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Spatial and demographic ecology of Texas horned lizards within a conservation framework

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SPATIAL AND DEMOGRAPHIC ECOLOGY OF TEXAS HORNED LIZARDS WITHIN A CONSERVATION FRAMEWORK

by

Alexander J. Wolf

B.S., Beloit College, 2006

A Thesis

Submitted in Partial Fulfillment of the Requirements for the

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Department of Zoology

in the Graduate School

Southern Illinois University Carbondale

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Alexander J. Wolf, for the Master of Science degree in Zoology, presented on April 20, 2012, at Southern Illinois University Carbondale.

TITLE: SPATIAL AND DEMOGRAPHIC ECOLOGY OF TEXAS HORNED LIZARDS WITHIN A CONSERVATION FRAMEWORK

MAJOR PROFESSOR: Eric C. Hellgren

Disturbance due to habitat restoration and urbanization can threaten populations of sensitive wildlife species. I examined 2 aspects of the ecology of Texas horned lizards (*Phrynosoma cornutum*), a Species of Special Concern in Oklahoma. I studied the effects of native prairie restoration and urban development on a population of *P. cornutum* on an urban wildlife reserve at Tinker Air Force Base, Oklahoma. I also studied population vital rate variation in 2 populations of *P. cornutum* using deterministic elasticity and life-stage simulation analyses.

My research on the effects of habitat disturbance on urban *P. cornutum* focused on Wildlife Reserve 3 (WR3) at Tinker Air Force Base, which has a population of *P. cornutum* that has persisted for many years. I quantified daily movement rates, home-range size, changes in spatial distribution, survival rates, and population size and density over 9 years (2003-2011). Movement rates of *P. cornutum* were affected by a 3-way interaction of sex, period (reproductive vs. non-reproductive), and study stage (2004-2005, 2007-2008, and 2009-2011). Stages represented variation in the type and level of anthropogenic disturbance on the site. Home-range size did not vary by sex, but was smaller during the non-reproductive period than the reproductive period. Spatial analyses indicated that disturbances due to restoration activities had little effect on the spatial distribution of *P. cornutum* on WR3. Survival was affected by season (inactive-season survival was higher), stage (declining survival in later stages with more disturbance), an interaction of season and stage, and disturbance (covariate of proportion of an individual's home range in disturbed areas for a given year; small negative effect), with little evidence for variation in survival by sex. Major causes of mortality included depredation and anthropogenic causes. I estimated a population size of 32.9 ± 4.7 (95% CI of 28.1–49.0) individuals (excluding hatchlings) with a corresponding density of 2.68 lizards/ha. Spatial analyses did not support the hypothesis that disturbance associated with restoration activities affected the spatial ecology of *P. cornutum* on WR3. However, these results were not entirely conclusive, due to the logistical constraints of working on a single site with an uncommon species. Size and density of the *P. cornutum* population has apparently declined since 2005. This decline is likely a consequence of 2 factors: the 2008 translocation of 17 adult lizards from an area adjacent to WR3 impacted by housing development coupled with a decrease in the annual survival rate of adults over time.

I compared the vital rates of the population of *P. cornutum* on WR3 to a site in south Texas, the Chaparral Wildlife Management Area (CWMA). The Chaparral WMA population had lower adult survival and higher fecundity than WR3. I predicted a trade-off between the effect of adult survival and fecundity on population growth rate (λ). I found that recruitment in *P. cornutum* most affected λ at both sites. Stochastic life-stage simulation analysis indicated that hatchling survival most affected λ in both populations. There was a trade-off in effect on λ between juvenile survival and fecundity between the two sites; fecundity affected λ more at the CWMA. Adult survival had minimal effects on λ in both populations. My study suggests that managers can address *P. cornutum* declines in similar ways across the species' range.

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CHAPTER 1

EFFECTS OF HABITAT DISTURBANCE ON TEXAS HORNED LIZARDS: A CASE STUDY OF AN URBAN POPULATION

INTRODUCTION

Habitat restoration in grasslands is an increasingly common conservation tactic, and can involve severe (although ideally short-term) habitat disturbance, such as mowing, tilling, and spraying herbicides (e.g., Wilson and Gerry 2006). However, restoration projects are rarely designed to adequately evaluate their effects on wildlife populations (Block et al. 2001). One challenge is selecting appropriate variables to measure wildlife responses to restoration (Block et al. 2001). Additionally, anthropogenic disturbances often represent events that cannot be replicated in an experimental approach (Michener 1997), which forces restoration projects to rely on quasi-experiments and observational studies such as before-and-after studies of restoration (Block et al. 2001). Complicating before-and-after monitoring of restoration activities are the natural factors that vary temporally and may not be related to the treatment (Block et al. 2001), such as climate. Another issue with habitat restoration and wildlife conservation is that habitat restoration often is initiated only after a population is identified as at risk of extinction (Schrott et al. 2005). However, some populations may already be below their extinction threshold (the population size below which it cannot sustain itself; Schrott et al. 2005) at the time of identification.

Urbanization is more permanent than other types of habitat disturbance (McKinney 2002). In the U.S., urban and suburban areas occupy more land area than all national and state parks and Nature Conservancy lands combined (McKinney 2002). Despite the many studies that have examined the effect of habitat change on reptiles and amphibians, few have examined urban populations of herpetofauna (Gardner et al. 2007). Of those that have, many use diversity indices as measurement variables rather than looking at temporal declines of a given species after habitat change (e.g., Dickman 1987, Germaine and Wakeling 2001, Hamer and McDonnell 2009). Studies often note a marked decline of reptile species richness in urban environments. For example, only 46% of historically present reptile species had a ≥ 95% probability of being extant in urban areas of Melbourne, Australia (Hamer and McDonnell 2009), indicating a considerable loss of the native species of reptiles. Abundance, species diversity, and species evenness of lizards were higher in less-developed areas along an urbanization gradient in Tucson, Arizona (Germaine and Wakeling 2001). Gardner et al. (2007) recommended more studies to examine the specific mechanisms by which habitat loss and degradation affect herpetofauna populations instead of focusing on correlations between patch size and diversity, as effective conservation planning can be best achieved after the effects of habitat loss are quantified and understood (Gardner et al. 2007).

Texas horned lizards (*Phrynosoma cornutum*) have declined throughout much of their native range (Donaldson et al. 1994). Possible causes of the decline include many of the anthropogenic habitat disturbances mentioned above, including land treatments (e.g., tilling, disking, mowing), habitat destruction (e.g., urban development), and use of pesticides on ants, their main food source (Donaldson et al. 1994, Endriss et al. 2007). Donaldson et al. (1994) noted that current land-use (housing, agriculture, etc.) was an accurate predictor of *P. cornutum* presence because of human-induced mortality. Previous studies comparing the effects of different disturbances such as prescribed burns and grazing on *P. cornutum* (Fair and Henke 1997, Hellgren et al. 2010) have used plots with different disturbance treatments (comparison between sites) rather than monitoring specific individuals or populations throughout the disturbance event (comparison across time) to identify the proximate effects of the disturbance.

Texas horned lizard populations appear to fare best in habitats with a moderate level of disturbance (Fair and Henke 1997, Hellgren et al. 2010). These results support the hypothesis that *P. cornutum* require a mosaic of bare ground and cover vegetation (Hellgren et al. 2010). However, the ideal amount of disturbance for *P. cornutum* habitat may differ across the species' range. Some authors have proposed that species with wide ranges require different successional stages in ecoregions of differing productivity, with more productive regions requiring a greater amount of disturbance to maintain optimal habitat structure (Spears et al. 1993, Kazmaier et al. 2001). The areas at the northeastern edge of *P. cornutum* range, which generally constitute mixed-grass prairie, are more productive than the mesquite- and thorn-scrub habitats found in much of the area inhabited by *P. cornutum*. In mixed-grass prairies, a regime of disturbance that promotes a mix of habitat types on a microhabitat scale should provide the best habitat for *P. cornutum*, with too little disturbance resulting in thick vegetation and no areas for feeding and basking, and too much disturbance eliminating cover from thermal extremes and predators (Burrow et al. 2001, Hellgren et al. 2010).

Because *P. cornutum* have relatively small home ranges compared to the scale of human development and require some disturbance (Hellgren et al. 2010), populations of the species in fragmented urban habitats may be viable. However, these populations are more susceptible to stochastic extirpation than larger, contiguous populations, and may be isolated to the point that they are completely separated from other populations, eliminating the chance of metapopulation rescue (Gotelli 2008). Therefore, it is important to assess the fates of individual lizards within these isolated populations, as well as examining how their spatial ecology is affected by habitat disturbance. I studied a population of *P. cornutum* on Tinker Air Force Base (TAFB), Oklahoma County, Oklahoma, that has been exposed to anthropogenic disturbance because of native prairie restoration (e.g., pesticide application, disking, mowing) and urban development (habitat loss). This population has been monitored since 2003 and presents a unique opportunity to quantify the effects of anthropogenic disturbances on the survival and spatial ecology of a reptile population in an urban setting.

I predicted that the *P. cornutum* population on TAFB will selectively use areas with intermediate amounts of disturbed habitat, that survival and population growth rates will be highest following limited disturbance events, and that survival and population growth rates will not decline following disturbance for prairie restoration. I further predicted that developed areas will not support *P. cornutum*. To test these predictions, my specific objectives were to quantify changes in daily movement rates, home-range size, shifts in spatial distribution, survival rate, and population size following disturbances.

STUDY SITE

Tinker Air Force Base (Midwest City, Oklahoma County, Oklahoma, 35° 24’ 58” N, 97° 24’ 41” W) is a largely urban base on the outskirts of Oklahoma City. Of the 2000-ha Base, approximately 500 ha were natural habitat. These areas were dominated by oak-hardwood forests and a mixture of native and non-native grasslands. Research activities were focused on the population of *P. cornutum* on Wildlife Reserve 3 (WR3; Fig. 1) and the surrounding areas. Wildlife Reserve 3 was a natural area (ca. 15 ha) on the southwestern side of TAFB, dominated by grassland with patches of woody vegetation and gravel trails. It was centered around 2 man-made ponds, with the surrounding area sloping towards the ponds. Although most areas of WR3 were gently sloped, some areas, especially immediately around the southern-most pond, had slopes > 45°. The soil on WR3 is primarily composed of clay. The average annual temperature for Oklahoma County is 15.7 °C, with an average annual high temperature of 21.8 °C and an average annual low temperature of 9.6 °C (Oklahoma Climatological Survey 2003). The average daily maximum and minimum in January are 8.4 and -3.2 °C, respectively, and average daily maximum and minimum temperatures in July are 33.9 °C and 21.6 °C, respectively (Oklahoma Climatological Survey 2003).

Dominant vegetation species on WR3 include big bluestem (*Andropogon gerardii*), little bluestem (*Schizachyrium scoparium*), plains bluestem (*Bothriochloa ischaemum*), indiangrass (*Sorghastrum nutans*), side oats grama (*Bouteloua curtipendula*), Maximilian sunflower (*Helianthus maximiliani*), tall fescue (*Lolium pratense*), and eastern redcedar (*Juniperus virginiana*; Endriss et al. 2007). As of 2011, the northern, northeastern, southern, and western sides of the Reserve are bounded by residential housing, whereas the eastern side borders several military buildings. Horned lizards have been sighted on a sporadic basis in other areas of TAFB, but targeted searches have yielded few if any captures by researchers (unpublished data).

Habitat restoration on WR3 since 2005 (Tables 1, 2, Fig. 2) and construction of a military housing development in a 7.4-ha area directly adjacent to WR3 in 2008-2010 (Fig. 1) have disturbed this key *P. cornutum* habitat patch. Management activities designed to restore prairie habitat have included tree removal, disking, mowing, spraying with herbicides, and seeding with native grasses and forbs.

METHODS

Field Methods

I captured lizards on WR3 during April-August through intensive visual searching and fortuitous encounters, and recorded basic morphometric information for each lizard, including snout-vent length (SVL), total length (TL), mass, and sex. Intensive visual searches consisted of slowly walking back and forth across search areas while looking for lizards. I attempted to evenly and thoroughly search all areas of the field site except areas where vegetation was so thick and high that lizard detectability would be near 0. Following Endriss et al. (2007), I implanted lizards > 5.0 g with a passive integrated transponder (PIT) tag (0.5 g), or clipped a unique combination of toes for smaller lizards. I attached a 0.95-1.95-g radiotransmitter (BD-2, Holohil Systems Ltd., Carp, Ontario, Canada or SOPR-2038, Wildlife Materials Inc., Murphysboro, Illinois, USA) to each lizard if the transmitter was < 10% of the lizard's body mass. Transmitters were attached by gluing them to the dorsum immediately posterior to the head. I secured the transmitters with an elastic band around the neck of the lizard to ensure that the transmitters were retained after shedding. After each shedding event, I re-glued the transmitters to the dorsum (Endriss et al. 2007).

I monitored the locations of radiotelemetered lizards 1-5 times weekly during the active lizard season (Apr–Aug) and at least bi-weekly from August until they entered hibernation (generally Oct-Dec). I homed to the telemetry signal and recorded each lizard location with a Trimble GPS Pathfinder Pocket Receiver (Trimble GeoXT, Terrasync 2.3, Strategic Consulting International, Oklahoma City, Oklahoma, USA) and stored location data in a geodatabase. Locations were recorded in Universal Transverse Mercator (UTM) coordinates using the North American Datum 1983 (NAD83). I varied the times during which I tracked lizards each day to obtain a representative sample of locations across all daylight hours. Radiolocations that I collected during 2010–2011 were added to a geodatabase containing lizard locations for WR3 from 2003 to 2009. This geodatabase, maintained at Tinker AFB, contained spatial, morphometric, and behavioral data for all lizards captured on the site from 2003 to 2011. It included a UTM location for all captures, recaptures, and radio-locations; stored data on SVL, TL, mass, sex, and incorporated descriptive notes on nesting, causes of mortality, environmental conditions and notable behaviors.

Daily Movement Rates

I calculated the rate of movement between each successive radio-location for lizards from 2004 to 2011. Based on observations of mating and nesting lizards, I defined a reproductive period (emergence–15 Jul) and a non-reproductive period (16 Jul–hibernation). For statistical analysis, I used only individuals for whom ≥ 5 locations had been recorded in both periods. However, to estimate means for each period separately, I used all individuals with ≥ 5 locations during that period. For individuals tracked during 2 different years, I randomly censored the data recorded for that individual in 1 of the years to ensure independence. I pooled individuals from different years by stage, which I defined as pre-restoration (2004-2005), pre-construction (2007-2008), and post-construction (2009-2011). I censored 2003 and 2006 due to lack of sample size during those years. If >1 location had been recorded for an individual on the same day, I randomly selected 1 location per day for use in analyses. I censored time intervals of < 0.5 day (i.e., <12 h) to ensure independence between locations, and censored time intervals of >2 days (>48 h) to minimize the likelihood than lizards were moving long distances undetected between observations. Rates were calculated as m/d, and I accounted for locations recorded at different times of day (e.g., the distance between a location at 0700 on one day and 1900 on the next was divided by 36 hrs, i.e., 1.5 days).

I analyzed movement rates for differences among stages, periods, and sexes using a 3-way repeated-measures ANOVA with all interactions in PROC MIXED in SAS 9.2 (SAS Institute, Cary, North Carolina, USA), with the reproductive and non-reproductive periods for each individual representing the repeated measures. I detected unequal variances using graphic examination of residuals, and log-transformed movement rates accordingly (Zar 1999). I used PROC GLM to calculate means and standard errors for each group in the analysis. I set a significant level of $\alpha = 0.05$.

Home-range Estimates

I estimated home-range sizes using minimum convex polygons (MCP) and fixed-kernel-density estimators (KDE; Kernohan et al. 2001). MCPs were calculated at the 95% level using the adehabitat package in ‘R’ v. 2.12.2 (R Core Development Team 2008). KDEs were also calculated at the 95% level using adehabitat in ‘R’, and I used a bivariate normal kernel. The least-squares cross validation (LSCV) method for selecting a kernel smoothing parameter, recommended by Seaman and Powell (1996), failed to minimize for most home-range estimates in the study. The failure of LSCV to find a minimum for many home ranges may have been because the distributions of locations for individuals in this study population are often clumped, resulting in locations immediately on top of each other, which often causes LSCV to fail (Kernohan et al. 2001). I therefore used the reference bandwidth for all KDEs (Kernohan et al. 2001). I retained the adehabitat default settings, in which the KDE for each individual home range is estimated using a separate grid of 40 x 40 cells.

I assumed that home ranges for individuals with ≥20 radio-locations in a period (reproductive or non-reproductive) were adequately represented for that period (Rose 1982) because preliminary examination of data showed that home-range size approached an asymptote after about 20 radio-locations, aside from obvious home-range shifts. This number of minimum locations matched the minimum set previously by Endriss (2006) for the study population. I randomly chose one year for each individual tracked for consecutive years. I anecdotally observed several individuals move across the entire study area between successive radio-locations ~1 day apart, therefore spatial autocorrelation (Swihart and Slade 1985) is not an issue for these data.

I analyzed home-range sizes for differences by stage (see ‘Movements’ section), period, and sex using a 3-way repeated-measures ANOVA with all interactions in PROC MIXED in SAS 9.2 (SAS Institute, Cary, North Carolina, USA), with the reproductive and non-reproductive periods for each individual representing the repeated measures. I censored individuals with <20 locations in both periods. I detected unequal variances using graphic examination of residuals, and log-transformed home-range sizes accordingly (Zar 1999). I used PROC GLM to calculate means and standard errors for each group in the analysis. Reported means for each period were based on all individuals in that sample, although I censored individuals not tracked across both periods from the ANOVA.

Spatial Shifts in Response to Management Activities

To assess the effects of restoration-related habitat disturbances on home range at the individual level, I identified individual lizards radio-tracked before and after a given disturbance (Table 2) and compared home ranges before and after the disturbance (Table 3). I assessed these changes in spatial distribution using the kernel-density-estimator (KDE) volume of intersection (VI; Fieberg and Kochanny 2005). This index yields a proportion of volume that two KDEs overlap each other; KDEs that do not overlap at all have a VI of 0, indicating a complete home-range shift, whereas KDEs that overlap completely have a VI of 1, which would indicate the individual’s home range has not changed at all.

After calculating the VI for each lizard’s pre- and post-disturbance home ranges, I regressed VI values against the proportion of each individual’s radio-locations in the disturbed area before the disturbance. If the disturbance has a positive effect, one would expect a lizard to shift its home range to overlap more with the disturbed area; individuals with less of their pre-disturbance home range in the disturbed area should display greater home-range shifts and thus lower VI values (yielding a positive slope in the regression model). Conversely, if the disturbance has a negative effect, one would expect lizards with more pre-disturbance home range in the disturbed area to shift their home ranges substantially, resulting in less overlap of the old home range with the new one and therefore a lower VI value. Therefore, a negative effect of disturbance would cause the regression model to have a negative slope. I omitted individual home ranges with a proportion of in-disturbed volume that was <0.01, as these individuals were likely nowhere near the disturbed area and the resulting proportion in disturbed area was due simply to the outer edges of the 95% KDE. I tested for significant regression slopes using PROC GLM in SAS.

I also assessed population-wide shifts in spatial distribution of lizard home ranges following disturbance by testing for differences between the population-wide mean proportion of home range within a disturbed area before and after said disturbance. For all such analyses, home ranges were only estimated for individuals with at least 5 radio-locations for the time period (pre- or post-disturbance). Because I was assessing the mean home-range proportion at a given time at the population-level, individuals included in the pre-disturbance home-range mean proportion were not necessarily present for the post-disturbance mean proportion and vice versa.

I performed this analysis by first constructing a 100% KDE raster for each individual using the Home Range Tools Version 1.1 (HRT; Ontario Ministry of Natural Resources, Centre for Northern Forest Ecosystem Research, Thunder Bay, Ontario, Canada.) extension for ArcGIS 9.3 (ESRI, Redlands, California, USA) with the reference smoothing parameter (Figs. 3a, 3b).

Output options for the KDE function in Home Range Tools were set as following: raster cell size = 1; scaling factor = 1,000,000; every utilization distribution (UD) calculated to the full extent of the input layer. Because this population is on a small study area compared to home-range sizes and UD tails are negligible (especially for the 100% KDE), calculating UDs to the extent of the input layer should affect home-range estimates minimally. I verified this by comparing a representative subsample (*n* = 6) of individuals' 95% KDEs calculated on the same extent to those individuals' KDEs calculated individually without a shared extent; a paired sample t-test (PROC TTEST) revealed no difference in home-range size between the two methods ($t_5 = 1.00$, P = 0.36).

In addition to generating 100% KDE rasters for each home range, I also created 95% KDE polygons using Home Range Tools, and then clipped each 100% KDE raster by its respective 95% KDE polygon to obtain a 95% KDE raster (Figs. 3b, 3c). These rasters were then clipped by the disturbed area polygon (Figs. 3c, 3d), and I compared the proportion of the KDE's volume within the disturbed area to the volume of the 95% KDE to create a proportion of home range within the disturbed area (Fig. 3e). These proportions were then used as the response variable to test whether the mean proportion of home range in the disturbed area for the population changed during the disturbance. As I did for individual-level analyses, I omitted individual home ranges with a proportion of in-disturbed area that was <0.01, as these individuals were likely nowhere near the disturbed area and the resulting proportion in disturbed area was due simply to the outer edges of the 95% KDE.

I could only perform the above analysis in situations for which there were sufficient numbers of radio-tagged lizards (both individuals and locations per individual) in and around the disturbed area before and after the disturbance. I identified 9 situations in which to test for disturbance effects; 5 were within-year tests, with before and after periods in the same year. The remaining 4 analyses were performed across years (Table 4). For each analysis, after calculating the proportion of home ranges in the disturbed area for each lizard in the population, I assessed differences in proportion of home ranges in the disturbed area using a t-test (PROC TTEST in SAS) in cases for which only pre- and post-disturbance samples were available. I dealt with inequality of variances as described for juvenile movement rate analysis. In cases where the pre- and post-disturbance samples were in the same year, I omitted locations during the disturbance and for a week after the disturbance to account for acute disturbance factors and only test longer-term effects (e.g., testing for an effect of herbicide spraying on habitat but not the direct effect of the tractor used to spray the herbicide). For longer-term analyses, a during-disturbance sample was sometimes included, or the population was pooled for a whole season and compared across multiple years; in these cases I used ANOVAs (PROC GLM in SAS) to assess differences in proportion of home ranges in the disturbed area. To account for non-normality in the data, I transformed data using the arc-sin square-root transformation for ANOVAs (Zar 1999).

I also examined overall population-wide changes in spatial distribution using KDE VI. I grouped individual locations (initial captures, recaptures, and telemetry locations) for all individuals in each of the 3 study stages (2004–2005, 2006–2008, 2009–2011). I then assessed spatial overlap among the 3 stages using VI. I ran this analysis twice, first assessing comparisons among all individuals on WR3, the area northeast of WR3 destined for housing development, and areas southeast of WR3 combined (Fig. 4). For the second comparison, I limited locations to those on WR3.

Survival Rates

I estimated survival rates of telemetered lizards that were tracked ≥10 days during 2004–2011 to compare survival rates to past studies on WR3 (Endriss et al. 2007). In a number of cases, I was unable to determine the fate of a lizard because of transmitter failure or removal from the study area by a predator (including humans). Because of this ambiguity, I estimated survival rates in 2 ways. Category 1 estimates assumed lizards with undetermined fates were alive; these individuals were censored from the analysis following their disappearance. Category 2 estimates assumed missing lizards were dead (Munger 1986, Endriss et al. 2007, Bogosian 2010). Lizards that died as a result of research activities (*n* = 10 for 2004–2011) were censored at the last date they were known to be alive.

I used the Known-Fates model in Program MARK (White and Burnham 1999), which is based on the Kaplan-Meier survival estimator with staggered entry (Pollack et al. 1989), to evaluate a priori hypotheses that sex, season (active vs. inactive), stage, and the proportion of home range in areas disturbed by restoration activities affect survival. Active season was considered to be 2 April–19 August and inactive season was 20 August–1 April (not to be confused with reproductive and non-reproductive periods [emergence–15 July and 16 July–hibernation, respectively]). Individuals tracked over multiple years were separated for the purposes of survival analyses, so experimental units for these analyses were individual-years. I used a weekly time interval starting on 2 April each year, with the first 20 weeks considered active season and the rest of the year considered inactive season. I also estimated cause-specific mortality rates using the Heisey-Fuller method (Heisey and Fuller 1985).

Population Size and Density Assessment

I selected three 4-6-day periods during May–June 2011 during which I intensively searched the Wildlife Reserve 3 study area for horned lizards. These periods are considered analogous to trapping occasions in mark-recapture terminology. Number of new captures and recaptures were tallied in each trapping occasion. Captures and recaptures outside these occasions were not included in mark-recapture analysis. Because of low capture and recapture numbers during 2010, in 2011 I adjusted my methods to multiple capture occasions earlier in the season (May–June), when *P. cornutum* are more active, to ensure a more accurate population assessment.

I used a closed population model in program MARK (White and Burnham 1999) to estimate population abundance on Wildlife Reserve 3. Although I was aware of telemetered individuals that died during the capture periods in 2011, natural mortalities do not violate the assumption of closure as long as marked and unmarked individuals do not have different survival rates (Seber 1973). I calculated the *P. cornutum* population density on WR3 by dividing the abundance estimate by the area enclosed by a 100% MCP defined by relocations of all lizards captured. This MCP encompassed the two large ponds on WR3; I subtracted the area of these ponds from the MCP area before calculating a lizard density.

RESULTS

Daily Movement Rates

I analyzed the daily movement rates of 44 individuals that were tracked in both periods (reproductive and non-reproductive) over 6 years. I censored data from 2003, 2004, and 2006 from analyses because of lack of adequate sample size. Overall daily movement rate was 19.2

m/d (SE ± 2.0), with estimated mean movement rates of 24.5 m/d (SE ± 1.4, *n* = 118) for the reproductive season and 11.9 m/d (SE ± 1.0, *n* = 56) for the non-reproductive season (Table 5).

The repeated-measures 3-way ANOVA for individuals tracked across both seasons (*n* = 44) showed that movement rates of *P. cornutum* on WR3 were affected by the interactions of sex*period ($F_{1,38}$ = 10.13, P = 0.003; Fig. 5) and stage*period ($F_{2,38}$ = 8.50, P = 0.001), as well as by the 3-way interaction of sex*stage*period ($F_{2,38}$ = 4.00, P = 0.03; Fig. 6). There were also significant effects of stage ($F_{2,38}$ = 5.89, P = 0.006) and period ($F_{1,38}$ = 13.95, P = 0.001) on daily movement rate of *P. cornutum* on WR3, but no main effect of sex ($F_{1,38}$ = 0.33, P = 0.57) or an interaction effect of sex*stage ($F_{2,38}$ = 1.05, P = 0.36). The sex*period interaction was manifested by a greater decline in male movement than female movement from the reproductive to the non-reproductive period (Fig. 5). The 3-way interaction is explained as males exhibiting movement rates with larger between-period declines than females, as well as larger annual variation in those declines than females (Fig. 6). Overall, the highly significant effect of period across all stages and sexes, in concert with temporal variation, appear to be driving the significant effects of the stage*period and stage*year*period interactions.

Home-range Estimates

I estimated home-range size for 31 individuals that were tracked across both periods in a year. For all individuals across all years, mean (± SE) annual home-range size was 3.30 ± 0.07 ha using KDEs and 0.93 ± 0.19 ha using MCPs. I could only include the 2007-2008 and 2009-2011 stages in the 3-way analysis due to inadequate sample sizes in 2004 and 2005.

I found a significant effect of reproductive period ($F_{1,27}$ =23.03, P < 0.0001) on KDE home-range sizes. During the two stages in the analysis (2007-2008; 2009-2011), home-range sizes were larger during the reproductive season (Fig. 7). Mean home-range size across both stages for the reproductive period was 4.65 ± 0.77 ha, whereas for the non-reproductive period it was 1.94 ± 0.56 (Table 6). Effects of sex, stage, sex*stage, sex*period, period*stage, and the 3-way interaction did not affect KDE home-range size (all $F_{1,27} < 1.5$, all $P > 0.23$).

Analyses of home-range size calculated using MCPs revealed a pattern similar to that of KDEs (Fig. 7); period was the only significant factor affecting home-range size ($F_{1,27} = 36.10$, $P < 0.0001$). Additionally, there was weak evidence for an effect of stage ($F_{1,27} = 3.41$, $P = 0.08$), as 2007-2008 home-range sizes were marginally but consistently larger than those in 2009-2011. All other factors and interactions did not affect MCP home-range size (all F values < 2.27, all P values > 0.14).

Spatial Shifts in Response to Management Activities

For individual-scale comparisons of home ranges before and after disturbances, there was no relationship between the proportion of home range in a disturbed area before disturbance and VI for each individual (Table 3). Only 1 comparison of 6, herbicide spraying that occurred during 2007 in Area D, had a P-value < 0.10 (slope of -0.45, indicating a negative response by lizards to the treatment; Fig. 8); none of the analyses yielded an r^2 value > 0.4.

Similarly, population-wide analyses yielded a single comparison (herbicide spraying in 2005 in Area A) in which there was a difference between mean proportion of home range in a disturbed area pre- and post-disturbance (Table 4, Figs. 9, 10). The proportion of locations in the disturbed area increased after the disturbance.

Anecdotally, few lizards entered developed areas after construction was completed (Fig 4). Although these low numbers prohibited any quantitative analyses of the effect of construction, it appeared that construction of the developments and paving of Mitchell Avenue (which separated the housing development and WR3) constrained *P. cornutum* travel across the road and into housing developments. However, I observed one individual in 2011 leave the north side of WR3 and travel through the housing development north of Mitchell Avenue for several days before returning to the east side of WR3. These observations suggest that although *P. cornutum* generally avoided crossing Mitchell Avenue, it may occur rarely.

The population-wide overlap (68%), as measured by VI, between lizard locations in the 2003–2005 (*n* = 1233) and the 2006–2008 (*n* = 2111) stages was higher than the overlap between the 2009–2011 stage (*n* =5035) and either of the former two (58 and 56%, respectively; Fig. 4). Because of the effort to find individuals impacted by construction and translocate them, much more search effort was spent to the northeast of WR3 during the 2006–2008 stage. This difference can be seen in the distribution of lizard locations (Fig. 4). After accounting for this by restricting the comparison to only WR3, the overlap in lizard distributions increased. I found 68% overlap between the 2003–2005 (*n* = 929) stage and both the latter two stages. The 2006–2008 stage (*n* = 994) overlapped the 2009–2011 stage (*n* = 4504) by 75%.

Survival Rates

There were several competing models explaining survival rate, although these differed between Categories 1 and 2 (Table 7, *n* = 147 individuals). Both categories of survival analysis showed strong evidence for different survival rates between active and inactive season. For models assuming missing individuals were alive (Category 1), there were 2 competitive models, both of which included an interaction of study stage and season. The individual covariate of proportion of home range in a disturbed area in a given year was also in the second-ranked model. These results indicate strong evidence for an interacting effect of stage and season (Table 8), and some support for an effect of the disturbance covariate. During 2009-2011, there were more hibernation deaths than the other stages (Table 9), making inactive-season survival much lower and causing the interaction between stage and season (Table 8). Otherwise, the active season generally has lower survival rates. The best model that included the individual covariate indicated a covariate effect strength of -0.39 ± 0.18.

For Category 2, which assumes missing individuals are dead, the most competitive model provided weak evidence of an effect of season on survival rates (Table 7). The second-best model was the null, and 8 of the 16 models run were within 2 AIC_c units. Although these results support an effect of season, the number of competitive models, including the null, indicate that the data are not well explained by the *a priori* models I constructed. The best model including the covariate effect, similar to Category 1, showed a negative effect with a slope of -0.46 ± 0.15.

Causes of mortality of telemetered lizards on WR3 included depredation (*n* =23), anthropogenic causes (*n* = 11), study-related (*n* = 10), uncertain causes (*n* = 8), and unknown causes during hibernation (*n* = 3; Table 9). Cause-specific mortality rates for depredation were greater in the latter two study stages; otherwise there were no obvious trends in cause-specific mortality rates over time (Table 9).

Population Size and Density Assessment

My data set was too small to allow Program MARK to fit complex models, similar to Endriss et al. (2007). I therefore followed their example and assumed constant survival, recapture probability, and population rate of increase (λ) between capture occasions. The top-ranked model that was properly estimated was a null model, which did not incorporate an effect of time on capture probability or population size. The population estimate for adult and juvenile lizards in 2011 was 32.9 ± 4.7 (SE; 95% CI: 28.1–49.0). Using a 100% MCP for all lizards telemetered or captured during 2011 on WR3 (Endriss et al. 2007), I calculated a survey area of 12.25 ha (not including the areas of the two ponds), yielding a density of 2.68 individuals/ha.

However, I captured and tracked lizards in areas adjacent to but not on WR3 during 2010 and 2011 (Fig. 4), suggesting the population is not limited to WR3. Capture rates for our searches (mean = 0.75 captures/person-hr, *n* = 3 occasions) were lower than Endriss et al. (2007; mean = 1.31 captures/person-hr, *n* = 4 occasions).

DISCUSSION

I was unable to detect changes in spatial distribution of *P. cornutum* following disturbances, and the continued occupancy of areas with more diverse microhabitat resources supports the hypothesis that *P. cornutum* need a mix of habitat types (Hellgren et al. 2010). However, estimates of survival and abundance indicated that the *P. cornutum* population on WR3 declined following habitat disturbance and loss. Quantitative results for the effects of construction were unobtainable, but my telemetry observations supported the prediction that developed areas adjacent to WR3 would see a drastic decline in *P. cornutum* use.

The interactions between *P. cornutum* and habitat disturbances can be complex and delayed. For example, survival rates increased in the second year after prescribed burning for a population of *P. cornutum* in Texas (Hellgren et al. 2010). I was not able to observe this type of interaction in this study because management and restoration actions on WR3 often occurred in consecutive years, preventing conclusions about any delayed effects of disturbance in a given year or stage of the study. The inability to investigate the effects of disturbance over time on wildlife highlights the need to design restoration projects to allow better opportunities for quantifying these effects (Block et al. 2001).

Daily Movement Rates

Estimates of daily movement rates were smaller that those reported in the literature, but the effects of period and sex matched those reported by Endriss (2006), Fair and Henke (1999), and Stark et al. (2005). Using a subset of the data included here, Endriss (2006) reported a mean daily movement rate of 25.1 ± 4.7 m/d on WR3 during 2003–2005. The overall mean rate in this study was less than that of Fair and Henke (1999), who estimated a rate of 36.5 m/d (SE ± 3.2), and that of Stark et al. (2005), who reported a mean rate of 45 m/d. Endriss (2006) and Stark et al. (2005) reported a decrease in male movement rates from the reproductive period to the non-reproductive season, but did not observe a corresponding decrease for females, similar to my findings. Fair and Henke (1999) noted a continual decrease in movement rates from June to October. Stark et al. (2005) posited that the change in male *P. cornutum* movement rates during the reproductive period was due to males searching for mates, a hypothesis echoed by Sherbrooke (2002) based on capture-frequency data from road-cruising surveys. My movement data seem to corroborate this, and males were seen mating several times during the reproductive period on WR3.

The relatively constant rate of female movements across periods, however, remains unexplained in the literature. I observed females on WR3 shift home ranges and/or move relatively long distances after nesting. For example, in 10 of 15 known nesting events in 2011, I observed daily movement rates of >100 m/d (maximum: 274 m/d) within 2 days of nesting. Sherbrooke (2003) noted that females may make several attempts at digging a nest before finding a suitable nest site. Searching for nesting sites might constitute the type of “occasional sallies” mentioned in Burt’s (1943) definition of a home range. In other words, females may inflate their mean movement rates (and home-range sizes) through a few large movements made while searching for a nest site. Nevertheless, my analyses show average movement rates of females were less than those moved by males in the reproductive period.

Females may limit movements as much as possible to minimize energetic needs beyond trips associated with nesting, provided their resource requirements (e.g., thermoregulation, energy intake, safety from predators; Pough et al. 2004) are met. Similarly, males probably limit movements after the reproductive period to the minimum necessary for survival. Several studies have tied *Phrynosoma* movements and home-range shifts to prey. These studies indicate that *Phrynosoma* often feed at an ant colony or along a foraging column of ants until the prey react to the continued depredation, at which point the lizard is forced to find a new area to feed (Baharav 1975, Whitford and Bryant 1979, Munger 1984). The reliance of *P. cornutum* on crypsis also may discourage movements, and it therefore follows that beyond male mate-searching and female nesting, *P. cornutum* movements would remain as low as possible as long as lizards can meet their requirements. Fair and Henke (1999) suggested that heat and low humidity may reduce movements during the hottest part of the summer, July-August in southern Texas, which is consistent to my observations in central Oklahoma.

Several alternatives may explain variation in movement rates among stages from 2004 to 2011. Movement rates declined from reproductive to non-reproductive period in every stage, but the declines for each stage differed from each other. Climatic variation and habitat change associated with restoration activities could play a role in causing movement rates to vary year-to-year. Examination of yearly temperature and precipitation trends (National Weather Service 2012*a*) provides some clues regarding the yearly trends in movement rates I observed. Non-reproductive period movement rates were lowest in 2011, a year with above-average temperatures, including a number of heat records (National Weather Service 2012*b*). This year also saw the greatest decline in male movement between the reproductive and non-reproductive periods. In a similar light, the lowest movement rates during the reproductive period for both sexes occurred in 2005, which had the lowest precipitation levels of any year included in the analysis. On the other hand, 2007 was a notably wet year, and cool, moist conditions may be a driving factor behind the relative consistency in male and female movement rates across periods in that year. These correlative observations are consistent with the hypothesis that high heat and low humidity depress horned lizard movements (Fair and Henke 1999). A more in-depth evaluation of weather records against movement rates may reveal more direct causative relationships between weather and movement rates.

Prairie restoration efforts on WR3 may have confounded the variation in annual patterns of movement rates. Because of the time scale of the restoration efforts and the spatial distribution of restoration activities relative to WR3 and habitat occupied by *P. cornutum*, it is difficult to draw conclusive parallels between movement rates and restoration activities. For example, during the reproductive period in 2004 and 2005 (the years preceding restoration activities), both sexes had the lowest movement rates for the overall study. However, it is unknown if movement rates were low due to lack of disturbance or to dry weather during 2005, or higher during other years due to disturbance or wetter weather. Tracking lizards in an area disturbed by restoration concurrently with a control group might address this question. Although an attempt to create such areas on WR3 was made by spraying herbicide on approximately half the area occupied by *P. cornutum* during the winter of 2010-2011, most telemetered lizards moved freely from the sprayed area to the area that was not sprayed and vice versa during the active season in 2011, making it difficult to draw inferences. The logistical and biological constraints imposed on the restoration project at WR3 and the corresponding study of *P. cornutum* underscore why restoration projects often fail to assess effects on wildlife and highlights the importance of designing restoration projects to address this very issue (Block et al. 2001).

Home-range Estimates

Previous KDEs of mean home-range size for *P. cornutum* on WR3 are smaller than those I calculated, although they represent a subset of the data that I analyzed. Endriss (2006) estimated mean 95% KDE home-range size to be 0.87 ± 0.11 ha (*n* = 24) and mean 95% MCP to be 0.50 ± 0.09 ha. The greater estimates for the latter years of the study compared to those of Endriss (2006) may be accounted for by methodological differences, including the length of monitoring each season and different kernel smoothing parameters (bandwidths). Endriss (2006) did not extend field work into August, and I qualitatively observed some individuals display home-range shifts as the number of observations surpassed the minimum of 20 set by myself and Endriss (2006). Longer observation periods may have therefore inflated home-range sizes relative to earlier work (Endriss 2006). Also, whereas Endriss (2006) used the least-squares cross validation (LSCV) method, I used the reference bandwidth method, which tends to overestimate home-range size to a greater extent than LSCV (Worton 1995, Seaman and Powell 1996, Kernohan et al. 2001).

Similar to daily movement rates, home-range sizes exhibited a significant decline from the reproductive period to the non-reproductive period, as observed by Burrow et al. (2002) for *P. cornutum* in southern Texas. Unlike movement rates, however, home-range size did not differ between sexes for either period. This combination of results implies that males are moving more than females within similarly sized home ranges during the reproductive period. Home-range size may be dictated by resource needs outside of mating (e.g., food, cover from thermal extremes and predators; Pough et al. 2004). Therefore, males and females may be meeting their needs for non-reproductive resources (i.e., food, refugia) within similarly-sized home ranges; males simply move more often within their home range while searching for female mates.

Patterns in annual home-range size variation and the period*year interaction follows those seen in daily movement rates. Meteorological variation between years could be the cause of this variation, and the decrease in home-range size from reproductive to non-reproductive period for both MCP and KDE estimates was greatest in 2011, a year with record-breaking heat (National Weather Service 2012*b*). Although Burrow et al. (2001) detected changes in home-range size in response to prescribed burning, changes in home-range size due to restoration and construction activities in this study are hard to tease apart from environmental and temporal variation, especially considering that the pre-disturbance years of 2004 and 2005 were censored from analyses.

Spatial Shifts in Response to Management Activities

Individual- and population-level spatial analyses provided little evidence of an effect of restoration activities on lizard spatial use and distribution. Although there was a single treatment with a marginal effect, namely herbicide spraying in Management Area A in July 2005 (Fig. 8), the relationship overall does not appear to be strong. Moreover, when evaluating significance of effect at an α-level of 0.05, one can expect, on average, to reject the null hypothesis of no effect when the null is true once out of every 20 trials; the total number of spatial trials was 15. Examining a map of lizard locations before spraying herbicide in June and after spraying in August, there appears to be more *P. cornutum* locations in the sprayed Area A after spraying (Figs. 8, 9). However, whether this is due to spraying or some other effect (perhaps merely stochasticity) would need to be assessed more directly. Overall, it appeared that the spatial distribution of lizards on WR3 proper has not changed in the past 8 years despite numerous prairie restoration activities. The WR3-only comparison showed higher overlap between the two later stages, which may be due to a variety of slight differences from the 2003–2005 stage, including more points on the north-western portion of WR3, a greater number of locations in the center of Area D (Fig. 2), and a larger sample size.

The results of these analyses do not indicate that disturbance due to restoration activities affected the spatial ecology of *P. cornutum* on WR3. However, they are not entirely conclusive, due to the logistical constraints of working on a single site with a Species of Special Concern. An experimental design with multiple sites, randomly assigned to prairie restoration treatments or controls, would provide more conclusive results. Hellgren et al. (2010) found an increase in survival of *P. cornutum* in the second year after a prescribed burn, but this sort of effect would be confounded in this study by repeated management actions in the same area in consecutive years.

I was unable to assess changes in spatial ecology due to construction projects adjacent to WR3 because of several confounding factors. The effort to translocate all *P. cornutum* whose home ranges overlapped the construction area in the earlier stage (2006–2008; Bogosian 2010) resulted in no resident lizards in the affected area. Although this unfortunate logistic constraint was necessary to attempt to minimize mortalities of a State of Oklahoma Species of Special Concern, no lizards remained in the construction area whose home ranges could be evaluated. Additionally, lizards with home ranges adjacent to the construction areas were also affected by restoration activities occurring on WR3 during the years of construction. Finally, I did not search housing developments for *P. cornutum* for a variety of logistical reasons: fenced backyards and respecting residents' privacy precluded realistically searching housing areas, telemetered lizards rarely ventured into this area, and the apparent lack of habitat suitability in the area directed me toward searching for lizards in more suitable areas. As a result, I could not detect the unlikely scenario in which lizards were actively living entirely in the housing developments.

Factors driving lizard spatial distribution on WR3 may be more related to habitat structure than disturbance. Long-term trends in lizard occupancy (Fig. 4) are generally in keeping with the habitat-niche model created by Bogosian et al. (2012). Areas of low *P. cornutum* density, especially the south-western corner of WR3 (Area B; Fig. 2), were shown as less suitable by Bogosian et al. (2012), and were dominated by thick monocultures of grasses (e.g., big bluestem, plains bluestem). Areas consistently occupied by *P. cornutum* were characterized by greater forb density and diversity and more bare ground, and therefore greater diversity of habitat structure. Presence of *P. cornutum* in these areas was consistent with the literature, which suggests that *P. cornutum* require a mosaic of habitat types including open areas and refugia (Pianka 1966, Whiting et al. 1993, Fair and Henke 1998, Burrow et al. 2001, Hellgren et al. 2010) and may be less adapted to dense monocultures of grass (Newbold 2005).

Areas with a mosaic of bare ground and forbs may be the required habitat for *P. cornutum* although some researchers proffer that horned lizards prefer disturbed areas per se (Whiting et al. 1993, Fair and Henke 1997). If such habitat requirements were met in perpetuity without disturbance, *P. cornutum* may thrive. Spears et al. (1993) proposed an interaction between bobwhite quail (*Colinus virginianus*) abundance and seral stage across different ecoregions: bobwhite abundance should be greater in early seral stages in more productive areas and greater in later seral stages in less productive areas. A similar effect has been proposed for Texas tortoises (*Gopherus berlandieri*; Kazmaier et al. 2001). This phenomenon could be acting on *P. cornutum* habitat use, as the mixed-grass prairies of WR3 are more productive than the mesquite- and thorn-scrub or short-grass prairie habitats that dominate much of the range of *P. cornutum*. The higher productivity of mixed-grass prairies may necessitate more disturbance to maintain the heterogeneity of habitat structure required for *P. cornutum* occupancy.

Survival Rates

The distribution of deaths among mortality causes supported my results from the known-fates survival analysis regarding the effects of season (Tables 7, 9). Depredation was the leading cause of death, followed by anthropogenic factors (not including signal loss, which is ambiguous). Depredation was also a major cause of death in other studies of *P. cornutum* survival (Munger 1986, Hellgren et al. 2010). *P. cornutum* hibernate under thin layers of soil (Sherbrooke 2003, personal observations), which reduces their inactive-season exposure to predators and human factors. Additionally, time spent out of hibernation during the inactive period (20 August–1 April) involves less movement and smaller home ranges (see previous sections; Fair and Henke 1999, Stark et al. 2005, Endriss 2006). Many common *P. cornutum* predators are mammalian or avian (Table 9, Tyler 1977, Munger 1986, Tyler 1991, Middendorf and Sherbrook 1992, Holte and Houck 2000, Sherbrooke and Middendorf 2004, Endriss et al. 2007, Hellgren et al. 2010), and movement by lizards likely attracts attention and undermines their main predator-avoidance strategy of crypsis. By reducing movements in late summer and autumn and remaining still and buried during winter, *P. cornutum* decrease the likelihood of being detected by a predator. Similarly, remaining motionless and buried during hibernation reduces the risk of encountering a human-made threat (Table 9).

Survival estimates on WR3 were higher than those reported by Hellgren et al. (2010) for *P. cornutum* on managed habitats in southern Texas. The leading cause of death in both populations was depredation. Because the Texas population was on a wildland preserve >6000 ha, it is possible that the abundance of predators was greater compared to the urban surroundings for my study site. Urban areas often have fewer predators (Woodroffe and Ginsberg 1998, Randa and Yunger 2006) and therefore mortalities due to predation should be lower on WR3 than in contiguous wildland areas. Several known *P. cornutum* predators were absent from WR3, including roadrunners (*Geococcyx californianus*), coachwhips (*Masticophis flagellum*), and Western diamondback rattlesnakes (*Crotalus atrox*). In addition, depredation accounted for a lower proportion of known causes of death at WR3 than in southern Texas (Hellgren et al. 2010).

Habitat characteristics and suitability also play a role in *P. cornutum* survival. There is some disagreement in the literature over habitat use of *P. cornutum*, particularly regarding the use of open vs. thickly vegetated areas. Some authors posit that horned lizards prefer open areas over those with thick vegetation at ground level, as open areas facilitate thermoregulation and feeding (ants prefer open areas) and the lizards' dorso-ventrally compressed bodies inhibit movement in thick vegetation. For example, Whiting et al. (1993) found that *P. cornutum* inhabited areas with less ground cover as opposed to areas with thick grass. Wilgers and Horne (2006) reported that *P. cornutum* preferred areas that were burned annually over those that were burned every 4 years or unburned for long periods of time. Newbold (2005) demonstrated that horned lizards (*P. platyrhinos*) had difficulty fleeing predators suddenly through thick grass, which was interpreted as support for the hypothesis that horned lizards prefer bare ground. Conversely, Burrow et al. (2001) found that *P. cornutum* in southern Texas used bare ground and herbaceous vegetation similar to their availability in the morning and evening, and avoided bare ground during the afternoon. Similarly, Endriss (2006) found that *P. cornutum* on WR3 sought out shade during the afternoon. Hellgren et al. (2010) suggested that although open areas are important to *P. cornutum* for ant foraging, survival data suggested that heavier levels of grazing and recent burns may increase vulnerability to predation. Similar dynamics may be occurring on WR3. Although some open areas are necessary, less cover and more disturbance may expose *P. cornutum* to greater risk of predation.

The progressive decline in survival rates across study stages, along with the negative effects of proportion of home range in disturbed area (the individual covariate), provides evidence that *P. cornutum* survival was detrimentally affected by disturbance due to prairie restoration on WR3. The frequency of depredation increased in conjunction with declining survival rates (Tables 8, 9). Indeed, the additional deaths reported in 2009–2011 drove the decreased survival rates.

The mechanism linking survival to disturbance may involve the effect of edge habitat in an urban environment, which could represent an ecological trap for *P. cornutum*. During the 2009-2011 temporal stage, the population had not only been exposed to repeated restoration activities, but housing construction was completed adjacent to WR3 (Table 4). Urban edge-effects, and a greater perimeter-to-area ratio as the habitat patch has gotten smaller, might increase the risk of coming into contact with anthropogenic threats and exotic predators (domestic/feral cats and dogs), as seen in the rising number of anthropogenic deaths during 2009-2011.

Lehtinen et al. (2003) found that some species of Malagasy herpetofauna tended to be edge-avoiders, whereas others tended to be interior-avoiders. All species in their study designated as interior-avoiders, i.e., those that prefer habitat edges, were lizards. Based on the hypothesis that *P. cornutum* need a mosaic of bare ground and vegetative cover to meet their needs (Hellgren et al. 2010), one would expect *P. cornutum* to prefer edges. Indeed, spatial data from WR3 showed that *P. cornutum* avoided homogeneous areas of grass and inhabited areas with a mixture of bare ground and vegetation (Bogosian et al. 2012). Although *P. cornutum* are capable of moving through unsuitable habitat such as thick grass monocultures and wooded areas, they clearly do not linger in these places, instead spending most of their time in areas with patches of bare ground, forbs, and grasses, including along trails and fences in WR3. Use of edges by *P. cornutum* may be particularly common in late-succession areas of high-productivity habitats such as mixed-grass prairie (Spears et al. 1993), which includes some areas of WR3 and the surrounding undeveloped areas. This utilization of edges may be an ecological trap (Gates and Gysel 1978), particularly in urban fragments. Edges provide the thermal and nutritional resources needed by horned lizards in high-productivity ecoregions, while simultaneously exposing them more frequently to anthropogenic and predatory threats. Indeed, 4 of the 7 anthropogenic-caused deaths in the 2009-2011 study stage were direct results of lizards living on the shared edge of WR3 and adjacent housing developments (1 lizard was hit by a lawn mower and 3 became tangled in plastic netting left by landscapers).

Population Size and Density Assessment

The estimate of the population size on WR3 was 38% smaller than the 53 ± 11 estimate for 2005 made by Endriss et al. (2007), and represented an annual λ of 0.92 for 2005–2011. I replicated the methods of Endriss et al. (2007) to minimize bias, so these results likely indicate a decline in population size. This result is not surprising, given the amount of *P. cornutum* habitat adjacent to WR3 lost during 2008–2011 via housing construction. Although past and current census methods were performed only on WR3 proper, more adjacent habitat likely allows an overall larger population, and individuals whose home ranges were partially on WR3 could have been surveyed in the initial estimate. The 2008 translocation of 17 adult lizards, (Bogosian 2010) all of whose home ranges were partially on WR3, likely represented the bulk of the decline in population size. Although there was an apparent reduction in adult survival over time, this decrease was probably not the only factor driving the population decline; recruitment, particularly the survival of non-reproductive stages, likely plays a key role in population growth and decline (see Chapter 2). However, the loss of any individuals due to stochastic events in such a small population can be devastating, and take on great importance relevant to population persistence. For example, the deaths of 3 adult lizards due to plastic netting entanglement in 2011 represented a stochastic event. The netting fell off the back of sod being laid in housing areas adjacent to WR3 and was blown by wind onto WR3. This random, presumably rare event resulted in a loss of ~10% of the estimated adult population on WR3.

Confounding factors that may have affected the results of the population census included variation in weather, searcher proficiency, detectability, and effort. The effects of variation in weather are difficult to assess quantitatively, especially because differences between the weather at times throughout the day and between micro-climates can affect *P. cornutum* behavior. Searcher proficiency and effort are also hard to quantify with such a small sample size. However, if the population has declined, one would expect lower capture rates even with equal search proficiency, which was the case. The lower capture rate in this study is further evidence of a population decline.

Conclusion

The above findings indicate a population under stress from anthropogenic factors. Stone (2007) found that small-mammal populations at prairie-restoration sites underwent a decline immediately following habitat-restoration treatments, but recovered to some degree after 3-5 years. Cunningham et al. (2002) also documented recovery of a lizard community in chaparral after a severe wildlife over the course of 4 years (though the *Phrynosoma* species in the study, *P.*

douglassi, was more frequently caught in unburned habitat). The population of *P. cornutum* on WR3 may be experiencing a similar temporary decline following disturbance. However, the ability of the *P. cornutum* population to recover may be lower than in the 2 studies above. Whereas small mammals are often r-selected species with high population densities, horned lizards have much lower densities (Pianka and Parker 1975*a*, Cunningham et al. 2002, Bateman et al. 2008), a more K-selected life history compared to many small mammals, and presumably lower dispersal rates. The isolation of the WR3 poses another challenge to *P. cornutum* recovery on Tinker AFB. The recovery of a lizard community described in the study by Cunningham and colleagues (2002) took place on a wildland that was 24,500 ha. The WR3 population has experienced not only habitat disturbance, but also a significant loss of adjacent habitat through housing construction, and a significant loss of individuals during the translocation preceding said construction (Bogosian 2010). Because WR3 is an urban reserve and is relatively isolated, immigration may be much less likely than large areas of contiguous habitat.

The spatial scale of *P. cornutum* ecology may be compatible with population persistence in urban areas. However, isolated populations are still subject to certain threats, such as catastrophes, stochasticity, and inbreeding, from which they may not be able to recover. Assessments of *P. cornutum* dispersal ability, genetic diversity, and minimum viable population size are necessary to determine whether isolated urban populations will be able to persist into the future.

Gardner et al. (2007) recommended studies that examine the specific mechanisms by which habitat loss and degradation affect herpetofauna. The results of this study have revealed specific causes of mortality and patterns of spatial use in altered habitat, and have advanced the knowledge of proximate factors affecting *P. cornutum* populations. However, future restoration projects should be designed to assess effects on herpetofauna and other wildlife to provide more detailed and robust information on the causative agents of decline (Gardner et al. 2007).

CHAPTER 2

VITAL RATE SENSITIVITY IN TWO POPULATIONS OF TEXAS HORNED LIZARDS USING LIFE-STAGE SIMULATION ANALYSIS

INTRODUCTION

Perturbation analyses (Caswell 2001) examine the potential effects of changes in an independent variable on a dependent variable (e.g., population growth rate[λ]),and are a valuable technique for planning species conservation and recovery efforts. Sensitivity analyses, which are a subset of perturbation analyses, are based on matrix models, and provide estimates of how absolute changes in vital rates will affect λ (Caswell 2001, Morris and Doak 2002). Related elasticity analyses (Caswell 2001) reflect the proportional change in λ following a proportional change in a vital rate (Caswell 2001, Morris and Doak 2002).

Life-stage simulation analysis (LSA), a form of matrix perturbation analysis (Wisdom et al. 2000), has been used to complement sensitivity/elasticity analyses. Wisdom and colleagues (1997, 2000) developed LSAs to better model populations by including variation in perturbation analyses. This type of model has been heralded as an improvement over deterministic sensitivity models because of the ability to incorporate variance (either stochasticity in the system or uncertainty in vital rate estimates) into analyses. Life-stage simulation analyses are performed by first creating a probability distribution for each vital rate and then using Monte Carlo simulations to create matrices composed of randomly drawn elements. Lambda for each randomly created matrix is calculated, and a regression of λ on each vital rate reveals which vital rate drives variation in λ.

Life-stage simulation analyses have been conducted for a variety of taxa, including reptiles, amphibians, birds, and mammals (Wisdom and Mills 1997, Wisdom et al. 2000, Biek et al. 2002, Johnson et al. 2010, Taylor et al. 2012). A variety of management implications have been drawn from these studies, including the importance of vital-rate variation in population growth and recovery, and consideration of differences between vital rates among populations (Wisdom et al. 2000, Johnson et al. 2010). For example, Johnson et al. (2010) found that vital rates of a species may vary among populations based on conservation status. They concluded that effective management for recovery of endangered species may require population- and situation-specific strategies.

Vital-rate variation among different species or populations often corresponds to differing life-history strategies, and has long been theorized to represent evolutionary trade-offs between survival and reproduction (Stearns 1976, 1977). For example, Murphy (1968) theorized that high or variable adult mortality should exert selective pressure toward earlier sexual maturity and higher fecundity, as the likelihood of subsequent opportunities to reproduce in such a situation is lower than in a population with consistently high adult survival.

Lizards have been widely used as models to explore trade-offs among life-history traits (Tinkle 1969, Tinkle et al. 1970, Tinkle and Ballinger 1972, Pianka and Parker 1975*a*, 1975*b*, Ballinger 1979, Ferguson et al. 1980, Ballinger et al. 1981, Ballinger 1983, Pianka 1986, Niewiarowski 1994). This taxon attracts study because lizards exhibit wide variation in life-history traits such as age at maturity, survival of various stages, annual and lifetime clutch frequency, and clutch size in relation to body size (Tinkle et al. 1970). Tinkle et al. (1970) proposed a network of interrelated reproductive strategies, with early-reproducing, multiple-clutching species with large clutches at one extreme and late-reproducing, viviparous species with one brood per year at the other extreme. A large number of studies have examined differences in life-history traits among *Sceloporus* species and populations (e.g., Tinkle and

Ballinger 1972, Ferguson et al. 1980, Ballinger et al. 1981, Tinkle et al. 1993) in an attempt to elucidate the connection between intraspecific variation in life-history traits and the environmental variation between locations of populations. Many authors suggest that greater reproductive effort in a given season is negatively related to adult survival rate in lizards (Tinkle 1969, Tinkle and Ballinger 1972, Pianka and Parker 1975*a*, 1975*b*, Ballinger 1979, Ferguson et al. 1980, Ballinger et al. 1981, Ballinger 1983, Pianka 1986, Niewiarowski 1994).

Horned lizards (*Phrynosoma* spp.) have much larger clutch sizes than many North American lizards, but generally have lower adult survival rates (Tinkle et al. 1970, Pianka and Parker 1975*a*). Horned lizards are a useful model for examining the theory of trade-offs in life-history traits, as they lie on one extreme of the clutch-size spectrum among lizards yet exhibit considerable variation in clutch size across their range (Ballinger 1974, Endriss et al. 2007). Additionally, many species of horned lizards are believed to be threatened, sensitive, or in decline (Carpenter et al. 1993, Donaldson et al. 1994, Jennings and Hayes 1994, Grant and Doherty 2007), and therefore represent a suitable taxon for applying life-history and sensitivity-analysis theory to real-world conservation issues. Assessing not only which vital rates are most important for restoring horned lizard populations, but also whether the most important vital rates differ between populations is of immediate application in management contexts (Johnson et al. 2010). Because thorough demographic data are often scant, especially for threatened populations, results regarding the magnitude of variation of vital rates between populations of horned lizards would benefit managers and conservation planners, whose resources are generally very limited. Sensitivity analysis and LSA also have the potential to address theoretical questions regarding trade-offs among life-history traits.

Johnson et al. (2010) found that different populations across a species' range can have different sensitivities to vital rates, especially among populations with different population trajectories or conservation statuses. Texas horned lizards (*Phrynosoma cornutum*) have declined throughout much of their range (Carpenter et al. 1993, Donaldson et al. 1994), and exhibit geographically varied vital rates (Ballinger 1974, Endriss et al. 2007). I sought to examine differences between vital rates among populations of *P. cornutum* with regard to conservation and management efforts. My specific objectives were to conduct deterministic elasticity analyses and LSAs using long-term demographic data from 2 populations of *P. cornutum* with markedly different adult survival rates and fecundity. Based on the literature relating to elasticity analyses and life-history theory, I predicted variation in the importance of adult survival and fecundity in different areas, wherein populations with lower adult survival would exhibit a stronger relationship between λ and fecundity parameters, as they are less likely to survive to reproduce again.

STUDY SITES

Tinker Air Force Base (Oklahoma County, Oklahoma, 35° 24' 58" N, 97° 24' 41" W) is a largely urban base on the outskirts of Oklahoma City. Of the 2000-ha Base, approximately 500 ha were natural habitat. These areas were dominated by mixed oak-hardwood forests and a mixture of native and non-native grasslands. Research activities were focused on the population of *P. cornutum* on Wildlife Reserve 3 (WR3) and the surrounding areas. Wildlife Reserve 3 was a natural area (ca. 15 ha) on the southwestern side of TAFB, dominated by grassland with patches of woody vegetation and gravel trails and centered around 2 man-made ponds, with the surrounding area sloping towards the ponds. Although most areas of WR3 were gently sloped, some areas, especially immediately around the southern-most pond, had slopes > 45 degrees.

The soil on WR3 is primarily composed of clay. The average annual temperature for Oklahoma County is 15.7 °C, with an average annual high temperature of 21.8 °C and an average annual low temperature of 9.6 °C (Oklahoma Climatological Survey 2003). The average daily maximum and minimum in January are 8.4 and -3.2 °C, respectively, and average daily maximum and minimum temperatures in July are 33.9 °C and 21.6 °C, respectively (Oklahoma Climatological Survey 2003).

Dominant vegetation species on WR3 include big bluestem (*Andropogon gerardii*), little bluestem (*Schizachyrium scoparium*), plains bluestem (*Bothriochloa ischaemum*), indiangrass (*Sorghastrum nutans*), side oats grama (*Bouteloua curtipendula*), Maximilian sunflower (*Helianthus maximiliani*), tall fescue (*Lolium pratense*), and eastern redcedar (*Juniperus virginiana*; Endriss et al. 2007). As of 2011, the northern, northeastern, southern, and western sides of the Reserve were bounded by residential housing, whereas the eastern side borders several military buildings. Horned lizards have been sighted on a sporadic basis in other areas of TAFB, but targeted searches have yielded few if any captures by researchers (unpublished data).

Habitat restoration since 2005 and construction of a military housing development in a 7.4-ha area directly adjacent to WR3 in 2008-2010 have disturbed the Reserve. Management activities designed to restore prairie habitat have included tree removal, disking, mowing, spraying with herbicides, and seeding with native grasses and forbs.

The Chaparral Wildlife Management Area (hereafter CWMA; Dimmit and La Salle counties, Texas, 28° 19’ 40” N, 99° 24’ 39” W) is a 6,150-ha area managed by the Texas Parks and Wildlife Department (Hellgren et al. 2010). The site, which is predominantly honey-mesquite woodlands or parklands, experiences managed grazing and prescribed burns (Flanders et al. 2006, Hellgren et al. 2010). A detailed site description is available in Flanders et al. (2006).

METHODS

Field Methods

Research on *P. cornutum* at Tinker Air Force Base has been ongoing since 2003, and I replicated previously used methods (Endriss et al. 2007, Bogosian 2010) to ensure continuity of data from 2003 to 2011. I captured lizards during April-August in 2010 and 2011 on WR3 through intensive visual searching and fortuitous encounters, and recorded basic morphometric information for each lizard, including snout-vent length (SVL), total length (TL), mass, and sex. Intensive visual searches consisted of slowly walking back and forth across search areas while looking for lizards. I attempted to evenly and thoroughly search all areas of the field site except areas where vegetation is so thick and high that I probably would not have been able to detect lizards when they were present. Following Endriss et al. (2007), I implanted lizards > 5.0 g with a passive integrated transponder (PIT) tag (0.5 g), or clipped a unique combination of toes for smaller lizards. I attached a 0.95-1.95-g radiotransmitter (BD-2, Holohil Systems Ltd., Carp, Ontario, Canada or SOPR-2038, Wildlife Materials Inc., Murphysboro, Illinois, USA) to each lizard if the transmitter was < 10% of the lizard's body mass. Transmitters were attached by gluing them to the dorsum immediately posterior to the head. I secured the transmitters with an elastic band around the neck of the lizard to ensure that the transmitters were retained after shedding. After each shedding event, I re-glued the transmitters to the dorsum (Endriss et al. 2007).

I monitored the locations of radiotelemetered lizards 1-5 times weekly during the active lizard season (Apr–Aug) and at least bi-weekly from August until they entered hibernation (generally Oct-Dec). I homed to each lizard's location and recorded it with a Trimble GPS Pathfinder Pocket Receiver (Trimble GeoXT, Terrasync 2.3, Strategic Consulting International, Oklahoma City, OK) and stored location data in a geodatabase. Locations were recorded in Universal Transverse Mercator (UTM) coordinates using the North American Datum 1983 (NAD83). I varied the times during which I tracked lizards each day to obtain a representative sample of locations across all daylight hours.

Radiolocations that I collected during 2010–2011 were added to a geodatabase containing lizard locations for WR3 from 2003 to 2009. This geodatabase, maintained at Tinker AFB, contains spatial, morphometric, and behavioral data for all lizards captured on Tinker AFB from 2003 to present, including a geographic (UTM) location for all captures, recaptures, and radio-locations, as well as data on SVL, TL, mass, and sex and descriptive notes on nesting, causes of mortality, environmental conditions, etc.

I also used observations of telemetered lizards to gather data on the vital rates that compose fecundity (see below). By tracking females during nesting periods, for instance, I observed nesting activity and gathered data on clutch frequency. By monitoring each nest over time and digging it up after hatching, I could estimate nest survival, the number of eggs in each clutch (clutch size), and hatch rate for each nest.

Field methods used to collect data at CWMA were very similar to those described for WR3 (Hellgren et al. 2010, E. C. Hellgren, personal communication). Data on vital rates were collected from 1998 to 2005. The present study draws on published and unpublished data (Hellgren et al. 2010, R. T. Kazmaier, West Texas A & M University, unpublished data).

Parameter Estimates

Vital rates (survival and fecundity), as well as demographic parameters such as proportion of females nesting, nest survival, and clutch size, make up each element of the Leslie matrix used in LSA. Below, I detail how I estimated the mean and variance of each parameter, as well as how these parameters were used to calculate each matrix element.

Life-stage simulation analysis relies on randomly drawing vital rate values from a probability distribution based on the estimated mean and variance of said vital rate. Ideally, the mean and variance for each vital rate should be estimated from empirical data, and estimates of process variance and sampling variance should be separated. (Morris and Doak 2002). I attempted to use White's (2000) method for variance decomposition, but in all instances, I failed to calculate realistic estimates of process variance, probably because sampling variance was too great relative to process variance (Gould and Nichols 1998). Because I was unable to reliably decompose variance, I incorporated empirical estimates of variance (process and sampling variance combined) into my LSA wherever possible (Wisdom et al. 2000).

I modeled vital rates limited to a 0-1 scale (survival rates, proportion of females breeding, proportion of females double-clutching, and hatch rates) using β distributions, and modeled clutch sizes using a stretched β distribution (Wisdom et al. 2000, Morris and Doak 2002). The shape of a β distribution is dictated by the parameters α and β; mean and variance estimates can be transformed to α and β estimates for a β distribution (Morris and Doak 2002). However, if the variance is too great relative to the mean for a parameter (e.g., due to sampling variance, see above), the resulting β distribution often does not match the distribution that one would expect based on biological information for the study species. The distribution may become bimodal, or the distribution may have a mode much closer to 0 or 1 than to the mean, which biologically would represent more extreme values or a more skewed distribution than is realistic based on empirical data and known information about the species. This unrealistic skew and/or high frequencies of 0 and 1 occurred in a number of vital rate distributions for *P. cornutum* at WR3 and CWMA. In several cases, I therefore adjusted the variance for some parameter estimates to better match biological expectations. All means, however, were empirically based.

Fecundity.—I defined fecundity as the number of female offspring per female per year. Similar to Wisdom and Mills (1997), I calculated fecundity using a number of vital rates, with fecundity = sex ratio × hatch rate × nest survival × [(proportion females breeding × first clutch size) + (proportion females double-clutching × second clutch size)].

Sex ratio.—Following Endriss et al. (2007), I assumed *P. cornutum* populations to have a proportion of 0.5 female.. For the purposes of LSA, I fixed the sex ratio instead of drawing a random value from a probability distribution for each model iteration, as this vital rate seemed constant over time (Endriss et al. 2007, unpublished data).

Hatch rate.—I defined hatch rate as the proportion of hatchlings that successfully emerged from the nest (hatchlings divided by estimated clutch size). Successful eggs were easily distinguished from those that failed to hatch by appearance; white, papery eggs with a slit were assumed to be successful. I assumed eggs that were dark brown and shriveled, with no evidence of an opening, to be failed eggs. I estimated hatch rate for WR3 using field data from 2010 (n = 3 nests) and 2011 (n = 7). Two nests on WR3 in 2011, which had record heat and below-average precipitation (National Weather Service 2012*a*), contained the skeletal remains of hatchlings that apparently hatched but failed to exit the nest before succumbing to dehydration. These skeletons (I tallied the number of individuals by counting skulls) were subtracted from the number of apparently successful eggs to determine the number of successfully emerged hatchlings.

I pooled the estimates from both years and from 1st and 2nd clutches, and used a mean of all 10 nests for the probability distribution of hatch rate. Because eggs in the same nest are not independent, I used an unweighted average of hatch rate. I used the sampling variance as defined by White (2000), i.e., the sum of each individual nest's variance divided by the number of nests in the sample (10). For CWMA, I based my estimated hatch rate on 16 excavated nests using similar methods to those used for WR3.

Nest survival.—I defined nest survival as the probability of at least one hatchling surviving incubation to hatch. Nests did not survive if the nest was depredated, flooded, or laid incorrectly. For example, in 2010, a female on WR3 laid her eggs outside the nest and backfilled an empty hole. The eggs were consumed quickly by ants. Some nests on WR3 had eggs that hatched successfully but whose hatchlings could not escape the nest chamber and subsequently died. I considered these nests to have survived, and incorporated the deaths of hatchlings into the hatch rate (above). Similar to hatch rate, I assumed that nest survival rates were the same for first and second clutches.

I combined the nest survival estimate from Endriss et al. (2007, 0.60, $n = 10$ over 2 years) with field data from 2010 ($n = 7$) and 2011 ($n = 11$) to calculate this vital rate at WR3. I used a weighted mean of nest survival (White 2000), which I calculated using the rates and sample sizes from 3 periods: 2004-2005 pooled (Endriss et al. 2007), 2010, and 2011. I was unable to estimate process variance (White 2000), and therefore used the sample variance. I calculated sample variance as the average yearly variance. Nest survival at CWMA was estimated based on 16 nests monitored between 1998 and 2001. I calculated a sample mean and variance for all years pooled; variance was equal to $p \times (1-p) / n$, where p is the probability of a nest survival and n is the number of nests in the sample.

Proportion of females reproductive.—I estimated the proportion of adult females who were reproductively active using data from Figure 2 in Ballinger (1974), which reported the number of reproductive, post-reproductive, and non-reproductive females from a population of *P. cornutum* in San Angelo, Texas, in the center of the *P. cornutum* range. The proportion I calculated, 0.9636, seemed appropriate for WR3, as all adult females that were telemetered during the first nesting periods of 2010 ($n = 9$) and 2011 ($n = 12$) displayed nesting behavior. Because of low survival at CWMA, very few females were monitored throughout the long nesting period that occurs in southern Texas. However, the length of the nesting period and the abundance of food (*Pogonomyrmex* spp.) at the site, should promote breeding by nearly all females. I therefore assumed the estimate I obtained from Ballinger (1974) was applicable to CWMA.

The greatest possible variance to be used in a β distribution with a mean of 0.9636 would be ~0.03. However, when drawing randomly from a β distribution with the mean above, a variance of 0.03 tended to result in a random draw of 1 almost all the time. Assuming that in resource-poor years some females may be unable to reproduce and to incorporate a small amount of variance into the model, I used a variance of 0.01. This combination of mean and variance resulted in values > 0.9 for almost 90% of draws ($n = 10{,}000$).

First clutch size.—Body size of *P. cornutum* differs across latitudes, and clutch size correlates with body size (Ballinger 1974, Endriss et al. 2007); therefore, I expected clutch size estimates to differ between WR3 and CWMA. For WR3, whenever females were observed nesting, I recorded the nest location and checked the nest regularly for signs of hatching. After hatching, I dug up each nest and counted the number of eggs. I estimated the mean number of eggs in the first clutch laid by females each season using data from Endriss et al. (2007; $n = 8$

nests during 2004–2005), and field data from 2010 (*n* = 4 nests) and 2011 (*n* = 7 nests). The weighted mean proposed by White (2000) incorporates estimated environmental variance, which I was unable to calculate for this vital rate. Consequently, I used an unweighted mean of the first clutch size for each time period as the estimated mean for the probability distribution. For the variance estimate, I used the sampling variance (White 2000) across all years, calculated by adding the variance of each time period's sample (2004–2005, 2010, 2011) and dividing this variance by the number of sample years (4). I based the minimum and maximum possible clutch size needed to calculate a stretched β distribution (Morris and Doak 2002) on the minimum and maximum number of eggs in a first clutch found by either Endriss et al. (2007) or myself, which was 12 and 24, respectively.

Field methods for estimating clutch size at CWMA were similar to those I used on WR3. However, estimates at CWMA were complicated by continual nest-laying throughout the active season. An overall sample of clutch size observations resulted, without knowledge of which nests were first, second, or even perhaps third clutches. Evidence of triple-clutching in south Texas could not be confirmed at CWMA, so I assumed all clutches were first or second nests. To estimate first and second clutch sizes, I assumed the total sample mean (*n* = 16 nests) was a weighted mean of first and second clutches. I used the proportion of females nesting (Ballinger 1974), the proportion double clutching on CWMA (see below), and the ratio of first: second clutch size on WR3 to solve algebraically for first and second clutch sizes on CWMA. Because variance estimates for clutch size on WR3 were similar between the first and second clutches, I assumed the same variance for both first and second clutches at CWMA. I calculated the minimum and maximum used for the stretched β distribution as the mean clutch size ± (2 × SD from the overall sample). The maximum clutch size for first clutches calculated in this manner was plausible when compared to the overall maximum in the observed sample of clutch sizes (maximum observed = 42, maximum calculated = ~49). This matching provided evidence that the mean and variance, as well as the method used to calculate the minimum and maximum possible clutch sizes for the stretched β distribution, were reasonable and conservative, in that I included variance slightly beyond the observed sample.

Proportion females double-clutching.—In 2011, I documented 6 of 9 telemetered females laying >1 nest on WR3. Whereas double- and even triple-clutching is known to occur in populations of *P. cornutum* farther south (R. T. Kazmaier, personal communication), double-clutching had not been documented previously at TAFB. I used the number of females double-clutching (6) divided by the number of females telemetered during the reproductive period (n =9) to estimate a mean (p = 0.667). I calculated variance using the formula $var(p) = p\ (1-p) / n$.

I calculated the mean proportion and variance of double-clutching females for CWMA using the same method as that used for WR3. The sample variance associated with the proportion of double-clutching females on CWMA resulted in a probability distribution heavily weighted with values of 1.0, creating a probability distribution that seemed more skewed than is biologically realistic. I therefore used a smaller variance to mimic biological expectations and create a probability distribution that had a lower frequency of unrealistic values.

Second clutch size.—Second clutch sizes for *P. cornutum* are generally smaller than first clutches (personal observation; R. T. Kazmaier, personal communication). For WR3, I determined the mean clutch size of second clutches (n = 3) during 2011 using the methods described for first clutch-size estimates. Because this estimate was based on data from 1 year, I simply used the sampling variance from these 3 nests for the LSA. Because of the small sample of second nests, I estimated the smallest and largest possible second clutches needed for a stretched β distribution as the estimated mean ± 2 standard deviations. I calculated the mean, variance, minimum, and maximum for second clutch size at CWMA from a sample of all nests as described above (see *First clutch size*). Similar to the maximum number I calculated for first clutch size, the minimum size I calculated by subtracting 2 SD from the mean estimate was slightly smaller than the minimum observed in field data (minimum observed = 6; minimum calculated = ~3), providing further support for my calculations of first and second clutch sizes.

Adult survival.—I estimated annual survival rates of telemetered lizards that were tracked ≥10 days during 2004–2011 on WR3 (n = 147 individuals) and during 1998-2005 on CWMA (n = 229 individuals). In a number of cases, I was unable to determine the fate of a lizard on WR3 because its transmitter signal disappeared, probably due to either transmitter failure or removal from the study area by a predator. Because of this ambiguity, I estimated survival rates in 2 ways that bracket the range of possibilities (defined as Categories; Munger 1986, Endriss et al. 2007, Bogosian 2010). Category 1 estimates assumed that lizards with undetermined fates were alive; these individuals were censored from the analysis following their disappearance. Category 2 estimates assumed that missing lizards were dead (Munger 1986, Endriss et al. 2007, Bogosian 2010). Lizards that died as a result of research activities were censored at the last date they were known to be alive.

I used the Known-Fates model in Program MARK (White and Burnham 1999), which is based on the Kaplan-Meier survival estimator with staggered entry (Pollock et al. 1989), to evaluate a priori hypotheses that sex, season (active or inactive), and study stage (for WR3, see Chapter 1) or year (for CWMA) affect survival. Active season was considered to be 2 April–19 August and inactive season was 20 August–1 April. Individuals tracked over multiple years were separated for the purposes of survival analyses, so experimental units for these analyses were individual-years. I used a weekly time interval starting on 2 April each year, with the first 20 weeks considered active season and the rest of the year considered inactive season.

Model selection results, based on AIC_c (Anderson et al. 2000), showed strong support for an effect of season in both populations. There was support for an effect of study stage on WR3, but no support for a year effect at CWMA. I constrained models to obtain overall mean and variance estimates for annual survival (accounting for season effects) at both sites to use for the LSA. For WR3 data, I averaged Category 1 and Category 2 estimates of the mean and variance of survival rates. Because I was unable to successfully decompose variance estimates following White's (2000) method, I used the highest-ranked model including an effect of year (CWMA) or stage (WR3) to estimate variance among year/stage survival rates for input into the LSA. For CWMA, the estimated among-year variance combined with the low adult survival rate resulted in a distribution skewed towards 0 more than biologically likely based on survival analyses. I therefore reduced the variance to create a distribution with a mode closer to the mean and farther from 0. This adjustment, from 0.028 to 0.020, did not change the coefficient of determination of λ on adult survival by >0.02.

Juvenile survival.—I calculated juvenile survival on WR3 for each year by dividing the number of juveniles recaptured as adults the following year by the total number of juveniles marked. I averaged the survival rate across all years, and calculated an overall variance using the simple average of yearly variances. Data were missing from the geodatabase for 2003–2004 (recaptures in 2004 and 2005), and I used Endriss et al. (2007) to provide pooled data for the 2 years. Too few juveniles were recaptured to calculate juvenile survival for CWMA, and I therefore assumed it to be equal to the rate for WR3.

Hatchling survival.—Detection and recapture rates of hatchlings were too low to provide an estimate of survival for either site. Moreover, very little is known about the causes of mortality in hatchling horned lizards. Both unimodal and bimodal distributions seem plausible, depending on whether main causes of death act on individuals (such as predators) or cohorts (such as climatic and meteorological effects like drought). Large variation in hatchling survival has been documented for other species of North American lizards in climatically variable ecoregions (Tinkle et al. 1993). Because of this uncertainty, I used a uniform probability distribution of hatchling survival for the LSA to include a wide range of possibilities. It is highly unlikely that hatchling survival is 1, so I used Euler’s equation to estimate what hatchling survival rate would have to be for $\lambda = 1$ given estimates of survival rates and fecundity for other stage classes (Hellgren et al. 2000, Endriss et al. 2007). I created a uniform distribution from 0 to twice the estimated hatchling survival rate to obtain a wide but plausible range of possible hatchling survival rates.

Model Construction and Analysis

Using the parameters and distributions from above, I populated a 3 × 3 Lefkovitch matrix (Crouse et al. 1987). This matrix was based on a life-history diagram that assumed 3 stage classes (hatchling, juvenile, and adult; Fig. 11). Lizards are hatchlings during the active season in which they hatch, juveniles between their first and second hibernations, and breeding adults after the second hibernation of a lizard’s lifetime. In this model, I assumed that all hatchlings that survive grow to be juveniles, and likewise juveniles grow to be adults (i.e., the probability of surviving and not progressing to the next stage was 0 until adulthood). Adults surviving a year remained in the adult stage class the following year.

I used the PopTools extension (v. 3.2, G. Hood, Canberra, Australian Capital Territory, Australia) for Microsoft Excel to calculate λ, deterministic elasticities, and perform Monte Carlo simulations. The Monte Carlo simulations drew 10,000 random values (Taylor et al. 2012) for each matrix element from their respective probability distributions, as well as calculated the resulting λ for each set of randomly drawn matrix elements. I regressed λ against each matrix element (vital rate) and against each of the demographic parameters used to calculate fecundity to determine which, of these parameters most affects λ (Wisdom and Mills 1997).

I used PROC GLM in SAS 9.2 (SAS Institute, Cary, North Carolina, USA) to regress λ against each set of randomly drawn vital rates, and calculate the coefficient of determination, r^2, between each parameter and λ (Wisdom and Mills 1997, Zar 1999). Several authors have suggested calculating covariance matrices for matrix elements in demographic populations, and these should ideally be incorporated into LSAs (Wisdom et al. 2000, Morris and Doak 2002, Johnson et al. 2010). However, this examination of covariance requires corresponding data over time (i.e., estimates of each vital rate for a number of years). Because many of the parameter estimates in this study were not available for multiple years (e.g., second clutch sizes are only available from 2011), it was impossible to calculate these covariance matrices.

Because of uncertainty surrounding the probability distribution for hatchling survival, I also conducted a perturbation analysis for hatchling survival. I conducted LSAs for CWMA and WR3 with a variety of other minima and maxima for the uniform distribution (Biek et al. 2002, Taylor et al. 2012), encompassing a wide range of both means and sets of upper and lower bounds (which are analogous to variance in a β or normal distribution). Following preliminary regressions of λ on hatchling survival, I selected 2 sets of bounds for the uniform distribution for hatchling survival in addition to the distribution based on the mean hatchling survival rate calculated from Euler’s equation. I set one distribution such that both the minimum and maximum shifted slightly away from 0 and towards 1 (representing an increase in mean survival rate) and one with a smaller breadth (higher minimum and lower maximum, analogous to less variance). I ran LSAs and generated r^2 values from regressions of λ on all vital rates for both populations using these 2 adjusted uniform distributions for hatchling survival rate. I report results for a subset of hatchling survival perturbations.

The Category 1 estimates for adult survival on WR3 that I calculated in Program MARK were approximately double those calculated for Category 2 in each stage (see Chapter 1, Table 8 for details). To examine the effects of the assumptions involved in each Category, I also conducted the LSA for WR3 using only Category 1 mean and variance estimates for adult survival, using only Category 2 estimates, using the mean survival rate of both Categories but the variance estimates from Category 1, and the mean of both survival rates but the variance estimate from Category 2. During these perturbations, I held all other vital rates constant. I used a lower bound of 0.05 and an upper bound of 0.65 for the hatchling survival distribution, thereby avoiding using hatchling distributions whose lower bound was 0 for adult survival perturbations so that the effects of changing adult survival variance would be more noticeable.

RESULTS

The vital-rate estimates for WR3 differed from those for CWMA in several aspects (Table 10). Adult survival at WR3 was more than double that at CWMA, whereas fecundity at WR3 was about 70% of the corresponding estimate for CWMA. Clutch sizes at CWMA were larger than those at WR3, and this effect is compounded by the greater proportion of females double-clutching at CWMA.

Deterministic matrix elasticity results based on mean vital-rate estimates (Table 10, Fig. 12, Appendix A) indicated that recruitment, including survival of the hatchling and juvenile stages and adult fecundity, had the greatest relative effect on λ for both WR3 and CWMA (Table 11). However, elasticity of λ to adult survival was much closer to the elasticities of the other vital rates at WR3 than at CWMA, where it had less than one third the effect on λ compared to the other vital rates. Distributions of hatchling survival rates with a lower bound <0.01 led to the greatest effect of hatchling survival on λ (Table 12, Fig. 13). Results of perturbation analysis involving hatchling survival were similar for the 2 sites, and thus results from WR3 are not reported. As the lower bound increased, the strength of the relationship between hatchling survival and λ decreased incrementally (Table 12). However, if the minimum for the distribution was 0, the maximum of the distribution did not affect the r^2 values. For distributions with the same range between the minimum and maximum, those with upper bounds closer to 1 had lower r^2 values. Distributions with the same means but different ranges (e.g., 0.15–0.75 vs. 0.30–0.60) led to explanations of similar amounts of variation in λ.

Unlike hatchling survival, perturbations in the variance of adult survival had a greater effect on λ than perturbations in the mean annual survival rate of adults for WR3 (Table 13, Fig. 14). In all perturbations, hatchling survival still had the highest r^2 values by far, followed by juvenile survival. However, as adult survival variance increased, adult survival had greater effects on λ to the point where it was approximately equal to fecundity.

Among the 3 versions of the LSA I ran for WR3, the version with hatchling survival with a lower bound of 0 explained the greatest variance in λ (Table 14, Fig. 15). Under that scenario, the effects of hatchling survival on λ as hatchling survival rates approached 0 dominated the other vital rates. As the minimum hatchling survival rate increased, the effect of other vital rates increased and the effect of hatchling survival rates on λ decreased accordingly. In each version, juvenile survival had a greater effect on λ than did fecundity. Overall, these results show that recruitment had a greater effect than adult survival on the growth of the population at WR3. Contrary to WR3, the effect of fecundity on λ was consistently greater than that of juvenile survival rate at CWMA (Table 15, Fig. 15). Additionally, adult survival in CWMA had extremely small effects on λ for all versions.

All demographic parameters that compose fecundity had similarly low effects on λ (Tables 14, 15). As with the matrix elements (survival rates and adult fecundity), increasing minimum hatchling survival increased the effect of fecundity components on λ. For WR3, nest survival, followed by hatch rate, consistently had the greatest effect on λ of the vital rates that make up fecundity. Other demographic parameters (proportion females reproductive, first clutch size, proportion females double clutching, and second clutch size) had very small effects on λ that were comparable to those of adult survival. For CWMA, there were similar patterns of an increasing importance of vital rates composing fecundity as hatchling survival rates were increased. Hatch rate, followed by first and second clutch size, were the most important demographic parameters rates for CWMA among those composing fecundity.

DISCUSSION

The results of the deterministic elasticity analysis indicated that fecundity, hatchling survival, and juvenile survival were equally important at both sites, and outranked other adult survival in importance. However, adult survival had a greater relative importance at WR3 than CWMA. The prediction of a trade-off between adult survival and fecundity had some support, as the site with lower adult survival rates (CWMA) had higher fecundity and much greater differences between the elasticities of λ to adult survival and fecundity. However, at CWMA, the elasticity of λ to non-reproductive stages (hatchling and juvenile) survival was equal to that of fecundity. Adding stochasticity to the analysis using the LSA indicated that recruitment was the main driver of population growth for *P. cornutum*. The prediction of a life-history trade-off between adult survival and fecundity also was supported to some degree by the LSA.

Hatchling survival was the top-ranked parameter in its effect on λ at both sites, and this result was robust to perturbations of hatchling survival and adult survival (Tables 14, 15). The inclusion of 0 in hatchling survival distributions depressed the effects of all other parameters, but a hatchling survival rate of 0 does not seem implausible. Personal observations indicate that hatchlings may be very quickly overcome by exposure to heat or dehydration. As they often hatch at the height of summer in hot, dry conditions, a year with extreme weather could conceivably kill an entire cohort of hatchlings. Even if a small proportion of hatchlings do survive, using a uniform distribution with a minimum of 0.05 did not change the rank-order results of the LSAs (Tables 12, 14, 15). Highly variable hatchling survival rates have been documented in other lizards. For example, hatchling survival of *Sceloporus graciosus* can vary annually from 0.12 to 0.59 (Tinkle et al. 1993). These dramatic fluctuations in hatchling survival may be more likely at a fragmented site that has reduced habitat diversity, refugia, or resources.

Recruitment was driving population growth rates in both study populations. In addition, although the *P. cornutum* populations differed in the rank orders of fecundity and juvenile survival, adult survival had the weakest effect on λ. Recent work with *Xenosaurus grandis*, a xenosaurid lizard with higher survival among all stages and lower fecundity than horned lizards (Zuniga-Vega et al. 2007), also documented the important influence of non-reproductive vital rates on λ. For *X. grandis*, transition of hatchlings and juveniles to the next stage, as well as adult survival, had the greatest effects on λ (Zuniga-Vega et al. 2007).

The LSA indicated a contrast between the importance of juvenile survival rate and fecundity, contrary to the prediction that adult survival rates would offset the importance of fecundity. The effect of fecundity on λ at both sites was smaller than the effect of hatchling survival. However, fecundity played a greater role in changing λ compared to juvenile survival at CWMA, in contrast to WR3 where juvenile survival consistently affected λ more than fecundity. A trade-off between juvenile survival and fecundity also was observed in the demographic parameters of the species studied by Biek et al. (2002); boreal toads (*Bufo boreas*) exhibited lower juvenile survival than two frog species (*Rana* spp.), but much higher fecundity. I did not have an estimate of juvenile survival for CWMA, but lower adult survival rates often correlate to lower juvenile survival rates (Pike et al. 2008). Logically, areas with lower survival rates must have higher fecundities to maintain a stationary population; CWMA may actually have a lower juvenile survival rate than WR3, which was reflected in the rankings of juvenile survival and fecundity at the 2 sites in this LSA.

Biek et al. (2002) showed that highly variable vital rates can have large effects on λ. This effect is seen in the present LSA, insofar as hatchling survival rate, which was modeled with a uniform distribution and large variance, had the greatest effect on λ. Uniform distributions for hatchling survival rate that had the same mean but different upper and lower bounds (analogous to difference variances for a β distribution) had similar r^2 values. These results indicate that the tendency of a vital rate to take on extreme values stochastically, as opposed to its variance per se, may be causing the large contributions to variance in λ. In other words, it is not only the variance that affects the importance of a vital rate, but also the proximity of the mean rate to 1 or particularly to 0. This finding bears noting in further LSAs. If a vital rate, when modeled on a β distribution, has too great a variance in relation to its mean, the shape of the β distribution may be bimodal at 0 and 1. This property of β distributions may be useful in modeling boom-and-bust phenomena, but modelers should be aware of the potential for creating a bimodal distribution when a unimodal distribution is more biologically accurate based on prior knowledge of the study species. This scenario is particularly common when field data yield wide sampling variances, which may or may not reflect process variance accurately. Moreover, mean vital rates closer to 0 or 1 are more susceptible to an accidentally generated bimodal distribution.

The results of this LSA have implications for conservation of threatened and endangered species. Whereas Johnson et al. (2010) found that differing vital rates between populations of Sierra Nevada bighorn sheep (*Ovis canadensis sierrae*) required different management strategies to increase population sizes, the results of this study suggest the opposite. Although the strength of each demographic parameter's effect on λ varied between populations, management strategies focusing on recruitment, and in particular hatchling survival, would strongly benefit both populations. As a consequence, managers across the range of *P. cornutum* could potentially adopt similar management priorities with respect to stage classes, despite intra-population differences in population vital rates. Biek et al. (2002) and Johnson et al. (2010) both suggest that widely varying vital rates may drive λ more than the top-ranked vital rate identified by deterministic elasticity analysis. Results from this study do not disagree, although whether variance itself or how frequently a vital rate stochastically approaches extremes (as a result of mean and variance) affects λ more strongly needs further exploration.

My results emphasize the importance of studying non-reproductive stages by managers and biologists. Due to the relative ease of capture and radiomonitoring adult P. *cornutum*, the adult cohort is more commonly studied. This trend holds true for many reptiles, with information on non-reproductive stages grossly lacking (Pike et al. 2008). Studies of adult survival, however, may be largely wasted if recruitment is driving population dynamics; it is therefore vital that managers identify cause-specific mortalities for juvenile and hatchling horned lizards. However, it should be noted that demographic parameters composing fecundity can only be studied by radio-tagging reproductive females (which lead researchers to finding nests).

Head-start programs, in which young animals are born and partially raised in captivity before release into the wild, have been attempted for a variety of reptiles and amphibians (Dodd and Siegel 1991, Ramo et al. 1992, Heppell and Crowder 1998, Spinks et al. 2003, Sprankle 2008). Generally, long-lived species (those with high adult survival) do not benefit substantially from head-start programs, as improving survival of young stages does not adequately compensate for adult mortality because adult survival is the key vital rate in these species (Crouse et al. 1987, Heppell and Crowder 1998, Enneson and Litzgus 2008). However, there are cases of successful head-start programs among species such as chiricahua leopard frogs (*Lithobates chiricahuensis*; Sprankle 2008), and a variety of *Iguana* spp. (Escobar et al. 2010). Results from both elasticity analysis and LSAs for *P. cornutum* indicate that augmenting non-reproductive stage classes has the potential to be an effective strategy for boosting wild populations of *P. cornutum* and other species with similar distributions of vital rates.

Potential pitfalls in head-start programs include genetic considerations and a failure to address the causes of decline in wild populations (Dodd and Siegel 1991, Spinks et al. 2003). It is important to consider the genetic composition of source populations for captive breeding programs and whether the genotypes in the source population are suitable for the release site in any head-start programs (Dodd and Siegel 1991). Dodd and Siegel (1991) also warn against releasing fewer individuals than that required to maintain a sustainable and genetically viable population. Both Dodd and Siegel (1991) and Spinks et al. (2003) comment that the causes of decline should be positively identified in any declining population. Releasing individuals into a population doomed to extirpation is merely a waste of conservation resources. With regard to *P. cornutum*, causes of decline in wild populations of *P. cornutum* must be identified before successful reintroductions or population augmentation programs can take place.

The importance of fecundity and its components (nest survival, hatch rate, clutch size) in affecting λ, although less than hatchling survival, are of interest to management. Minimizing human and habitat disturbances at a site may decrease the risk of depredation for nests (and lizards). Depredation of adults has increased over the years at WR3 following human-induced habitat disturbance (see Chapter 1). Clutch size and hatchling health upon emergence may be affected by female nutritional condition and body size, which may in turn be affected by habitat quality and food abundance (Ballinger 1983, Ford and Seigel 1989, James and Whitford 1994), factors that managers can conceivably modify. Unfortunately, hatch rate may be largely determined by climatic conditions. Hot, very dry weather at WR3 during 2011 seemed to prevent some hatchlings from emerging from the nest; this type of attrition may be unavoidable for managers (with the exception of collecting and incubating eggs in captivity).

In the wider arena of sensitivity analyses and wildlife population management, the inclusion of variance and stochasticity in analyses can provide surprising results not predicted by prior deterministic studies. Quality demographic data for all stage-classes must be obtained for populations of interest, as focus on those stages of life most easily monitored can risk missing the key factors that are driving population growth rates. However, drastic differences in vital rates between populations do not necessarily require different management strategies, as is seen in the case of Texas horned lizards. These findings support claims that LSAs are a valuable tool for assessing conservation needs of, and developing management plans for, wildlife populations.

Table 1. Detailed summary of management activities on Tinker Air Force Base, Oklahoma, that occurred on Wildlife Reserve 3 in management zones (Fig. 2), 2005-2010.

Zone	Year	Management activities
A	2005	Removed select deciduous and evergreen trees from area; treated entire area with Roundup Pro and Monument herbicides (May); treated entire area with mixture of Roundup Pro and 2,4-D amine herbicides (July); treated entire area with Roundup Pro and Monument herbicides (September); installed silt fencing along shorelines surrounding Prairie and Wood Duck Ponds
	2006	Drill-seeded entire area [except north side of Prairie Pond between gravel trail and north edge of pond (A2) with native grass mix; sloped areas on south side of pond between southern shoreline and terrace at top of slope to the south (A1) and western half of dam (A4) were covered with Futerra erosion control fabric following seeding; on north side of Prairie Pond (A3), trenched and installed about six subsurface corrugated piping (6” diameter) extensions from existing outlets on south side of trail to northern shoreline of pond.
	2007	Treated entire area with Roundup herbicide 21-27 Jun; ~18 large dead trees staged btwn Wood Duck and Primrose Ponds (October time frame, A1)
	2008	Reinstalled portions of silt fencing around Prairie and Wood Duck Pond shorelines; treated entire area with Roundup herbicide; moved (10K loader) stockpiled dead trees from east side of Wood Duck Pond into southern half of Wood Duck Pond and into south side of Prairie Pond (A1); drill-seeded area with native grass 5 June except western half of Prairie Pond dam (A4), north and east sides of northern half of Wood Duck Pond (A2), and between gravel trail and pond shoreline on north side of Prairie Pond (A3)
	2009	Spot-sprayed for Johnson grass control on east side of Prairie Pond dam (A5)
	2010	Seeded, rolled (compacted) and laid down erosion control fabric week of Feb. 15 (A4 only). Sprayed with herbicides around eastern end of Prairie Pond and around Wood Duck Pond during winter of 2010 – 2011.
B	2005	

Table 1. Continued.

Zone	Year	Management activities
	2006	Mechanically removed ~ 700 young (i.e., <10 years old) deciduous and evergreen trees and sprayed stumps of deciduous trees with Garlon herbicide; sprayed entire area with Remedy herbicide to control *Sericea lespedeza*
	2007	
	2008	Treated south and west edges of prairie area immediately adjacent to firebreak with Plateau herbicide to control Johnsongrass and tall fescue
	2009	Sprayed ¾ of area with Remedy herbicide for Sericea lespedeza control (primarily west, south, and east areas, basically excluding central and north central areas); mechanically (chainsaws and weed trimmers) removed ~ 870 young deciduous and evergreen trees and sprayed deciduous tree stumps with Garlon herbicide
	2010	Prescribed burn 18 Mar. Spot spraying last week of Jul.
C	2005	
	2006	
	2007	Spot treated area for Johnson grass, plains bluestem, Bermuda grass, and Sericea lespedeza; mechanically (chainsaws/weed trimmers) removed young deciduous/evergreen trees and sprayed deciduous tree stumps with Garlon herbicide (5 – 11 Jul)
	2008	Lightly disked areas that were previously spot-treated in (C2); treated disked areas with Roundup to control Johnsongrass, plains bluestem, and Bermuda grass (C2)
	2009	Mechanically (chainsaws and weed trimmers) removed ~ 295 young to median-aged deciduous and evergreen trees (Jul); mowed and drill-seeded Area C2 with native grass following same procedure outlined in 3D below (same dates as below); planted approximately 20-30 cedars along northern edge of area

Table 1. Continued.

Zone	Year	Management activities
	2010	Spot spraying last week of Jul.
D	2005	
	2006	
	2007	Mechanically (chainsaws and weed trimmers) removed select young deciduous and evergreen trees; treated entire area with Roundup
	2008	Treated entire area with Roundup herbicide 12 May; lightly disked entire area after vegetation die-off; resprayed entire area with Roundup herbicide 20 Sep
	2009	Planted approximately 50 cedars along northern edge of area; mowed entire area in early June to 4-6” height; following mowing, entire area was drill-seeded with native grass (9 Jun)
	2010	Southeast half sprayed during winter of 2010 – 2011
E	2005	
	2006	
	2007	
	2008	
	2009	
	2010	Last week of Jul: extensive spot spraying around border with B; most of E away from pond slopes sprayed.
F	2005	
	2006	Spot-treated weeds with Roundup herbicide
	2007	Spot-treated weeds with Roundup herbicide
	2008	Spot-treated weeds with Roundup herbicide
	2009	Area cleared for construction of new roadway
	2010	

Table 2. Timeline of management activities on WR3, Tinker Air Force Base, Oklahoma (see Fig. 2). B = prescribed burn; D = disking; M = mowing; H = herbicides sprayed; S = seeding; T = tree removal; O = other.

	Management Area					
Month/Year	A	B	C	D	E	F
2005*	O					
May 2005	TH					
Jul 2005	H					
Sep 2005	H					
2006*	SO	TH				H
2007*				TH		H
Jun 2007	H					
Jul 2007			HT			
Oct 2007	T					
2008*	OHT	H	DH			H
May 2008				HD		
Jun 2008	S					
Sep 2008				H		
2009*	H	HT	MS	S		O
Jun 2009				MS		

Table 2. Continued.

Month/Year	Management Area					
	A	B	C	D	E	F
2010*						
Feb 2010	SO					
Mar 2010		B				
Jul 2010		H	H		H	
Dec 2010	H			H		

* Management activities without a corresponding month either were on-going or the specific date of the activity was not recorded.

Table 3. Results of regressing volume of intersection (VI) between pre- and post-disturbance home ranges against proportion of home range in disturbed area before disturbance for *Phrynosoma cornutum* on Wildlife Reserve 3, Tinker Air Force Base, Oklahoma. Locations refer to management areas on Wildlife Reserve 3 (see Fig. 2). Sample sizes (n) are individual lizards used to calculate VI.

Disturbance type	Disturbance period	Location	Treatment groups (n)	Results
Mowing and seeding	1–9 Jun 2009	D	Pre-disturbance: 1 April–31 May 2009 Post-disturbance: 17 June–31 August 2009 (7)	$F_{(1.5)} = 2.96$, $P = 0.15$, $r^2 = 0.37$
Herbicide spraying	July 2005	A	Pre-disturbance: 1–30 June 2005 Post-disturbance: 1–31 August 2005 (10)	$F_{(1,8)} = 0.13$, $P = 0.72$, $r^2 = 0.02$
Herbicide spraying	5–11 July 2007	D	Pre-disturbance: 18 May–4 July 2007 Post-disturbance: 19 July–2 September 2007 (10)	$F_{(1,8)} = 3.91$, $P = 0.08$, $r^2 = 0.33$
Herbicide spraying	12 May 2008	D	Pre-disturbance: 1 April – 11 May 2008 Post-disturbance: 20 May - 30 November 2008 (9)	$F_{(1,7)} = 0.17$, $P = 0.69$, $r^2 = 0.02$
Herbicide spraying	20 September 2008	D	Pre-disturbance: 1 May - 18 September 2008 Post-disturbance: 29 September–31 October 2008(5)	$F_{(1,3)} = 1.87$, $P = 0.27$, $r^2 = 0.38$
Herbicide spraying	Winter 2010-2011	A, D	Pre-disturbance: 1 March–31 December 2010 Post-disturbance: 1 March–31 August 2011 (8)	$F_{(1,6)} = 0.13$, $P = 0.73$, $r^2 = 0.02$

Table 4. Comparisons of population-wide mean proportion of home ranges of *Phrynosoma cornutum* on Wildlife Reserve 3, Tinker Air Force Base, Oklahoma in disturbed areas before, during, and after disturbance. Locations refer to management areas on Wildlife Reserve 3 (see Fig. 2). Treatment group sample sizes (*n*) are home ranges for individual lizards. Results are *t* or *F* statistics for *t*-tests and ANOVAs, respectively, with accompanying P-values.

Disturbance type	Disturbance period	Location	Treatment groups (*n*)	Results
Mowing and seeding	1–9 June 2009	D	Pre-disturbance: 1 April–31 May 2009 (7)	$t_{(6.13)}$ = -1.71, P = 0.14
			Post-disturbance: 17 June–31 August 2009 (7)	
Herbicide spraying	July 2005	A	Pre-disturbance: 1–30 June 2005 (8)	$t_{(12)}$ = 2.21, P = 0.05
			Post-disturbance: 1–31 August 2005 (6)	
Multiple	2 July 2007–30 June 2009	D	Pre-disturbance: 1 March 2004–1 July 2007 (28)	$F_{(2,85)}$ = 0.42, P = 0.66
			During-disturbance: 2 July 2007–30 June 2009 (34)	
			Post-disturbance: 1 July 2009–31 December 2010 (26)	
Herbicide spraying	5 –11 July 2007	D	Pre-disturbance: 18 May–4 July 2007 (4)	$t_{(6)}$ = 0.13, P = 0.90
			Post-disturbance: 19 July–2 September 2007 (4)	
Herbicide spraying	12 May 2008	D	Pre-disturbance: 1 April–11 May 2008 (7)	$t_{(14)}$ = -0.20, P = 0.85
			Post-disturbance: 20 May–30 November 2008 (9)	
Herbicide spraying	20 September 2008	D	Pre-disturbance: 1 May–18 September 2008 (4)	$t_{(7)}$ = 0.16, P = 0.88
			Post-disturbance: 29 September–31 October 2008 (5)	

Table 4. Continued.

Disturbance type	Disturbance period	Location	Treatment groups (*n*)	Results
Herbicide spraying	Winter 2010–2011	A, D	Pre-disturbance: 1 March–31 December 2010 (7)	$t_{(12)}$ = 0.11, P = 0.92
			Post-disturbance: 1 March–31 August 2011 (7)	
Multiple	2004 – 2005	A	1–31 August 2004 (3)	$t_{(9)}$ = -1.19, P = 0.27
			1–31 August 2005 (8)	
Multiple	2005 – 2009	D	1–31 August 2005 (14)	$F_{(3,38)}$ = 1.02, P =0.39
			1–31 August 2007 (14)	
			1–31 August 2008 (4)	
			1–31 August 2009 (10)	

Table 5. Daily movement rates (m/day) of *Phrynosoma cornutum* on Wildlife Reserve 3, Tinker Air Force Base, Oklahoma, 2004–2011. Active season refers to any time an individual was not hibernating, generally from early April to October–December, and estimates are based on individuals tracked in both periods. Reproductive period refers to any time between ending hibernation and 15 July, when all reproductive activity (i.e., mating and nesting) is generally completed. 'Non-reproductive period' is from 16 July to when an individual enters hibernation. Reproductive estimates are based on individuals tracked in that period, but not necessarily across both periods.

Sub-sample	*n* (individual-years)	Mean	SE
Active Season			
Males	24	17.9	2.1
Females	20	20.4	3.4
Reproductive Period			
Both sexes	118	24.5	1.4
Males	56	32.0	2.1
Females	62	17.7	1.4
Non-reproductive Period			
Both sexes	56	11.9	1.0
Males	31	9.3	1.0
Females	25	15.1	1.8

Table 6. Summary statistics for home-range size estimates for *Phrynosoma cornutum* on Wildlife Reserve 3, Tinker Air Force Base, Oklahoma, during 2003-2011. All estimates are reported as mean ± SD ha. 'Active season' refers to any time an individual was not hibernating, generally from early April until sometime in October-December, and estimates are from individuals for whom ≥20 locations per period were made. 'Reproductive period' refers to any time between the end of hibernation and 15 July, when all reproductive activity (i.e., mating and nesting) is generally completed. 'Non-reproductive period' is from 16 July to entry into hibernation. Period estimates include individuals not tracked during both periods.

		95% KDE		95% MCP	
Sub-sample	*n* (individuals)	Mean	SE	Mean	SE
Active Season					
Males	16	2.30	0.31	0.74	0.12
Females	15	4.36	0.95	1.14	0.25
Reproductive Period					
Both sexes	95	4.14	0.48	1.22	0.15
Males	40	3.16	0.38	1.04	0.11
Females	55	4.85	0.77	1.35	0.24
Non-reproductive Period					
Both sexes	45	1.84	0.44	0.31	0.07
Males	22	1.85	0.44	0.31	0.07
Females	23	1.83	0.75	0.30	0.12

Table 7. Results of known-fates survival analysis of telemetry data collected for *Phrynosoma cornutum* on Wildlife Reserve 3, Tinker Air Force Base, Oklahoma during 2004–2011. Category 1 represents analysis assuming individuals with unknown fates are alive, and Category 2 represents analysis assuming individuals with unknown fates are dead. AIC_c = Akaike's Information Criterion adjusted for small sample sizes; k = number of parameters in model; Stage = study stage effect (see text for detail on stages); season = seasonal effect (active vs. inactive season); covar = proportion of home range in disturbed area; sex = male or female.

Category	Model	AIC_c	Δ AIC_c	AIC_c Weights	Model Likelihood	k	Deviance
1	{stage * season}	339.000	0.000	0.638	1.000	5	328.982
1	{stage * season + covar}	340.421	1.421	0.314	0.492	6	328.396
1	{stage + season}	346.543	7.543	0.015	0.023	4	338.531
1	{stage * covar}	347.312	8.311	0.010	0.016	5	337.294
1	{stage + season + covar}	348.405	9.404	0.006	0.009	5	338.386
1	{stage}	348.962	9.962	0.004	0.007	3	342.955
1	{season + covar}	349.461	10.461	0.003	0.005	3	343.454
1	{season}	349.563	10.563	0.003	0.005	2	345.560
1	{stage + covar}	350.773	11.772	0.002	0.003	4	342.761
1	{season + sex}	350.883	11.883	0.002	0.003	3	344.876
1	{season * covar}	351.048	12.048	0.002	0.002	4	343.036
1	{covar}	352.550	13.550	0.001	0.001	2	348.547
1	{season * sex}	352.885	13.885	0.001	0.001	4	344.873
1	{null}	353.332	14.332	0.000	0.001	1	351.331
1	{sex}	354.506	15.506	0.000	0.000	2	350.503
2	{season}	615.083	0.000	0.175	1.000	2	611.079
2	{null}	615.416	0.333	0.148	0.847	1	613.415

Table 7 Continued.

Category	Model	AIC$_c$	Δ AIC$_c$	AIC$_c$ Weights	Model Likelihood	k	Deviance
2	{stage}	616.114	1.031	0.104	0.597	3	610.106
2	{stage + season}	616.538	1.455	0.085	0.483	4	608.524
2	{season + sex}	616.688	1.606	0.078	0.448	3	610.680
2	{season + covar}	616.829	1.747	0.073	0.418	3	610.821
2	{covar}	616.925	1.842	0.070	0.398	2	612.921
2	{sex}	616.971	1.889	0.068	0.389	2	612.967
2	{stage + covar}	617.993	2.910	0.041	0.233	4	609.979
2	{season + stage + covar}	618.387	3.304	0.034	0.192	5	608.366
2	{stage * season}	618.391	3.308	0.033	0.191	6	606.362
2	{season*covar}	618.688	3.605	0.029	0.165	4	610.674
2	{season * sex}	618.691	3.608	0.029	0.165	4	610.677
2	{stage * covar}	619.408	4.326	0.020	0.115	6	607.379
2	{season * stage + covar}	620.346	5.263	0.013	0.072	7	606.307
2	{season * stage * covar}	626.681	11.598	0.001	0.003	12	602.572

Table 8. Annual, active-, and inactive-season survival rates for *Phrynosoma cornutum* on Wildlife Reserve 3, Tinker Air Force Base, Oklahoma, during each study stage, 2004-2011. Category 1 assumes missing individuals are alive, Category 2 assumes missing individuals are dead.

Study Stage	Time frame	Category 1 survival rate	95% CI	Category 2 survival rate	95% CI	*n*
2004–2005	Annual	0.86	0.64–0.95	0.44	0.27-0.62	33
2006–2008	Annual	0.63	0.43–0.79	0.28	0.14-0.48	41
2009-2011	Annual	0.51	0.35-0.66	0.26	0.16-0.40	58
2004–2005	Active	0.90	0.77-1.00	0.69	0.54-0.83	33
2006–2008	Active	0.63	0.44-0.82	0.56	0.39-0.73	41
2009-2011	Active	0.77	0.64-0.89	0.55	0.41-0.68	58
2004–2005	Inactive	0.95	0.85-1.00	0.64	0.48-0.80	33
2006–2008	Inactive	1.00	1.00-1.00	0.50	0.30-0.70	41
2009-2011	Inactive	0.66	0.48-0.84	0.48	0.32-0.65	58

Table 9. Individual mortality causes for *Phrynosoma cornutum* on Wildlife Reserve 3, Tinker Air Force Base, Oklahoma during 2003–2011. Heisey-Fuller cause-specific mortality rates are included in parentheses.

Category	Specific cause	2003-2005	2006-2008	2009-2011	Total
Depredation		2 (0.14)	7 (0.33)	14 (0.33)	23
	Probable mammalian	2	6	6	14
	Probable avian		1	3	4
	Unknown[1]			5	5
Signal loss[2]		1 (0.07)	7 (0.33)	11 (0.26)	19
Anthropogenic		2 (0.14)	2 (0.09)	7 (0.17)	11
	Mowing	1	1	1	3
	Fence post hole	1			
	Disking (restoration)		1		1
	Plastic netting entanglement			3	3
	Culvert[3]			3	3
Study death[4]		5 (0.36)	1 (0.05)	4 (0.09)	10
	Collar entanglement	4	1	4	9
	Euthanasia (weight loss)	1			1
Uncertain		1 (0.07)	4 (0.19)	3 (0.07)	8
Hibernation[5]				3 (0.07)	3

[1] In these cases, we recovered transmitters for these individuals with no sign of the lizard. We assumed these to be removed by predators.

[2] Animals with transmitters around their necks after shedding them have a low change of survival, although these were treated as censored individuals for Category 1 survival analyses.

[3] These animals were found in drainage culverts under the gravel paths in WR3 for which drainage outflows had been buried. We assumed these individuals would eventually die and removed them from the culverts. We treated these events as mortalities for survival analyses.

[4] Not included in survival analyses.

[5] Unknown proximate cause of death, but did not awake from hibernation.

Table 10. Population vital rates for *Phrynosoma cornutum* at Wildlife Reserve 3 (WR3), Tinker Air Force Base, Oklahoma and Chaparral Wildlife Management Area (CWMA), Texas. All vital rates are proportions (0-1) unless otherwise indicated.

	WR3			CWMA		
Vital rate	Mean	Variance	*n*	Mean	Variance	*n*
Hatch rate	0.669	0.008	10 nests	0.579	0.02	16 nests
Nest survival	0.741	0.015	28 nests	0.77	0.007	27 nests
Females reproductive	0.964	0.01	55 females	0.964	0.01	55 females
First clutch size (eggs)	19.014	6.17	19 nests	31.110	78.62	16 nests[a]
Females double clutching	0.66	0.24	9 females	0.83	0.009	6 females
Second clutch size (eggs)	12.667	6.33		20.73	78.62	16 nests[a]
Fecundity (female young/female/yr)	7.32			10.53		
Adult survival	0.474	0.02	147 lizards	0.210	0.02	229 lizards
Juvenile survival[b]	0.252	0.006	92 lizards	0.252	0.006	
Hatchling survival[c]	0.332			0.298		

[a] Sample size represents a pooled sample of all nests. First and second clutch sizes were derived algebraically (see text for details).

[b] Juvenile survival estimate unavailable for CWMA; WR3 estimate used for CWMA in elasticity and life-stage simulation analyses.

[c] Mean hatchling survival estimated using Euler's equation with $\lambda = 1$ for each population. Uniform distribution from 0 to (2 × mean estimate) used for life-stage simulation analysis.

Table 11. Elasticity of λ to fecundity and survival rates of various stages of *Phrynosoma cornutum* at Wildlife Reserve 3 (WR3), Tinker Air Force Base, Oklahoma, and Chaparral Wildlife Management Area (CWMA), Texas.

	Elasticity	
Vital Rate	WR3	CWMA
Hatchling survival	0.26	0.31
Juvenile survival	0.26	0.31
Adult survival	0.23	0.08
Adult fecundity	0.26	0.31

Table 12. Results of perturbations of hatchling survival distributions used in life-stage simulation analyses for *Phrynosoma cornutum* at Chaparral Wildlife Management Area, Texas. Columns are: minimum and maximum of the uniform distribution, range between minimum and maximum, and coefficient of determination (r^2) for regression of λ on hatchling survival rate. For all perturbations, mean and variance of all vital rates was held constant.

Minimum–maximum	Range	r^2
0.00–0.90	0.90	0.64
0.00–0.60	0.60	0.62
0.00–0.30	0.30	0.61
0.05–0.55	0.50	0.53
0.05–0.60	0.55	0.51
0.05–0.35	0.30	0.45
0.10–0.60	0.50	0.44
0.10–0.50	0.40	0.39
0.15–0.75	0.60	0.38
0.30–0.90	0.60	0.27
0.30–0.60	0.30	0.13

Table 13. Coefficients of determination (r^2) for population growth rate (λ) regressed on adult survival rate resulting from perturbations of variance in adult *Phrynosoma cornutum* survival for Wildlife Reserve 3 (WR3), Tinker Air Force Base, Oklahoma. For all perturbations, mean and variance of all vital rates was held constant except those of adult survival. For sources of rates and variances, "mean" represents the mean of Categories 1 and 2.

Source of rate	Source of variance	Annual survival rate	Variance among stages	Adult fecundity r^2	Adult survival r^2	Juvenile survival r^2	Hatchling survival r^2
Mean	Mean	0.4740	0.0207	0.13	0.08	0.18	0.58
Mean	Category 1	0.4740	0.0316	0.11	0.11	0.16	0.56
Mean	Category 2	0.4740	0.0097	0.14	0.04	0.19	0.61
Category 1	Category 1	0.6303	0.0316	0.12	0.11	0.16	0.56
Category 2	Category 2	0.3177	0.0097	0.13	0.05	0.17	0.61

Table 14. Amount of variation explained in population growth rate (λ) by each vital rate, as measured by coefficients of determination (r^2), in life-stage stimulation analyses (LSA) for *Phrynosoma cornutum* at Wildlife Reserve 3 (WR3), Tinker Air Force Base, Oklahoma. Results for 3 perturbations are presented, with varying uniform distribution bounds for hatchling survival. All vital rates are proportions (0-1) unless otherwise indicated.

	r^2 for each perturbation (hatchling survival bounds)		
Vital rate	(0.0 – 0.7)	(0.05 – 0.65)	(0.175 – 0.875)
Nest survival	0.04	0.06	0.07
Hatch rate	0.02	0.03	0.05
Females reproductive	0.01	0.01	0.02
First clutch size (eggs)	0.01	0.01	0.02
Females double clutching	0.01	0.01	0.02
Second clutch size (eggs)	0.01	0.01	0.01
Fecundity (female young/female/yr)	0.09	0.13	0.19
Adult survival	0.05	0.09	0.10
Juvenile survival	0.12	0.17	0.26
Hatchling survival	0.67	0.57	0.46

Table 15. Amount of variation explained in population growth rate (λ) by each vital rate, as measured by coefficients of determination (r^2), in life-stage stimulation analyses (LSA) for *Phrynosoma cornutum* at Chaparral Wildlife Management Area (CWMA), Texas with varying uniform distribution bounds for hatchling survival. All vital rates are proportions (0-1) unless otherwise indicated.

	r^2 for each perturbation (hatchling survival bounds)		
Vital rate	(0.0 – 0.6)	(0.05 – 0.55)	(0.15 – 0. 75)
Nest survival	0.01	0.02	0.03
Hatch rate	0.06	0.09	0.12
Females reproductive	0.01	0.01	0.01
First clutch size (eggs)	0.04	0.06	0.08
Females double clutching	0.00	0.00	0.00
Second clutch size (eggs)	0.03	0.05	0.06
Fecundity (female young/female/yr)	0.15	0.22	0.30
Adult survival	0.04	0.05	0.05
Juvenile survival	0.11	0.17	0.22
Hatchling survival	0.62	0.53	0.38

FIGURES

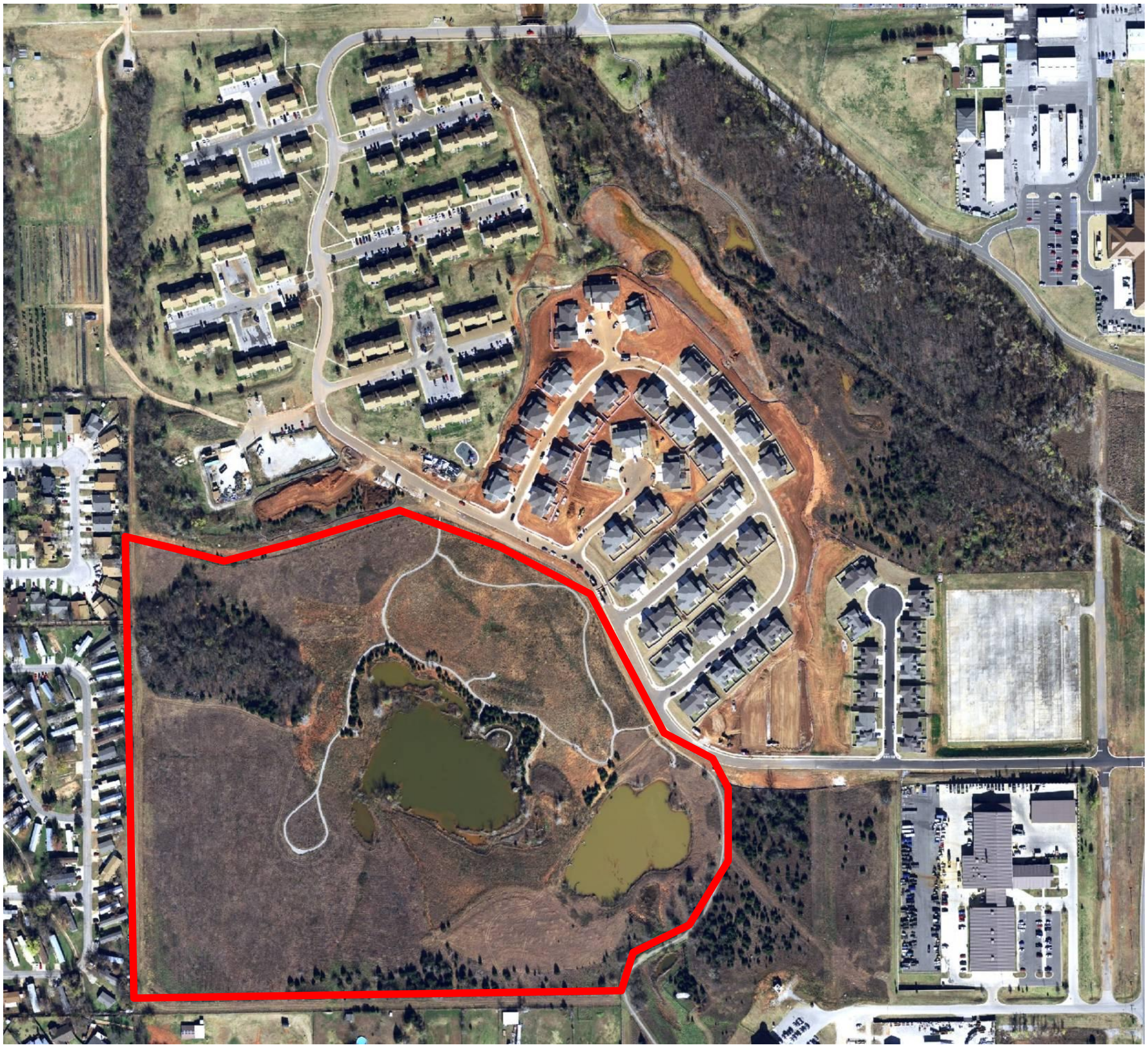


Figure 1. Wildlife Reserve 3 (outlined in red), Tinker Air Force Base, Oklahoma, during 2009–2011 study period. Housing subdivision northeast of Wildlife Reserve 3 was completed in early 2010.

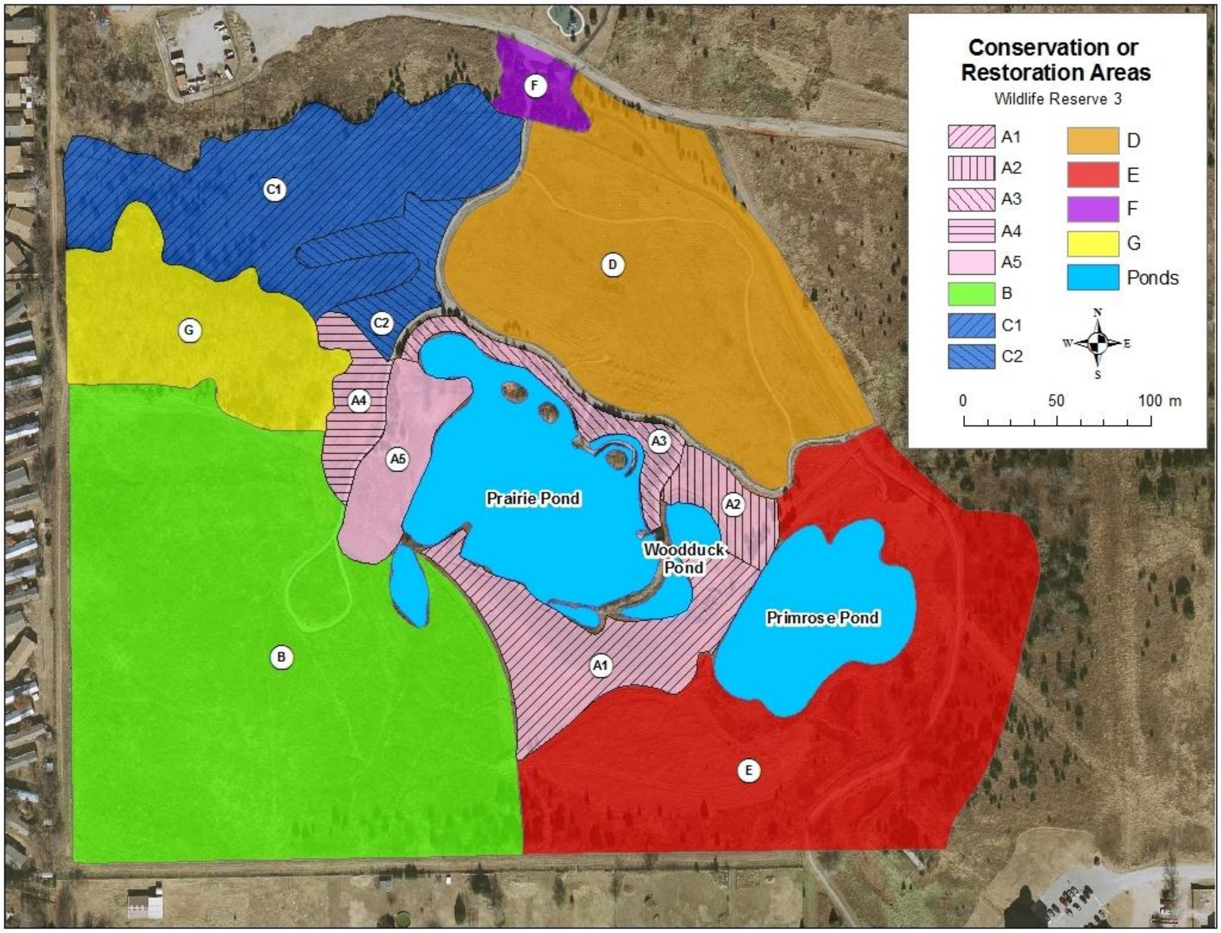


Figure 2. Areas of conservation or restoration activities on Wildlife Reserve 3, Tinker Air Force Base, Oklahoma, during 2005–2011. See Table 1 for details and Table 2 for a timeline of management activities.

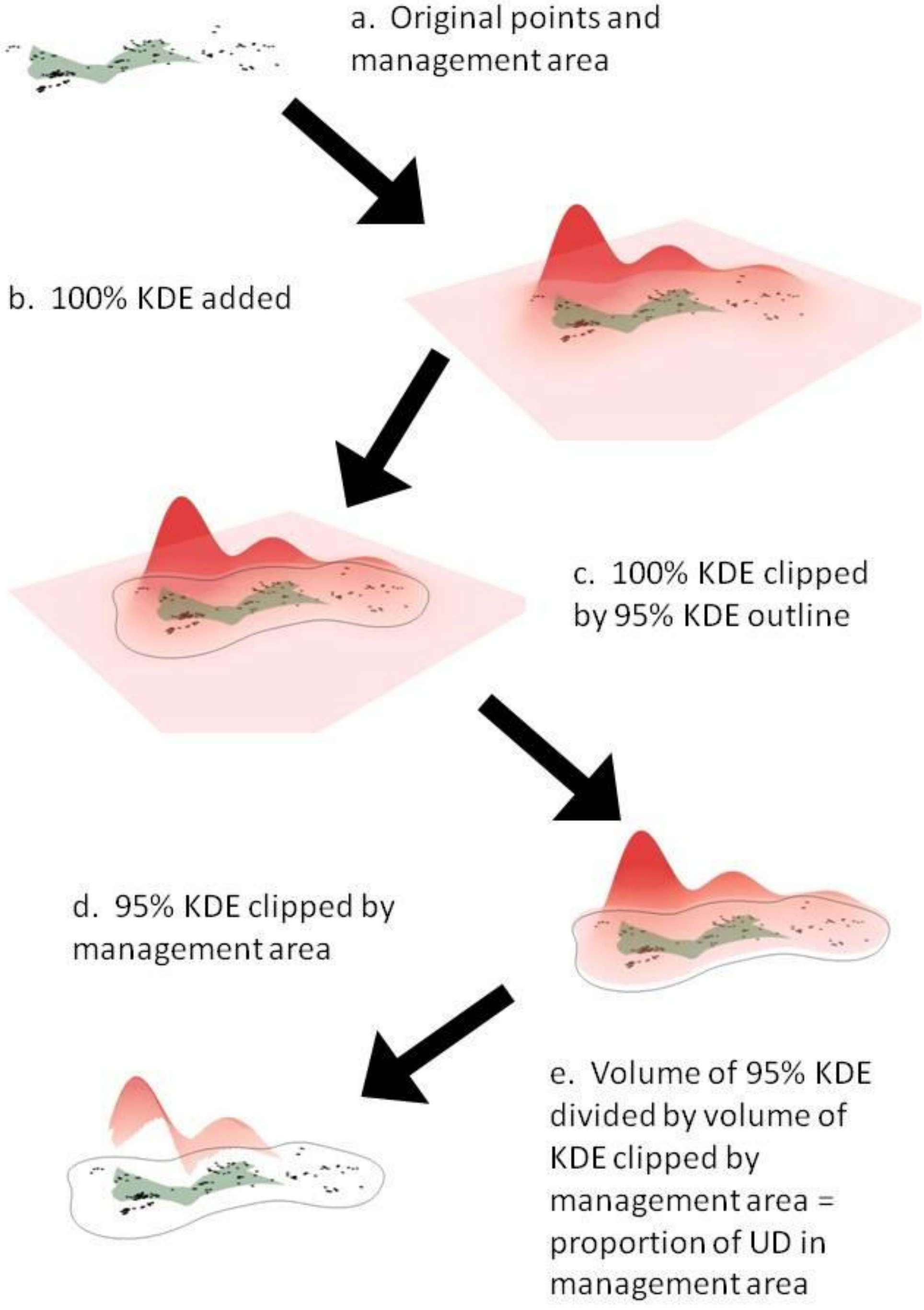


Figure 3. Flow chart of spatial analyses method for detecting shifts in individual *Phrynosoma cornutum* home range in response to habitat disturbance on Wildlife Reserve 3, Tinker Air Force Base, Oklahoma.

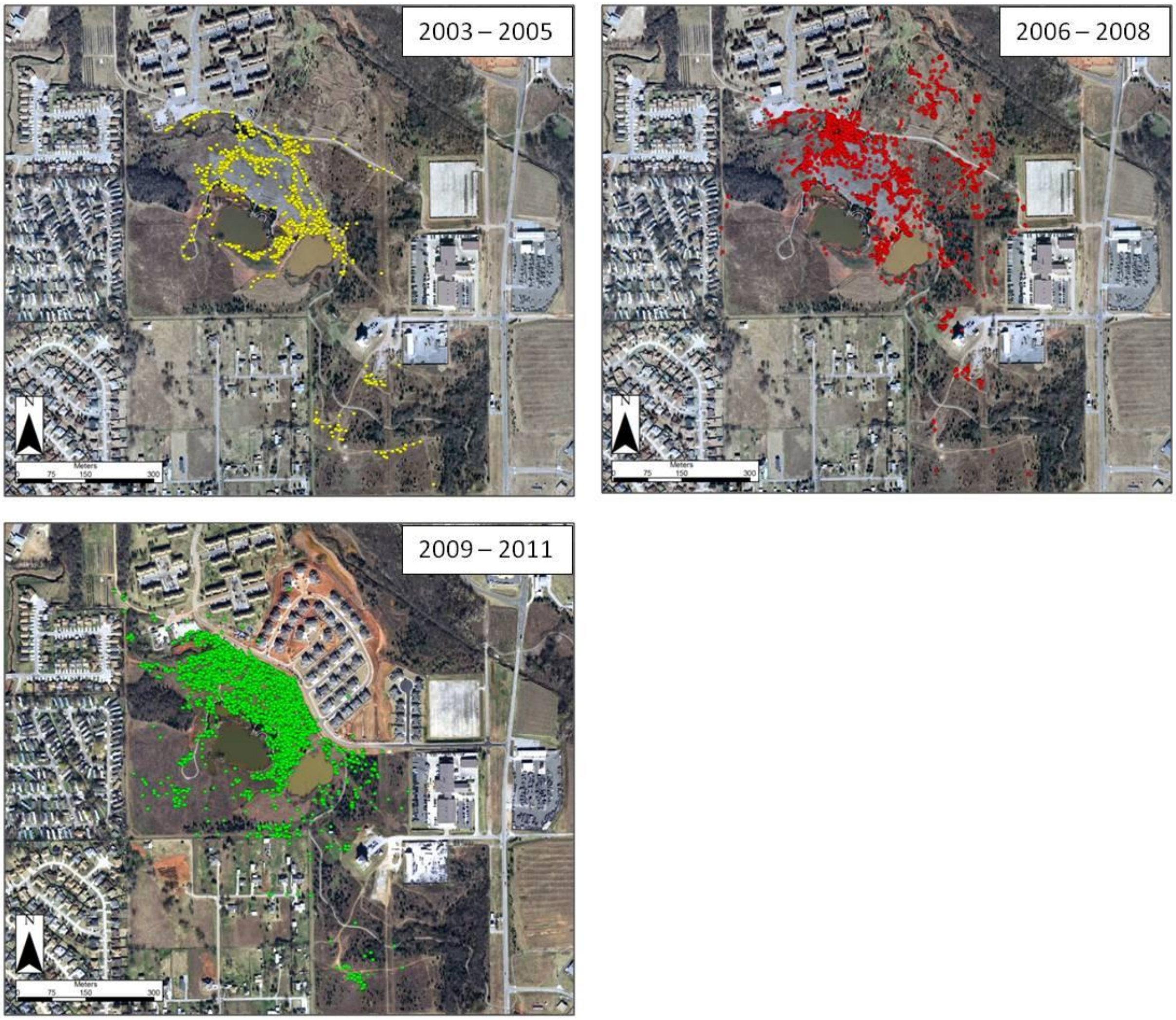


Figure 4. *Phrynosoma cornutum* locations on Wildlife Reserve 3 and surrounding areas, Tinker Air Force Base, Oklahoma during 3 study periods. 2003-2005 and 2006-2008 maps used an aerial photograph taken in 2007; 2009-2011 map used an aerial photograph taken in 2009. Note new housing development northeast of Wildlife Reserve 3 completed in 2009.

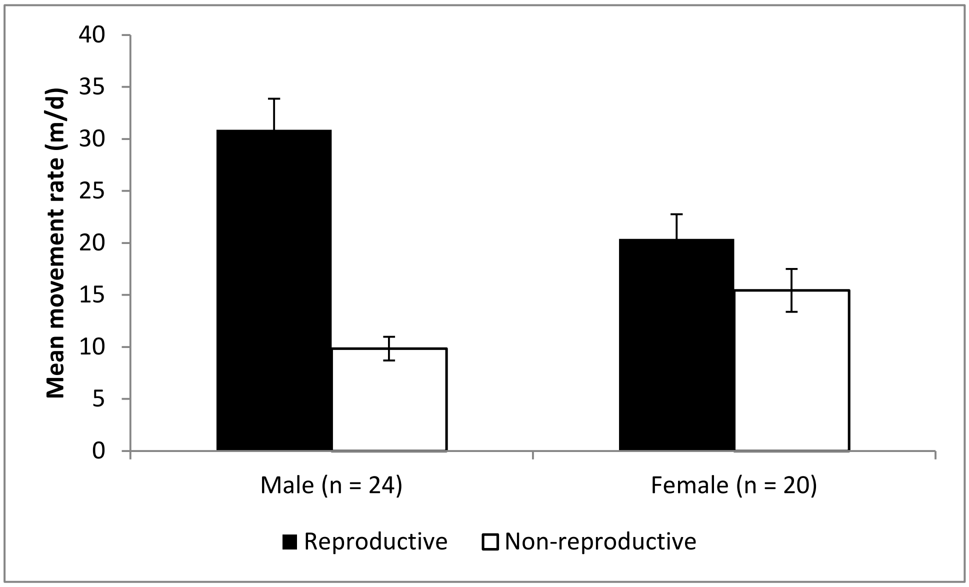


Figure 5. Interaction of daily movement rates (m/day; mean ± SE) by sex and period for *Phrynosoma cornutum* on Wildlife Reserve 3, Tinker Air Force Base, Oklahoma. Reproductive period is from emergence from hibernation (generally early April) to 15 July. Non-reproductive period is from 16 July until entering hibernation (generally October to December).

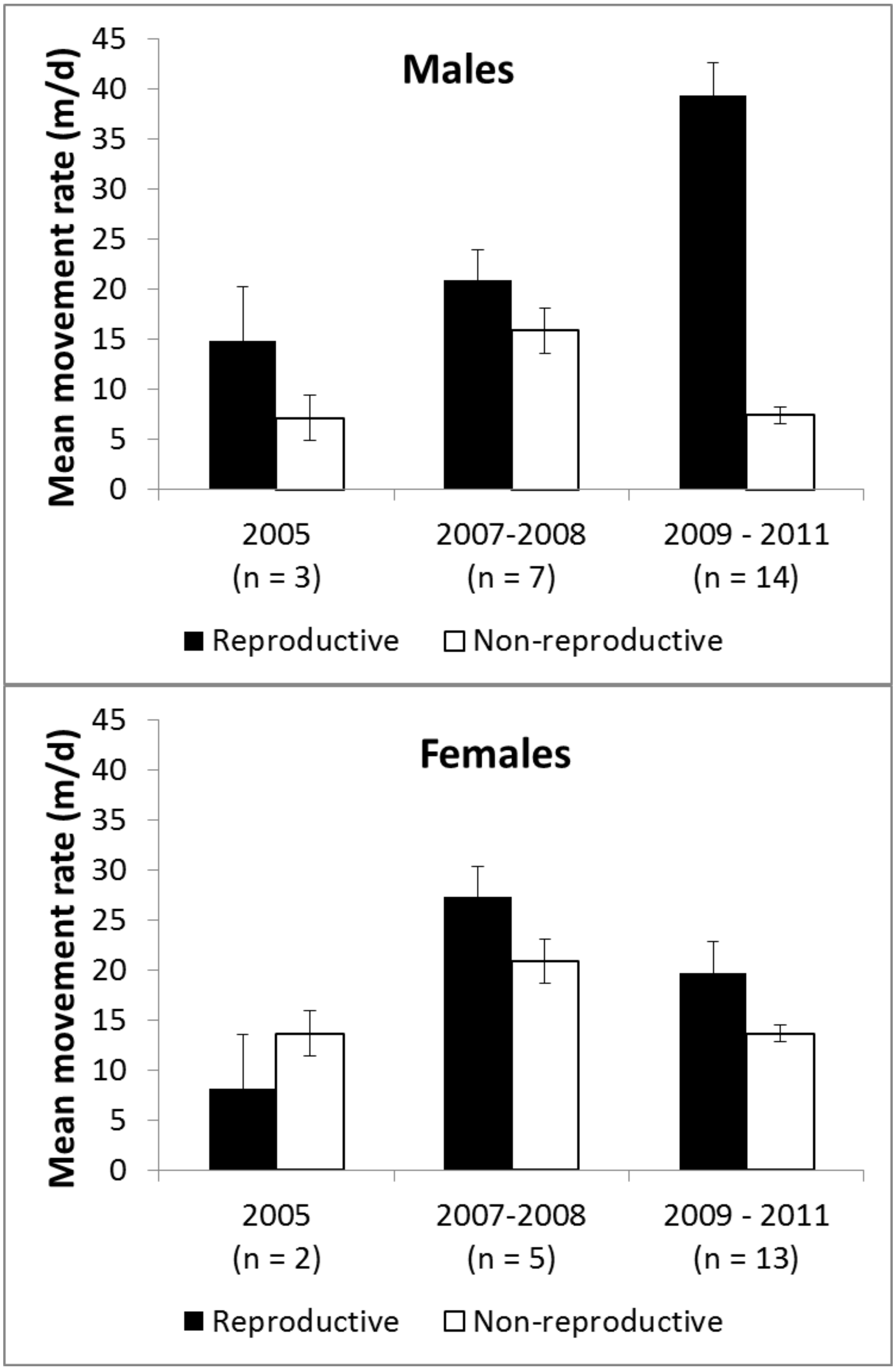


Figure 6. Interaction of daily movement rates (mean ± SE) by sex, period, and study stage for *Phrynosoma cornutum* on Wildlife Reserve 3, Tinker Air Force Base, Oklahoma. Reproductive period is from emergence from hibernation (generally early April) to 15 July. Non-reproductive period is from 16 July until entering hibernation (generally October to December).

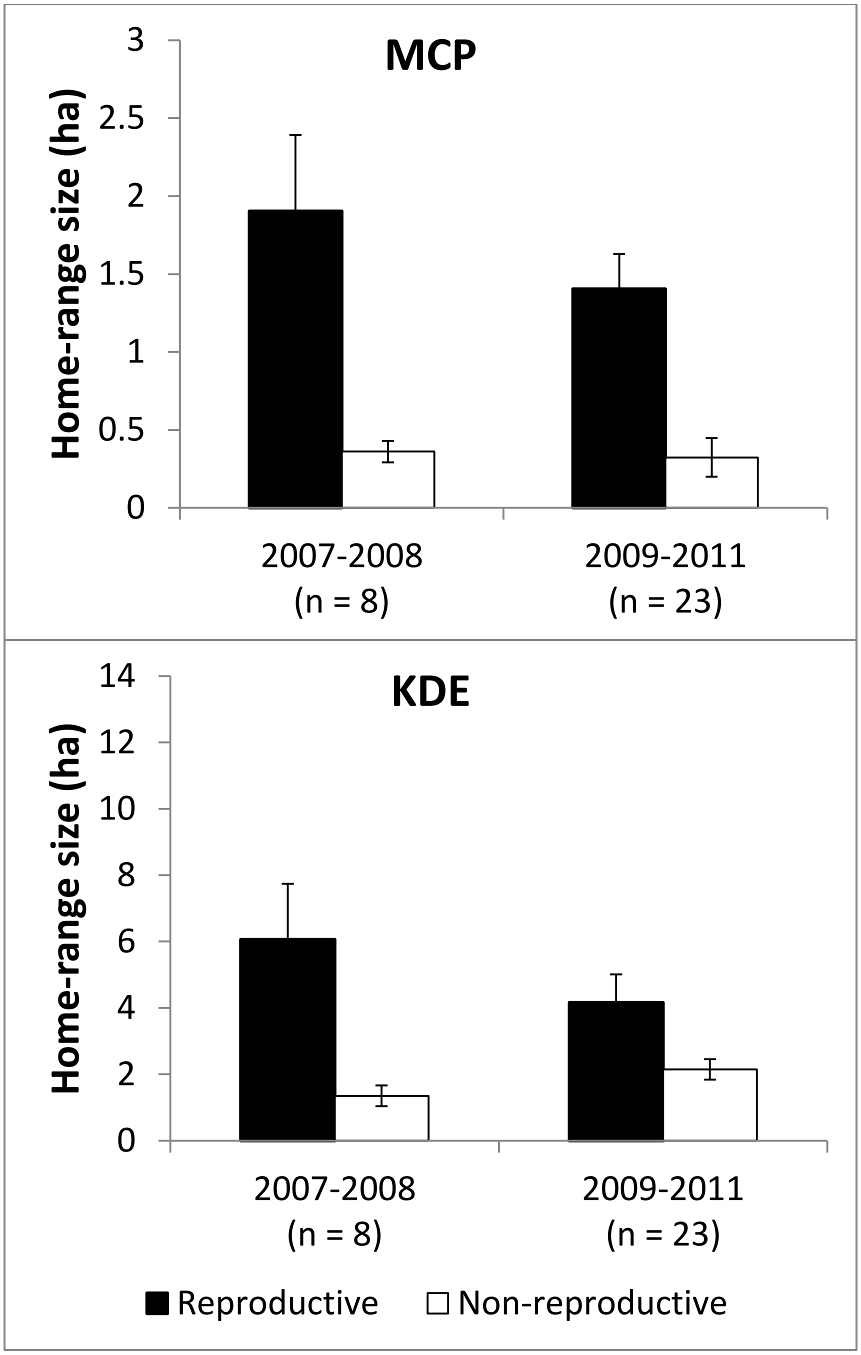


Figure 7. Home-range sizes (mean ± SE) by period and study stage for *Phrynosoma cornutum* on Wildlife Reserve 3, Tinker Air Force Base, Oklahoma. Home-range sizes were calculated by minimum convex polygon (MCP) and kernel-density estimate (KDE). Reproductive period is from emergence from hibernation (generally early April) to 15 July. Non-reproductive period is from 16 July until entering hibernation (generally October to December).

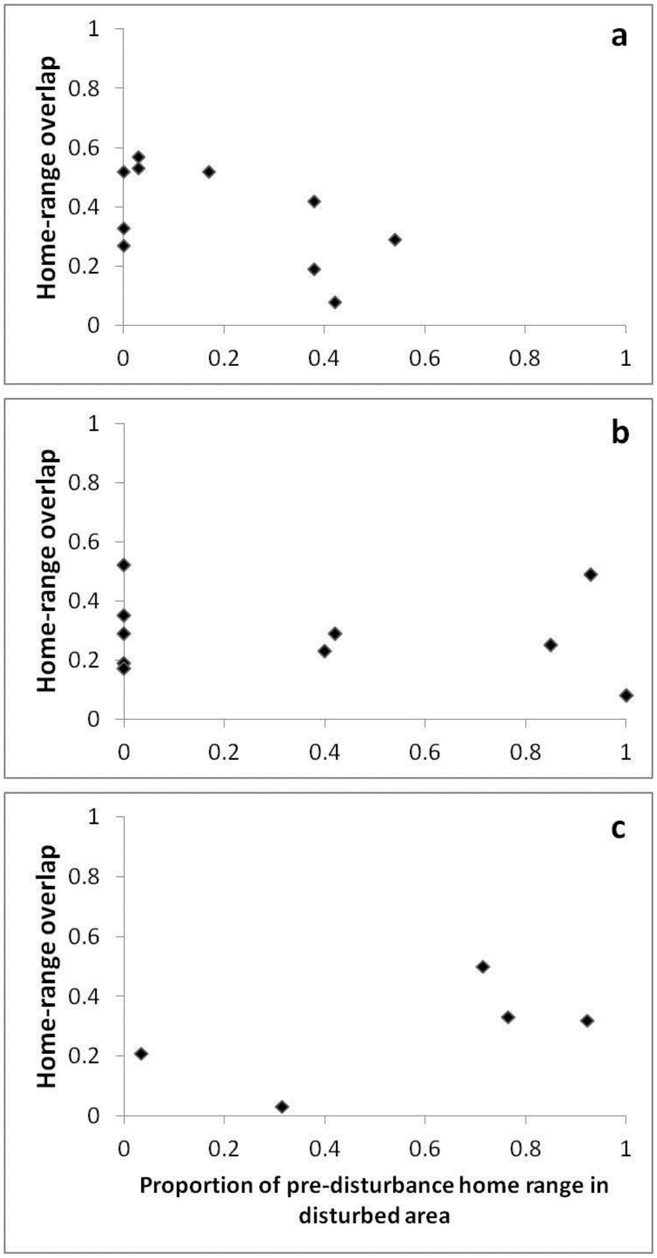


Figure 8. Sample comparisons of proportion of pre-disturbance *Phrynosoma cornutum* home range in disturbed area and overlap of pre- and post-disturbance home range. Panels represent three different herbicide applications: Area D (Fig. 2) in 2008 ($F_{(1,8)} = 3.91$, $P = 0.08$, $r^2 = 0.33$, panel a); Area A in 2005 ($F_{(1,8)} = 0.13$, $P = 0.72$, $r^2 = 0.02$, panel b); and Area D in 2008 ($F_{(1,7)} = 0.17$, $P = 0.69$, $r^2 = 0.02$, panel b).

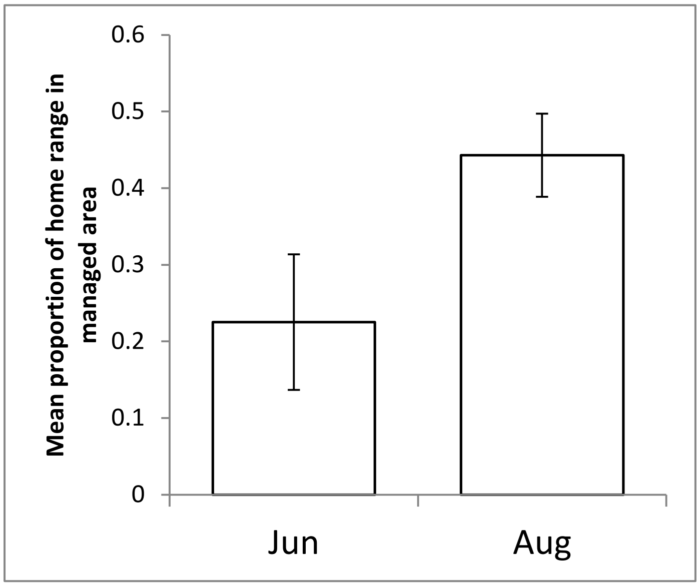


Figure 9. Mean (± SE) proportion of *Phrynosoma cornutum* home range in Management Area A, for the months before and after herbicide spraying of Wildlife Reserve 3, Tinker Air Force Base, Oklahoma during 2005.

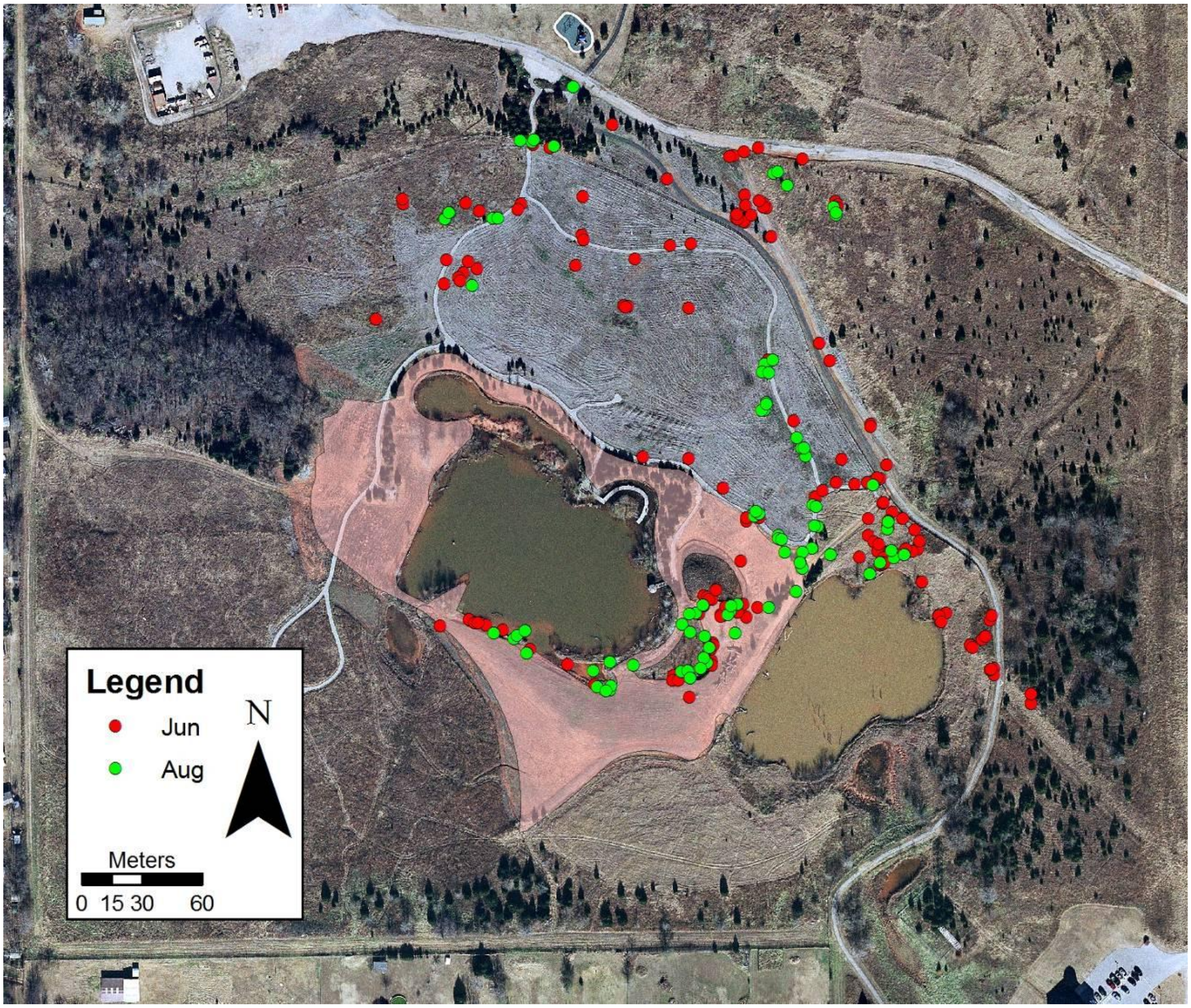


Figure 10. Radiolocations of *Phrynosoma cornutum* on Wildlife Reserve 3, Tinker Air Force Base, Oklahoma in June and August of 2005. Management Area A (shaded in pink) was sprayed with herbicide in July of 2005.

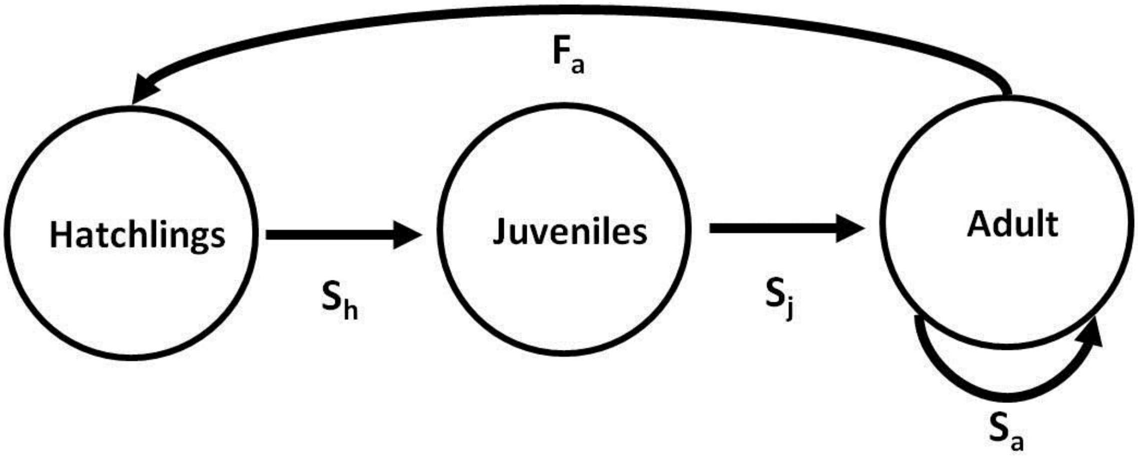
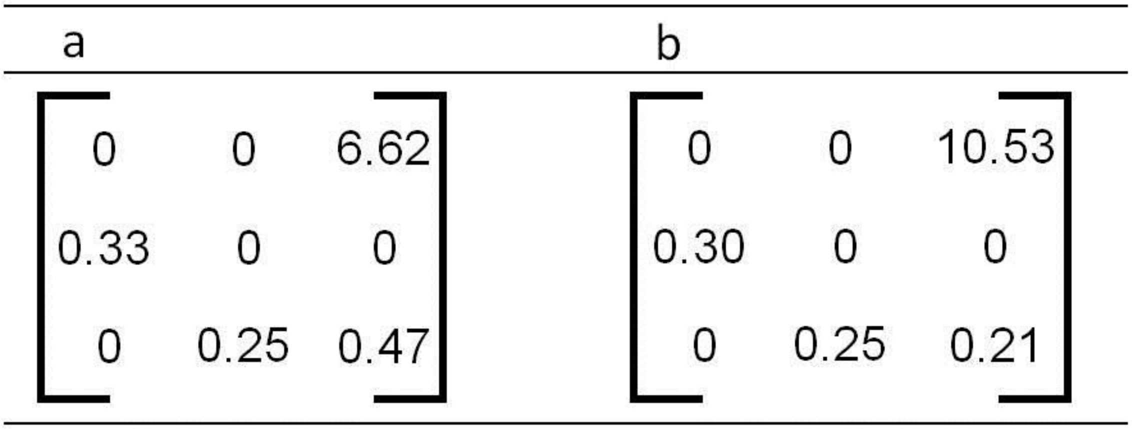


Figure 11. Life history diagram for *Phrynosoma cornutum*. S_h: hatchling survival rate; S_j: juvenile survival rate; S_a: adult survival rate; F_a: adult fecundity.



a

$$\begin{bmatrix} 0 & 0 & 6.62 \\ 0.33 & 0 & 0 \\ 0 & 0.25 & 0.47 \end{bmatrix}$$

b

$$\begin{bmatrix} 0 & 0 & 10.53 \\ 0.30 & 0 & 0 \\ 0 & 0.25 & 0.21 \end{bmatrix}$$

Figure 12. Stage-based matrices for populations of *Phrynosoma cornutum* at Wildlife Reserve 3, Tinker Air Force Base, Oklahoma (a) and Chaparral Wildlife Management Area, Texas (b).

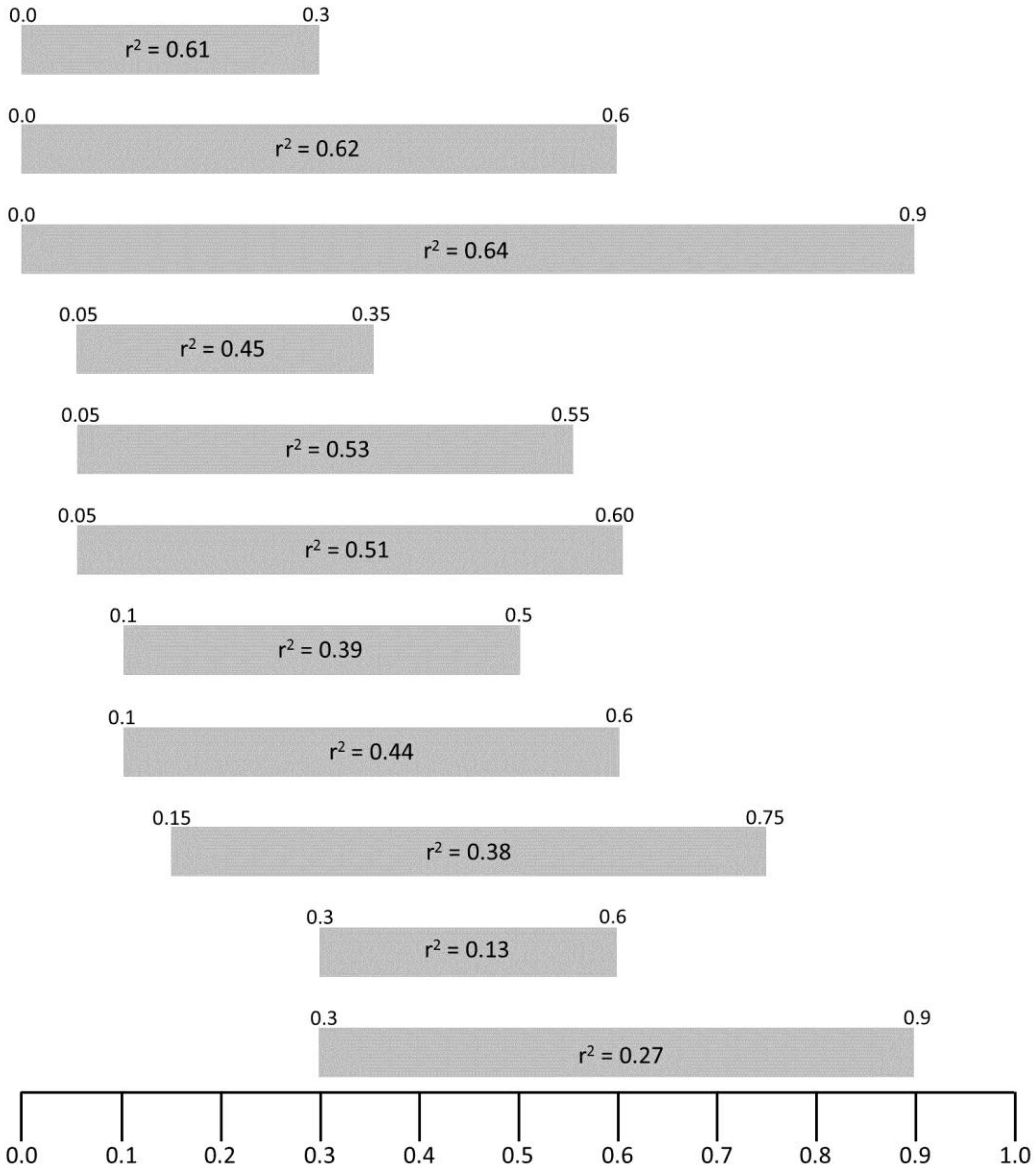


Figure 13. Results of perturbations of hatchling survival distributions used in life-stage simulation analyses for *Phrynosoma cornutum* at Chaparral Wildlife Management Area, Texas. For all perturbations, mean and variance of all vital rates was held constant except the variance of adult survival. Bars represent the range of the distribution input into the LSA for each perturbation, with minima and maxima at the upper corners of each bar. The coefficient of determination (r^2) of hatchling survival and population growth rate (λ) for each distribution is reported within each bar.

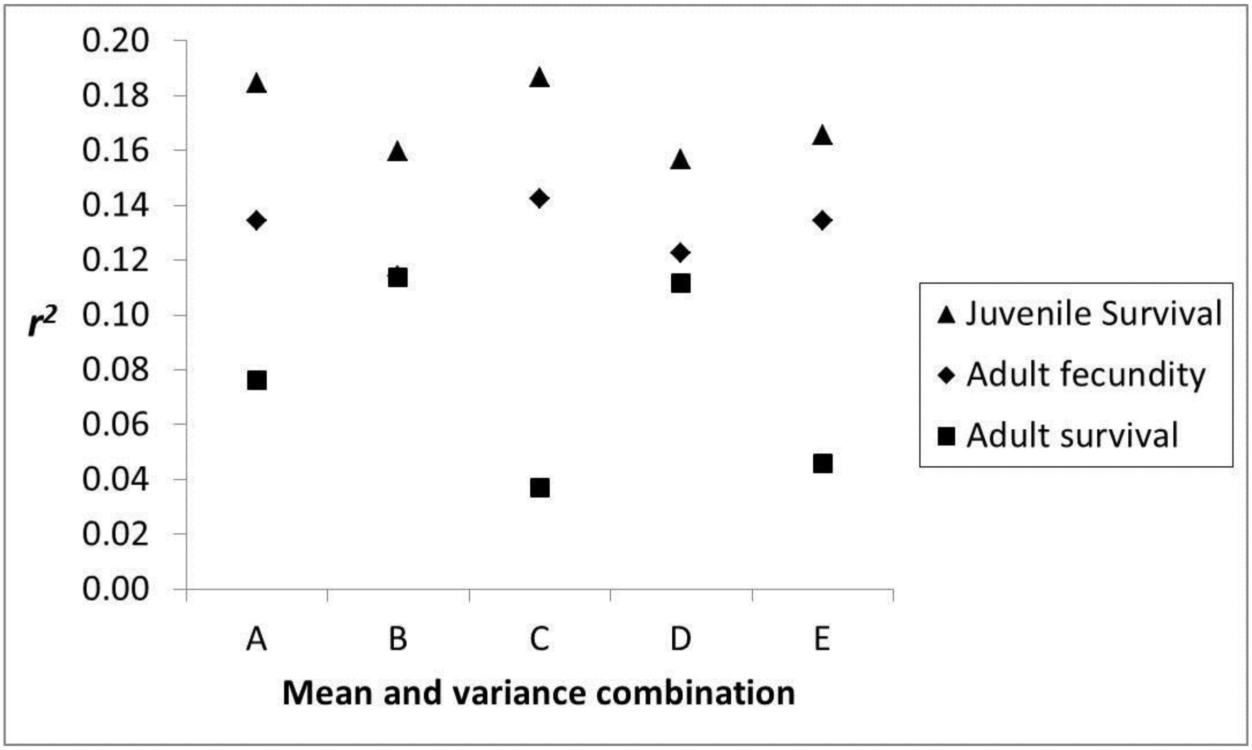


Figure 14. The coefficient of determination (r^2) of population growth rate (λ) regressed on three vital rates for perturbations of adult *Phrynosoma cornutum* survival rate and variance of said rate for Wildlife Reserve 3, Tinker Air Force Base, Oklahoma. Mean and variance combinations: (A) Means of Category 1 and Category 2 survival rates and variances; (B) mean of Category 1 and 2 survival rates and Category 1 variance; (C) mean of Category 1 and 2 survival rates and Category 2 variance; (D) Category 1 survival rate and variance; (E) Category 2 survival rate and variance. Category 1 survival rate and variance estimates assumed unknown fates were alive, Category 2 assumed unknown fates were dead. Survival rates, variances, and r^2 values for the above Categories and vital rates, as well as hatchling survival, are reported in Table 13.

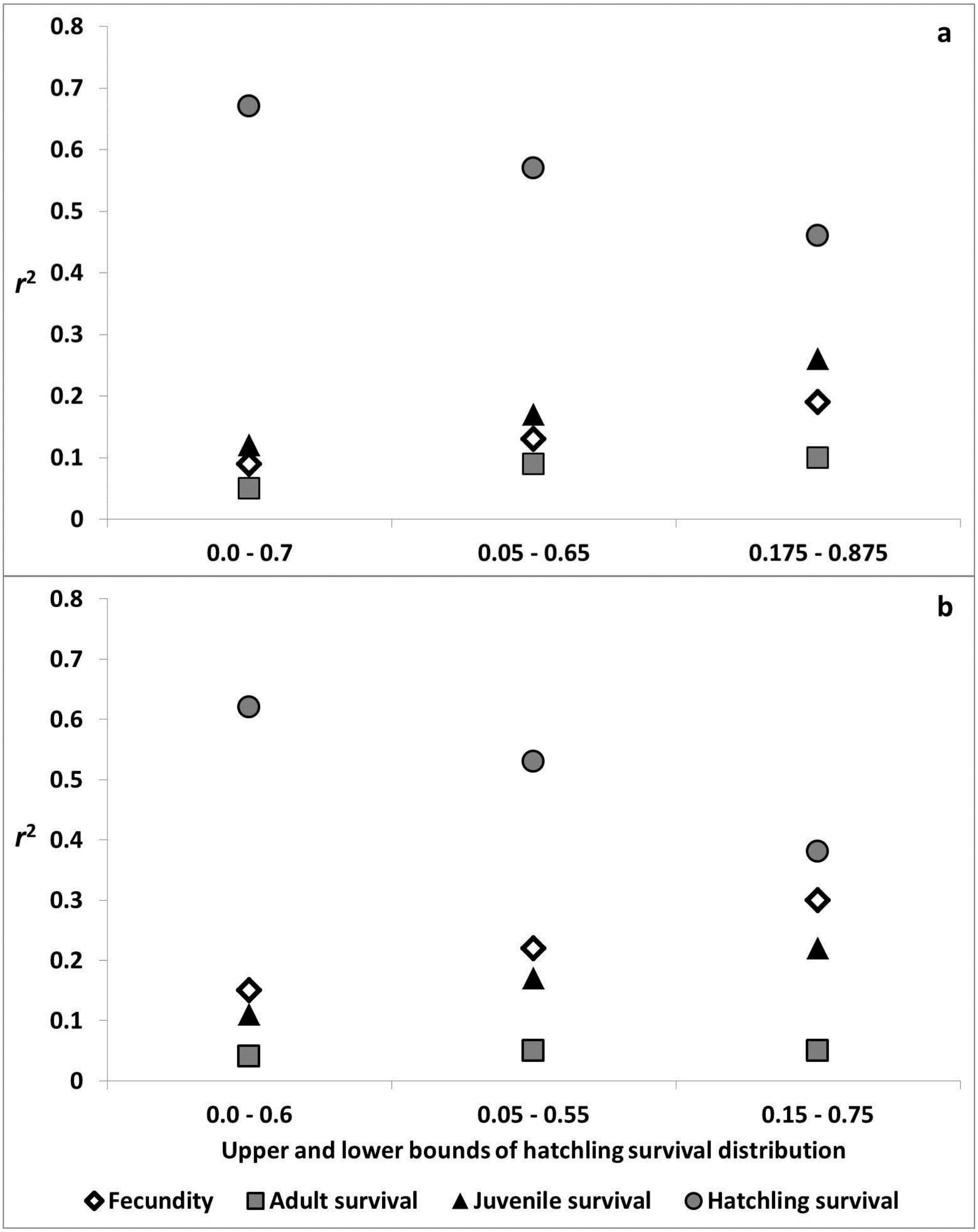


Figure 15. The coefficient of determination (r^2) of population growth rate (λ) regressed on individual vital rates for 3 different hatchling *Phrynosoma cornutum* survival distributions for Wildlife Reserve 3, Tinker Air Force Base, Oklahoma (a) and Chaparral Wildlife Management Area, Texas (b). Vital rates included are adult fecundity (F_a), adult survival (S_a), juvenile survival (S_j), and hatchling survival (S_h).

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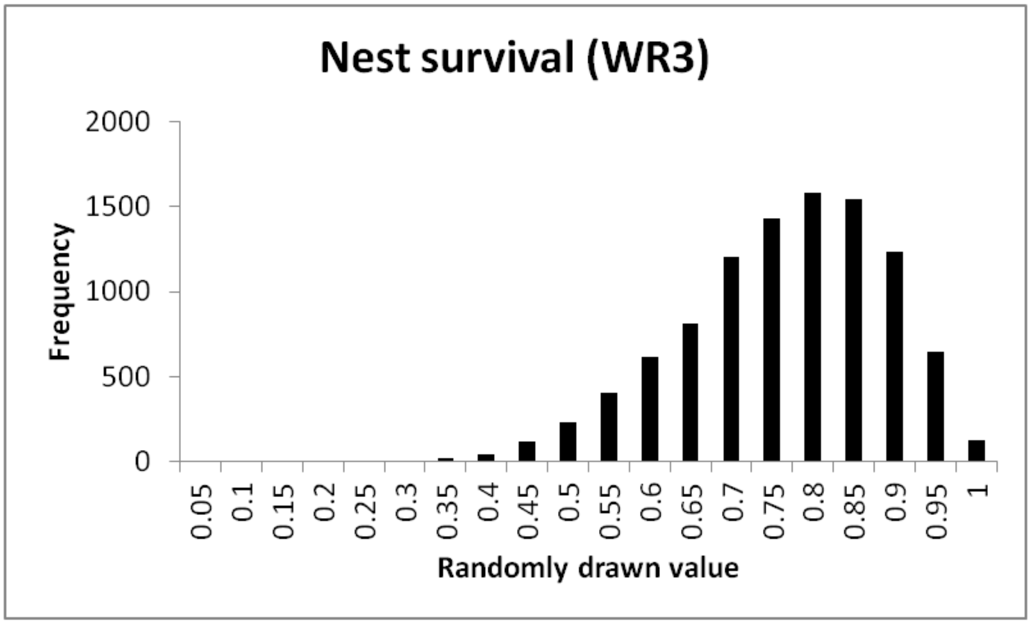
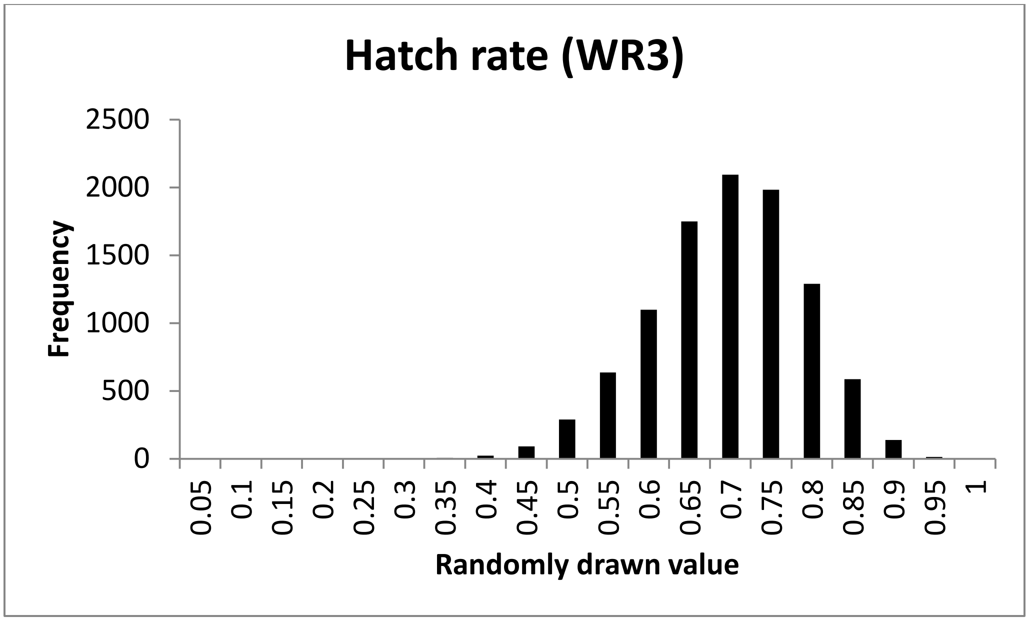
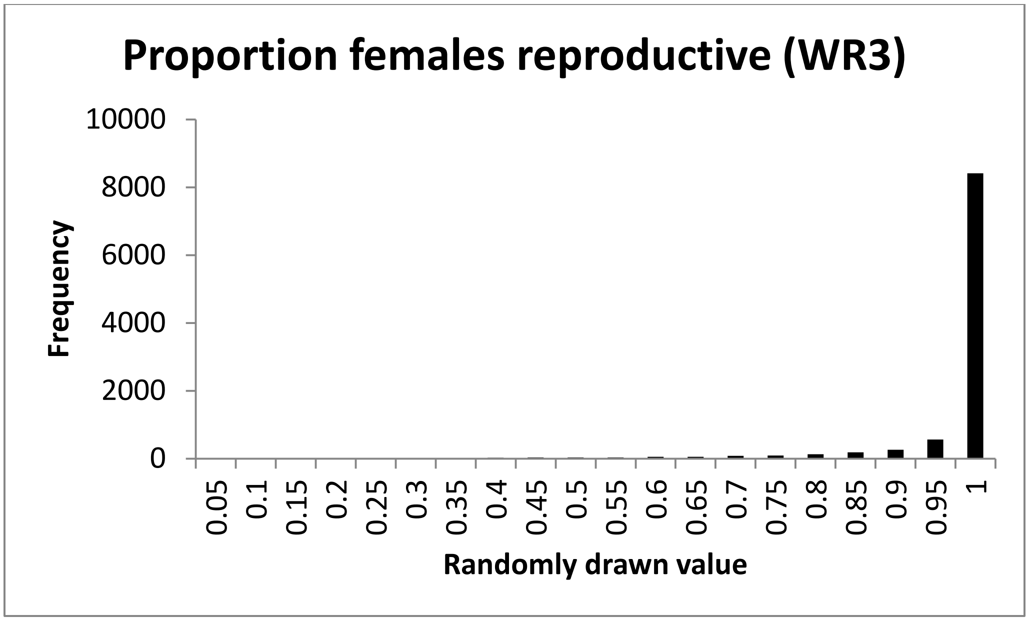
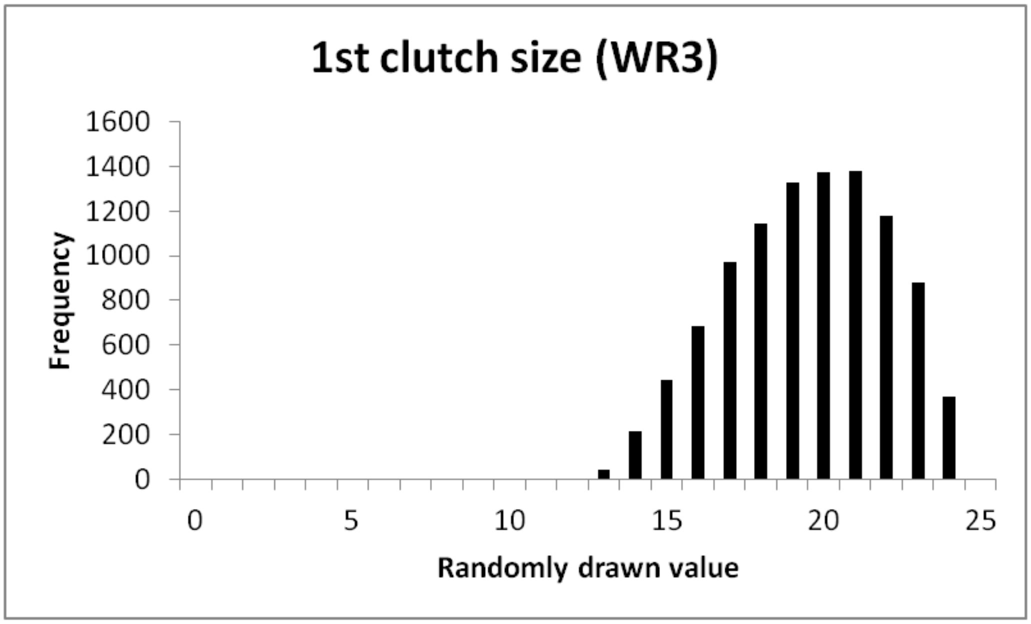
APPENDICES

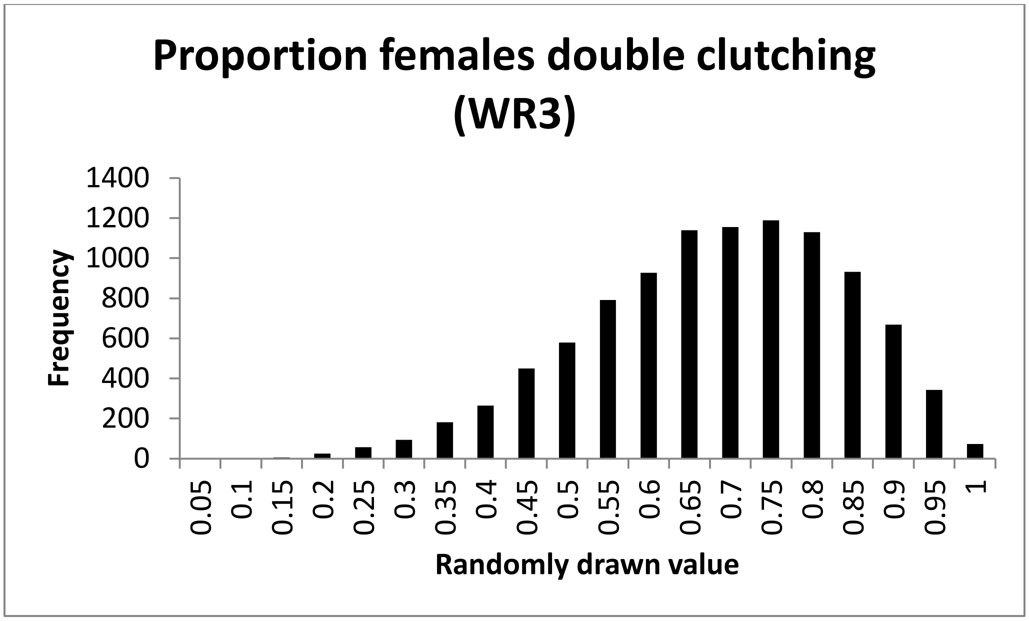
Appendix A. Frequency distributions for 10,000 randomly drawn values of each vital rate for Wildlife Reserve 3 (WR3), Tinker Air Force Base, Oklahoma, and Chaparral Wildlife Management Area (CWMA), Texas. Uniform distribution for hatchling survival was 0.0-0.7 for WR3 and 0.0-0.6 for CWMA.



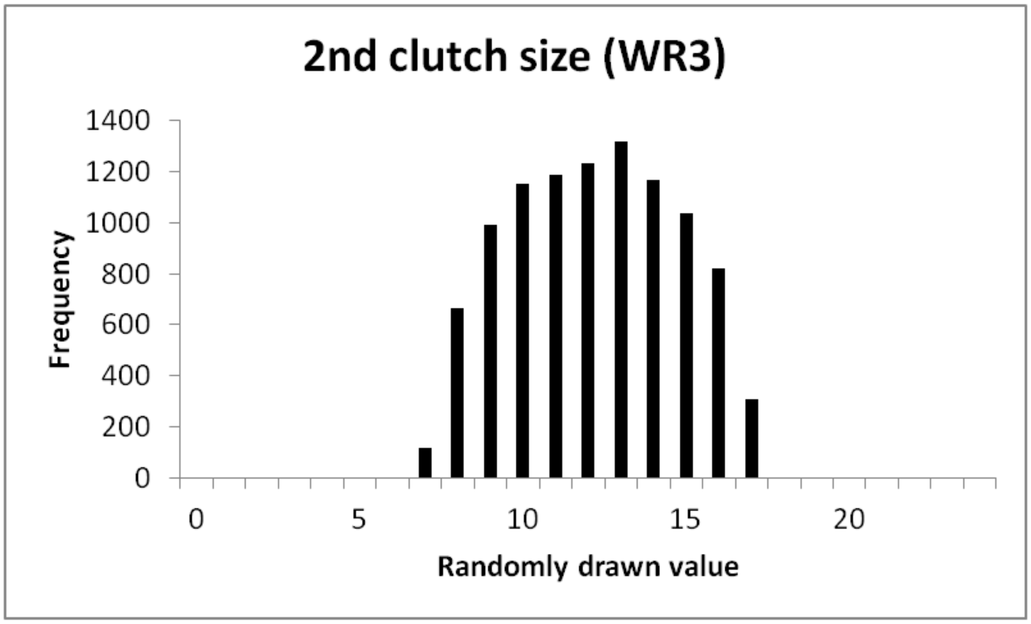



Proportion females reproductive (WR3)
10000
8000
6000
4000
2000
0
Frequency
0.05
0.1
0.15
0.2
0.25
0.3
0.35
0.4
0.45
0.5
0.55
0.6
0.65
0.7
0.75
0.8
0.85
0.9
0.95
1
Randomly drawn value

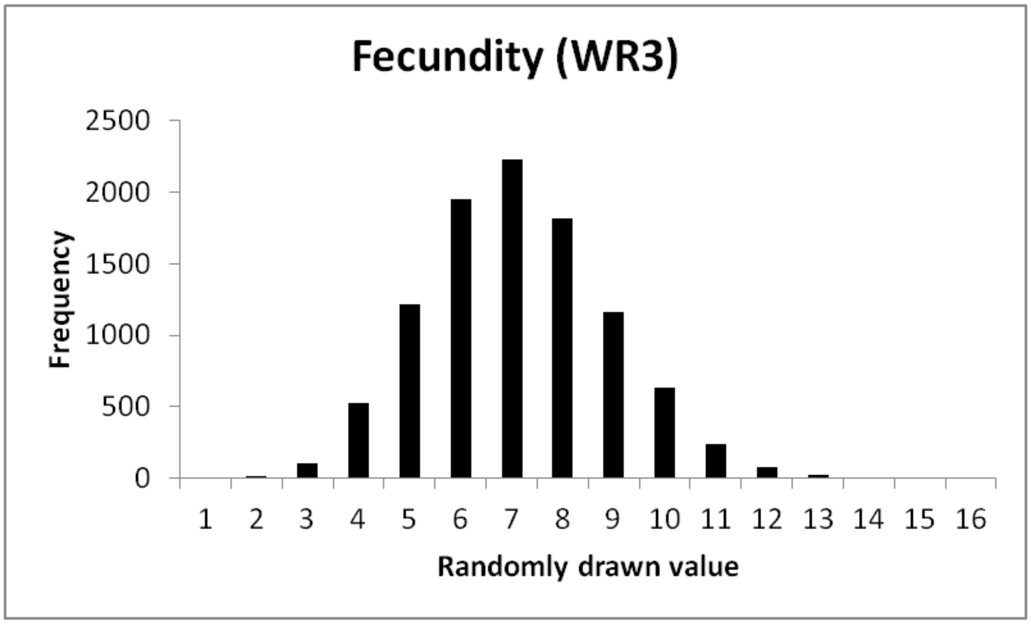

1st clutch size (WR3)
1600
1400
1200
1000
800
600
400
200
0
Frequency
0
5
10
15
20
25
Randomly drawn value

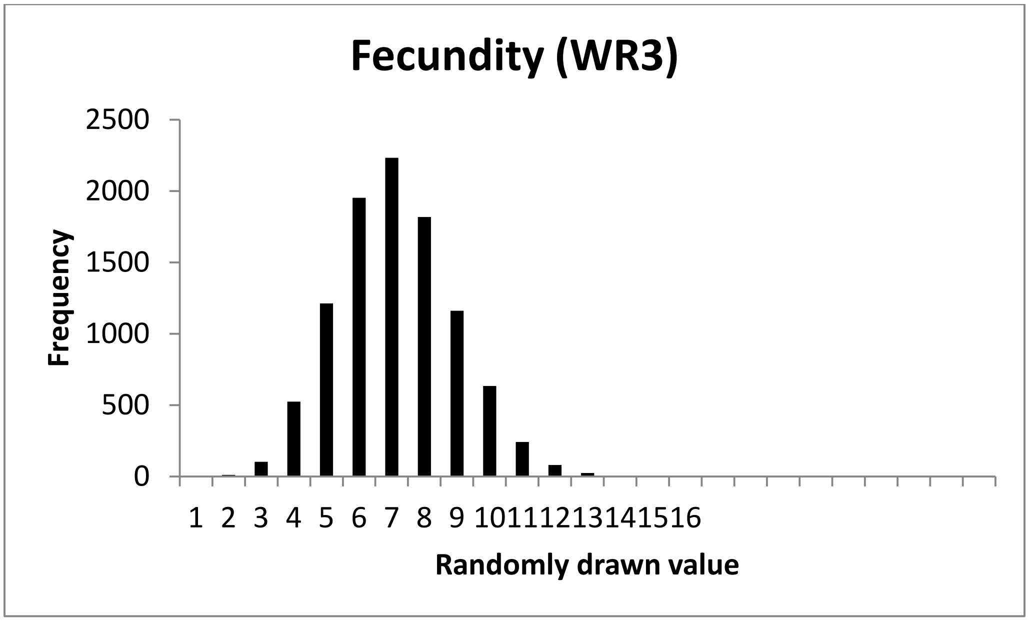


Proportion females double clutching (WR3)
Frequency
1400
1200
1000
800
600
400
200
0
0.05
0.1
0.15
0.2
0.25
0.3
0.35
0.4
0.45
0.5
0.55
0.6
0.65
0.7
0.75
0.8
0.85
0.9
0.95
1
Randomly drawn value



2nd clutch size (WR3)
Frequency
1400
1200
1000
800
600
400
200
0
0
5
10
15
20
Randomly drawn value


Fecundity (WR3)
Frequency
2500
2000
1500
1000
500
0
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
Randomly drawn value


Fecundity (WR3)
Frequency
2500
2000
1500
1000
500
0
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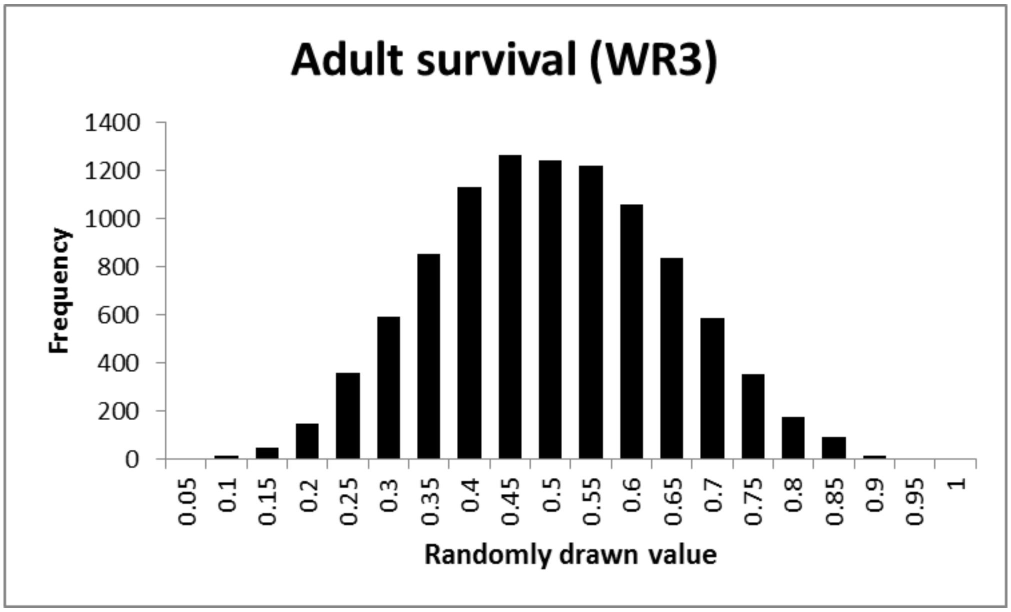
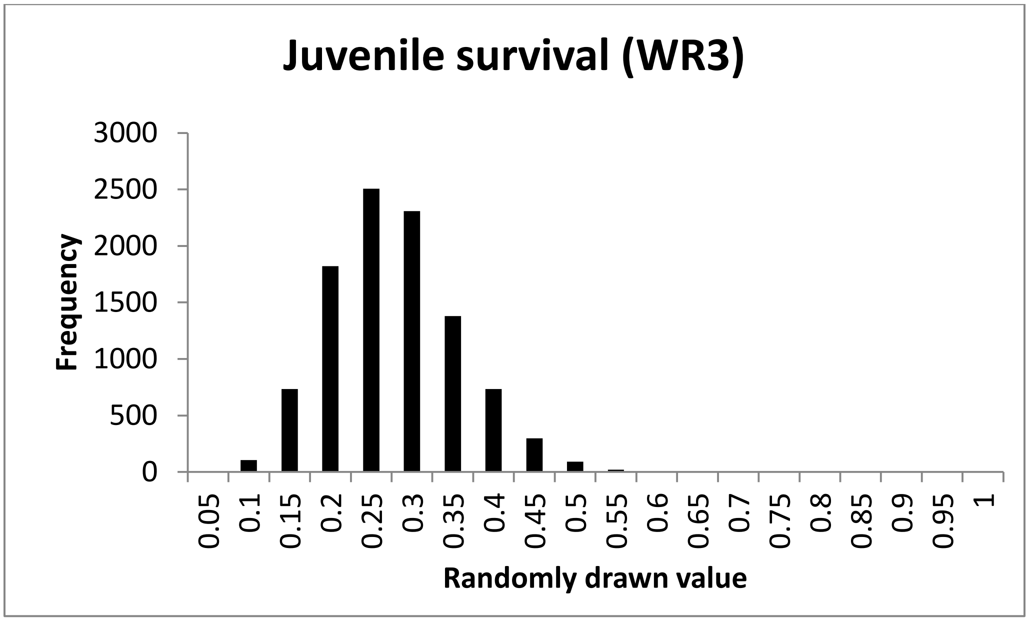
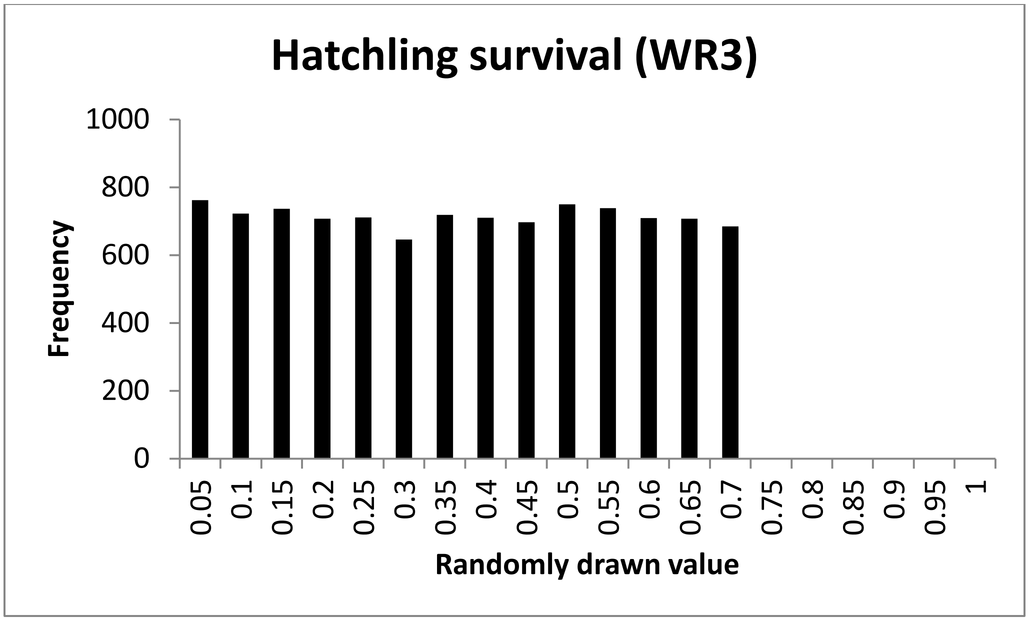
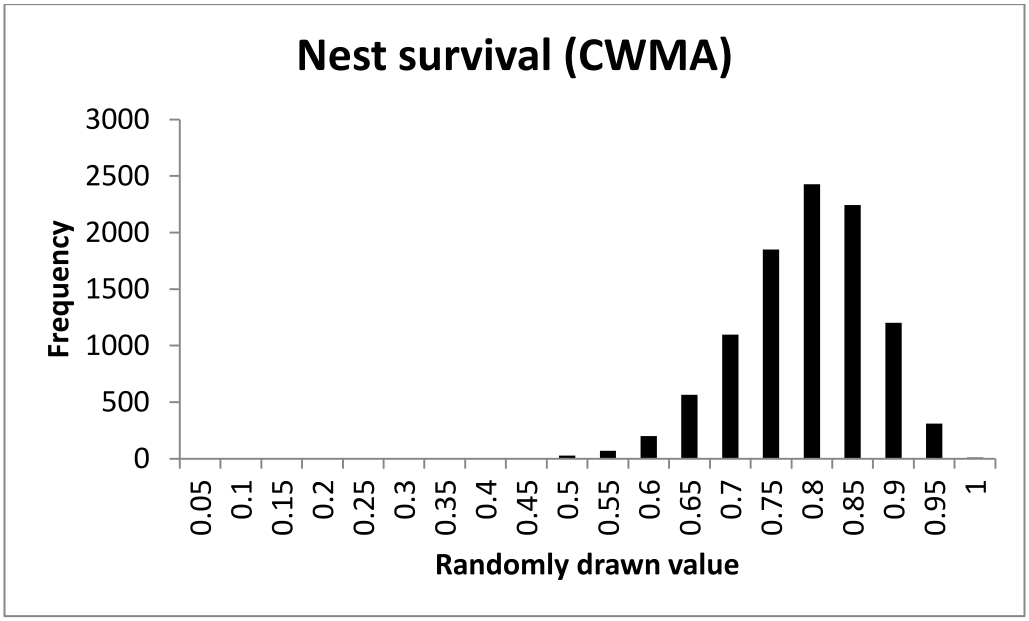
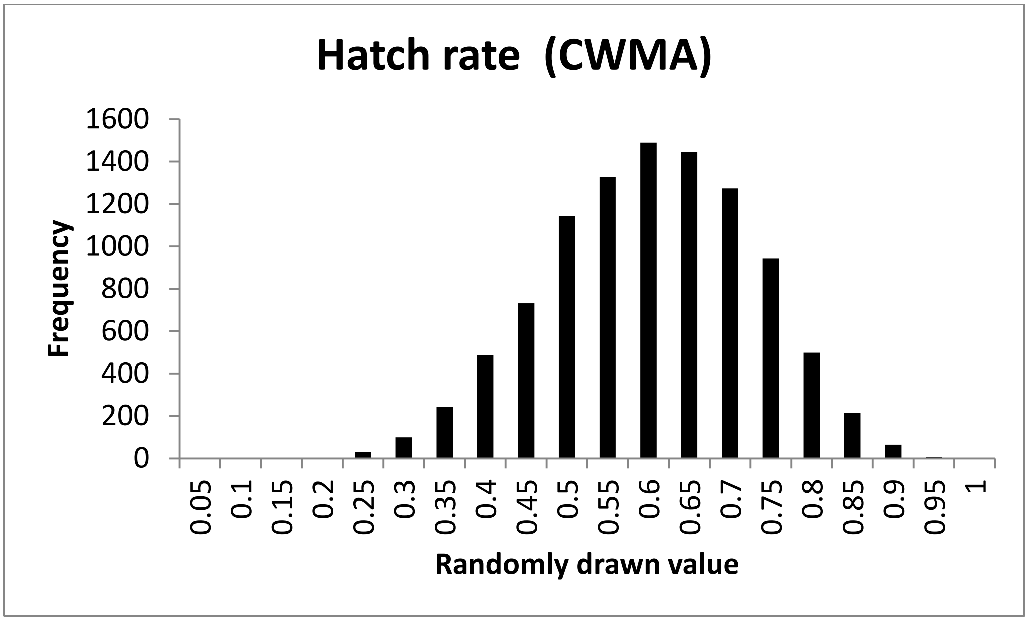
Randomly drawn value

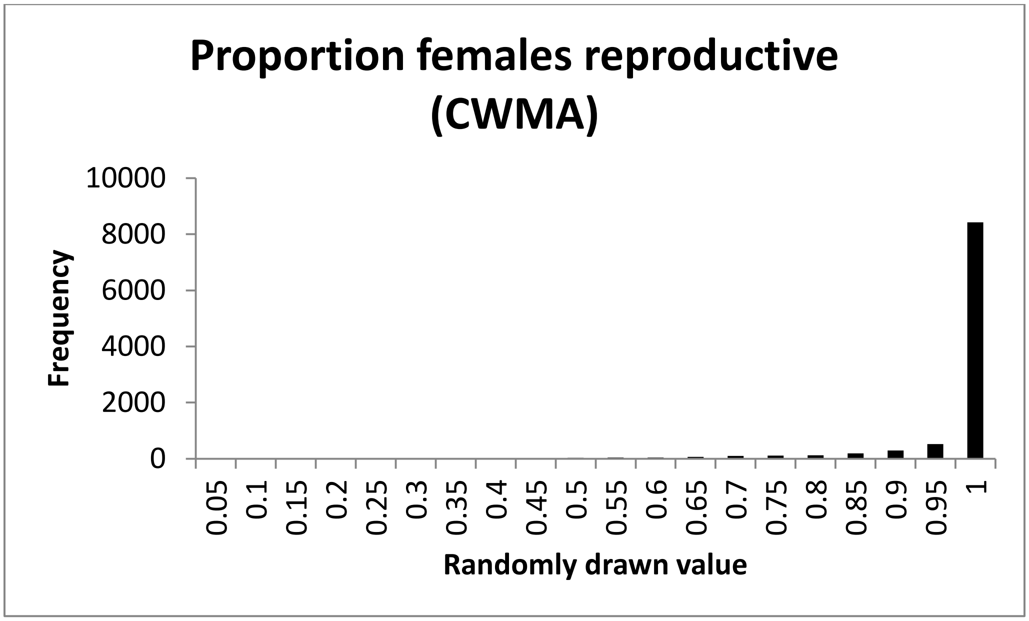

Adult survival (WR3)
Frequency
1400
1200
1000
800
600
400
200
0
0.05
0.1
0.15
0.2
0.25
0.3
0.35
0.4
0.45
0.5
0.55
0.6
0.65
0.7
0.75
0.8
0.85
0.9
0.95
1
Randomly drawn value

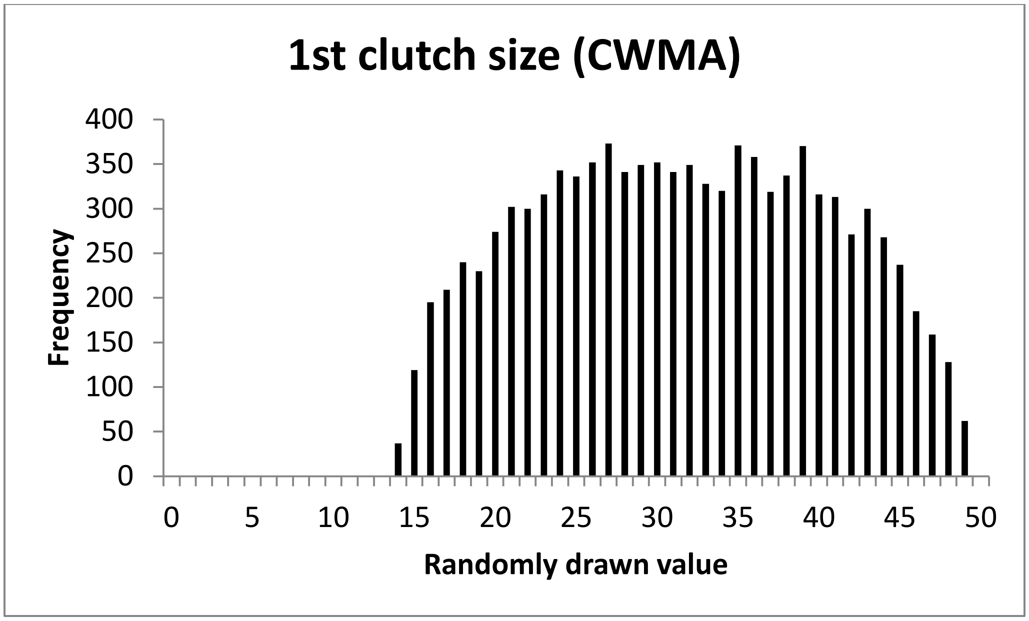

Juvenile survival (WR3)
Frequency
3000
2500
2000
1500
1000
500
0
0.05
0.1
0.15
0.2
0.25
0.3
0.35
0.4
0.45
0.5
0.55
0.6
0.65
0.7
0.75
0.8
0.85
0.9
0.95
1
Randomly drawn value

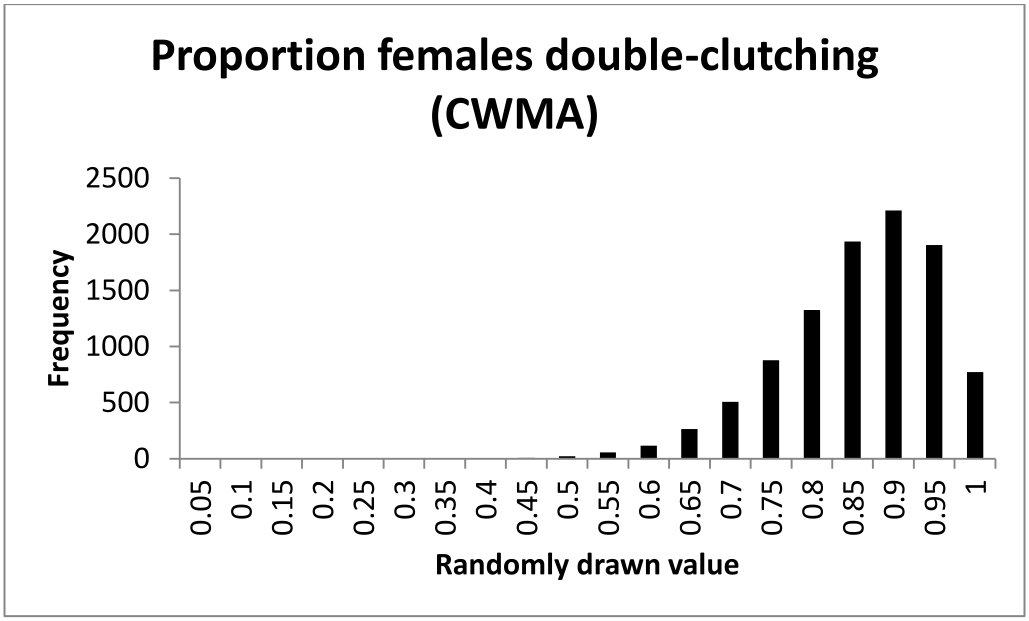

Hatchling survival (WR3)
Frequency
1000
800
600
400
200
0
0.05
0.1
0.15
0.2
0.25
0.3
0.35
0.4
0.45
0.5
0.55
0.6
0.65
0.7
0.75
0.8
0.85
0.9
0.95
1
Randomly drawn value

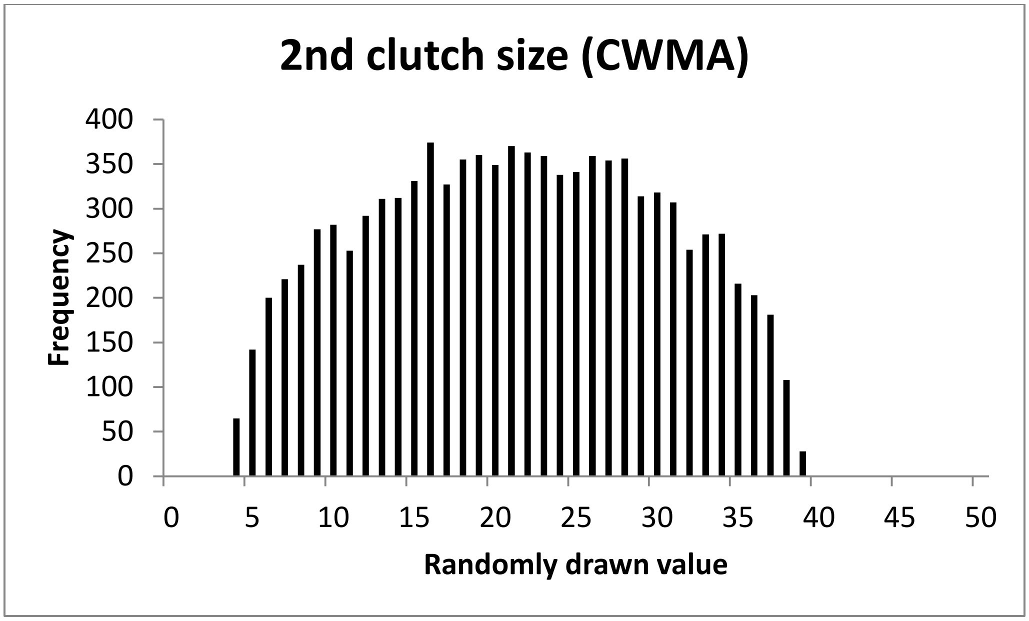

Nest survival (CWMA)
Frequency
3000
2500
2000
1500
1000
500
0
0.05
0.1
0.15
0.2
0.25
0.3
0.35
0.4
0.45
0.5
0.55
0.6
0.65
0.7
0.75
0.8
0.85
0.9
0.95
1
Randomly drawn value

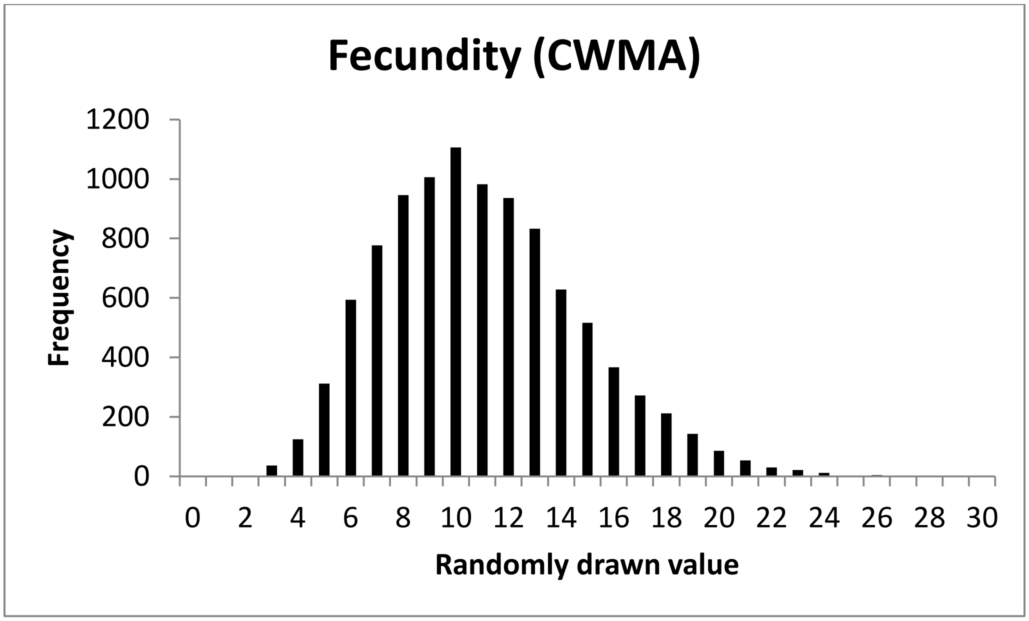

Hatch rate (CWMA)
Frequency
1600
1400
1200
1000
800
600
400
200
0
0.05
0.1
0.15
0.2
0.25
0.3
0.35
0.4
0.45
0.5
0.55
0.6
0.65
0.7
0.75
0.8
0.85
0.9
0.95
1
Randomly drawn value

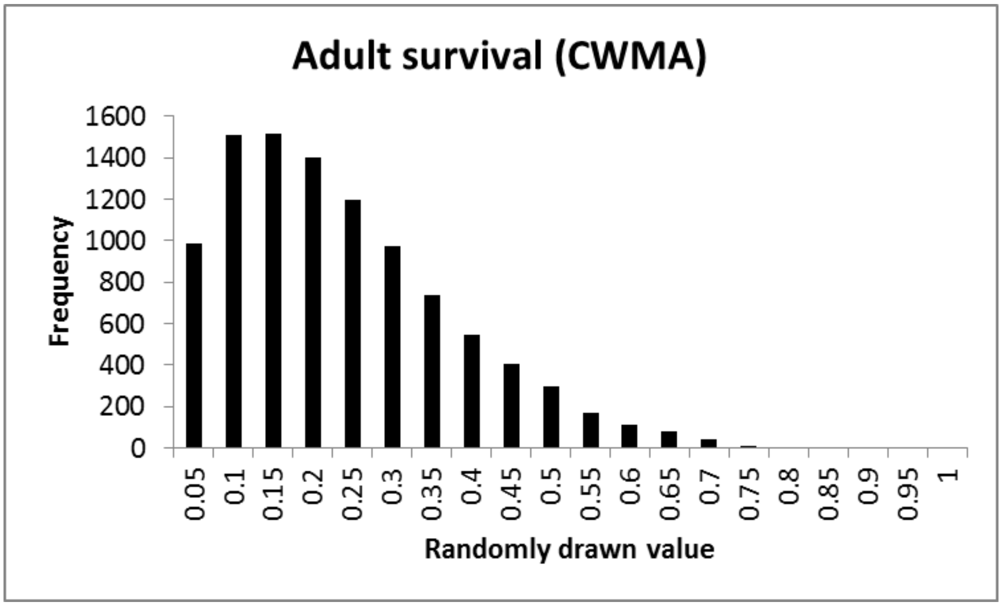

Proportion females reproductive (CWMA)
Frequency
10000
8000
6000
4000
2000
0
0.05
0.1
0.15
0.2
0.25
0.3
0.35
0.4
0.45
0.5
0.55
0.6
0.65
0.7
0.75
0.8
0.85
0.9
0.95
1
Randomly drawn value

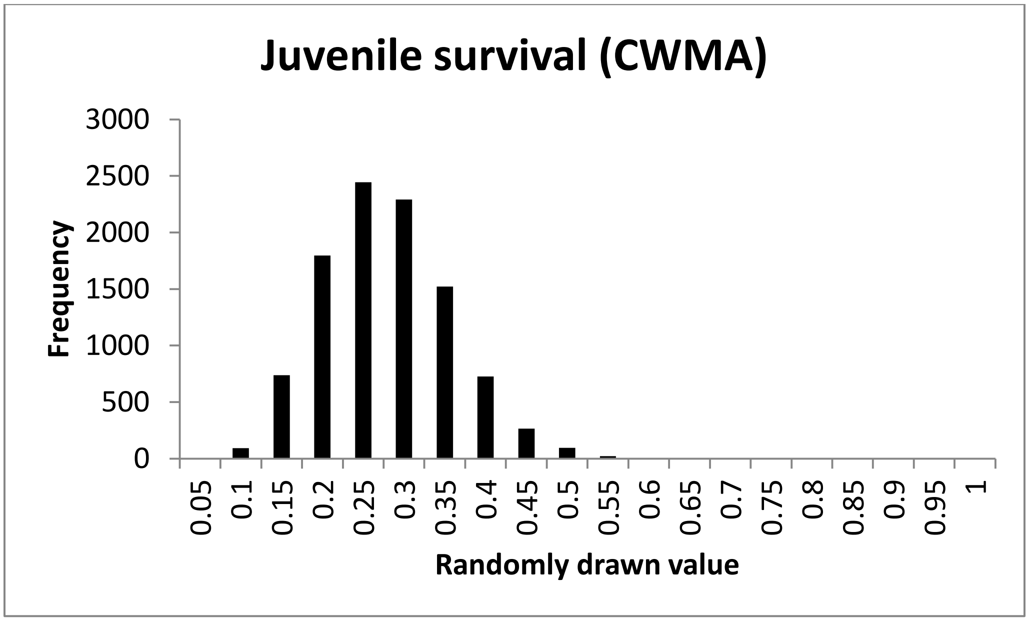

1st clutch size (CWMA)
Frequency
400
350
300
250
200
150
100
50
0
0
5
10
15
20
25
30
35
40
45
50
Randomly drawn value

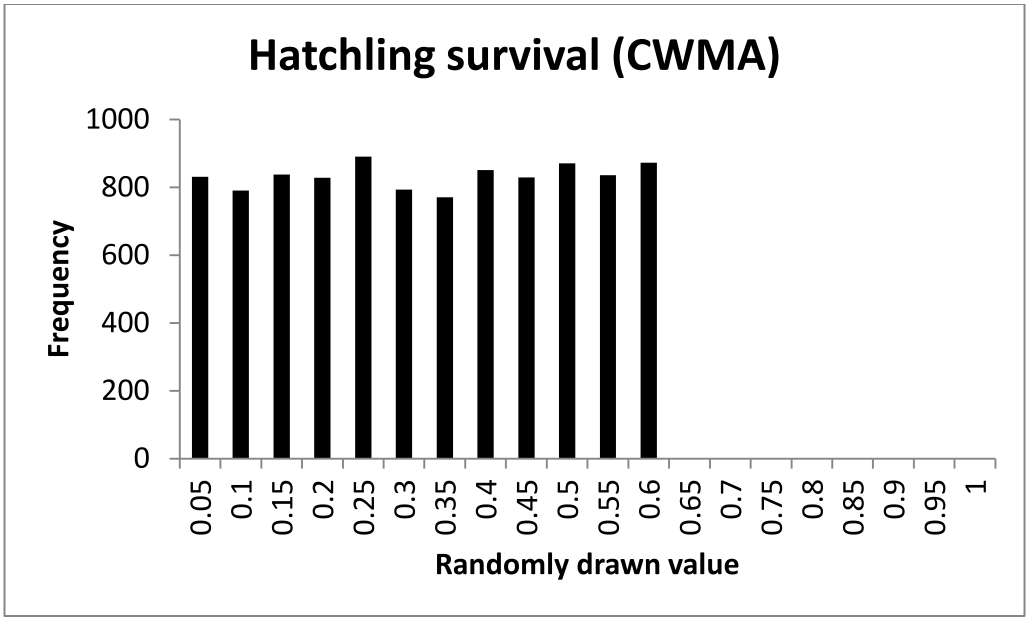

Proportion females double-clutching (CWMA)
Frequency
2500
2000
1500
1000
500
0
0.05
0.1
0.15
0.2
0.25
0.3
0.35
0.4
0.45
0.5
0.55
0.6
0.65
0.7
0.75
0.8
0.85
0.9
0.95
1
Randomly drawn value


2nd clutch size (CWMA)
Frequency
400
350
300
250
200
150
100
50
0
0
5
10
15
20
25
30
35
40
45
50
Randomly drawn value


Fecundity (CWMA)
Frequency
1200
1000
800
600
400
200
0
0
2
4
6
8
10
12
14
16
18
20
22
24
26
28
30
Randomly drawn value


Adult survival (CWMA)
Frequency
1600
1400
1200
1000
800
600
400
200
0
0.05
0.1
0.15
0.2
0.25
0.3
0.35
0.4
0.45
0.5
0.55
0.6
0.65
0.7
0.75
0.8
0.85
0.9
0.95
1
Randomly drawn value


Juvenile survival (CWMA)
Frequency
3000
2500
2000
1500
1000
500
0
0.05
0.1
0.15
0.2
0.25
0.3
0.35
0.4
0.45
0.5
0.55
0.6
0.65
0.7
0.75
0.8
0.85
0.9
0.95
1
Randomly drawn value


Hatchling survival (CWMA)
Frequency
1000
800
600
400
200
0
0.05
0.1
0.15
0.2
0.25
0.3
0.35
0.4
0.45
0.5
0.55
0.6
0.65
0.7
0.75
0.8
0.85
0.9
0.95
1
Randomly drawn value

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Alexander J. Wolf

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Beloit College
Bachelor of Science, Evolution, Ecology and Behavioral Biology, May 2006

Thesis Title:
Spatial and demographic ecology of Texas horned lizards within a conservation framework

Major Professor: Eric C. Hellgren