Notes

Documenting Extinction in Real Time: Decline of the Houston Toad on a Primary Recovery Site

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Abstract

The Houston toad Bufo (Anaxyrus) houstonensis is a federally endangered amphibian endemic to east central Texas and is primarily found in the Lost Pines ecoregion. In 2010, we became cautiously optimistic regarding the recovery of the species on the Griffith League Ranch, one of the toad’s primary recovery sites, after an unusually successful reproductive season. Subsequently, the extreme drought throughout Texas deepened, culminating in the fall 2011 high-severity wildfires throughout the Lost Pines ecoregion. After the drought and wildfires, we continued to intensively monitor Houston toads via anuran call surveys, drift fence arrays, and visual observations of reproduction. Our objective was to investigate the dynamics of the Houston toad population on the Griffith League Ranch during these dramatic impacts to its habitat and to discuss the potential for Houston toad recovery in the ecoregion. In summary, both a simulation model and our field monitoring data suggest the Houston toad population on the Griffith League Ranch is at critically low numbers and may be extirpated in the near future if human-mediated recovery strategies are not continued and refined. We do not discern any evidence to suggest the 2011 wildfires have had any direct detrimental impacts on subsequent Houston toad population dynamics. Still, high-resolution data will be needed in the future to quantify how the wildfires affected Houston toad viability over the medium and long term.

Keywords: amphibian decline; Bufo houstonensis; endangered species; population dynamics; simulation model

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Introduction

Amphibian communities are currently experiencing worldwide declines in both abundance and diversity (Pechmann et al. 1991; Wake 1991; Pechmann and Wilbur 1994; Alford and Richards 1999; Stuart et al. 2004; Beebee and Griffiths 2005; Adams et al. 2013). These declines are often the result of the additive effects of multiple environmental and anthropogenic stressors and thus will require an integrative approach in research to identify causes of and reverse negative amphibian population trends (Wake 2012). However, there are relatively few documented long-term amphibian studies focused on a species of interest that incorporate such an integrative research approach.

The Houston toad Bufo (Anaxyrus) houstonensis was the first amphibian listed under the Endangered Species Conservation Act (Bureau of Sports Fisheries and Wildlife 1970), the precursor to the Endangered Species Act (U.S. Endangered Species Act 1973, as amended; Figure 1). Subsequent to listing, the Houston toad has decreased in abundance throughout the entirety of its distribution and has been extirpated from 3 of the 12 counties with known historical occupancy (Forstner et al. 2007). As with other amphibians, population declines can be linked to an assortment of causes, although habitat loss and
fragmentation have long been considered the primary drivers of negative Houston toad population dynamics (Brown 1971). The Lost Pines ecoregion in Bastrop County has historically supported the majority of Houston toads, and until recently it has been the only county thought to contain fairly robust populations (Brown 1971; McHenry 2010; Duarte et al. 2011).

Since the Houston toad was first listed as endangered, biologists have learned a great deal about the species’ habitat preferences, reproductive biology, and population dynamics. The Houston toad is a habitat specialist, showing strong preference for deep sandy soils and forest cover in proximity to breeding ponds (U.S. Fish and Wildlife Service [USFWS] 1984; Buzo 2008; Vandewege et al. 2013). Breeding sites consist of pools of water with variable depths and hydroperiods, with increased reproductive success occurring in ponds with gentle sloping banks (slope < 10°; Forstner and Ahlbrandt 2003).

Houston toad reproductive behavior is sex dependent. Males typically form large aggregations at breeding ponds at irregular intervals between late January and early May (Hillis et al. 1984; Swannack 2007). Breeding events have a greater probability of occurring on nights with relatively high absolute humidity and low wind speed, and subsequent to Houston toad breeding activity the previous night (Brown et al. 2013b). Notably, mating success does not appear to be influenced by the size of the individual male toad (Jones et al. 2011), nor does mating success appear to deter males from returning to breeding ponds on subsequent nights (Hillis et al. 1984; Jacobson 1989). Females, in contrast, typically will only visit breeding ponds where large aggregations of chorusing males are present (Gaston et al. 2010), and they generally will not revisit the breeding ponds once successful mating occurs within a given season (Jacobson 1989). Hatfield et al. (2004) calculated a mean Houston toad clutch size of approximately 1,773 eggs per reproducing female using data reported by Kennedy (1962) and Quinn and Mengden (1984). A 50:50 juvenile sex ratio for individuals that emerge from breeding ponds has been confirmed from captive reared Houston toads (M.R.J.F. and P. Crump, unpublished data). Yet, data collected on a wild population suggest there is a 5:1 male-biased sex ratio for adult Houston toads (Swannack and Forstner 2007). The disparity between the two sex ratios may be linked to female Houston toads not reaching sexual maturity until 2 y of age, whereas males reach sexual maturity at 1 y of age (Swannack and Forstner 2007), a finding supported by lab experiments (Quinn and Mengden 1984).

Survival probabilities have been estimated for the species. Hatfield et al. (2004) analyzed more than 10 y of female Houston toad capture–recapture data and estimated annual apparent survival to be 0.20 for females that were at least 1 y old. Swannack (2007) conducted a 5-y adult male Houston toad capture–recapture study and estimated annual apparent survival to be between 0.15 and 0.27. Although juvenile survival has not been directly estimated, Swannack et al. (2009) were able to narrow the range in plausible Houston toad juvenile survival probabilities by using a pattern-oriented modeling approach. Through a series of simulations, they found that an annual juvenile survival probability (i.e., from egg life stage to the next breeding season) of 0.0075 to 0.015 when paired with an adult male survival probability of 0.15 yielded population projections that were similar to that resulting from intensive field sampling. Surprisingly, there is currently no evidence that amphibian chytrid fungus Batrachochytrium dendrobatidis is negatively impacting Houston toad or other local anuran populations in the Lost Pines ecoregion, despite being present generally and within the Houston toad population specifically (Gaertner et al. 2010, 2012). Results from a population viability analysis suggest that Houston toads in Bastrop County can achieve a low probability of extinction if two or three subpopulations that are connected via dispersal corridors are protected and managed for the species (Hatfield et al. 2004). However, long distance (i.e., >100 m) Houston toad dispersal is rare (Vandewege et al. 2013).

Because of the generally negative outlook for Houston toad viability, Texas State University in conjunction with the Houston Zoo Inc., the Texas Parks and Wildlife Department, and the USFWS, concurrent with a strong commitment by the Capitol Area Council of the Boy Scouts of America, has integrated a Houston toad headstarting (i.e., captive rearing) program into recovery initiatives, with headstart releases at all life stages occurring on the Griffith League Ranch (GLR) since 2008. Notably, these efforts have led to successful Houston toad reproductive events in the wild (M.R.J.F., unpublished data). Indeed, there was cautious optimism for the future of Houston toad recovery on the GLR, particularly in 2010 after documenting a relatively large number of toads attempting to breed (Duarte et al. 2011). In 2010, we captured 112 individuals (92 males, 20 females), which is more than three times the number of individual toads captured during each of the previous breeding seasons (2006–2009). However, in 2011...
extreme drought conditions in Bastrop County resulted in no detected Houston toad reproductive activity for the first time since we began annual monitoring of the property in 2000. Furthermore, the drought, coupled with >60 y of fire suppression, lack of forest thinning management strategies, and wind gusts in excess of 58 km/h caused by the passage of tropical storm Lee, culminated in high-severity wildfires in the Lost Pines ecoregion from September through October 2011. Those fires burned ca. 39% of the ecoregion and 55% of the GLR.

Notably, population model results suggest wildfires and drought conditions reduce Houston toad population growth rates by more than 75% when these events occur independently (Seal 1994). Moreover, because of the catastrophic nature of the wildfire, the immediate concern from agencies and landowners was the possibility of substantial direct mortality to native flora and fauna (Lost Pines Recovery Team 2011). Thus, our objective was to document the status of the Houston toad on the GLR after years of drought and the occurrence of high-severity wildfires. Through the use of a simulation model, we also provide quantitative evidence for why individual Houston toad captures are critically low on the property, despite continued intensive monitoring of the Houston toad and other herpetofauna throughout Bastrop County after the drought and subsequent wildfires.

**Study Area**

The Lost Pines ecoregion in Bastrop County, Texas, has historically supported the largest populations of Houston toads across the species’ geographic distribution (Brown 1971; USFWS 1984). Within Bastrop County, Bastrop State Park and the GLR are considered primary Houston toad recovery sites because they are large conservation-oriented properties located within critical Houston toad habitat. This study was conducted on the GLR, a 1,948-ha ranch owned by the Boy Scouts of America. The GLR is a primarily forested ranch with an oxbow dominated by loblolly pine *Pinus taeda*, post oak *Quercus stellata*, blackjack oak *Quercus marilandica*, and eastern red cedar *Juniperus virginiana* and an understory dominated by yaupon holly *Ilex vomitoria*, American beautyberry *Callicarpa americana*, and farkleberry *Vaccinium arboreum*. The GLR contains 3 permanent ponds (i.e., ponds have not dried in at least 12 y, inclusive of exceptional drought), 10 semipermanent ponds (i.e., ponds typically dry several times per decade), and 10 or more ephemeral pools (i.e., pools hold water for weeks to months annually, depending on rainfall). The high-severity wildfire on 4 September 2011 burned 987 ha of this habitat patch, followed by a second wildfire on 4 October 2011 that burned an additional 80.5 ha, for a total fire effect on ca. 55% of the property (Figure 2).

**Methods**

**Sampling design**

We monitored Houston toad activity on the GLR in the 2011–2013 breeding seasons through anuran call surveys, drift fence arrays, and visual confirmation of reproduction. For drift fence monitoring, we used 18 Y-shaped and 7 linear drift fence arrays. Y-shaped arrays consisted of three 15-m arms with a 19-L center bucket and a 19-L bucket at each arm terminus. Linear arrays consisted of a 15-m arm with a 19-L bucket at each end, and a double-throated funnel trap in the center of the array on each side of the flashing. We equipped pitfall traps with flotation devices to mitigate mortality during bucket flooding, and both pitfall and funnel traps were supplied with wet sponges to provide a moist environment. We also equipped pitfall traps with predator exclusion devices (Ferguson and Forstner 2006). Wildfires that occurred in fall 2011 resulted in 14 traps (11 Y-shaped arrays and 3 linear arrays) located in burned areas, and 11 traps (seven Y-shaped arrays and four linear arrays) located in control areas.

In addition to sampling herpetofauna using traps, we carried out anuran call surveys following the protocol of Jackson et al. (2006). We focused call surveys on nights when Houston toads were most likely to be active based on environmental preferences derived from long-term data collected on the GLR (Brown et al. 2013b). Furthermore, each year we greatly exceeded the 12 call surveys required to surpass 95% confidence regarding presence–absence of the species at a given pond (Jackson et al. 2006). We began surveys at dusk and surveyed each pond retaining water once per survey night for 5 min. When we detected calling Houston toads, we searched the ponds and surrounding areas, and we captured the toads that were present. We individually marked all toads captured in drift fence arrays and at ponds via toe clipping (Ferner 2007).

Successful reproductive events were monitored through visual searches for anuran egg strands and tadpoles in ponds, visual searches for emerging toadlets, and captures of toadlets in drift fence arrays. Visual searches for anuran egg strands in all ponds were conducted during daylight hours by trained observers after detected calling activity. If we did not find evidence of a successful reproductive event (i.e., no egg strands, no tadpoles, and no emergent toadlets), we assumed Houston toad reproduction did not occur on the property in the given year.

**Simulation model**

Individual captures on the GLR were insufficient to calculate robust estimates of Houston toad abundance in breeding seasons post-2010. To understand why individual captures have decreased since 2010, despite continued high sampling effort, we used a simulation model. Demographic and abundance estimates incorporated into our simulation came from previous Houston toad studies. Within our simulation model, we incorporated demographic stochasticity (i.e., random variation in demographic estimates). The inclusion of this type of stochasticity in simulation models is typical, particularly when modeling populations with low abundance (Morris and Doak 2002; Akçakaya et al. 2004). The sampling distribution for each population parameter was selected based on that distribution’s shape, range, and standard
use in population models (Caswell 2001; Beissinger and McCullough 2002; Morris and Doak 2002; Akcakaya et al. 2004). In addition, in years in which there was a lack of evidence for a successful reproductive event, our simulation assumed no reproduction occurred (i.e., we fixed clutch size to zero for those years). In all other years, the simulation model assumed every 2-y-old female was an adult and that all adult females successfully reproduced.

The initial adult male abundance was randomized by sampling an integer between 148 and 360 (mean ± 2 SE), assuming a uniform distribution (Duarte et al. 2011). We used a uniform distribution to incorporate the uncertainty associated with the abundance estimate. Using a uniform distribution meant each value within the possible range had an equal probability of being selected in each iteration. The initial adult female abundance was randomized by dividing the selected number of adult males by 5 and rounding this number to the nearest integer to incorporate the adult sex ratio (Swannack and Forstner 2007). The number of initial immature females (1-y-old female toads) was difficult to predict because no empirical data are available. However, we know that 47 adult male toads were captured in 2009 (M.R.J.F., unpublished data) and that we captured roughly 35.2% of the adult male Houston toads in 2010 (Duarte et al. 2011). We assumed we captured the same proportion of total adult male toads present in 2009 as we did in 2010, and we used the adult sex ratio reported by Swannack and Forstner (2007) to estimate the total number of adult female toads present in 2009 (ca. 27 individuals). We then calculated the number of eggs deposited in 2009, and by extension, the number of surviving immature females for 2010 using the methods described below. The clutch size per adult female for each year (except years in which there was a lack of evidence for a successful reproductive event) was randomized by sampling from a Poisson distribution for each adult female present that particular year, while setting the mean clutch size ($\lambda$) to 1,773 (Hatfield et al. 2004).

The juvenile survival probability was randomized in each iteration by sampling from a uniform distribution.

Figure 2. Aerial image of the Griffith League Ranch (GLR), Bastrop County, Texas, and its location with respect to a 13,406-ha wildfire that occurred in the Lost Pines ecoregion in September 2011, and a 125-ha wildfire that occurred in October 2011. Overlain on the image are the wildfires and the locations of the drift fence arrays and ponds. The September 2011 wildfire burned 987 ha (50.7%) of the GLR, and the October 2011 wildfire burned 80.5 ha (4.1%) of the GLR. On the right are images of the terrestrial habitat around a drift fence array on the GLR before (A), shortly after (B), and ca. 1 y after (C) the high-severity wildfires. Nearly all of the understory vegetation, litter, duff, and coarse woody debris were consumed within the burned area, alongside nearly complete overstory tree mortality. However, natural understory revegetation occurred quickly after the wildfires.
that ranged from 0.0075 to 0.015 (Swannack et al. 2009). We chose a uniform distribution for this process because these estimates were derived using a pattern-oriented modeling approach, not a capture-recapture study. Thus, a mean estimate and its associated variance were not available, and there is considerable uncertainty with this estimate. The number of eggs in year $t$ that resulted in a new individual surviving to year $t + 1$ was estimated by sampling from a binomial distribution for each egg in year $t$ with a probability of success equal to the selected juvenile survival probability. To estimate how many of these surviving juveniles were male, we sampled from a binomial distribution for each surviving juvenile with a probability of success $= 0.5$ (assuming a 50:50 sex ratio). The difference between the number of juvenile survivors and the number of male juvenile survivors was calculated to determine how many of the surviving juveniles were immature females. The number of adult males that survived from year $t$ to $t + 1$ was estimated by sampling from a binomial distribution for each adult male in year $t$ with a probability of success $= 0.15$, because this estimate is considered the more realistic adult male survival probability based on intensive field data (Swannack et al. 2009). Thus, the total number of adult males for each time step was calculated as the sum of the number of juvenile and adult males that survived from the previous year. The number of adult females that survived from year $t$ to $t + 1$ was estimated by sampling from a binomial distribution for each adult female in year $t$ with a probability of success $= 0.20$ (Hatfield et al. 2004). Likewise, the number of immature females that survived to be an adult from year $t$ to $t + 1$ was estimated by sampling from a binomial distribution for each immature female in year $t$ with a probability of success $= 0.20$ (Hatfield et al. 2004). Thus, the total number of adult females for each time step was calculated as the sum of the number of immature and adult females that survived from the previous year.

We ran the simulation model for 10,000 iterations. Each iteration was run for 5 y, with the first year corresponding to the 2010 breeding season. The 0.025, 0.5, and 0.975 quantiles for the abundance estimates of adult male and female toads in each year across all iterations were used to track adult Houston toad abundance over time. The simulation model was conducted in program R (R Core Team 2013; Supplemental Material, Text S1, DOI: 10.3996/112013-JFWM-071.55).

### Results

In 2011, we conducted 33 call surveys and trapped for 102 nights, with no detected calling activity and two adult females captured in traps. In 2012, we conducted 33 call surveys and trapped for 72 nights, with 13 unique adult males detected during call surveys and no captures in traps. For the 13 individuals detected during call surveys, we obtained 21 total recaptures, including one toad recaptured six times over a 2-wk period. In 2013, we conducted 24 call surveys and trapped for 50 nights. During call surveys, we captured one adult male and one adult female, and we detected two additional calling males that we were unable to capture. In addition, for 2013 a total of two amplexant pairs were observed at a single breeding pond, and two other individuals were captured in traps, both of which were 2013 adult headstart releases. We had released 50 adult headstarted individuals on the GLR 8 d before, and an additional 75 individuals 1 d before, the observed breeding event. Based on the size of individuals (assessed by visual observation, recently released headstart Houston toads are much larger than wild Houston toads), the amplexant toads likely included one wild male, one headstart male, and two headstart females from headstart releases 1 or 8 d before capture. The pairs were not disturbed during amplexus to prevent disrupting reproduction. Refer to Table 1 for a summary of the survey effort and detections of unique non-headstarted Houston toads on the GLR, 2010–2013.

The simulation model results indicated both adult males and females had a decrease in abundance on the GLR from 2010 to 2013 (Figure 3). In the 2013 breeding season, our simulation model suggested there were ca. 12 (95% CI = 4–23) adult male toads and 22 (95% CI = 9–40) adult female toads. In the 2014 breeding season, our simulation model suggested there were ca. 4 (95% CI = 1–10) adult female toads, however, the number of adult male toads increased to ca. 215 (95% CI = 71–504).

### Discussion

We have captured a remarkably low number of Houston toads on the GLR since the 2010 breeding season, particularly given the high sampling effort. We do not consider low captures in a single year to be conclusive evidence of a dramatic reduction in abundance because of the strong connection between spring weather and breeding activity (Brown et al. 2013b); but low captures, along with a lack of detected reproduction events, over three consecutive years is certainly cause for alarm. The intuitive association would be to link this decline in captures and detected reproductive events on the GLR to the seemingly catastrophic wildfires in fall 2011. However, there is no empirical evidence to suggest immediate adverse effects of the wildfires on abundance and diversity of other herpetofauna on the GLR (Brown et al. 2014a), and we detected individuals and reproduction within the burn zones on the GLR and elsewhere in both the 2012 and 2013 breeding seasons. Furthermore, individual Houston toad captures and reproduction were compar-
attractively high at Bastrop State Park in 2013, despite the same high-severity wildfires on the property (M. C. Jones, Department of Biology, Texas State University, personal communication). If wildfire impacts were driving the Houston toad decline on the GLR, then we would expect similar effects on other anurans as well as at other properties within the burn zone. Moreover, our simulation model did not include detrimental effects on vital rates because of the wildfires, yet it predicted realistic abundance estimates for 2013 that agreed with our individual captures from intensive field sampling. Thus, it seems that the population of Houston toads on the GLR would have had dramatic declines in abundance regardless of the wildfires. The lack of empirical evidence to suggest immediate adverse effects of the wildfires on herpetological populations, including the Houston toad, in Bastrop County agrees with the current growing body of literature concerning herpeta-fauna–fire relationships (Guscio et al. 2007; Hossack and Corn 2007; Langford et al. 2007; Ashton and Knipps 2011; Brown et al. 2011; Hossack et al. 2013).

Our simulation model suggests the adult Houston toad population on the GLR was at a critically low number in 2013 (Figure 3). Although the abundance estimate for 2014 suggests the number of adult male Houston toads could potentially rebound to ca. 215 individuals, it should be noted that our simulation model was conservative and that such a rebound is unlikely. The simulation model assumed every individual adult female successfully reproduced. The density of Houston toads on the GLR may be inadequate for large enough aggregations of chorusing male toads to form to successfully attract female conspecifics to breeding ponds (Gaston et al. 2010). Thus, it is highly plausible that, given the estimated Houston toad densities, not every adult female toad in the wild will successfully reproduce every breeding season. Furthermore, the vital rate estimates used in our simulation model were conservative. These estimates were calculated based on data collected when Houston toad populations were experiencing more favorable environmental conditions. It is worth noting that our simulation model did not include the possibility of individuals entering the population via immigration, but it did incorporate the opportunity for individuals to emigrate. The survival estimates used in our simulation model were calculated as apparent survival, not true survival. Apparent survival is the probability that an individual survives and remains in the study area from one year to the next. This could potentially be driving our decreasing population projection. However, interpond movement of Houston toads on the GLR and long-distance dispersal events are rare (Vandewege et al. 2013). Thus, immigration of individuals from neighboring properties probably does not significantly affect GLR Houston toad population dynamics.

Currently, Bastrop State Park, the GLR, and the Welsh Tract are the only permanent recovery sites in Bastrop County that explicitly manage for the Houston toad as a priority goal. Given the high conservation value of a Houston toad population on the GLR to persistence in the Lost Pines ecoregion, supplementing the population with captive-bred or headstarted individuals may be the only viable recovery strategy in the immediate future. However, current research suggests adult return rates for Houston toad headstarts released at the tadpole and recently metamorphosed toadlet life stages are similar to those of wild toads (Vandewege 2011). Furthermore, preliminary research on the GLR suggests adult headstart releases have low initial survival probabilities at release, potentially much lower than the average for adult wild toads (D.J.B., unpublished data). Thus, a substantial captive breeding initiative is likely required to dramatically increase adult Houston toad numbers on the GLR. Nevertheless, headstarting toads does not address the causative agents of the decline and thus cannot be the long-term solution. However, we note that if adult headstarted toads are released on nights with optimal breeding conditions, and successful reproduction occurs (as we observed in 2013), that is still a valuable outcome of the adult headstarting effort.

To further understand factors that are contributing to the decline of Houston toad populations, we are currently investigating the impacts of annual weather variability and the long-term climate trend on Houston toad survival and reproduction using simulation modeling, the influence of habitat patch size and connectivity on site occupancy using historical imagery and site records, and the influence of red imported fire ants Solenopsis invicta on terrestrial juvenile and adult Houston toad survival using field observations (see initial studies by Brown et al. 2012, 2013a). Although negative short-term wildfire effects on Houston toad population dynamics are not apparent, potential medium- and long-term effects are possible, because negative wildfire impacts can take 6 y or more to become evident (Hossack et al. 2013), and impacts can be related to an
assortment of factors (reviewed in Pilliod et al. 2003). Therefore, we are also currently investigating the impact of the wildfires and postfire restoration actions on vegetation structure, microclimate parameters (i.e., air temperature, absolute humidity, mean wind speed, maximum wind speed, soil temperature, and soil moisture), water quality as well as the community composition of arthropods (both aquatic and ground dwelling) and understory vegetation (see initial studies by Brown et al. 2014b, 2014c).

In summary, individual captures through intensive field sampling post-2010, in concert with our simulation model, suggest that the wild Houston toad population on the GLR may be extirpated in the near future if human-mediated recovery strategies, such as headstarting and captive breeding with subsequent releases, are not continued and refined. Unique individual detections of non-headstarted adult Houston toads declined from 112 in 2010 to 5 in 2013. The use of headstarted individuals to supplement wild Houston toad populations, although promising, has led to a new set of research questions regarding strategies to increase the effectiveness of this management approach. The future success of the Houston toad may heavily depend on research related to the efficacy of headstarting practices, and we encourage future work centered on this management strategy. Although the fall 2011 wildfires in the Lost Pines ecoregion were high-severity fires, there is currently no evidence suggesting those fires have had immediate detrimental impacts on Houston toad populations in the burn zone. Nevertheless, high-resolution data (i.e., fine-scale data on microclimate, vegetation structure and community, and community composition of arthropods) will be needed in the future to quantify how the fires affected Houston toad viability in the Lost Pines ecoregion over the medium and long term. We are likely documenting the real-time extirpation of an endangered anuran on a primary recovery site, which has enormous implications with respect to the persistence of the species within its last remaining stronghold. Thus, it is imperative that the forces contributing to the distribution-wide decline of this species be addressed to prevent Houston toad extinction in the wild.

Supplemental Material

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Text S1. Program R code used in simulation model for Houston toad Bufo (Anaxyrus) houstonensis population dynamics on the Griffith League Ranch, Bastrop County, Texas, 2010–2014. This simulation model includes demographic stochasticity, fixes clutch size to zero for years in which reproduction was not detected, and assumes there is a 50:50 sex ratio for surviving juveniles, females mature at 2 y, and all mature females successfully reproduced in years that clutch size is not fixed to zero. Found at DOI: 10.3996/112013-JFWM-071.S5 (65 KB DOCX).

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