the applicability of this method to increase post-release survival might be explored for future horned lizard reintroductions (Tetzlaff et al. 2019*a*). Our study also used only a single release site near the portion of WR3 most heavily used by the residents during the time of our study. Although historically *P. cornutum* has been found throughout the reserve, this reintroduction site decision was made to prevent anthropogenic disturbance during release, account for our small sample size, and facilitate the successful integration of headstarted lizards into the population. Had the headstarted adult cohort been released elsewhere, or released at multiples sites throughout the reserve, they may have been less susceptible to localized mass predation events. Finally, if weather conditions are agreeable, we recommend opening soft-release enclosures for headstarted adults fully before the beginning of their breeding season to increase chances of finding a mate the same year of release.

Based on our findings, juvenile Texas horned lizards may be suitable candidates for future headstarting initiatives. The extent of the headstarted juvenile cohort's pre-release growth was unexpected, but most of that growth was concentrated in the two months prior to their release in May 2024. This accelerated growth was most likely a consequence of consistent foraging opportunities provided while in captivity, but the size of feeder insects may have also been influential. Once the lizards reached larger sizes, mealworms and small crickets were provided, which are generally larger than the large-bodied native ant species fed upon by wild Texas

horned lizards at TAFB (Ramakrishnan et al. 2018). Although our headstarted juveniles showed no difficulty acquiring native prey species or growing post-release, care must be made to prevent impaction while horned lizards are kept in captivity.

Research on smooth green snakes (*Opheodrys vernalis*) found that headstarted snakes that underwent brumation had rapid compensatory growth during the first two months of their active season, resulting in similar mean body sizes as snakes that were kept active year-round (Sacerdote-Velat et al. 2014). Consequently, recommendations were made to include brumation cycles during reptile headstarting efforts as a precautionary measure to preserve natural behaviors. The lizards at TAFB typically enter brumation in October and emerge between late March to April, though timing varies across years and individuals. Therefore, horned lizard headstart programs might encourage natural brumation behaviors while still achieving desired pre-release body sizes by slightly truncating their overwintering period (i.e. November to March). Furthermore, headstarted individuals will have less opportunity to form maladaptive behaviors if they are kept inactive for several months, especially if human handling is limited. Construction of enclosures containing natural habitat cues should also require less effort and financial investment given the hatchlings' small stature and limited home range.

Future research should focus on acquiring larger sample sizes and comparing releases of headstarted hatchlings to those that are raised to juvenile age, to determine if accelerated growth and reduced predation risk in early spring translates to a greater number of lizards surviving to sexual maturity. Given horned lizards limited dispersal abilities, careful consideration must be given before selecting insular urban environments for population augmentation. Predation risk should either be evaluated through surveys of the local fauna and identification of edge habitat or

reduced through predator-removal initiatives if appropriate (Lettink and Armstrong 2003, Phillips et al. 2005, Hansen et al. 2019).

MANAGEMENT IMPLICATIONS

The recovery of threatened species through headstart programs depends on thorough post-release monitoring to identify factors that enable the realization of short-term objectives. If headstarted animals are to reinforce existing populations or establish ones, they must first competently perform fitness-related behaviors similar to their wild counterparts. Findings from our study support the use of soft release techniques during Texas horned lizard reintroduction, but suggest that refinement of headstarting husbandry protocols is warranted. Areas that could be improved include time spent in captivity, enclosure conditions and complexity, handling frequency and predator recognition training, and replication of natural life cycles. Current headstarting initiatives for Texas horned lizards release captive-bred hatchlings before brumation. Given that our headstarted juveniles were protected from predation until late May, experienced accelerated growth in captivity, and demonstrated natural behaviors once released, managers should also consider including juveniles into existing release protocols. Despite the growing need for urban conservation, we caution against urban release sites unless reintroduction is coupled with predator management strategies.

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TABLES

Individual daily movement rates [meters/day]					
	Origin	**N**	**Mean (SD)**	**Median (IQR)**	**Range**
Adults 2023	Headstart	15	7.48 (4.61)	6.19 (2.84)	2.66–19.94
	Resident	17	12.95 (4.70)	11.10 (6.95)	5.18–22.53
Juveniles 2024	Headstart	8	8.75 (3.91)	7.57 (3.24)	3.73–16.85
	Resident	9	10.80 (7.48)	9.38 (2.48)	4.01–29.57

Table 1: Summary of mean daily movement rates over the study period for two age classes of headstarted and resident Texas horned lizards at Tinker Air Force Base, OK, USA. Movement rates are averaged from May 26th, 2023 – October 1st, 2023, for adult lizards and from May 20th, 2024 – October 1st, 2024, for juvenile lizards.

Home Range [hectares]								
			95 % MCP			**95% KDE**		
	Origin	**N**	**Mean (SD)**	**Median (IQR)**	**Range**	**Mean (SD)**	**Median (IQR)**	**Range**
Adults 2023	Headstart	13	0.13 (0.08)	0.13 (0.07)	0.04–0.32	0.14 (0.09)	0.11 (0.11)	0.01–0.30
	Resident	17	0.40 (0.41)	0.28 (0.24)	0.10–1.74	0.38 (0.31)	0.27 (0.08)	0.11–1.24
Juveniles 2024	Headstart	8	0.20 (0.20)	0.12 (0.35)	0.01–0.47	0.16 (0.16)	0.11 (0.10)	0.03–0.53
	Resident	8	0.53 (0.80)	0.13 (0.55)	0.01–2.02	0.21 (0.30)	0.12 (0.08)	0.03–0.94

Table 2: Summary of home range estimates over the study period for two age classes of headstarted and resident Texas horned lizards at Tinker Air Force Base, OK, USA derived from 95% minimum convex polygons and 95% kernel density using the plug-in bandwidth method. Estimates are from May 26th, 2023 – October 1st, 2023, for adult lizards and from May 20th, 2024 – October 1st, 2024, for juvenile lizards.

Survivorship							
					Survival rates (95% CI)		
	Origin	**N**	**Mortalities**	**Censored**	**To brumation**	**Post-brumation**	**Second brumation**
Adults 2023	Headstart	16	11	5	0.35 (0.11–0 .60)	0.35 (0.11–0.60)	0
	Resident	18	9	6	0.65 (0.34–0.84)	0.65 (0.34–0.84)	0.35 (0.12–0.60)
Juveniles 2024	Headstart	8	6/5*	1/2*	0.19 (0.01–0.54) 0.38 (.09–0.67)*	NA	NA
	Resident	9	4	1	0.52 (0.16–0.80)	NA	NA

Table 3: Summary of survival estimates using Kaplan-Meier estimation for two age classes of headstarted and resident Texas horned lizards at Tinker Air Force Base, OK, USA. The adult survival rates are calculated over the entire study period from April 2023 – October 1st, 2024. The juvenile rates are calculated from May 20th, 2024 – October 1st, 2024. The asterisk treats a headstarted juvenile's ambiguous mortality as deceased for the low survival estimate and right-censored for the high estimate.

FIGURES





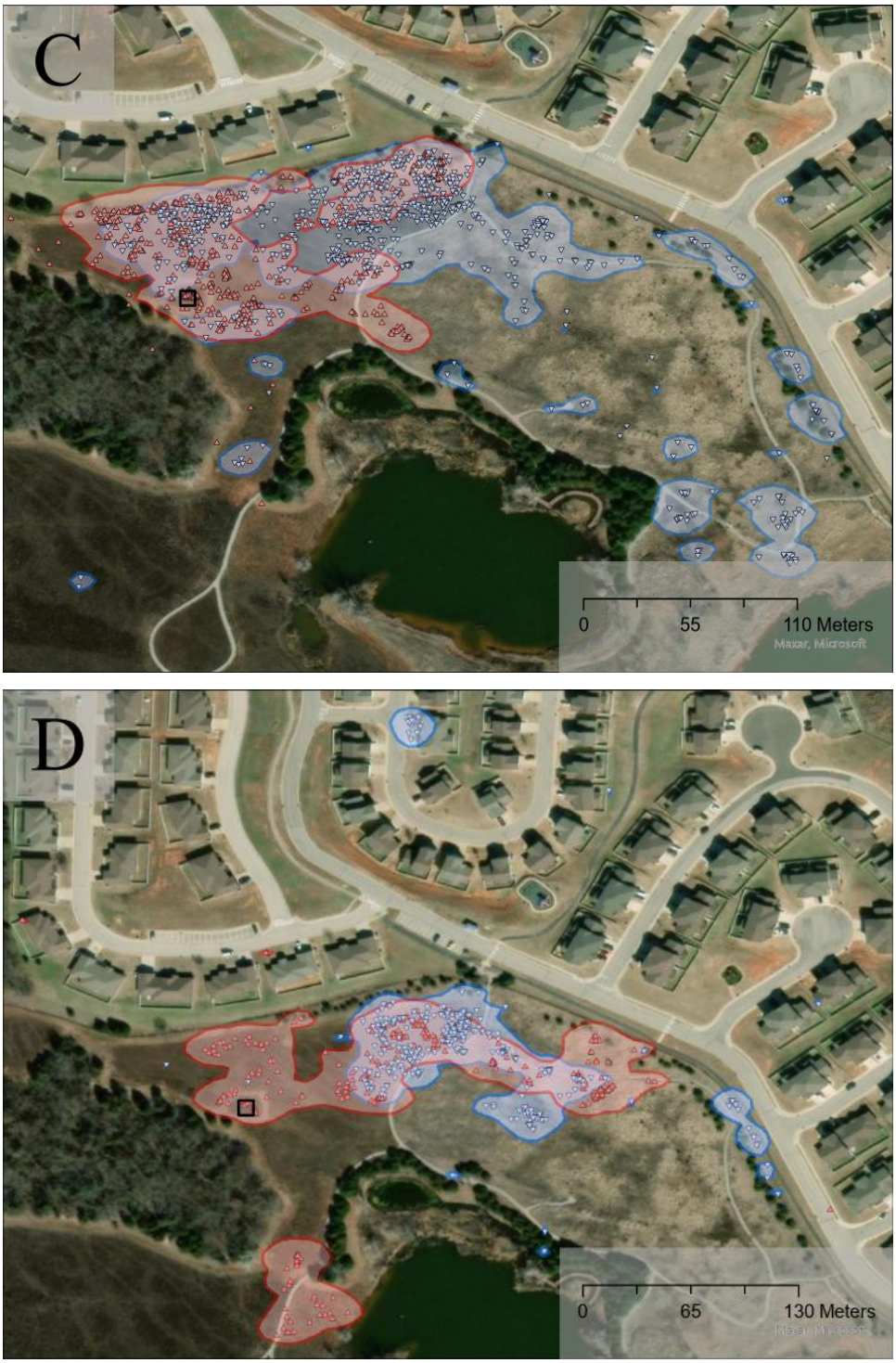
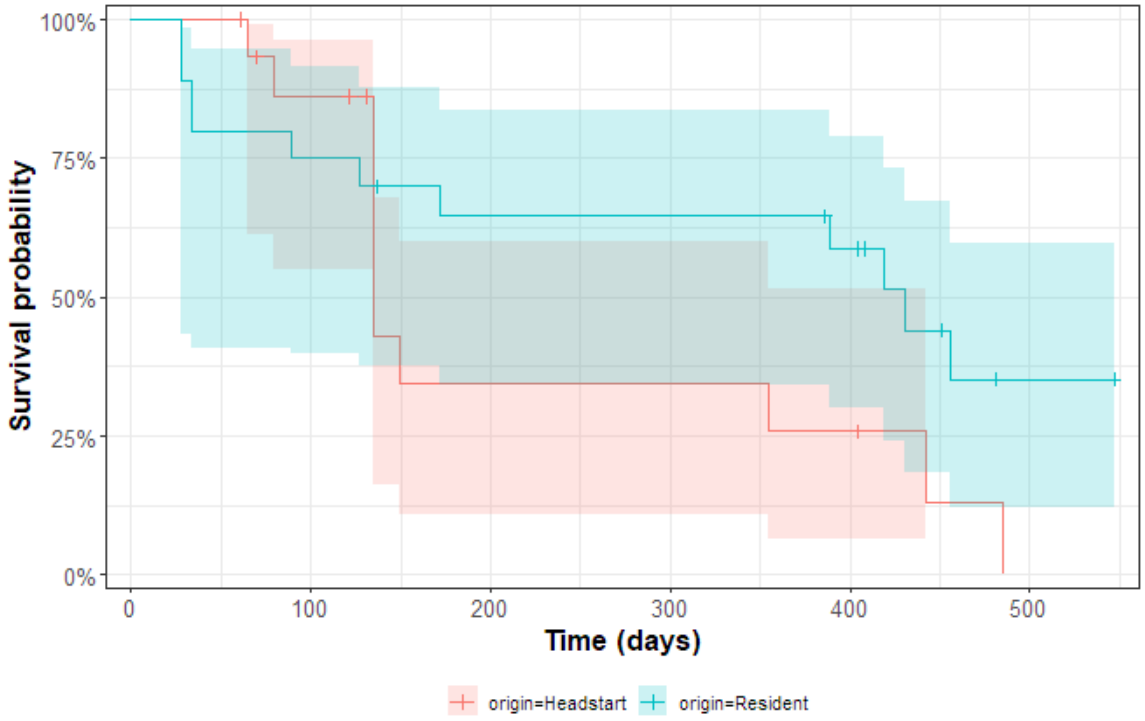


Figure 1: Area used by Texas horned lizards at Tinker Air Force Base, OK, USA. Individuals' home ranges outlined with 95% minimum convex polygons for **A)** adults in 2023 (headstarts: *n* = 13, residents: *n* = 13); **B)** juveniles in 2024 (headstarts: *n* = 8, residents: *n* = 8). Also, the total

area used by headstarted, and resident lizards, delineated with 95% isopleths derived from kernel density estimation using the plug-in method, overlayed with pooled individual relocations (triangles) for **C)** adults in 2023 and **D)** juveniles in 2024. Red polygons and triangles represent headstarted lizards, blue represents residents. The black square represents the soft release pen, and the black dotted line in frame A represents the wooden fence that runs along the northern boundary of the reserve.

A)


100%
75%
50%
25%
0%
Survival probability
0
100
200
300
400
500
Time (days)
origin=Headstart
origin=Resident

B)

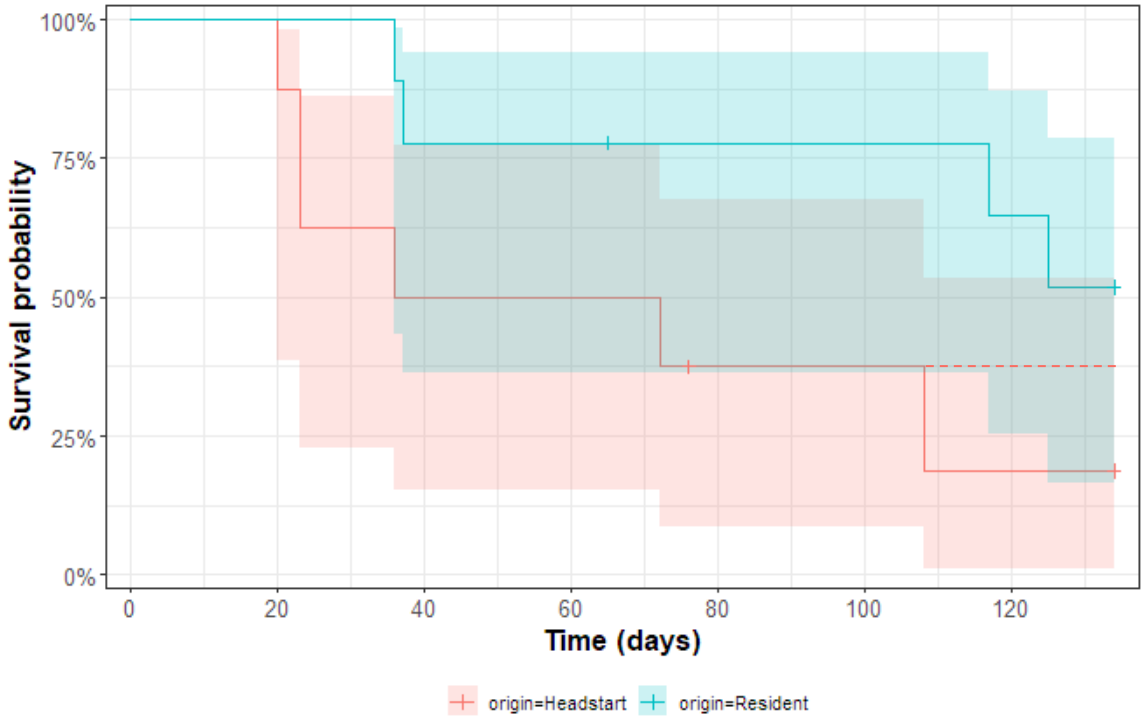

100%
75%
50%
25%
0%
Survival probability
0
20
40
60
80
100
120
Time (days)
origin=Headstart
origin=Resident

Figure 2*:* Kaplan-Meier survival curves for 2 age classes of headstarted and resident Texas horned lizards on Tinker Air Force Base, OK, USA; Blue shading represents 95% confidence intervals surrounding blue resident survival curves, red for headstarted survival curves for **A)** the adult cohort from April 2023 – October 1st, 2024 (headstarts: $n = 16$; residents: $n = 19$), and **B)** the juvenile cohort from (headstarts: $n = 8$; residents: $n = 9$). The dotted line represents the high estimate of survival for the headstarted juvenile cohort. Right-censored events are represented by tick marks.

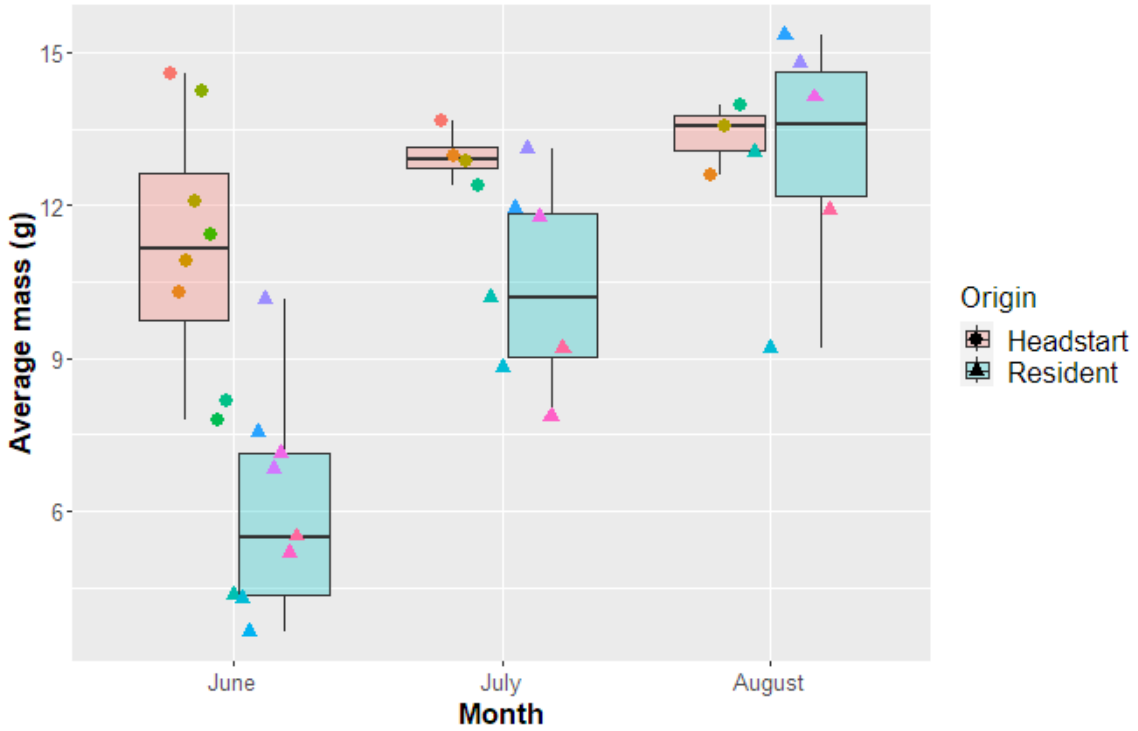


Figure 3*:* Average mass measurements for juvenile Texas horned lizards at Tinker Air Force Base, OK, USA during the 2024 study period. Colored circles or triangles represent individual lizards.

SUPPORTING INFORMATION

Adults							
ID	**Origin**	**Sex**	**Start Date**	**End Date**	**Days**	**Status**	**Note**
1126	H	F	5/25/2023	6/12/2023	18	0	Dropped tag. Last: 6/11. Found: 6/13.
1127	H	F	5/25/2023	5/11/2024	352	0	Tag failure or left reserve. Last: 5/10.
1128	H	M	5/25/2023	8/16/2023	83	1	Dropped tag. Possible mammalian. Last: 8/15. Found:8/17
1129	H	F	5/25/2023	8/16/2023	83	1	Dropped tag. Possible mammalian. Last: 8/15. Found:8/17
1130	H	M	5/25/2023	6/3/2023	9	0	Dropped tag. Last: 6/2. Found: 6/7. Tag stop: 6/5.
1132	H	M	5/25/2023	8/12/2023	79	0	Dropped tag. Shed. Last: 8/11. Found 8/15.
1133	H	M	5/25/2023	8/2/2023	69	0	Dropped tag. Shed. Last: 8/1. Found: 8/3.
1134	H	F	5/25/2023	8/30/2023	97	1	Dropped tag: Mammalian. Last: 8/29. Found: 8/30.
1135	H	M	5/25/2023	8/16/2023	83	1	Dropped tag. Possible mammalian. Last: 8/15. Found:8/17
1136	H	M	5/25/2023	6/21/2023	27	1	Depredated: Snake. Last: 6/20. Found: 6/22.
1137	H	F	5/25/2023	6/7/2023	13	1	Dropped tag. Possible avian. Last: 6/6. Found: 6/7.
1083	H	M	5/25/2023	7/31/2024	433	1	Found partially decapitated/ face removed. Euthanized same day. Found: 7/31
1087	H	M	5/25/2023	8/16/2023	83	1	Dropped tag. Possible mammalian. Last: 8/15. Found:8/17
1088	H	F	5/25/2023	8/16/2023	83	1	Dropped tag. Possible mammalian. Last: 8/15. Found:8/17
1089	H	M	5/25/2023	4/3/2024	303	1	Infection of cloaca. Euthanized.
1091	H	F	5/25/2023	6/18/2024	390	1	Predated, decapitated with arm off. Marks on transmitter. Last: 6/18. Found: 6/19.
1051	R	M	4/12/2023	5/1/2023	19	1	Depredated: Snake. Last: 4/28. Found: 5/3.
1076	R	F	4/3/2023	5/7/2023	34	1	Natural death: Dried carcass. Last: 4/28. Found 5/16.
1112	R	M	5/1/2023	4/23/2024	358	0	VHF signal loss.
1121	R	F	4/12/2023	5/26/2024	410	1	Found decapitated. Last: 5/24. Found: 5/27.
1122	R	F	4/14/2023	8/8/2023	116	1	Dropped tag. Possible mammalian. Last: 8/7. Found: 8/23.
1140	R	F	4/20/2023	7/2/2024	439	1	Found decapitated. Last: 7/1. Found: 7/2/2024.
1141	R	F	4/19/2023	5/15/2024	392	0	VHF signal loss.
1142	R	M	4/3/2023	10/1/2024	547	0	*End of study.*
1143	R	M	4/5/2023	6/27/2024	449	0	VHF signal loss.
1144	R	F	4/10/2023	7/1/2023	82	1	Dropped CTT tag. Last: 6/30. Found: 7/3.

1145	R	M	5/2/2023	6/7/2024	402	1	Found decapitated. Last: 6/4. Found: 6/10.
1146	R	M	5/18/2023	5/11/2024	359	0	VHF signal loss.
1147	R	M	5/25/2023	9/22/2023	120	1	Dropped CTT tag. Last: 9/21. Found: 9/27. No silicon on tag,
1148	R	F	5/30/2023	10/1/2024	490	0	*End of study.*
1149	R	M	5/30/2023	8/18/2023	80	0	CTT signal loss. Last: 8/17.
1150	R	F	5/31/2023	4/26/2024	331	1	Unknown cause.
1151	R	F	5/31/2023	10/1/2024	489	0	*End of study.*
1152	R	M	6/7/2023	7/27/2024	416	0	Shed.
1154	R	M	7/26/2023	6/15/2024	325	0	CTT signal loss.
				Juveniles			
1164	R	F	5/20/2024	9/14/2024	117	1	Found decapitated. Last: 9/12. Found: 9/16.
1165	R	F	5/20/2024	10/1/2024	134	0	*End of Study*.
1166	R	F	5/28/2024	6/26/2024	29	1	Transmitter attached to bone. Completely consumed. Last: 6/25. Found: 6/28
1167	R	F	6/4/2024	9/22/2024	110	1	Chewed transmitter. Possible Coyote. Last: 9/19. Found: 9/24.
1168	R	F	6/6/2024	10/1/2024	117	0	*End of Study.*
1169	R	F	6/7/2024	6/25/2024	18	1	VHF Found: 6/25, Found decapitated. Last: 6/24. Found: 6/26.
1170	R	F	6/7/2024	10/1/2024	116	0	*End of Study.*
1171	R	M	6/7/2024	7/24/2024	47	0	Tag failure. Last: 7/24. Left study site.
1172	R	M	6/14/2024	10/1/2024	109	0	*End of study.*
1155	H	F	5/20/2024	7/31/2024	72	1	Found decapitated. Last: 7/30. Found: 7/31.
1156	H	M	5/20/2024	9/5/2024	108	1	Found w/ broken jaw. Maybe from zoo volunteers. Euthanized. Last: 9/3. Found: 9/5.
1157	H	F	5/20/2024	6/9/2024	20	1	Found decapitated. Last: 6/8. Found: 6/10.
1158	H	F	5/20/2024	10/1/2024	134	0	*End of study.*
1159	H	F	5/20/2024	6/12/2024	23	1	Predation, transmitter only. Last: 6/11. Found: 6/13.
1160	H	F	5/20/2024	6/25/2024	36	1	Found decapitated. Last: 6/24. Found: 6/25.
1161	H	M	5/20/2024	6/12/2024	23	1	Predation, transmitter only. Last: 6/11. Found: 6/13.
1162	H	M	5/20/2024	8/4/2024	76	0	Left study site. Last: 8/3.

Table S1*:* Detailed survival data over the study period (2023 – 2024) for 2 age classes of headstarted and resident Texas horned lizards on Tinker Air Force Base, OK, USA.

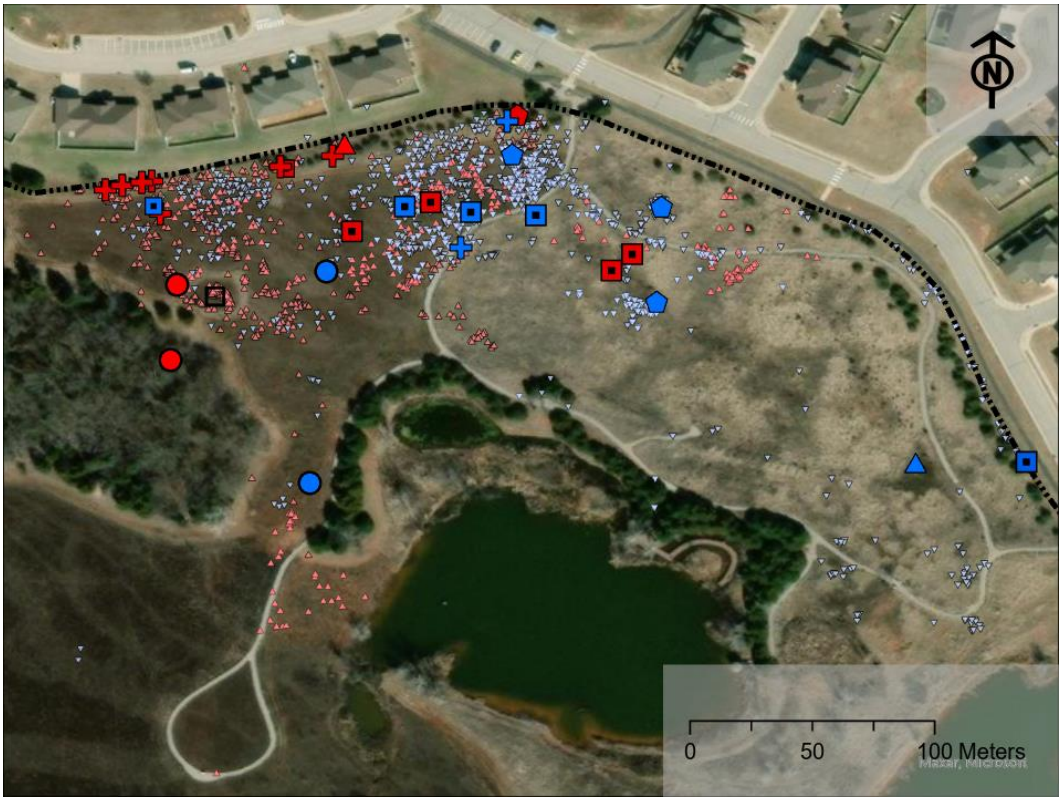


Figure S1*:* Map showing the locations of known mortalities over the entire study period (2023 – 2024) for 2 age classes of headstarted and resident Texas horned lizards on Tinker Air Force Base, OK, USA. Mortalities are overlaid over small triangles representing pooled relocations. Red shapes indicate headstarted lizards, while blue shapes indicate residents. Large triangles signify snake predations, crosses are presumed mammalian predations, circles are predations from unknown origin, and pentagons correspond to either natural or unknown causes of death. The black square represents the soft release pen, and the black dotted line corresponds to the wooden fence that runs along the northern boundary of the reserve.