MODELING ASPECTS OF THE ECOLOGICAL AND EVOLUTIONARY DYNAMICS OF THE ENDANGERED HOUSTON TOAD

A Dissertation

by

TODD MICHAEL SWANNACK

Submitted to the Office of Graduate Studies of
Texas A&M University
in partial fulfillment of the requirements for the degree of

DOCTOR OF PHILOSOPHY

August 2007

Major Subject: Wildlife and Fisheries Sciences

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Approved by:

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ABSTRACT

Modeling Aspects of the Ecological and Evolutionary Dynamics of the Endangered
Houston Toad.
(August 2007)
Todd Michael Swannack, B. A., Texas A & M University;
M.S., Southwest Texas State University
Co-Chairs of Advisory Committee: Dr. William E. Grant
Dr. James R. Dixon

The goal of my dissertation was to describe the dynamics of a group of Houston toads located at the Griffith League Ranch (GLR), Bastrop County, Texas. My research included using statistical modeling to predict activity and abundance, mark-recapture techniques to estimate survivorship, and simulation modeling to explore the impacts of the difference in age at first reproduction and to project the future dynamics of the population at the GLR.

From 2001 – 2005, 225 individual Houston toads (199 M : 26 F) were captured using two methods: breeding pond surveys and drift fences. Houston toads were neither caught equally among capture methods, nor across years. Toad activity was mostly confined within their breeding season, and activity was not continuous. A logistic regression indicated activity depended on time of year, mean precipitation, mean minimum daily temperature, and mean percent lunation as well as two-way interactions with moon-phase and other variables. Abundance depended on time of year, current precipitation, minimum temperature, and two-way interactions between time of year and the other two variables.

Twenty-one of the 199 males (10.5%) and no females were recaptured among years. The probability of male survival was estimated using program MARK. Eight of 16 candidate models were supported and all but one contained precipitation as a covariate, indicating precipitation is important for Houston toad survival. Survivorship estimates varied from 0.1 to 0.41.

The sex ratio was significantly male-biased. The odds of catching females in traps were 3.5 greater than capturing females in a pond, while the odds of capturing males in a trap were 0.28 compared to ponds. Results from a simulation model indicated the sex ratio is biased because of the difference in maturation times between males and females, coupled with high juvenile mortality.

Results from an individual-based, spatially-explicit, stochastic simulation model, indicated a relatively low probability (~ 0.013) of *B. houstonensis* going extinct at the GLR within the next 10 years. Emergent properties of the model were similar to results observed in the field or reported in the literature. The model also identified that dispersal of Houston toads should be a future research priority.

DEDICATION

This is dedicated to the memory of those who passed before me.

Jeffery
Grandpa
Grandma
Rico
Evie
Paw Paw
Grandma

Que en paz descanse

ACKNOWLEDGMENTS

First and foremost, I would like to acknowledge Dr. Michael Forstner's undying passion for the writings of Kurt Vonnegut. Mike's enthusiasm gave me a fierce desire to emulate Vonnegut's style the best I could, which is why you will not find a single semicolon in this manuscript. Not one. They are silly and unnecessary and all they do is prove you went to college. (Ok, there will be at least one to meet the formatting requirements – my principles are strong until graduation is involved). That being said, I am also glad that Dr. Forstner hired me those many years ago. Working for him is a life changing experience and I'm glad I did it.

I was very fortunate to have the advisors that I did. Both Dr. Grant and Dr. Dixon were excellent mentors and I learned more than I thought I could from both of them. Doc knows more about herps than anyone ever will and he always provided me with sound wisdom. Bill, on the other hand, knows very little about herps, but man, can he model stuff. He took a chance on me and I will be forever indebted to him for all of the opportunities he created. I really enjoyed my time in his lab.

Dr. Neal Wilkins and Dr. Mike Longnecker rounded out my committee and they were both terrific. They made themselves available to me and always answered my questions. I got lucky with my committee and they made this a positive experience.

I would like to acknowledge the Boy Scouts of America for allowing me access to the Griffith League Ranch. For 4 years, I chased toads all over that place, and it was a whole lot of fun, except when the monsters were chasing me.

Mary Dixon, Josie Duvall, and Ruth Forstner fed me when I looked hungry, which must have been often, because they always fed me. They are three of the nicest people I have ever met.

I did not work on this project alone and would like to thank my field crew. Kensley Greuter, Jake Jackson, and Shane Kiefer worked really hard and they deserve part of this degree. They're not getting any of it, but they deserve it. Diana McHenry has been a good friend for years and continues to be so. I was glad she was became my counterpart in the lab. Without her, things could have been a lot funkier. Bret Collier and Mike Sorice helped me with some of my stats, and I thank them both. My undergrad, Trey Towers, far exceeded what was expected of him. Thanks. Damon Hall knows more words than he should, which worked out well when I ran out of my own.

My lab mates from the Systems lab were flat-out awesome (Edith, Karine, Magui, Mike, Tulia). They embraced me and made me part of their group, even though I couldn't understand most of what was going on. ¡*Hijole*! Special thanks to Mike Kjelland for coming up with cool diversions – one day we will win a ba-zillion dollars. Tulia provided a lot of background information on the EMYCIN algorithm, helped me with some computer stuff I didn't understand (Camtasia, PowerPoint, ArcGIS), and was always there when I needed someone. She also kept me sane when I got a little stressed, so that was nice because I don't hold my crazy that well.

While I was here, I met a rock band from Spain, *Los Aggieñoles*, and they were great. They gave me a lot of cool music, and made me feel cooler than I probably am, but who keeps track of that stuff? So to Joack y Cris, y Agustín y Mar – *muchísimas* *gracias. Y Daniel – ¡Bienvenidos!* (Ok, I'm a little late on that, but I'm not quite sure how to say what I want to say in Spanish).

I have been fortunate to have great friends and they deserve some recognition. First, *The Boys,* without those guys, I don't think I would have had the courage to tackle half of the things I've faced. So, to Tim and Bryan: thanks for the last 20+ years. Suzy and Jodi came along at some point and I'm happy they did – who else would listen to me when I was making a big deal out of something small? Chris took me to a couple of football games (yeah, Gig 'em), and provided a voice of reason anytime I needed it, which was often. Leigh can make me laugh and has treated me very well, but she just doesn't wear enough maroon. Artie braved the outdoors to paint some beetles, and along with Vaden, Stacey, and Abe, made the trek to College Station to see me. If that's not friendship, I don't know what is. Brandon has always read anything I've asked him to, including the introductory chapter to this work. His comments have greatly improved anything I have written. Pickett and Lori answered their phones whenever I freaked out enough to call and I really value their opinions. I am really gland I worked at Origin. Mike Vayo and Cullen provided hours of distractions via *the email* – that was a lot of fun. The entire Schuelke family are some of my favorite people in the world – they're just great. The Koch family made the mistake of feeding me once, and I haven't left them alone since. Keith and Pam Blount did the same. Suckers. The Towns-Schwarzes or Schwarz-Townses (or Kathy and Tim for short), have treated me well for years – if I showed up in the middle of the week, they made sure the beer was cold, if I need a job writing captions, they offered, and if I needed to be reminded of how good Deadwood was, they reminded. I didn't watch it, but they reminded.

Finally, I would like to thank my family. Mom and Dad have been very supportive and I am grateful for that. Margie came along about halfway through this and she's added a new sense of vigor to our family. My uncles (and aunts) Charles (& Diane), Joe (& Suzy), Allen (& Scarlett), Jon (& Sandra), and Elaine (& Gary) were unquestioningly supportive. Ashley provided me with hours (and hours and hours) of conversation and has been become a great friend. John is a good brother, shoots straight, and I couldn't ask for anything else. Shawntel is still convinced that toads are creepy, but I have the rest of my life to change her mind. Flicker and Switters put up with a lot, especially during *go time*, so they probably deserve another mouse to chase. And then there's my brother Craig. What would I do without him? He is a truly great guy and I am going to enjoy watching him be an even better father.

This was a lot of fun.

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CHAPTER I

INTRODUCTION

Amphibian declines

Amphibian populations have been on the decline worldwide for the last 25 years (Barinaga 1990). Within the last fifteen years there has been a concerted effort, not only within the herpetological community, but also the scientific community as a whole, to determine the factors causing the decimation of these populations. A single factor does not appear responsible for the decline, and some regions and species are not affected (Pechmann et al. 1991). There are four major groups of hypotheses thought to be responsible for the decline of amphibian populations: emerging infectious diseases (EIDs), global climate change, human-mediated activities, and normal population fluctuations mistakenly identified as population declines (Collins and Storfer 2003).

Three main EIDs have been documented to cause heightened mortality in amphibian populations. The most prevalent EID is chytridiomycete fungus (*Batrachochytrium dendrobatidis*), an intracellular fungus which infects keratinized tissue of both larvae and adults. This fungus has been linked to amphibian population declines across the globe (Berger et al. 1998). Current data indicate *B. dendrobatidis* is detrimental to montane, stream breeding species with low fecundity (Green and Kargarise-Sherman 2001, Daszak et al. 2003). *Ranavirus spp*. was linked to declines in populations of *Ambystoma tigrinum* in North America (Jancovich et al. 1997), and *Rana temporia* in the United Kingdom (Cunningham et al. 1996). *Saproglenia* water molds, which cause egg

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This dissertation follows the style of *Ecology*.

mortality in amphibians was linked to declines in populations of *Bufo boreas* and *R. cascadeae* in the Northwest United States (Blaustein et al. 2003).

Historically, climate change occurred gradually and species were able to respond by either shifting their geographic distribution or by adapting to local conditions. Within the last 50 years, weather patterns have changed at an unprecedented rate (Pounds and Crump 1994). Current predictions foretell rapid changes in weather patterns and therefore species with limited dispersal abilities may not be able to move to favorable habitat, nor will they have the time to evolve to the new conditions. Climate change coupled with chytridiomycosis is thought to have caused the extinction of the golden toad (*B. periglenes*) as well as accelerated the decline of the harlequin frogs (*Atelopus* spp.) (Pounds and Crump 1994, Pounds et al. 2006).

Human-mediated activities that alter habitat in an irreversible way, such as residential or commercial development (and the associated infrastructure), clearing forests for logging or agricultural practices, or draining wetlands, are detrimental to any wildlife population (Soulé 1986). These activities fragment the landscape, creating a matrix of native habitat patches interspersed among untraversable, foreign habitat types. Connectivity among native patches is reduced. While each species can tolerate different levels of fragmentation (Kolozsvary and Swihart 1999), if habitats are altered too much or patches are too small, local populations will be displaced or become extinct (Hanski 1982, Wilcove et al. 1986). Taxa requiring multiple habitat types are especially vulnerable to the effects of anthropogenic habitat destruction. Many amphibian species depend on both aquatic and terrestrial habitats to complete their life cycles (Duellman and Trueb 1994) and if movement between these necessary habitat types (i.e., breeding ponds and upland foraging/aestivation sites) is hampered, then the probability of extinction increases for that population and/or species. Very few amphibian populations have not been affected by human development (Blaustein et al. 1994, Semlitsch 2000, Collins and Storfer 2003). While the literature is replete with examples of how amphibians have been affected with habitat fragmentation caused by humans (Fahrig 1997, Marsh and Pearman 1997, Kolozsvary and Swihart 1999, Marsh and Trenham 2001), it is important to understand these processes are irreversible and management decisions need to focus on the best possible strategies given the existing conditions (Semlitsch 2000).

All biological populations fluctuate in size due to stochasticity in birth or death rates caused by either intrinsic or environmental factors (demographic or environmental stochasticity, respectively) (Krebs 2001, Turchin 2003). Few studies on amphibians have collected enough data to determine if a population's decline is a descent to extinction or simply a low point in a normal population cycle (Connell and Sousa 1983, Pechmann et al. 1991). Without long-term datasets on the population dynamics of amphibians, it becomes impossible to distinguish between a population on the verge of extinction and one that has the potential to naturally rebound (Blaustein et al. 1994). Every species has a specific suite of life history characteristics (such as mortality rates, age at first reproduction, sex ratio, etc…) that shape its demography. Without obtaining data for these characteristics, as well as understanding the relationships among them, accurate predictions of how a species will react to perturbations to its environment –

such as fragmentation or the introduction of a disease – are difficult to make. Species with limited geographic distributions are of special concern because they are especially vulnerable to exogenous factors, and have a higher probability of extinction compared to species with large, continuous ranges (Wilcove et al. 1986). Since these species are generally rare and/or threatened, it is important to understand their biology, and therefore gather as much data as possible so that conservation actions can be effective.

The decline of amphibian populations is inherently complex and probably not the result of a single factor (Blaustein and Wake 1990). Each of the above hypotheses has been linked to population declines and /or extinctions. However, there are several species that appear to be on the verge of extinction, yet ecological data are sparse for those species. Without long-term monitoring of a population, management decisions will not effectively conserve the ecological and genetic fingerprints of these species.

There are 13 endangered amphibians in the United States. Each has a limited geographic distribution – eight of these species are salamanders which are restricted to specific spring-fed systems and the remaining five species are anurans: two frogs and three toads (Stebbins 1985, Conant and Collins 1991). One of these species, the Houston toad, *Bufo houstonensis* (Sanders (1953)) has received considerable media attention due to its endangered status. The species is currently perceived to be at critically low levels throughout its geographic distribution due to both human-mediated habitat destruction and recent drought like conditions in South Central Texas. Many aspects of the Houston toad's natural history remain unreported. Given that gaps exist in the knowledge of this species, it is imperative to collect more data on this species in order to establish a viable conservation plan.

Natural history of the Houston toad

The Houston toad (*Bufo houstonensis*) is a relict descendant of southernmost populations of the narrow-skulled *Bufo americanus* species group, diverging from southernmost populations of ancestral *B. americanus* within the last 10,000 years (Blair 1972). *Bufo houstonensis* was formally described in 1953 based on its geographic distribution and skeletal morphology (Sanders 1953). Hillis et al. (1984) reconfirmed *B. houstonensis*' specific status molecularly, through starch gel electrophoresis, and morphologically using a discriminate function analysis based on seven morphological characteristics: headwidth, distance between interocular crests, length of paratoid gland, width of paratoid gland, length of tibiofibula, snout-urostyle length, and the distance between paratoid glands and the transverse axis of postorbital crests.

Bufo houstonensis is restricted to areas with deep sandy soils, and is generally associated with pine (generally Loblolly *Pinus taeda*) or mixed hardwood forests (Brown 1971). The paucity of these habitats and the destruction of these habitat types associated with the urban expansion during the last half of the 20th century has limited the geographic distribution of *B. houstonensis* to nine Texas counties with the largest group occurring in the Lost Pines region of Bastrop County, with smaller, isolated groups found in adjacent Burleson and Lee counties (Dixon 2000, Gaston et al. 2001). This limited distribution alongside perceived declines caused *B. houstonensis* to be listed on both the national and international endangered species lists (Gottschalk 1970, Honegger 1970). Even though *B. houstonensis* has been listed as endangered for over 30 years, many natural history and demographic characteristics necessary for conservation remain unknown.

Early work on Houston toads focused mainly on pre- or post-mating isolating mechanisms, including vocalization (Blair 1956) and hybridization (Kennedy 1962, Brown 1971). The majority of population-level data came from two studies: Hillis et al. (1984), and Price (2003), with Jacobson (1989) building on the work of former. All of these studies occurred in Bastrop County, Texas. Data for all of these studies were collected during the breeding season and therefore the breeding behavior has been well documented.

Reproductive activity for *B. houstonensis* extends from late January through early May (Hillis et al. 1984), although poor environmental conditions can delay breeding (Kennedy 1962). *Bufo houstonensis* does not breed continuously throughout the season, instead activity is confined to 3 – 7 day spurts. Male toads assemble at ponds (either ephemeral or permanent) early in the season (generally around the middle of February) and attract females through chorusing. Females arrive at the ponds later in the season, during the peak of male activity (around the second week in March). Within a given season, individual males will return to the same pond (Jacobson 1989) and females rarely visit the pond more than once (Price 2003). In between these short breeding periods, and after the reproductive season is finished, adult Houston toads are rarely seen above ground. Both Hillis et al. (1984) and Price (2003) hypothesized that temperature, precipitation, and moon phase drive *B. houstonensis* activity, but specific levels of these environmental factors have not been quantified. Currently, there is not any information regarding the year around activity of Houston toads.

Bastrop County is composed of a matrix of forested and non-native pasture lands, and it is unknown how Houston toads utilize pastures composed of non-native grasses. Further, general movement patterns of Houston toads are not well understood. During the breeding season, adult males move to a pond and stay within 50 meters (m) of the pond throughout the season (Hillis et al. 1984, Jacobson 1989). Price (2003) documented movement through a long term (14 year) capture-recapture study at BSP and adult Houston toads moved a maximum of 1,600 meters between breeding seasons (Price 2003). Female movements have not been well documented and movement outside the breeding season for either sex has not been reported.

Using the capture-recapture data from the BSP, annual survivorship for female *B. houstonensis* was estimated at 0.2022 per year (Hatfield et al. 2004). These data were incorporated, along with recruitment data from a captive study (Quinn and Mengden 1984), into a population viability analysis (PVA) of female Houston toads (Hatfield et al. 2004). This PVA stated juvenile survivorship must be higher than 1% in order for populations to survive. Further, the PVA stressed the importance of maintaining multiple breeding populations as a way to maintain genetic variability (Hatfield et al. 2004). Caswell (2001) emphasized the necessity for these models to include survival estimates for both sexes. Survival estimates for male *B. houstonensis* have not been calculated.

Both Hillis et al. (1984) and Price (2003) reported male-biased sex ratios for populations of *B. houstonensis* in Bastrop County, Texas. Both of these studies were limited to individuals collected at chorusing ponds. Male Houston toads congregate at ponds and vocalize to attract females. Given this breeding strategy, the sex ratio at the ponds (termed the operational sex ratio (Wells 1977)) is expected to be skewed towards males and most likely does not reflect the actual proportion of each sex in the population. Sex ratios can be naturally biased because of an unequal sex ratio at birth, differential mortality between the sexes, differential migration rates between the sexes, or differential maturation rates (Wilson 1975, Gibbons 1990). Gibbons (1990) stressed the importance of the difference in age at first reproduction on the demography of turtles, but this has not been shown for anurans. Data gathered from a captive study on *B. houstonensis*, demonstrated a difference age at first reproduction between males and females (Quinn and Mengden 1984). Male *B. houstonensis* matured in one year while females matured in two. If males and females mature at different rates, the adult sex ratio is biased towards the earlier reproducing sex, which, in turn, lowers the effective population size (Gibbons 1990). The impacts of this life history characteristic on the demography of *B. houstonensis* have not been explored.

In order for conservation to be successful, the evolutionary history, ecological dynamics, and response to anthropogenic perturbations must be understood for the species (Meffe and Carroll 1997). The purpose of this research is to illuminate some of the enigmatic aspects of the natural history of the Houston toad and to reduce the uncertainty associated with specific life history characteristics through statistical and / or simulation modeling. The major objectives were as follows:

(1) To describe the dynamics of *B. houstonensis* located at the GLR.

(2) To quantify and predict the activity patterns of *B. houstonensis*.

(3) To estimate annual survivorship of male *B. houstonensis*.

(4) To determine the impacts of the difference in the age at first reproduction on the demography of *B. houstonensis* using a mathematical simulation model.

(5) To synthesize the results from the above objectives into an individual-based, spatially explicit simulation model to explore the ecological dynamics of *B. houstonensis*.

This study was completed in collaboration with Dr. Michael Forstner of Texas State University at San Marcos. Dr. Forstner provided data collected under the following permits (issued to Dr. Forstner: Unites States Fish and Wildlife: TE 039544-0 and TE 039544-1, Texas Parks and Wildlife: SPR-0102-191, Institutional Animal Care and Use Committee: Texas State University at San Marcos: 5Qrs45_02).

CHAPTER II

DYNAMICS AND ACTIVITY PATTERNS OF THE HOUSTON TOAD AT THE GRIFFITH LEAGUE RANCH, BASTROP COUNTY, TEXAS

Introduction

The federally endangered Houston toad, *Bufo houstonensis*, is currently limited to nine Texas counties (Dixon 2000, Gaston et al. 2001), with its largest and most robust population located in Bastrop County. Although *B. houstonensis* was listed as endangered in 1970 (Honegger 1970), very little published information is available regarding the population dynamics and general ecology of this species. Early work on the species explored the effects of hybridization with its sympatric congeners and provided little information on its ecological dynamics (Kennedy 1962, Brown 1971). Hillis et al. (1984) conducted the first study describing the reproductive ecology of *B. houstonensis*. Beginning in 1991, Price (2003) conducted a 14-year, mark-recapture study of *B. houstonensis* at Bastrop State Park (BSP). Hatfield et al. (2004) estimated female survivorship from the BSP data, but these data are from a single location within Bastrop County and are only from a subset of ponds at BSP. According to results reported by Price (2003), the *B. houstonensis* population in Bastrop County is currently declining and abundance is the lowest it has been in the last 20 years.

While both Hillis et al. (1984) and Price (2003) did extensive work on *B. houstonensis*, their studies were inherently restricted to the breeding season (late January – early May) and individuals were only collected at ponds where chorusing occurred. Since Houston toads have only been monitored during the breeding season, year-around activity and movement patterns of the species are unknown. If the data from Price (2003) are accurate, and *B. houstonensis* is declining, then more information must be gathered on the species for conservation efforts to be successful.

During the breeding season, activity is not continuous and occurs in 3-5 day periods (Hillis et al. 1984, Jacobson 1989, Price 2003). The specific environmental cues used by *B. houstonensis* to initiate breeding behavior during the breeding season remain enigmatic. Hillis et al. (1984) hypothesized that *B. houstonensis* emergence was correlated, in part, with minimum daily temperature, precipitation, and possibly algal growth. Price (2003) emphasized the importance of the phase of the moon on toad activity. Activity in other species of *Bufo* has been linked to several environmental factors. Temperature and precipitation were reported as the most important variables affecting *B. americanus* behavior (Fitzgerald and Bider 1974). Captures of adult *B. quercicus* increased with increasing precipitation (Greenberg and Tanner 2005b). *Bufo boreas* emerged from nightly refugia based on the temperature (Smits and Crawford 1984). Weather patterns are important in the life history of most Bufonids, however, quantitative models used to predict toad activity based on weather patterns do not exist. These models would be extremely useful for researchers and/or land managers as they would then have a tool to determine when Houston toads would be active.

Hillis et al. (1984) believed the biggest threat facing *B. houstonensis* was habitat destruction caused by an increasing human population. In Bastrop county, the Houston toad resides in the Lost Pines ecoregion, a remnant stand of loblolly pine (*Pinus taeda*) (Al-rabab'ah and Williams 2004). During the last several decades, this landscape has become fragmented and is now interspersed within a matrix of residential and agricultural lands. The Houston toad is predominately a woodland species (Brown 1971) and it remains unknown if non-native pasture lands are dispersal barriers for *B. houstonensis*. Given the continuous and currently high level of fragmentation of Bastrop County, it is imperative to determine how *B. houstonensis* utilizes patches of non-native passture grasses.

During the mid-1980s, Houston toads were discovered on the Griffith League Ranch (GLR) in Bastrop County (A. Price, 2002, pers. comm. to M. Forstner). The GLR is the last remaining undivided “league” ranch originally deeded to the men who fought in the Texas revolution by Sam Houston. It is a “league by a league” (1,948 ha) of mostly pine-oak woodlands. The Boy Scouts of America (BSA) inherited the land in the 1990s, but the land remained in dispute due to litigation. *Bufo houstonensis* has not been studied on the GLR and in 2000, when litigation was complete, the BSA dedicated resources to the conservation of the Houston toad on the GLR.

This study represents the first year-around study of Houston toads as well as the first study describing *B. houstonensis* at the GLR in Bastrop County. A long term monitoring project was established at the GLR in 2000 and the objectives of this study were 1) to determine the abundance and describe the dynamics of *B. houstonensis* at the GLR, 2) to monitor *B. houstonensis* year-around in multiple habitat types, 3) to determine if *B. houstonensis* utilized pastures composed of non-native grasses, and 4) to quantify how environmental factors affect *B. houstonensis* behavior throughout the year.

Methods

Study system

The Griffith League Ranch (GLR) is a 1,948 ha property owned by the Boy Scouts of America (BSA) in Bastrop County, 91% of the property is underlain by deep sandy soils of the Patilo, Demona, or Silstid series. The GLR was historically a pine and mixed hardwood forest. Three large tracts of approximately 200 ha each were cleared for cattle grazing early in the 20th century. Cattle were removed from the property in 2001 to improve pond quality for Houston toads. A herd of longhorn was donated to the BSA in 2003 and these animals are kept away from known *B. houstonensis* ponds. *Bufo houstonensis* was originally detected on the property during the early 1980s (A. Price, pers comm., 2002), but no program of monitoring was established until the BSA acquired the property in 2000. Audio surveys were conducted each year from 2000 – 2005 to determine the distribution of Houston toads on the GLR. *Bufo houstonensis* choruses were heard at 12 of the 17 ponds on the property (Fig. 2.1).

Trapping design and field methods

Based on the results of the 2000 call survey, a trapping design was conceived to maximize both the number of toads captured and to determine how *B. houstonensis* utilized the landscape by evaluating 5 treatment groups across different habitat types (Fig. 2.1). Treatment groups were numbered sequentially based on their proximity to the front gate of the GLR. Due to limited funding initially, this design was implemented over time. In March 2001, five linear drift fences (two 121 m, three 153 m), with 1.9 liter pitfalls every 30 m, were placed along the border of the forest and non-native pastures to determine if toads utilized these non-native pasture grass habitats (henceforth referred to as tmt 5). In addition to the pasture traps, three Y-shaped drift fence arrays were placed in 3 habitats (one trap per habitat type): 30 m from a breeding pond (Pond 2) in pine forest, in mixed oak woodland, and in a small (~2 ha) natural clearing, composed of both native and introduced grasses. In February 2002, the remaining traps from the original conceptual design were added – seven additional Y-shaped arrays and pitfalls, completing the following trapping design: 4 traps surrounding Pond 2, one at each cardinal point, at randomly chosen distances from the pond's edge (10m, 30m, and two at 50m) (henceforth referred to as tmt. 1). Two treatments of 3 traps placed 150 m apart, with the first traps in each treatment being equidistant from a known *B. houstonensis* breeding pond (tmt. 2 & 3, placed near ponds 5, and 6 & 7, respectively). Additional funding allowed another treatment identical to treatments 2 & 3, near Pond 12 (tmt. 4) (Fig. 2.1). Each Y-shaped array had a funnel trap placed along each side of each arm (6 total per trap, 72 total). The funnel traps were covered with a piece of flashing for shading.

Traps were checked every morning beginning on 12 March 2001 and ending 30 June 2004, with the exception of a total of 3 non-continuous weeks when the traps were closed due to excessive temperatures (below 3°C or above 37°C) or precipitation events (generally above 15 mm). Snout-urostyle length (SUL), head width (HW), and weight were recorded for all anurans. Each adult *B. houstonensis* received a passive integrated transponder (PIT) (Camper and Dixon 1988). Juvenile *Bufo sp.* and all other vertebrate

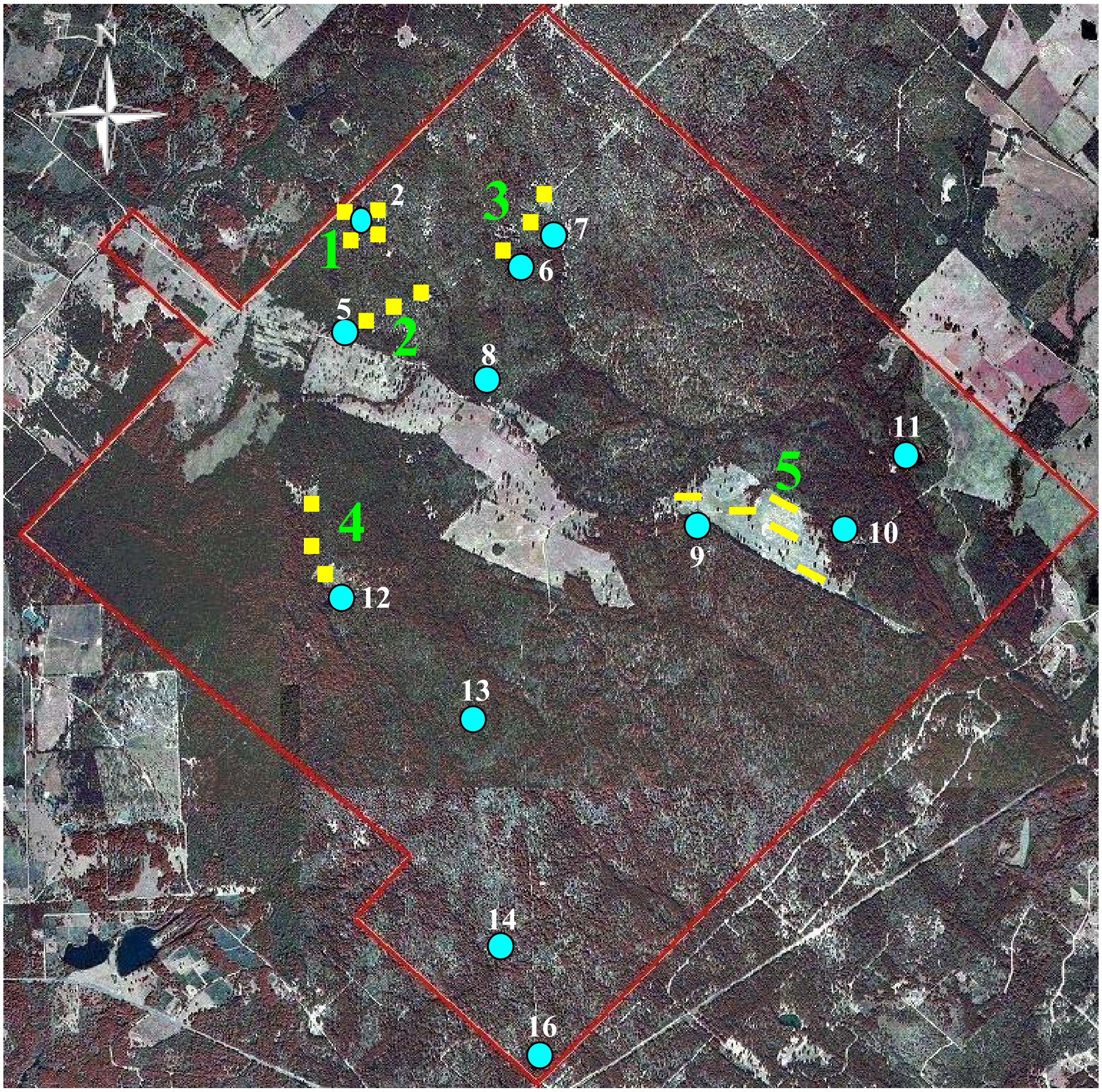

Fig. 2.1. Map of the trapping design on the Griffith League Ranch, Bastrop County, TX. Circles represent ponds where Houston toads have either chorused or bred. White numbers refer to the ID number of each pond. Boxes represent Y-shape drift fence arrays. Yellow lines represent linear drift fence arrays. Green numbers represent the numbers used for the treatment groups of the traps.

taxa were toe-clipped, scute-clipped, or scale-clipped, when appropriate. All organisms were released near their capture site shortly after collection.

Nightly surveys were conducted at each of the 17 ponds at the GLR during the active season (1 February – 30 April) of *B. houstonensis* during 2000 – 2005 (Jackson et al. 2006). Researchers performed standard auditory surveys (Scott and Woodward 1994) as well as walked the perimeter of each pond at the GLR. Any *B. houstonensis* captured were measured, marked, and released at the spot of capture within 10 minutes.

The type of capture method (either caught in a trap or hand-collected at a pond) was recorded for every capture. In 2001 and 2002, standard measurements were only taken at initial capture and from 2003 – 2005 measurements were taken every time an individual was captured. Two datasets were extracted from the capture data. One data set included only the initial capture of each toad (henceforth referred to the initial dataset) and the second dataset included both initial and recapture data (henceforth referred to as the total dataset).

Radio telemetry

Between 2003 – 2005, 21 (16 M : 5 F) *B. houstonensis* were fitted with external radio transmitters (model #: BD-2, weight: 1.8g, Holohil Systems, Ontario Canada). Toads were selected based on weight and body condition. Only toads weighing over 20 g were selected to remain within the recommended ratio of telemeter weight to body weight (White and Garrott 1990). Gravid females were not fitted with telemeters. In 2003, telemeters were sewn inside spandex jackets (jacket weight: 0.5 g), and the unit was placed over the toads head and front limbs (resembling a t-shirt, Fig. 2.2a). In 2004, telemeters were attached to stainless steel beaded chain using PC•7 heavy duty, waterproof epoxy paste (Protective Coating Company, Allentown PA). The chain weighed 0.8 g, and was fastened around the waist of the toads (Fig. 2.2b) (Rathburn and Murphey 1996). Extra beads were removed to tailor the unit for each individual. This method was not ideal because the chain had to be fastened tight enough around the toad so it would not slip off, and while this did not visibly hamper the movement of the toad, the constant pressure of the chain caused abrasions on the soft tissue on the ventral side of the toad. In 2005, the belt design was modified. A piece of nylon ribbon (3 mm width) was threaded through a stainless steel molar bracket (molar brackets were provided by J. Swannack, D.D.S.). The molar bracket and thread were fastened to the telemeter using PC•7. The nylon ribbon and molar bracket unit weighed 0.2 g (Fig. 2.2c). The unit was tied around the waist of the toad, with the telemeter located on the dorsal side. A single drop of tissue glue was put on the knot on the ventral side.

Toads fitted with telemeters were released at the edge of the pond closest to their capture point. Telemetered toads were located at least once every two days during the life of the telemeter. GPS coordinates were taken at each location using either a Garmin GPS V (2003 – 2004) or a Garmin 60CS (2005).

Fluorescent powder tracking

A black spandex jacket was placed on a single non-gravid female, captured on 2 May 2004. Inert fluorescent pigment (T1 series pigment, Radiant Color, Richmond, CA) was placed underneath the jacket, against the dorsum of the toad. As the female moved, the powder fell out of the jacket and she could be tracked with a portable UV light

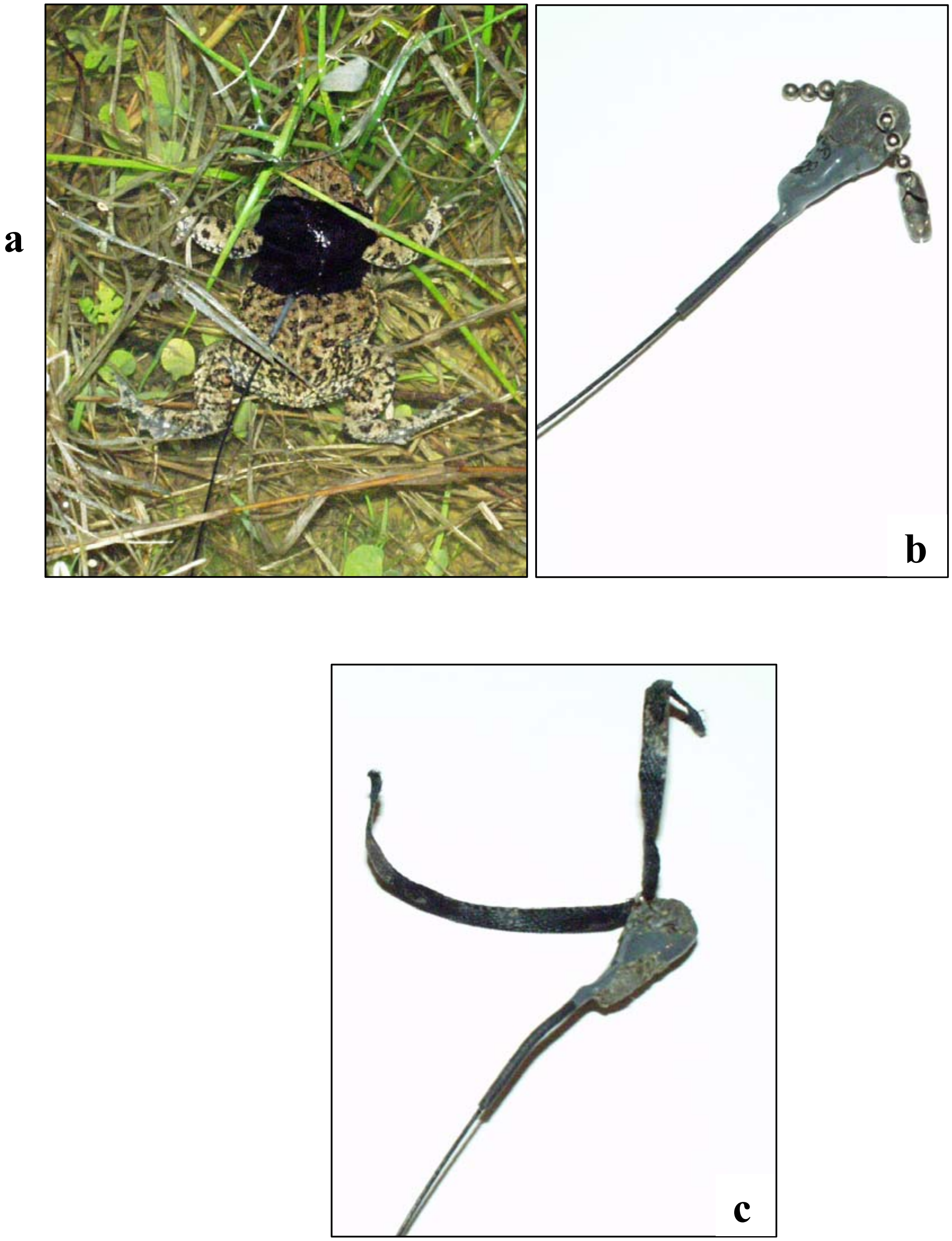

Fig. 2.2. Methods used for attaching radio telemeters to *Bufo houstonensis* captured at the GLR during a) 2003, b) 2004, and c) 2005.

(Raytector Portable UV Light, Raytech Industries, Middleton, CT). The female was tracked each subsequent night.

Recording environmental conditions

Outdoor min-max thermometers and rain gauges accurate to 0.01 inches were added in October of 2001. Weather data were recorded daily. Any missing data were taken from the National Climatic Data Center (NCDC) weather station in Elgin, Texas (station number: 412820), located approximately 10 miles west of the GLR. Standard measurements were converted to metric values using a conversion tool in Microsoft Excel.

Statistical analyses

Number of toads captured

The initial dataset was analyzed for differences in the number of toads captured among years. Differences in the number of males and females captured were also tested. A sex ratio was established from the initial dataset and was tested for differences from parity using a χ^2 test, corrected for one degree of freedom (*df*). Statistical analyses were completed using PROC FREQ in SAS v 9.0 (SAS Institute Inc).

Size at initial capture

Analysis of variance (ANOVA) was used to test differences in mean size at initial capture (weight, SUL, HW) between males and females to determine if there were any sexual dimorphisms in *B. houstonensis* captured at the GLR. Yearly differences in mean size were tested among years for each sex to determine if the size at initial capture changed across years. Statistical analyses for size at initial capture were completed using SPSS v.12.0 (SPSS Inc).

Spatial distribution of toads

In order to determine the spatial distribution of toads at the GLR, the numbers of toads captured in each treatment group were pooled with the toads captured at the pond nearest the traps. Locations were identified as follows (refer to Fig. 2.1 for a location of the ponds and traps): P2 included toads captured at pond 2 and in the tmt. 1 traps. P5 included the pond 5 and tmt. 2 captures. Due to their proximity, ponds 6 and 7 were included with the tmt. 3 traps. P9 represented the captures from pond 9 as well as the tmt. 5 traps. P12 represents toads captured at pond 12 and tmt. 4. The remaining ponds were classified represented by a 'P' then pond's ID number (e.g., P3 represents pond 3). The numbers of toads captured at each location were tested for differences in abundance using PROC FREQ in SAS.

More individuals were captured at ponds than in traps (refer to Chapter IV for an analysis of the capture method), so the individuals captured at the ponds were removed from the sample and the data were analyzed for differences in toad captures among treatment groups using PROC FREQ in SAS.

Capture histories

Capture histories were created for every individual in order to establish the number of times an individual was captured per-year as well as among years. Inter-year recaptures were used to estimate the probability of survival and are addressed in detail in Chapter III. For each year, the number of times an individual was captured was calculated in order to determine the proportion of individuals visiting the breeding areas once per year.

Activity

Hillis et al. (1984), Jacobson (1989) and Price (2003) reported males make multiple visits to ponds during the breeding season, so the total dataset was used to determine the activity patterns of *B. houstonensis.* The total number of toads captured per month (summed across years) was calculated and the date of first capture for each sex was recorded. The calendar year was divided into three-day increments (*td*), in order to summarize the intra-season variability in *B. houstonensis* activity. The first increment for each year was 1 – 3 January (*td* 1) and the last was 29 – 31 December (*td* 122). The total number of toads, separated by sex, captured per *td* was calculated for each year of the study. The mean number of toads captured per *td* across all years was calculated to establish a general trend of toad activity.

Weather conditions affecting toad behavior

Activity in many anurans depends on environmental factors, most commonly temperature and precipitation (Duellman 1995). The mean number of *B. houstonensis* captured per *td* was plotted against mean minimum temperature (per *td*) and mean precipitation (per *td*) to determine qualitatively if there was a relationship between toad activity and temperature or precipitation. Price (2003) reported toads were not active during a full moon. The daily fraction of the moon illuminated (U. S. Naval Observatory 2006) was divided into ten categories (0-10% illuminated, 11-20%, etc…) and the total number of toads captured per category was plotted.

Statistical models used to predict activity

There appeared to be a relationship between *B. houstonensis* activity and environmental factors. In order to quantify the relationship between toad activity or toad abundance and weather patterns, two statistical models were created: 1) a logistic regression model to predict if toads would be active, given certain environmental conditions, and 2) a negative binomial regression model to predict Houston toad abundance, given they were active. Variable selection for each model followed Hosmer and Lemeshow (2000) and used a likelihood ratio test approach for model selection (Simonoff 2003). The possible main effects for either model were: three-day period (*td*), mean precipitation per *td* during the entire study (*pr*), mean precipitation lagged one three-day period (*lp*), mean precipitation lagged two three-day periods (*lp2*), and average percent lunation during a three-day period (*mo*), defined as the fraction of the moon's disk illuminated by the sun, not taking cloud cover or other obstructions into account. Each independent variable was tested as a single effect and if the *p-value* was greater than 0.25, it was removed from consideration. Significant variables ($p < 0.25$) were included in a main effects model. From this preliminary main effects model, all possible interactions were added. For both models, interaction terms were created from centered variables to reduce collinearity (Tabachnick and Fidell 2000). Using a likelihood ratio test, variables were removed from the saturated model (model with all variables and interaction terms) until the model could not be reduced further (refer to Hosmer and Lemeshow (2000) for a more detailed description).

The dependent variable in the logistic regression model was coded as a binary variable and represented if toads were active during any specific *td* (0 = no toads captured per *td*, 1 = at least one toad captured per *td*). The normality of the standardize residuals, the assumption of linearity in the logit, and a Hosmer-Lemeshow test (Hosmer and Lemeshow 2000), were used to determine if the final model fit the data. A classification table was created using 0.5 as a cut-off point to determine the predictive power of the model (Agresti 1996, Hosmer and Lemeshow 2000).

A negative binomial regression model was used to predict the mean count of *B. houstonensis*, given that Houston toads were active. Periods when toads were not captured were removed from the dataset. The dependent variable was the mean count per three-day period of toads when they were captured. A negative binomial distribution was chosen because the Poisson distribution did not fit the data, based on the assumption of the Poisson distribution that the mean equals the variance ($\mu_{count} = 2.05$, $\sigma^2_{count} = 7.26$) (Agresti 1996, Simonoff 2003). The predicted and observed counts were plotted per *td* to determine if the model accurately predicted mean toad abundance. Additionally, both predicted and observed counts were pooled into three groups and represented abundances before, during, and after the breeding season. These groups were used to determine if the model accurately predicted abundance during those three times.

Results

General results

Over the course of the 5 year study, 225 individuals were captured using two capture methods: breeding ponds surveys (1,000 person hours: 5 years of surveys, 25 surveys per year, 4 hours per survey, 2 researchers per night) and drift fence / pitfall traps (411,768 trap hours). Houston toads were not caught equally each year. Likewise, precipitation varied across years (three years were above 100 mm (2001, 2002, and 2004) and two were below 70 mm (2003 and 2005). The most toads were captured in 2005, and the highest annual precipitation was in 2004. Toad activity was mostly confined to their breeding season, yet activity was not continuous throughout the season and was associated with precipitation, temperature, and moon phase.

Abundance

Between 5 March 2001 and 31 May 2005, 225 individual adult *B. houstonensis* (199 M: 26 F) were captured at the GLR (Fig. 2.3). Throughout the study, these individuals were recaptured 92 total times for a total of 317 observations. There was a significant difference in the number of toads captured per year ($\chi^2 = 18.4424$, df=4, $p = 0.001$). The most toads were captured in 2002 (67 M : 7 F) and fewest in 2001 (11 M : 2 F). The sex ratio was significantly male-biased ($\chi^2 = 133.02$, $df = 1$, $p < 0.0001$) and varied by capture method (refer to Chapter IV for analyses of the sex ratio and capture methods).

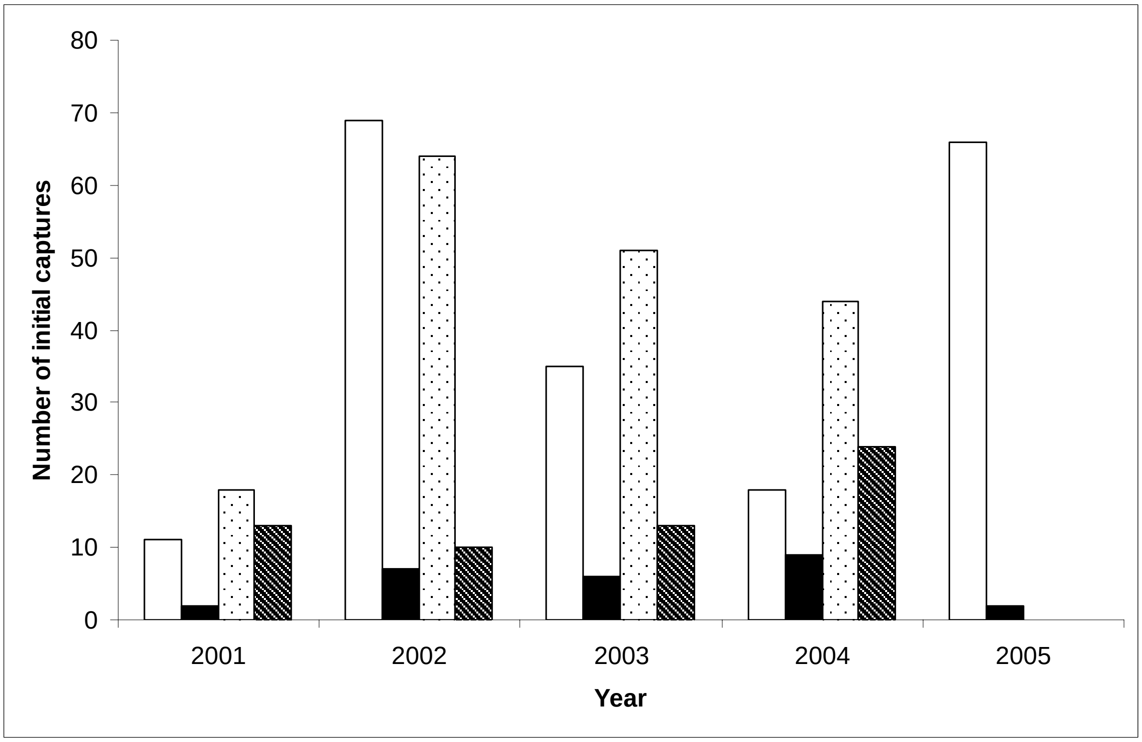

Fig. 2.3. Number of individual Houston toads (*B. houstonensis*) captured at the Griffith League Ranch (GLR) and Bastrop State Park (BSP), Bastrop County, TX from 2001 – 2005. Open and closed bars represent males and females captured at the GLR, respectively. Dotted bars and crosshatched bars represent males and females captured at BSP, respectively. Data from BSP were taken from Price (2003) and were not available in 2005.

Sexual dimorphisms

Females were larger than males for all three measurements (Table 2.1) and three one-way ANOVAs indicated these differences were statistically significant (Table 2.1A). For each sex, weight increased slightly from 2001 – 2005 (Fig. 2.4a), but the increase was not significant (males: F = 1.637, $p = 0.167$, females: F = 0.985, $p = 0.485$). Likewise, SUL increased across years (Fig. 2.4b) and there was a slightly significant difference in SUL of males (F = 2.486, $p = 0.045$) across years and no significant difference for females (F = 0.839, $p = 0.516$). Head-width appeared to decrease for initial captures during subsequent years (Fig. 2.4c), but the differences were not significant for either sex (males: F = 1.199, $p = 0.313$, females: F = 0.960, $p = 0.452$).

Spatial distribution

Bufo houstonensis were not distributed equally across the GLR. Houston toads were only captured at 11 of the 17 ponds on the property (Fig. 2.5). One adult male was captured at pond 13 (Fig. 2.1), but not measured. There was a significant difference in the number of individuals captured among these locations ($\chi^2 = 376.5455$, df = 9, $p < 0.0001$). The majority of toads were captured at or near ponds with the drift fence / pitfall traps. However, significantly more toads were captured at ponds than in traps (refer to Chapter IV for a detailed analysis of the capture data). The most toads were captured at P2 (89 M : 13 F). At P9, 35 *B. houstonensis* were captured. All of the individuals captured in the tmt. 5 traps were either captured within a canopied drainage leading to a known chorusing pond (Pond 9), or in the terminal buckets of the entire treatment group, which bordered on the forests no farther than 15 meters from the forest

Table 2.1. a) Average measurements of initial captures of Houston toads (*B. houstonensis*) captured at the Griffith League Ranch, Bastrop County, TX. b) ANOVA table examining statistical differences between the sexes of Houston toads. SUL represents snout-urostyle length and HW represents headwidth.

a

Sex	Measurements		
	Weight (g)	SUL (mm)	HW(mm)
Male	21.35	58.93	18.59
Female	31.93	63.94	21.53

b

Variable	Group	Sum of Squares	df	Mean Square	F	*p*
Weight (g)	Between	2652.527	1	2652.527	110.172	.000
	Within	5056.028	210	24.076		
	Total	7708.555	211			
SUL (mm)	Between	630.657	1	630.657	25.801	.000
	Within	5157.438	211	24.443		
	Total	5788.096	212			
HW (mm)	Between	199.051	1	199.051	15.865	.000
	Within	2584.596	206	12.547		
	Total	2783.647	207			

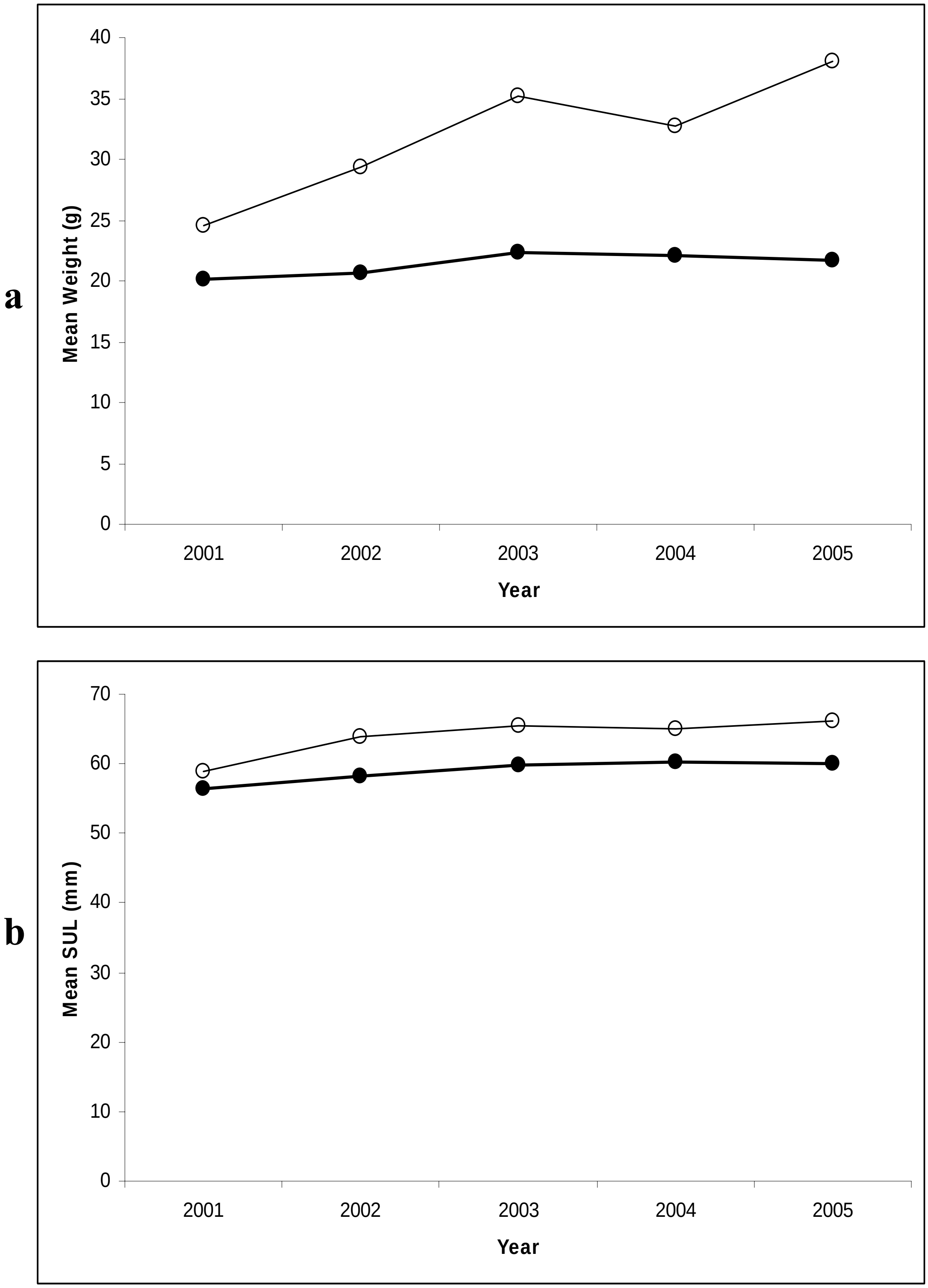

Fig. 2.4. Average measurements of *B. houstonensis* captured at GLR, Bastrop County, TX. a) weight (g), b) snout-urostyle length (mm), c) headwidth (mm). Open circles represent females, closed circles represent males.

c

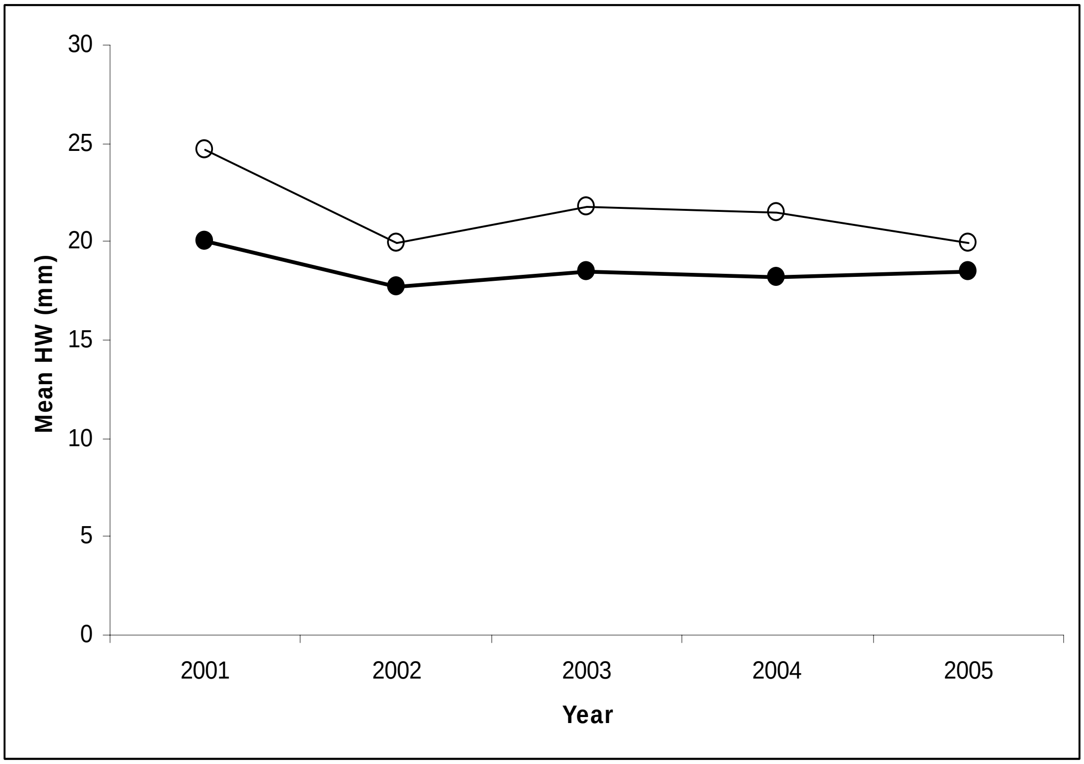

Fig. 2.4 continued.

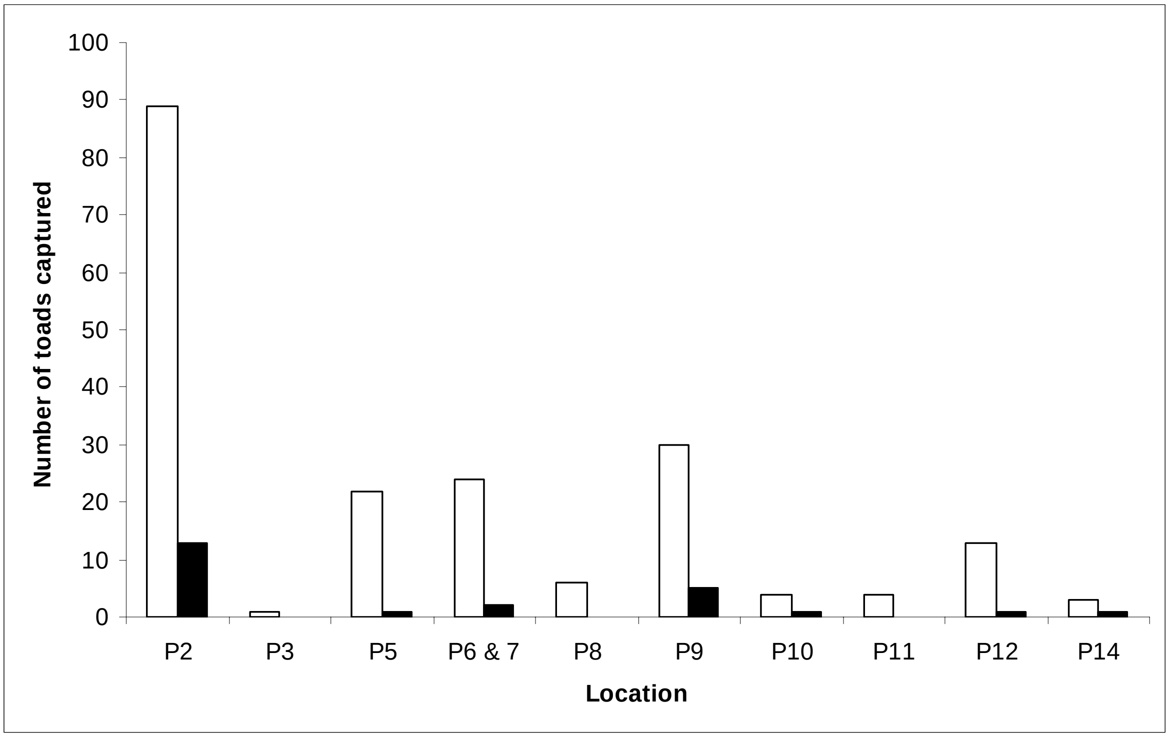

Fig. 2.5. Number of individual *B. houstonensis* captured at the GLR, Bastrop County, TX. The X-axis refers to a specific geographic location at the GLR (Fig. 2.1). P2 includes toads captured at pond 2 and in the tmt. group 1 traps P5 includes the pond 5 and tmt. group 2 captures. P6 & 7 includes toads captured at both ponds 6 and 7 as well as the tmt. group 3 traps. P9 represents the captures from pond 9 as well as tmt. group 5 (the pasture traps). P12 represents the pond 12 and tmt. group 4 captures. The remaining values represent specific ponds on the GLR (P3 = pond 3, etc…). Open bars represent males, closed bars represent females..

edge (refer to Fig. 2.1). There were not any mid-pasture captures for this treatment group. At the P5 location, 23 toads (22 M : 1 F) were captured. At P6 & 7, 25 toads (24 M: 1 F) were captured. There were fewer toads (13 M : 1 F) captured at the P12 location. When the pond captures were removed, there was a significant difference in the number of toads captured at each treatment location ($\chi^2 = 19.71$, $df = 4$, $p = 0.0006$), with the most toads being captured at tmt. 1 (Fig. 2.6).

Radio telemetry

Out of the three different attachment methods used for telemetry (Figs. 2a, 2b, 2c), the best method used was the nylon ribbon and molar bracket (Fig. 2.2c). The nylon ribbon did not cause abrasions on the ventral side of the toad like the steel chain, the unit was extremely light (0.2 g), and stayed on the toads longer than the other two methods (up to 5 weeks). The spandex jackets used in 2003 did not stay on the toads for more than 4 days. The stainless steel beaded chain used in 2004 worked relatively well, however, the chain did cause abrasions. The chain did not appear to hamper movement, but the abrasions were severe enough to abandon this method in favor of the nylon ribbon-molar bracket unit.

General movement patterns

Between 2003 – 2005, 21 (16 M : 5 F) *B. houstonensis* were fitted with radio telemeters. A total of 139 observations (63 in 2003-2004, 76 in 2005) were made. Telemetry began each year in during the first chorusing event in March. The latest a Houston toad with a telemeter was ever observed was 2 June. Telemeters fell off the

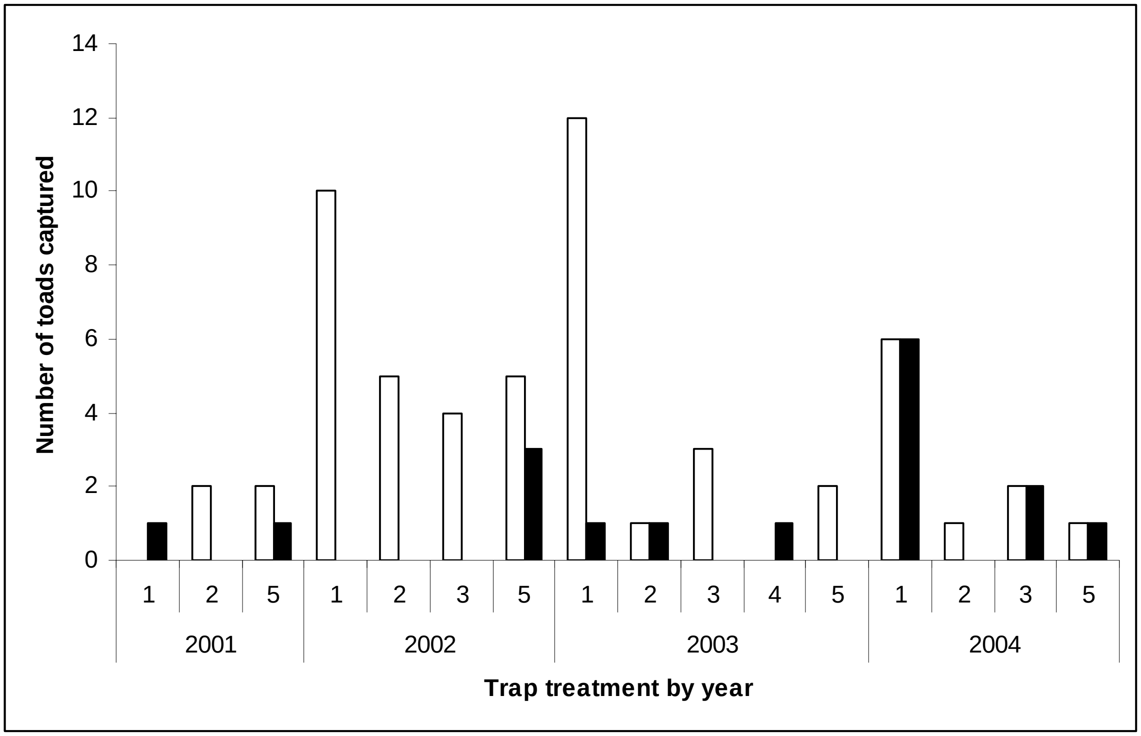

Fig. 2.6. Number of Houston toads captured at the Griffith League Ranch, Bastrop County, TX, per trap or trap type from 2001 – 2005. Treatments 1 – 5 represent drift fence arrays. Traps were closed permanently in June 2004. Open bars represent males, closed bars represent females.

toads frequently and all of the attachment methods proved problematic. While there are not enough data to determine a home range with any degree of accuracy, these data are valuable for qualitative descriptions of the post-breeding behaviors of Houston toads.

In general, Houston toads exhibited the same movement patterns across years. Once released, Houston toads found refuge, generally under fallen oak trees, and rarely moved from that refugia. From March to May, males remained within 75 meters of their respective breeding ponds. Females did not stay near the pond and within two days of being released, all females with telemeters moved at least 50 m from the pond's edge. With one exception, Houston toads did not burrow into the ground. The one toad found in a self-made burrow was a male and was buried 3 cm in the ground under pine-leaf litter. The remaining toads were always found in cavities under fallen trees, almost exclusively oaks (*Quercus spp.*). Telemetered toads were observed foraging at night, always within five meters of their hibernacula. Individuals often returned to the same hibernacula after foraging events. Toads were never observed more than 10 m from their respective refugia. One female moved between two refugia (both cavities under fallen oak trees) less than one meter apart. Foraging did not occur every night. Toads moved distances greater than 10 m only after a rainfall event, with the exception of one male captured at pond 7 in 2005. This male moved a total of 221 m from the pond, and was never more than 5 m from a water-filled drainage. The average movement of all toads was 74.8 ± 25.78 m. The median distance moved was 77.59 m.

Fluorescent powder tracking

The fluorescent powder method provided a different type of result than the radio telemetry. The female moved 3.2 m (straight line distance) from the release point, and situated herself underneath a fallen oak tree. She did not move in a straight line, however. The powder marks on the ground indicated she moved from the release point to the tree and moved along the tree, paused (indicated by a higher concentration of fluorescent powder), and then moved further down the length of the tree until she found a hollow spot large enough for her body. The female remained in the hollow for 48 hours after release (confirmed visually), and then the jacket was found *sans* toad.

Capture histories

Females were only captured once per year and were never recaptured among years. Most of the males from the total sample (76%) were only captured once per year (Fig. 2.7). The frequency of males visiting the ponds more than once year increased during the study period (Fig. 2.8).

The majority of toad captures were associated with breeding activity and confined between February and April (Fig. 2.9). Each year, males were captured earlier than females (Table 2.2). The earliest a male was captured was 15 January, while the earliest a female was captured was 24 February (Table 2.2). Activity subsided after the breeding season (generally by the end of April). During the entire five year study, only four individuals were captured outside of the breeding period (three in October and one in December, Fig. 2.9). These events occurred after the GLR received over 22 mm of rain and it is likely that the toads were flooded out of their refugia. On average, there were

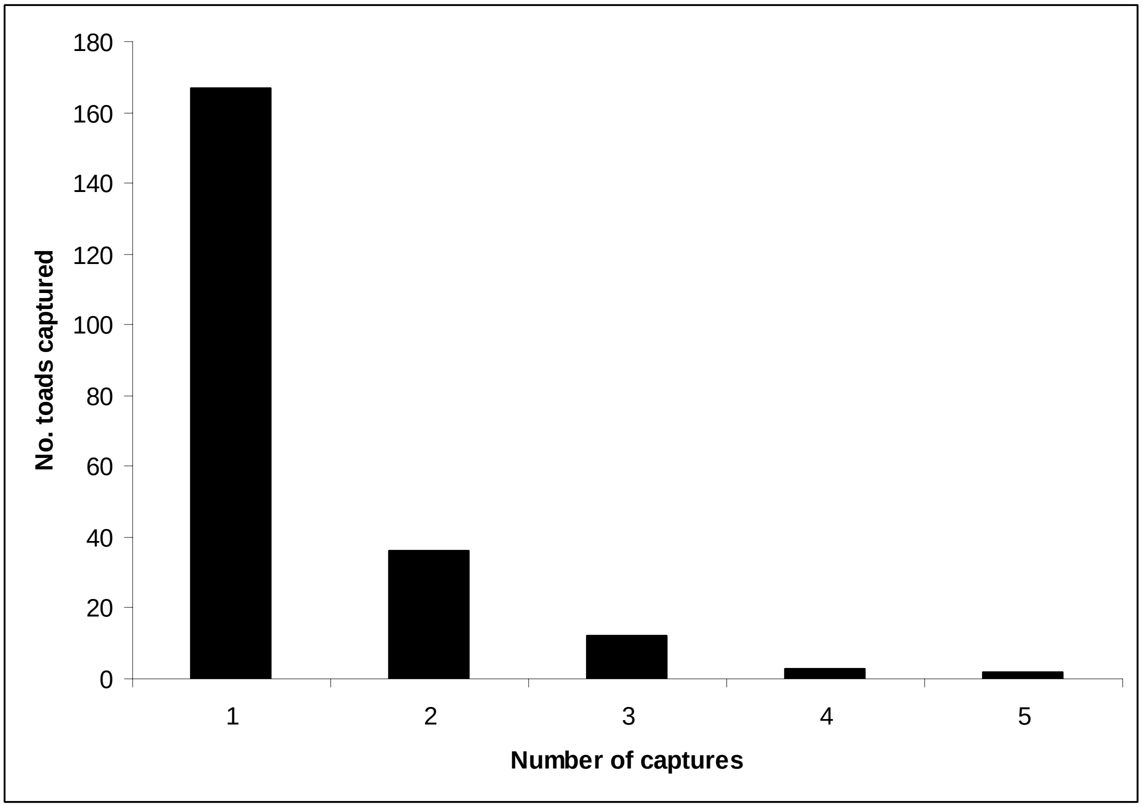

Fig. 2.7. Number of times male Houston toads (*B. houstonensis*) were captured on different days within a given breeding season. Data include all captures from 2001 – 2005, including the individuals recaptured in subsequent years.

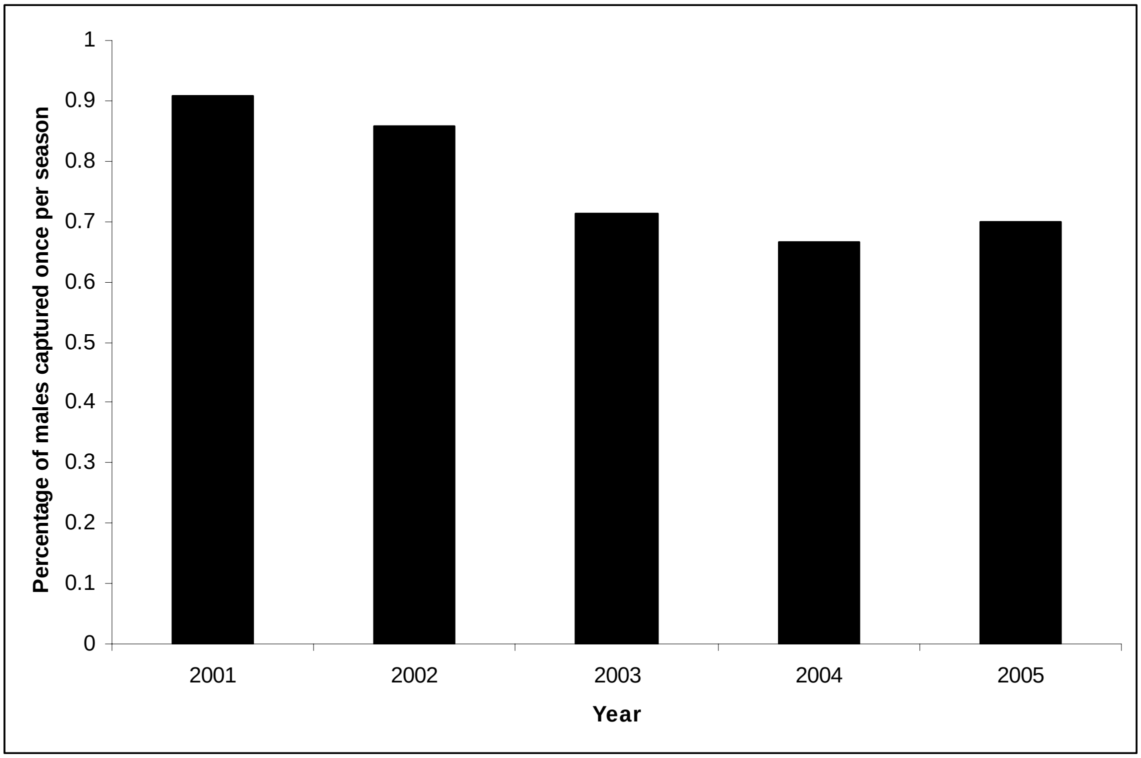

Fig. 2.8. Percentage of male Houston toads (*B. houstonensis*) captured only once per year at the GLR, Bastrop County, TX. Proportions based on number of males captured once / total number of males captured per year.

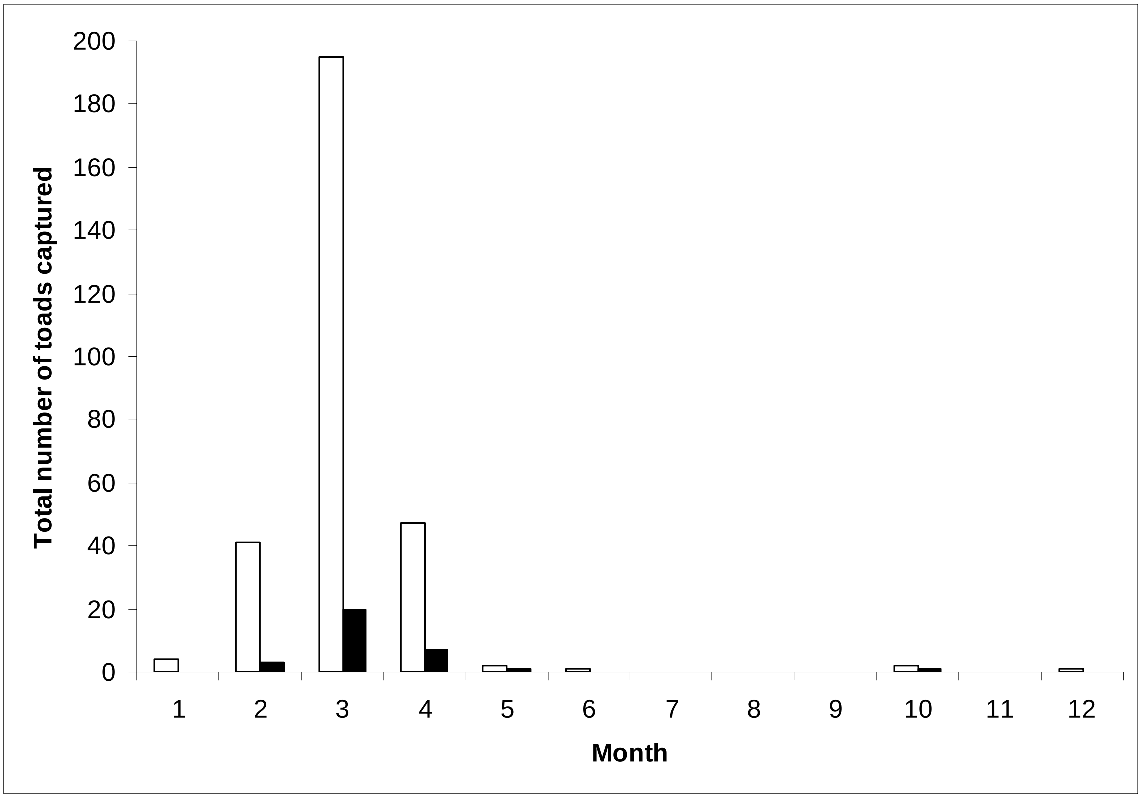

Fig. 2.9. Total number of Houston toads (*B. houstonensis*) captured per month at the GLR, Bastrop County, TX from 2001 – 2005. Month 1 represents January, Month 12 represents December. Open bars represent males, closed bars represent females.

Table 2.2. Date of first captures for male and female Houston toads (*B. houstonensis*) captured at the GLR, Bastrop County, TX.

	Date of first capture	
Year	M	F
2001	12 Mar.	16 Apr.
2002	18 Feb.	1 Mar.
2003	13 Feb.	11 Mar.
2004	15 Jan.	24 Feb.
2005	15 Feb.	7 Mar.

two main peaks of activity – one large peak in the middle of March, and a smaller peak in the middle of April (Fig. 2.9). Activity was not continuous through the breeding season and occurred in intervals of 3 – 5 days.

Yearly activity

Houston toad activity varied among years (Figs. 2.10 – 2.14). In 2001, a single male was captured on 12 March (*td* 24), eight males were captured between 29 – 31 March (*td* 30), one male was captured between 13 – 15 May (*td* 45), and one male was captured in December (*td* 112) after the GLR received substantial rainfall (Fig. 2.10). Two females were captured in 2001 (16 – 18 April, *td* 45) and were not captured at the same time as males (Fig. 2.10). In 2002, there were two peaks of activity (8 – 10 March and 7 – 9 April, *td* 23 and 33, respectively) when 21 males were captured. Immediately preceding the first peak, 5 males were captured. In between these peaks, the number of males captured fluctuated between 0 – 8 individuals (Fig. 2.11). Females were captured during both peaks of male activity in 2002 (Fig. 2.11). In 2003, the peak of Houston toad activity for both males and females occurred between 8 – 13 March (*td* 23 – 24) (Fig. 2.12). After the peak period, there were 9 males captured and 2 females captured (between 26 March – 3 April, *td* 29 – 31). In 2004, males were captured earlier than any other year (Table 2.2). The first peak of male activity in 2004 occurred earlier as well (between 1 – 3 March, *td* 21) while the second peak occurred between 9 – 11 April (Fig. 2.13, *td* 34). The peak of female activity in 2004 (13 – 15 March, *td* 25) did not overlap with the peaks in male activity (Fig. 2.13). There were four three-day periods in 2005 when over 10 males were captured: 21 – 23 February (*td* 18), 5 – 7 March (*td* 22), 20 –

22 March (*td* 27), and 9 – 11 April (*td* 34) (Fig. 2.14). The most males (40) were captured during *td* 27. Only two females were captured in 2005, one during *td* 22 and one during *td* 34 (Fig. 2.14). Both in 2004 and 2005, females were not captured during the largest peaks in male activity.

Mean activity patterns of B. houstonensis at the GLR

On average, male *B. houstonensis* were captured at breeding areas before females, while the majority of females were captured during peak male activity (Fig. 2.15). Mean Houston toad activity was not continuous, but occurs in 3 – 5 day intervals. Peaks in male activity did not occur without immediately being preceded by the presence of smaller groups of males at / or near potential breeding ponds (Fig. 2.15). After June, activity can be explained by rainfall events greater than 22 mm.

Weather patterns affecting toad behavior

In addition to the time of year, mean Houston toad activity appeared to be influenced by three environmental covariates: daily temperature, precipitation, and percent lunation. *Bufo houstonensis* were only captured between mean minimum three-day temperatures of 3° - 16° C (Fig. 2.16). During the breeding season, mean three-day precipitation events greater than 4 mm also seemed to influence toad activity (Fig. 2.17), as well as the mean precipitation three days prior (Fig. 2.18). Houston toads were not captured equally during different moon phases ($\chi^2 = 75.07$, $df = 9$, $p < 0.0001$). The fewest toads were captured when lunation was between 51 – 60% (Fig. 2.19).

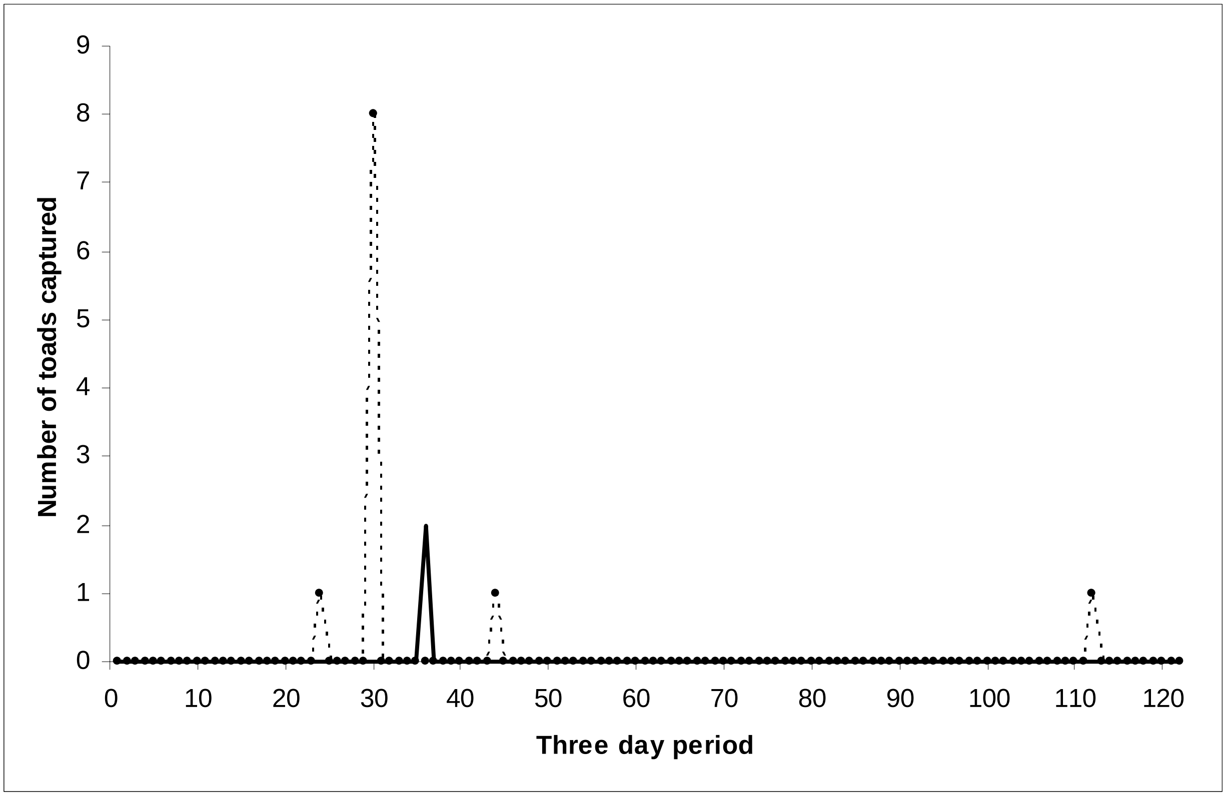

Fig. 2.10. Total number of Houston toads (*B. houstonensis*) captured at the GLR in 2001 per 3-day period. The X-axis represents annual three day periods with 1 representing January 1 – 3, etc… Dotted lines represent males, solid lines represent females.

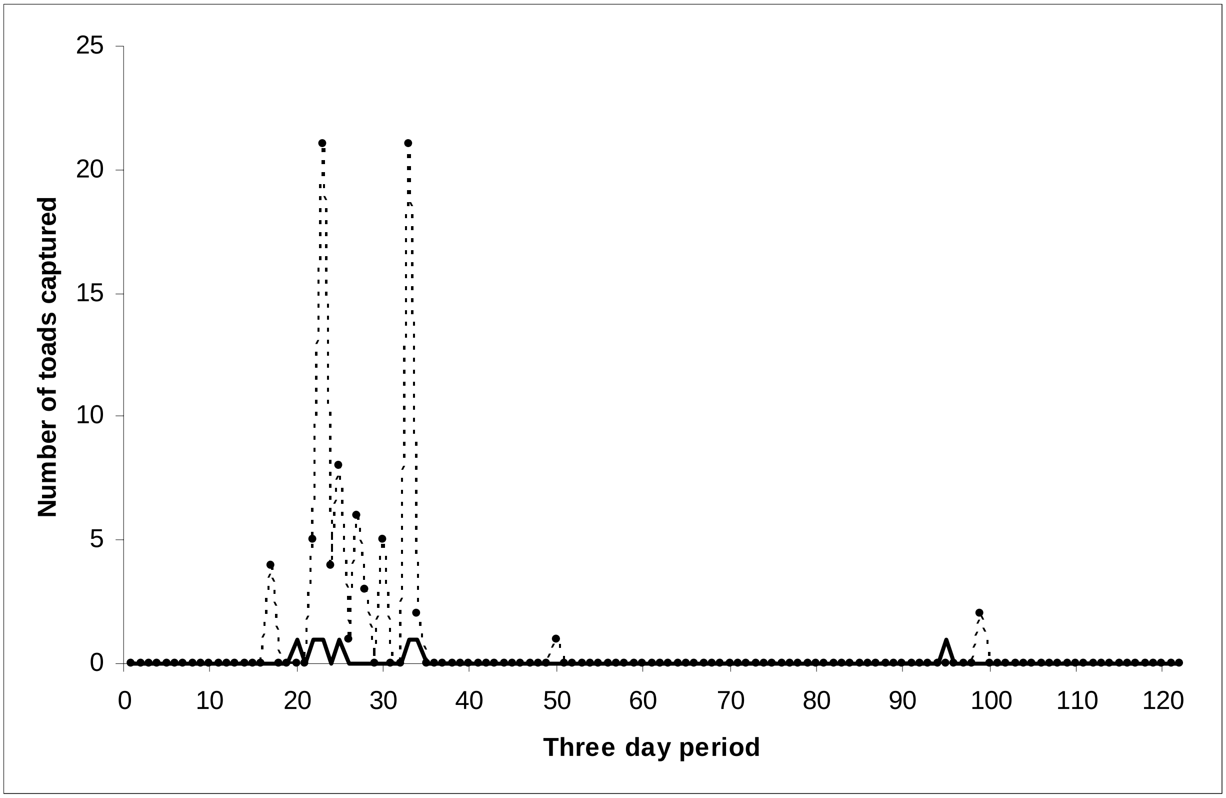

Fig. 2.11. Total number of Houston toads (*B. houstonensis*) captured at the GLR in 2002 per 3-day period. The X-axis represents annual three day periods with 1 representing January 1 – 3, etc… Dotted lines represent males, solid lines represent females.

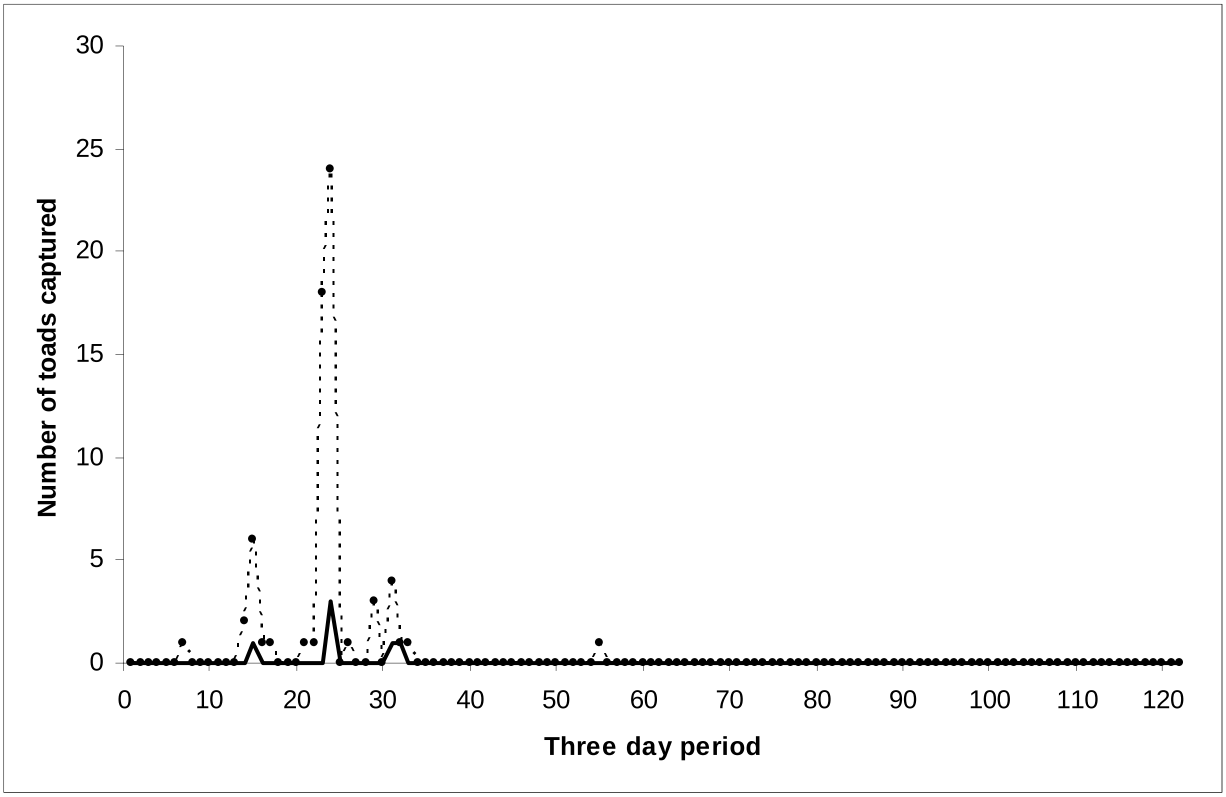

Fig. 2.12. Total number of Houston toads (*B. houstonensis*) captured at the GLR in 2003 per 3-day period. The X-axis represents annual three day periods with 1 representing January 1 – 3, etc… Dotted lines represent males, solid lines represent females.

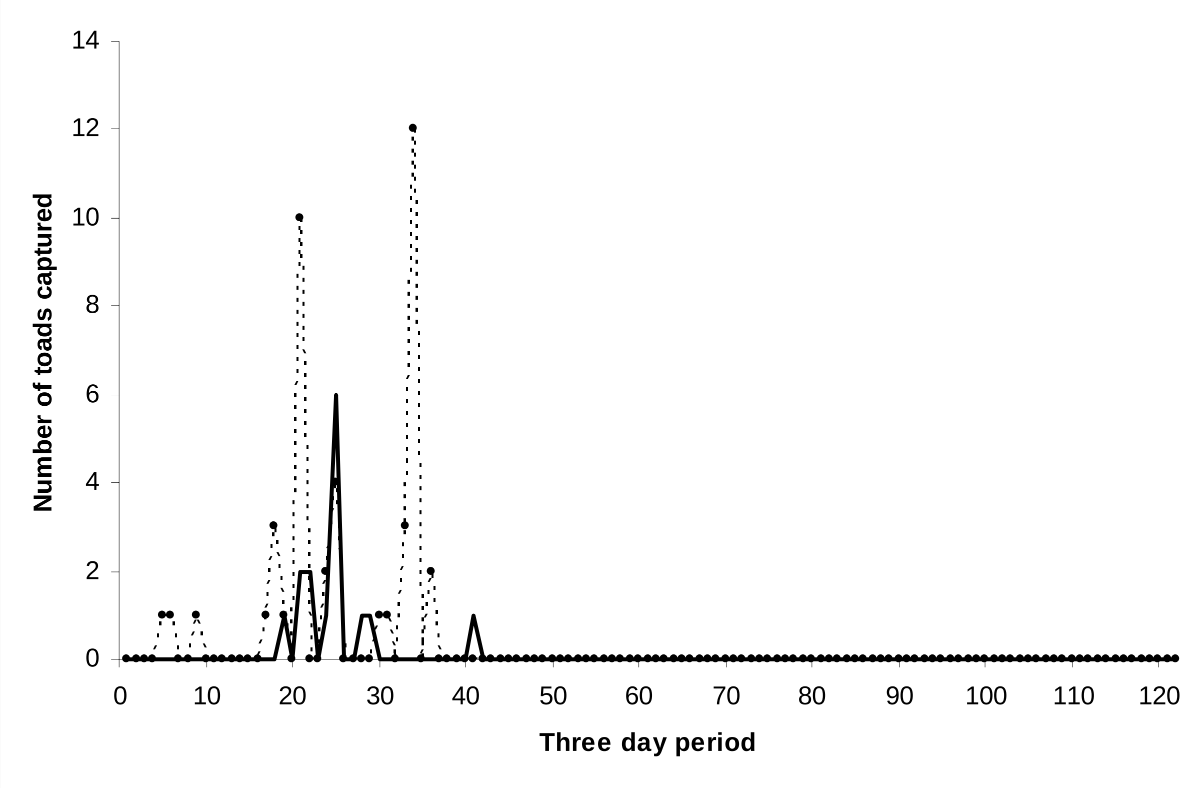

Fig. 2.13. Total number of Houston toads (*B. houstonensis*) captured at the GLR in 2004 per 3-day period. The X-axis represents annual three day periods with 1 representing January 1 – 3, etc… Dotted lines represent males, solid lines represent females..

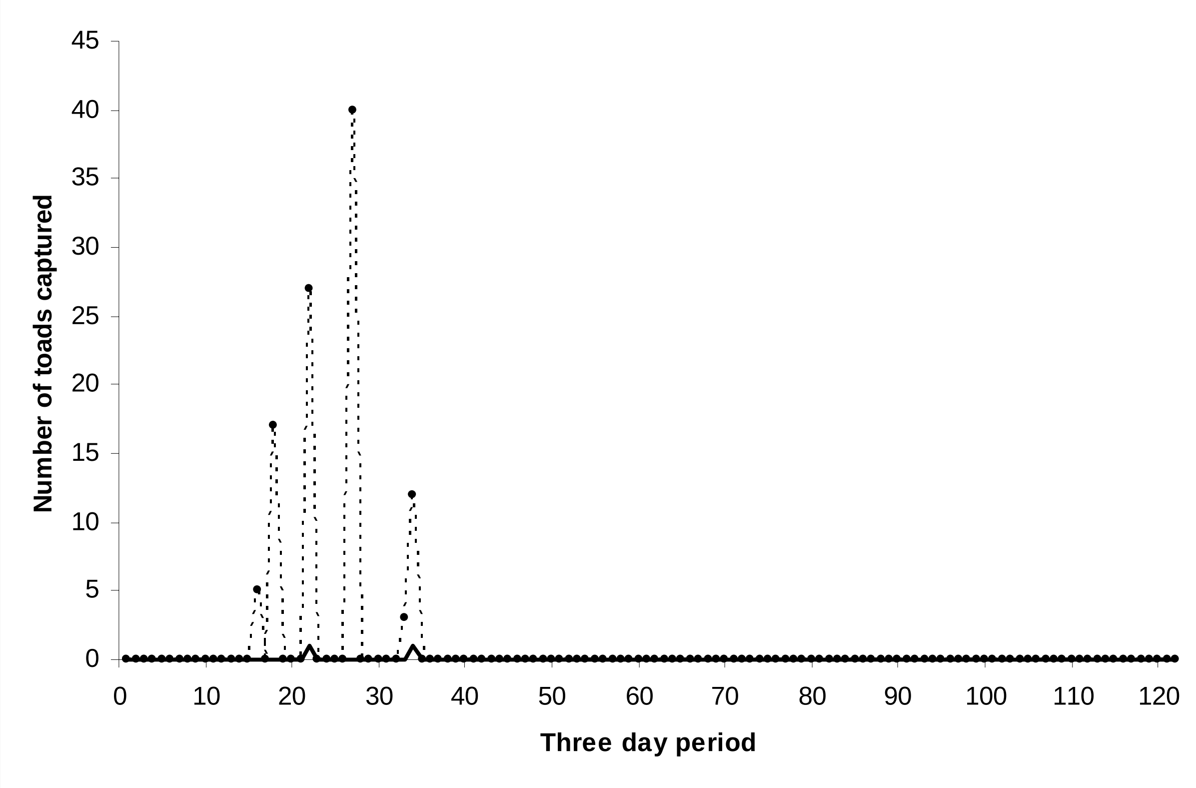

Fig. 2.14. Total number of Houston toads (*B. houstonensis*) captured at the GLR in 2005 per 3-day period. The X-axis represents annual three day periods with 1 representing January 1 – 3, etc… Dotted lines represent males, solid lines represent females.

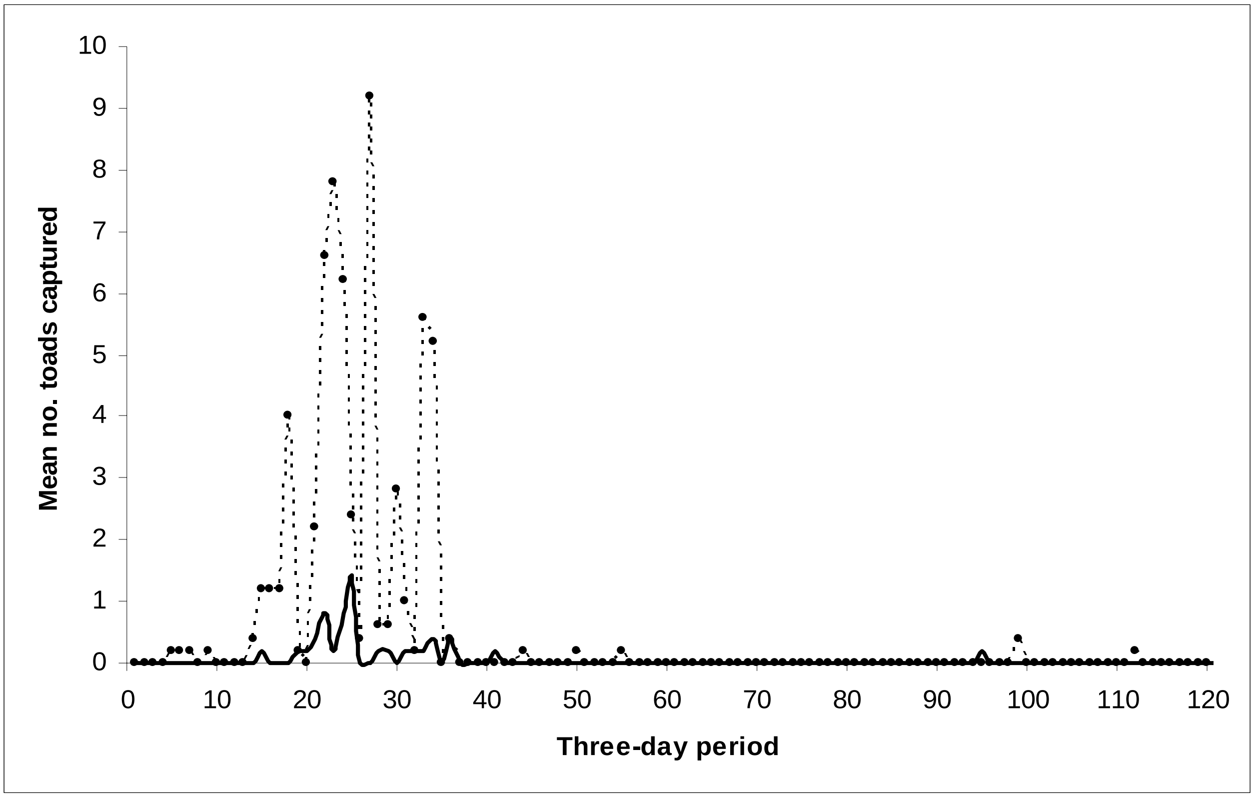

Fig. 2.15. Mean number of Houston toads (*B. houstonensis*) captured at the GLR from 2001 – 2005 per 3-day period. The X-axis represents annual three day periods with 1 representing January 1 – 3, etc…Dotted lines represent males, solid lines represent females.

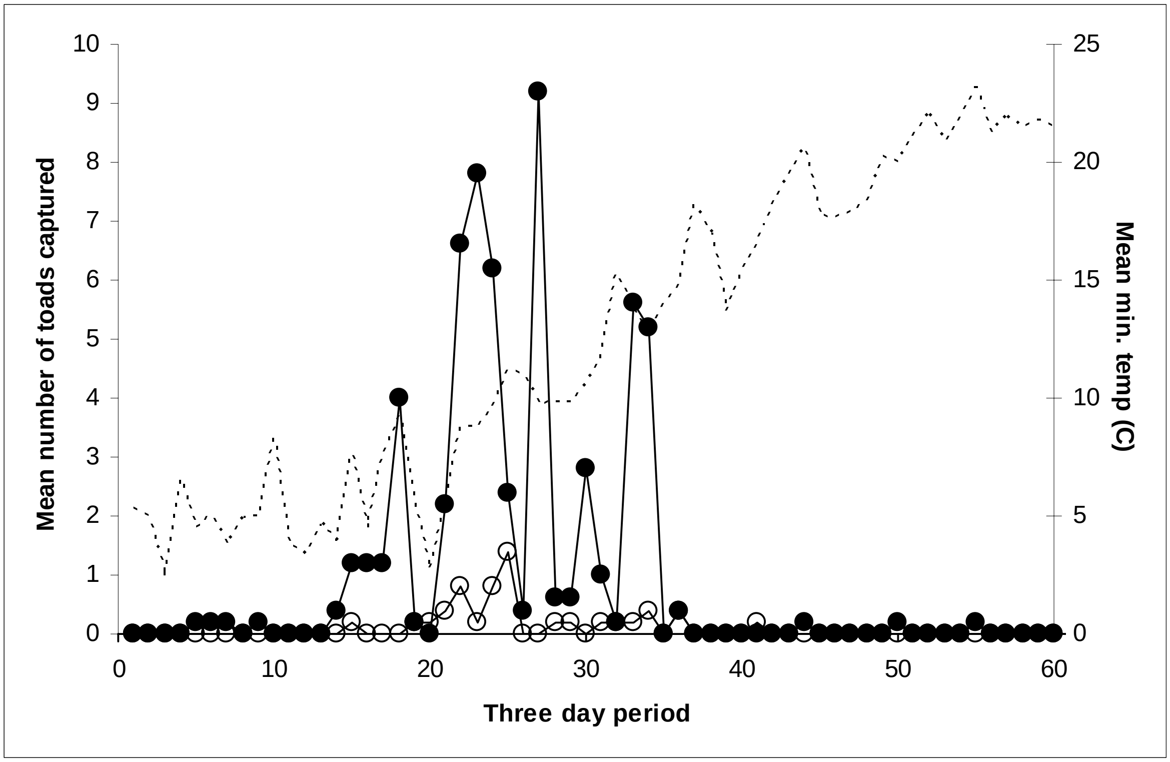

Fig. 2.16. Mean number of Houston toads (*B. houstonensis*) captured from 2001 – 2005 during the first 180 days of the year (divided into 3 day periods, where 1 represents January 1 – 3, etc…), based on toads captured at the GLR, Bastrop County, TX. Solid circles represent males, open circles represents females, and the dotted line represents mean minimum temperature (°C) per three day period (secondary Y-axis)..

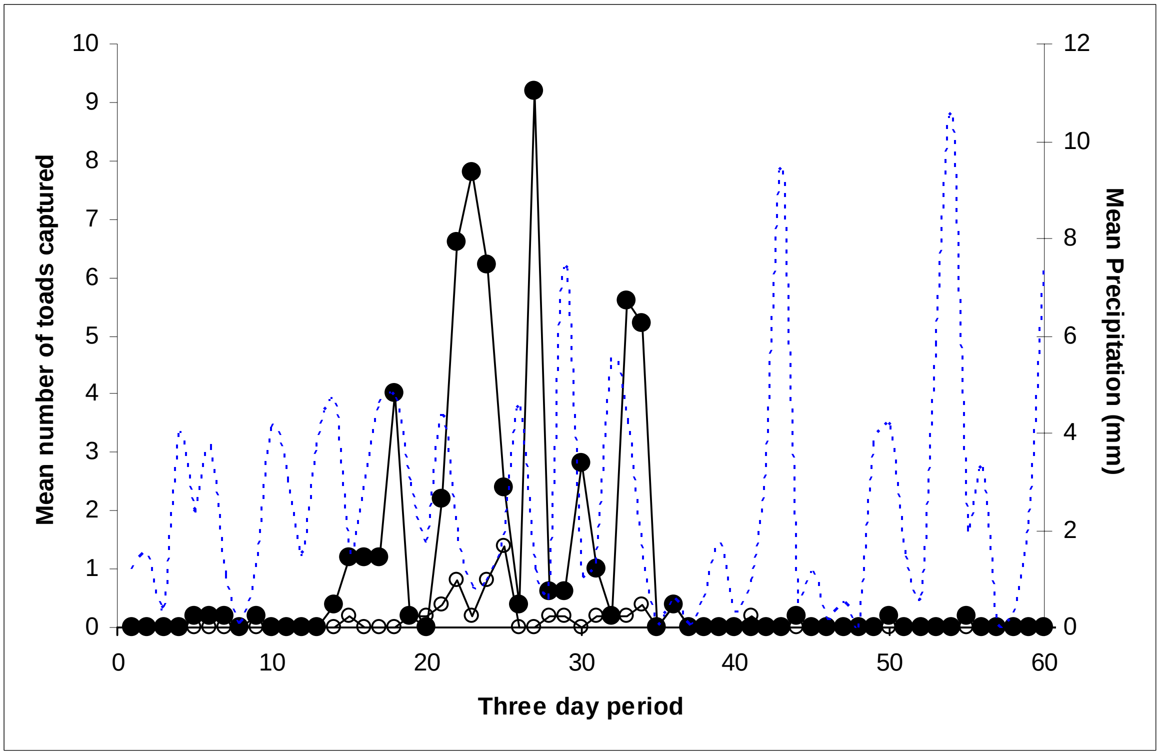

Fig. 2.17. Mean number of Houston toads (*B. houstonensis*) captured from 2001 – 2005 during the first 180 days of the year (divided into 3 day periods, where 1 represents January 1 – 3, etc…), based on toads captured at the GLR, Bastrop County, TX. Solid circles represent males, open circles represents females, and the dotted line represents mean precipitation (mm) per three day period (secondary Y-axis)..

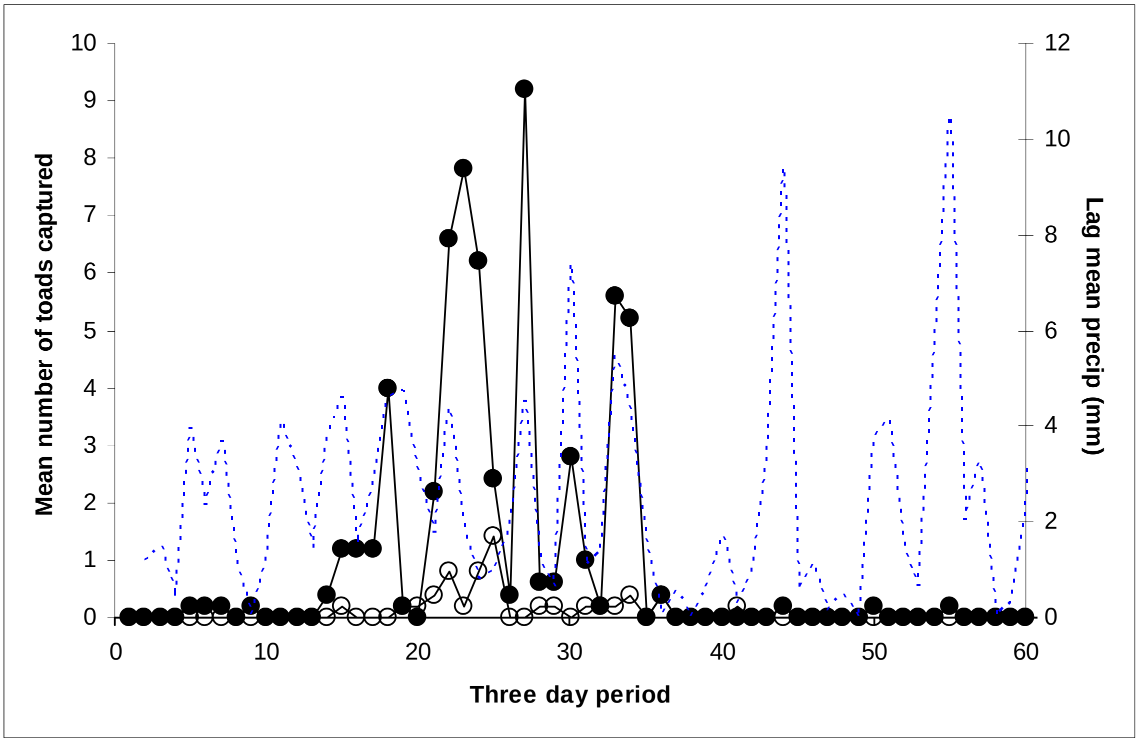

Fig. 2.18. Mean number of Houston toads (*B. houstonensis*) captured from 2001 – 2005 during the first 180 days of the year (divided into 3 day periods, where 1 represents January 1 – 3, etc…), based on toads captured at the GLR, Bastrop County, TX. Solid circles represent males, open circles represents females, and the dotted line represents mean precipitation (mm) three days prior (secondary Y-axis).

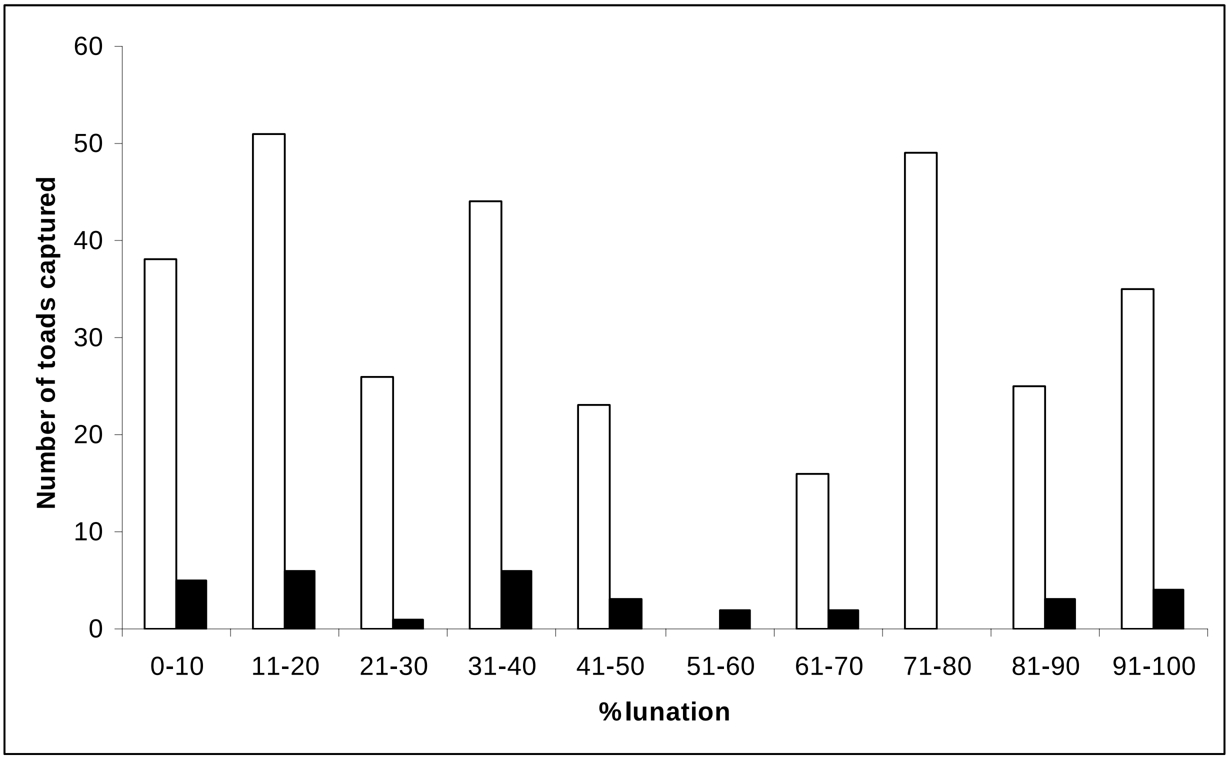

Fig. 2.19. Total number of Houston toads (*B. houstonensis*) captured at the GLR, Bastrop County, TX, during different percent lunation (amount of the moon's disk illuminated) varying percentages of lunation. Open bars represent males, closed bars represent females.

Predicting activity of B. houstonensis

The final logistic regression model used to predict toad activity included the following terms: *td, mt, mo, lp*, *td*mo, mt*mo, lp*mo* (Table 2.3a). The Hosmer-Lemeshow test indicated support for this model ($\chi^2 = 5.329$, df = 8, $p = 0.7218$). The residuals appeared normally distributed (Fig. 2.20) and there were not severe deviations from linearity in the logit (Fig. 2.21). Using 0.5 as a cut-off point (Hosmer and Lemeshow 2000), the model correctly predicted 86% of the observations (Table 2.3b). At the cut-off probability, the model predicted false negatives 9% of the time (model predicted a 0, when the observed value was 1) and false positives 4% of the time (predicting a 1 when the observed point was a 0). The prediction equation was:

$$E\left(\pi_i\right) = \frac{\exp(b_0 - b_1(td) - b_2(mt) - b_3(mo) + b_4(lp) + b_5(td * mo) + b_6(mt * mo) - b_7(lp * mo))}{\left(1 + \exp(b_0 - b_1(td) - b_2(mt) - b_3(mo) + b_4(lp) + b_5(td * mo) + b_6(mt * mo) - b_7(lp * mo)\right)}$$

where $E(\pi_i)$ represents the expected probability of *B. houstonensis* being active, *exp* is base of the natural logarithm, b_i represents the estimated values of the coefficients (Table 2.3a).

Predicting abundance of B. houstonensis

The final model used to predict the actual count of *B. houstonensis*, given they were active, differed from the logistic regression model. Using a likelihood ratio test approach to model selection, the best model included *td*, *mt*, *pr*, *td*mt*, *td*pr*. The prediction equation was:

Table 2.3. a) Coefficients for final logistic regression model used to predict Houston toad (*B. houstonensis*) activity at the Griffith League Ranch, Bastrop County, Texas. The dependent variable was coded as 0 if toads were not active and 1 if toads were active. Refer to the text for the regression equation. *td* represents the three-day period, *mt* represents mean minimum temperature, *mo* represents the mean percent lunation, *lp* represents mean three-day precipitation lagged one day. b) Classification table generated from the logistic regression model. The cut-off point was set at 0.5..

a

Parameter	DF	Estimate	S.E.	χ^2	*p*
Intercept	1	4.587	5.1966	0.7791	0.3774
td	1	-0.0464	0.0123	14.2584	0.0002
mt	1	-0.1412	0.056	6.3524	0.0117
mo	1	-4.7136	10.2251	0.2125	0.6448
lp	1	0.3834	0.1437	7.1175	0.0076
*td*mo*	1	0.7662	0.3411	5.0438	0.0247
*mt*mo*	1	3.5743	1.7237	4.3001	0.0381
*lp*mo*	1	-8.9776	4.2532	4.4555	0.0348

b

Classification Table

Prob. Level	Correct		Incorrect		Percentages		
	Event	Non-Event	Event	Non-Event	Correct (%)	False Pos.	False Neg.
0.5	22	83	5	11	86	4.1	9.1

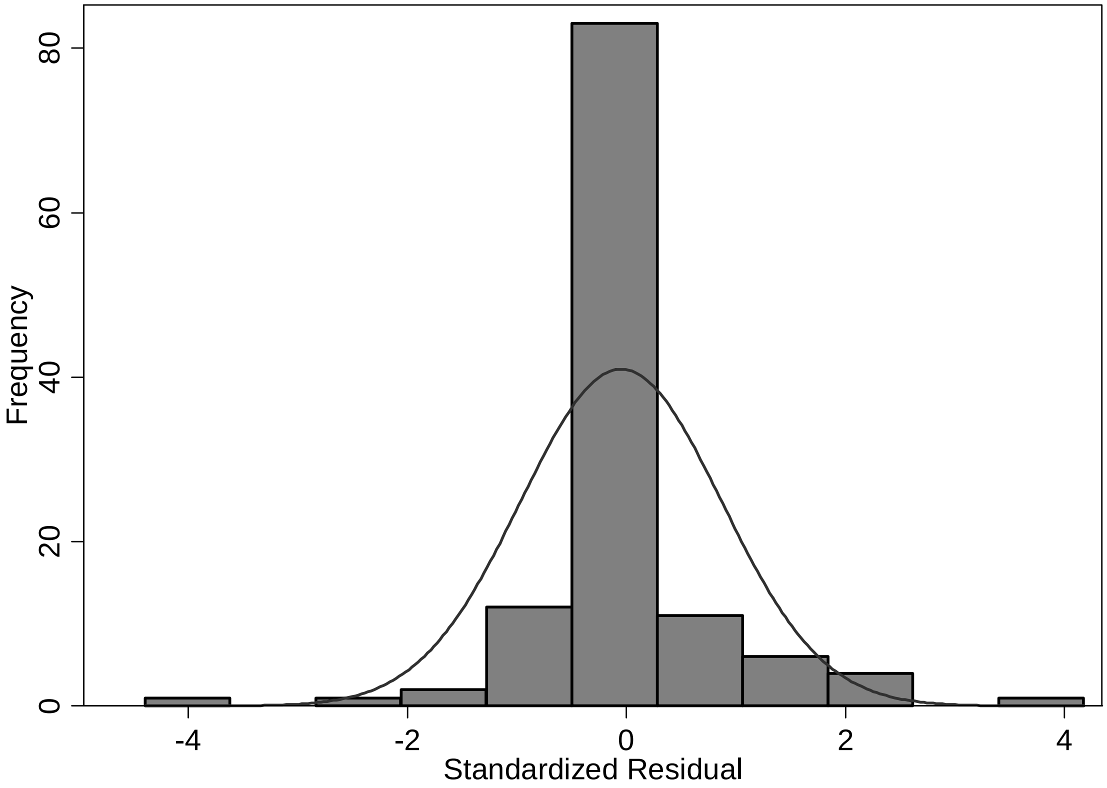

Fig 2.20. Standardized residuals of logistic regression model used to predict *B. houstonensis* activity (refer to table 2.3 for coefficients of logistic equation).

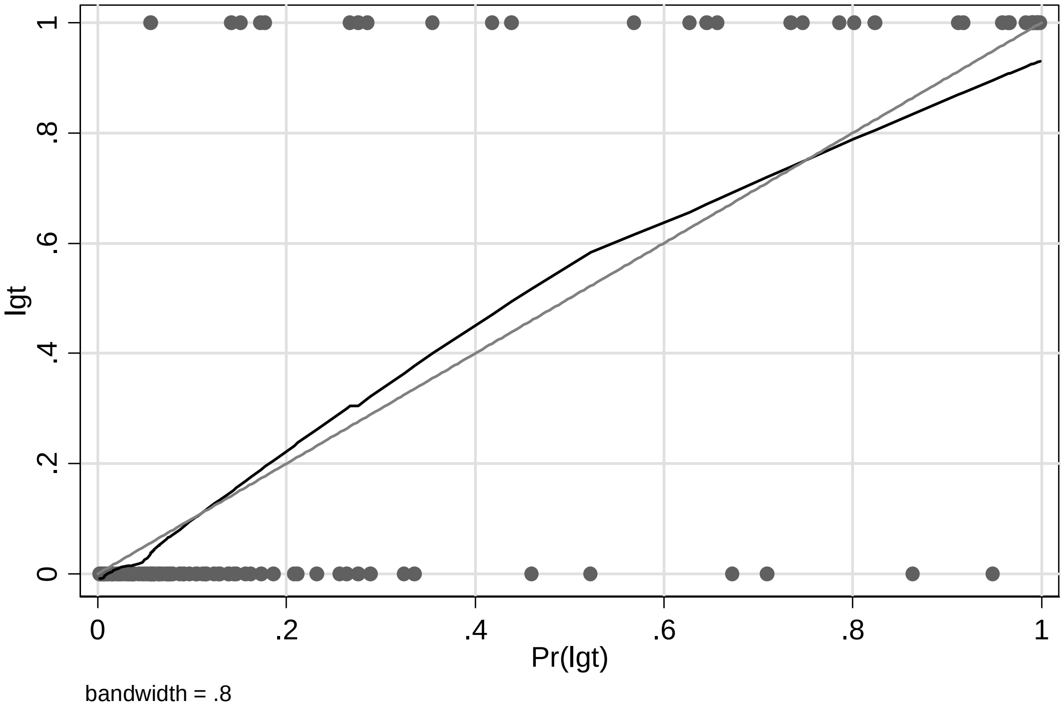

Fig. 2.21. Examining the assumption of linearity in the logit for the logistic regression model used to predict *B. houstonensis* activity. The black line represents the model the outcome predicted by the model. *Lgt* represents the dependent variable..

$$\ln(count) = b_0 - b_1(td) - b_2(mt) + b_3(pr) - b_4(td * mt) + b_5(td * pr)$$

where *ln* is the natural logarithm, *count* is average number of toads captured per 3-day period, and b_i represents the estimated values of the coefficients (Table 2.4). This model did not predict the average number of toads very well for any given 3-day period (Fig. 2.22). It over-estimated the average number of toads at the beginning of the breeding season and underestimated the number of toads active during most three-day periods during the breeding season (Fig. 2.22). However, the model predicted about the same mean number of toads being active before, during, and after the breeding season (Fig. 2.23).

Discussion

Abundance at the GLR

The GLR was monitored continuously from 2001 - 2004, with nightly visits from during the breeding season in 2005, and therefore these data should reflect the actual abundances of toads at the GLR. While numerically fewer toads were captured at the GLR from 2001 – 2004 than at BSP, these results are similar, in trend, to the data from BSP (Fig. 2.3) (Price 2003). From 2001 – 2004, *B. houstonensis* abundance at BSP was at the nadir of the 14 year study. The results from GLR and BSP support the contention that *B. houstonensis* abundance within Bastrop County is at a low point. Price (2003) attributed the low numbers to a regional drought negatively affecting recruitment. Variable environments cause population sizes to fluctuate (Turchin 2003), and throughout its evolutionary history, *B. houstonensis* has had to adapt to the drought

Table 2.4. Parameter estimates for the negative binomial regression model used to predict the count of *B. houstonensis* at the Griffith League Ranch, Bastrop County, Texas, given that Houston toads were active. The log link was used and the dispersion parameter was estimated using maximum likelihood. *td* represents the three-day period, *mt* represents mean minimum temperature, *lp* represents mean three-day precipitation lagged one day.

Parameter	DF	Estimate	S.E.	Confidence Limits		χ^2	*p*
Intercept	1	7.1731	1.8927	3.4635	10.8827	14.36	0.0002
td	1	-0.1202	0.0327	-0.1844	-0.056	13.48	0.0002
mt	1	-0.2699	0.1089	-0.4834	-0.0564	6.14	0.0132
pr	1	0.7168	0.3211	0.0874	1.3461	4.98	0.0256
*td*mt*	1	-0.0137	0.0039	-0.0213	-0.0061	12.5	0.0004
*td*pr*	1	0.0251	0.0091	0.0073	0.0428	7.62	0.0058
Dispersion	1	0.382	0.2268	-0.0626	0.8265		

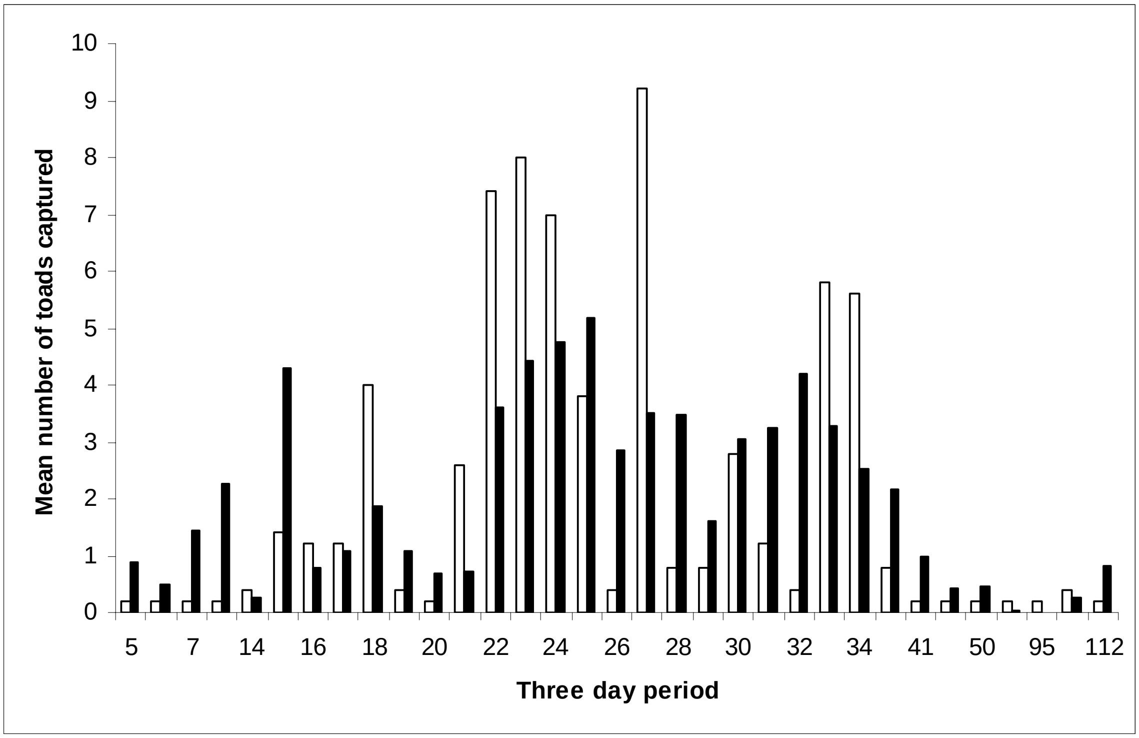

Fig. 2.22. The number of observed (open bars) and predicted (from the negative binomial regression model, closed bars) of Houston toads (*B. houstonensis*) per three-day period, at the Griffith League Ranch, Bastrop County, TX, from 2001 – 2005.

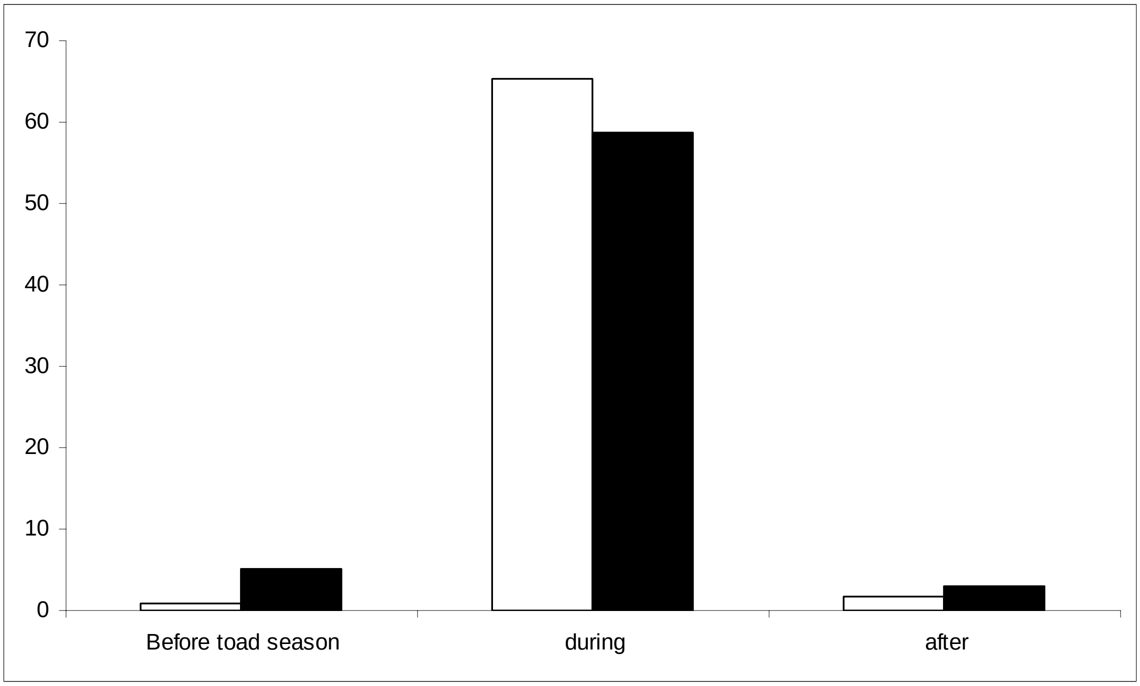

Fig. 2.23. The observed (open bars) and predicted (closed bars) number of toads before, during, and after the known active period of *B. houstonensis* at the Griffith League Ranch, Bastrop County, TX, from 2001 – 2005. Predicted values were calculated from the negative binomial regression.

cycles of southeast central Texas (Sorenson et al. 1976). Populations of *B. houstonensis* would naturally rebound in wetter conditions, however, drought is not the only negative influence on Houston toads.

During the 1950s, the majority of the then extant populations of *B. houstonensis* were exposed to a severe decadal drought (Stahle and Cleaveland 1988). The population in Bastrop county survived and rebounded, while the populations in Harris, Liberty, and Ft. Bend Counties did not (Price 2003). The urban expansion of Houston (located within Harris County) occurred during the same time and most of the available habitat in Harris County of *B. houstonensis* was destroyed, either through urbanization or agricultural modifications. The drought, which lowered recruitment into the population, coupled with the habitat destruction, created conditions from which the population could not recover.

Currently, Bastrop County is experiencing rapid urban growth – the human population of Bastrop County increased by 50% between the last two census periods (38, 263 individuals in 1990 and 57,773 in 2000 (US Census Bureau)). Central Texas is also experiencing a regional drought, similar to the conditions of Harris County during the 1950s. The continuing fragmentation along with the recent construction of several ranchette-style neighborhoods within the critical habitat region of *B. houstonensis* has severely fragmented the Houston toad's favorable habitat. However, two large tracts of land (GLR and BSP, over 1,900 ha each) have dedicated resources to Houston toad conservation. Monitoring the *B. houstonensis* populations in Bastrop County must continue in order to determine the effects of both ongoing fragmentation and drought conditions.

Spatial distribution of B. houstonensis at the GLR

Bufo houstonensis were not captured equally at every pond at the GLR (Fig. 2.5). Most of the toads were captured at the ponds with traps near them (Fig. 2.5), however, the distribution of toads on the GLR does not appear to be an artifact of the trapping design because the majority of toads were captured at chorusing ponds and every pond at the GLR was censused nightly during the breeding season. Houston toads captured in the tmt. 5 traps were never captured in pitfall traps more than 15 m from a forested edge. *Bufo houstonensis* did not appear to utilize non-native pasture habitat during the migrations to and from breeding ponds. Non-native pasture grasses and / or open canopy habitat can hinder dispersal of many amphibian species, especially juveniles (deMaynadier and Hunter 1999, Rothermel and Semlitsch 2002) and these data indicate non-native pasture habitat hinders adult movements as well. Excluding the GLR and BSP, forested habitat in rural Bastrop County exists in small patches, surrounded by a matrix of agricultural and non-native pasture grass patches. These closed canopy patches appear to be required for *B. houstonensis* and the lack of forested lands would logically be detrimental to the Houston toad.

Sexual dimorphisms in B. houstonensis

Bufo houstonensis is sexually dimorphic in size (Table 2.1 and Hillis et al. 1984), however, the size difference between the sexes is not as extreme as its congeners. Mean male body length in *B. americanus* ranges between 82 – 86 % of female body length (Licht 1976, Wilbur et al. 1978), whereas mean SUL length in *B. houstonensis* was reported at 91% (Hillis et al. 1984) or 92% (this study) of female body length.

Toads have indeterminate growth, which is rapid growth from birth to sexual maturity, then after maturity, growth slows (Duellman and Trueb 1994). The difference in size between the sexes results from the different evolutionary pressures each sex faces. Males benefit by maturing faster and breeding more often, while it is advantageous for females to delay maturation to reach a larger size and increase fecundity (fecundity is positively correlated with body size in toads (Reading 1991)).

Capture histories

Both Hillis et al. (1984) and Jacobson (1989) reported multiple visits to breeding sites by male *B. houstonensis*. At the GLR, most males were only captured once per year (Fig. 2.7). For any given year, the proportion of males captured once per year did vary but was always above 0.66 (Fig. 2.8). These results are similar to the results reported by Hillis et al. (1984). Twenty-one males (10.5% of the total sample) were recaptured across years (male capture-recapture data were analyzed in Chapter III). Females, conversely, were never recaptured inter-yearly, were rarely captured at ponds, and were more likely to be captured in traps (refer to Chapter IV for analysis of capture method). In 2005, sampling only included breeding pond surveys, so the number of females may be underestimated in 2005, however, from 2001 – 2004, trapping was extensive, so it is likely there are far fewer females than males at the GLR. Unlike previous studies (Hillis et al. 1984, Price 2003), males at the GLR did not congregate in large numbers at the breeding ponds. The maximum number of males captured on a single night at a single pond at the GLR was 16, compared to 104 individuals captured at one location on one night by Hillis et al. (1984). These results, however, are not meant as direct comparisons, only a point of reference for the dynamics of *B. houstonensis* over the last 20 years. Coupling the results from Hillis et al. (1984) and Price (2003), it is logical to assume to population has been declining since the mid-1990s. Direct competition among males for females was not observed and males were spaced at least one meter apart while chorusing. The sex ratio at the GLR was significantly male-biased (refer to Chapter IV).

The large number of single-visit males coupled with relatively few females indicates two things: the sex ratio could be intrinsically skewed (refer to Chapter IV for discussion of biased sex ratios), and if multiple-visit males are more successful at breeding, as indicated by Hillis et al. (1984), then a small number of males (i.e., the males that are captured more than once per breeding season) could be breeding with more than one female per year. Over time, this breeding strategy would reduce the effective population size, which is consists of only those individuals that contribute offspring to the next generation (Freeman and Herron 1998). In small breeding populations, like the Houston toad, when females are limited and only a few males contribute to the breeding population, then the population has a high potential for inbreeding, which increases both genetic homozygosity and the probability of fixing deleterious alleles (Dobzhansky et al. 1977). Data are currently not available regarding the breeding success of individual *B.*

houstonensis at the GLR, but this needs to be a central thesis of future research, despite the inherent intractability other than by genetic evaluation.

Activity patterns

The breeding strategy of *B. houstonensis* is typical for members of the genus *Bufo* (Licht 1976). Males arrived at potential breeding areas before females. With the exception of 2001, females were always captured during a peak in male activity. In 2001, it is likely the first peak of toad activity occurred before the study began and therefore the 2001 data do not reflect the dynamics of *B. houstonensis* during that year. Females did not arrive at the breeding ponds at once, nor were they captured more than once per year. This breeding strategy is defined as explosive breeding (Wells 1977).

Houston toad activity at the GLR was mostly confined between February and April and activity was correlated with reproductive behavior. Individuals captured after 15 May were always captured after precipitation events greater than 22 mm. When sessile, Houston toads often occupied small mammal burrows or holes under fallen trees (Hillis et al. 1984), and it is likely these refugia were flooded and the late-year captures were a result of toads moving across the landscape in search of a new burrow.

The lack of captures after the breeding season could be a result of migration away from the breeding area. The drift fence arrays would not have captured toads moving more than 100 m from a pond, other than outside suitable habitat. Another possibility is that toads were aestivating to avoid unfavorable environmental conditions. Radio telemetry indicated *B. houstonensis* did not migrate more than 200 m away from their respective breeding ponds. It is important to note that Houston toads were not radio-tracked after 2 June of any year because the telemeters fell off the individuals. Between the end of the breeding season and 2 June, *B. houstonensis* with telemeters did not move unless it rained. The lack of migratory movement of telemetered individuals coupled with lack of captures in the traps that were placed throughout the habitat (Fig. 2.1) does indicate adult *B. houstonensis* are relatively stationary after the breeding season and probably remain within 200 m of their respective breeding pond.

In other Bufonid species, post-metamorphic juveniles disperse from their nascent pond and find new breeding locations (deMaynadier and Hunter 1999). This appears to be the case at the GLR as well. In 2003 and 2004, juvenile Houston toads were marked as they emerged from their natal pond (Greuter 2004, Swannack et al. 2006) and at least one individual was marked at pond 6 and recaptured as an adult in 2005 at pond 2 (straight line distance of 950 m). The juvenile life stage was identified as the crucial life stage for Houston toad conservation (Greuter 2004, Hatfield et al. 2004). If juveniles are the main dispersers, and therefore colonizers, then conservation efforts must focus on conserving habitat connecting potential breeding sites.

Neither males nor females were captured continuously through the breeding season. Generally, there were two peaks of male activity, approximately 10 March (*td* 23) and 10 April (*td* 34) (Fig. 2.15). The single peak of male activity in 2001 is most likely an artifact of the study beginning after the first peak. In 2003, the GLR received very little rainfall and this might have suppressed the second peak. Drought-like conditions were reported to disrupt movement and arrival patterns of *B. quercicus* and *B. terrestris* (Dodd

1994) and it is likely this occurred with *B. houstonensis* during years with little rainfall (2003 & 2005).

Price (2003) reported *B. houstonensis* were not often captured during a full moon. At the GLR, *B. houstonensis* were not captured when the percent lunation was between 51 – 60% (Fig. 2.19). Houston toads were captured equally across all other levels of moonshine. Houston toad activity, like many other bufonids, depended on precipitation and temperature (Fitzgerald and Bider 1974, Smits and Crawford 1984, Greenberg and Tanner 2005b), as well as lunation and time of year. The logistic regression model used in this study predicted mean toad activity fairly well (~86%), based on time of year (three-day period), mean minimum temperature, mean precipitation three days prior, and lunation. The negative binomial regression model, while it did not predict well for a specific three-day period, it did accurately estimate average toad behavior at particular values of temperature and precipitation before, during, and after the breeding season. The two models differed in that the negative binomial regression model did not include *lp* or *mo* and the count only depended on *td*, *mt*, and *pr*, as well as the interaction terms. In general, Houston toad activity did not depend on current precipitation, but depended on the precipitation from three days prior, as well as the phase of the moon. The abundance of toads, given that they are already active, however, depended on the current precipitation (i.e., an increase in current mean three-day precipitation indicated an increase in the abundance of *B. houstonensis*, given the time of year and temperature). These models emphasize that the effects of weather on Houston toad activity are complex, resulting from the interactions of several variables. These interacting variables cannot be separated into component parts, thus the quantitative effect of a single factor is difficult to estimate (Fitzgerald and Bider 1974).

Current research for the Houston toad includes surveying the historical range to determine the current distribution of *B. houstonensis*. The detection of *B. houstonensis* is imperfect, and Jackson et al. (2006) determined it takes 12 visits to a specific site to determine absence with 95% confidence in a given year. These models provide researchers and land managers with quantitative tools to predict if Houston toads will be active during a specific three-day period, given certain environmental conditions and therefore maximizing search efforts.

Conclusions

Based on trends from both BSP and GLR, *B. houstonensis* appears to be declining. During the 1950s, the Houston toad population in Harris County experienced similar conditions, both weather- and anthropomorphic-related. Unlike Harris County, however, there are two large tracts of land (BSP and GLR) in Bastrop County that have dedicated significant resources to the conservation of the Houston toad, and this should buffer the species from immediately losing all of its critical habitat. However, it is important to note that BSP and GLR are not safe-havens, nor is Houston toad conservation the primary mission of either tract. Furthermore, landscape level processes occurring outside of the GLR and BSP, such as fragmentation, could negatively impact the ecological processes occurring inside the properties (Turner et al. 2001), which could further disrupt *B. houstonensis* dynamics. Further, if drought conditions continue, the effects consecutive years with low recruitment could decimate the population. Both the

BSP and GLR must be continually monitored in order to further understand the how landscape-level fragmentation and weather patterns affect the dynamics of this species.

Bufo houstonensis did not utilize pastures composed of non-native grasses. These pastures could be significant barriers for toad dispersal. Houston toads were not captured more than 15 m from a forested edge and movement across pastures only occurred in drainages. No toads were captured in the middle of a pasture. Habitat corridors connecting wooded patches are necessary to aid in dispersal between ponds and upland habitat.

The breeding dynamics of *B. houstonensis* at the GLR were similar to those reported by Hillis et al. (1984), Jacobson (1989), and Price (2003). Males emerged first, began chorusing, and females arrived at the ponds later in the season. Females do not remain at the pond more than one night, nor do they arrive all at once. This defines the Houston toad as an explosive breeder (Wells 1977). The peak in Houston toad activity is generally during the middle of March, the specific time depends on weather conditions. Breeding choruses mainly consisted of single-visit males, with few individuals (10% of the total sample) being recaptured across years.

Radio telemetry and fluorescent pigment tracking indicated that from March – May both male and female *B. houstonensis* remained within 200 m of chorusing ponds. If they burrowed, Houston toads did not burrow below 3 cm, however, all but 1 individual were found under fallen logs (generally oak). Long movements (>10 m daily) did not occur often, and only occurred after precipitation events. One individual utilized a water-filled drainage and its movements were within always within 5 m of the drainage.

The movement patterns of *B. houstonensis* depended on available water and during drought conditions, dispersal from nascent ponds could be limited.

Houston toads were only active during the breeding season. Toad activity appeared correlated with mean minimum daily temperature and mean precipitation. Further, no male and only one female *B. houstonensis* were captured when the percent lunation was between 51-60%. Using the data collected from the GLR, a logistic regression model accurately predicted mean toad activity during a given three day period based on time of year, mean precipitation during the prior three day period, mean minimum temperature, lunation, and the two-way interactions of lunation with each variable. A negative binomial regression model predicted the abundance of Houston toads for any given three day period based on time of year, mean minimum temperature, mean three-day precipitation, and the two-way interactions with time of year and the other two variables. Both models emphasize the complexities of predicting activity based on single environmental factors. These models can assist researchers determine when the probability of encountering Houston toads is the highest.

CHAPTER III

ESTIMATING SURVIVORSHIP FOR ADULT MALE HOUSTON TOADS (*BUFO HOUSTONENSIS*) USING AN INFORMATION-THEORETIC APPROACH

Introduction

Obtaining estimates for basic demographic parameters, such as probabilities of survival and capture, are important to they give insights of animal population dynamics (Schmidt et al. 2002). Understanding the population dynamics of rare or endangered species are especially important because natural resource managers rely on accurate estimates of a species' mortality in order to make informed management decisions to enhance rather than further threaten the survival of the species.

Species with ontogenetic and / or sexual differences in behavior or habitat selection will be exposed to different suites of environmental and interspecific pressures and therefore have age- and sex-specific mortalities (Freeman and Herron 1998). Many amphibians have biphasic life cycles (Duellman and Trueb 1994) and obtaining survival data for each life stage can be difficult because the eggs or larvae must be accurately counted and then censused immediately after emergence. The terrestrial adults must be captured, marked, and recaptured at least once throughout the study period. Commonly, sexually mature amphibians are captured as they immigrate and emigrate to and from breeding ponds or within the breeding site itself, when they are the most conspicuous. Once adults are sexually mature, they may not breed every year, which can make capturing or recapturing individuals difficult, especially during short-term studies (Semlitsch et al. 1996). Nevertheless, with the perception that amphibian populations are declining (Barinaga 1990, Green 2003) survivorship estimates are requisite for each life stage, not only for their use in population modeling (Krebs 2001, Turchin 2003), but also for their use in conservation efforts – identifying critical life stages can aid conservationists in protecting habitat by making sagacious decisions regarding the size of buffer zones required to protect specific life stages of the target species . Obtaining these estimates for open populations requires the use of statistical metrics that estimate probabilities of survival as well as probability of capture because it is almost impossible to capture every individual in a population (Schmidt and Anholt 1999, Schmidt et al. 2002).

During the last two decades, modeling techniques for estimating demographic parameters from mark-recapture (henceforth MR) studies have advanced considerably (Lebreton et al. 1992, Burnham and Anderson 2002). These advances along with the associated freeware used for the statistical analyses of MR data (White and Burnham 1999) have provided biologists with potent, reliable tools for estimating demographic parameters. Recently, MR studies have used a model selection approach within an information-theoretic framework to estimate survival probabilities (Burnham and Anderson 2002, Schmidt et al. 2002). This approach allows biologists to test different biologically-relevant hypotheses (i.e., models) and determine which model best fits the data, based on a selection criterion, most commonly Akaike's information criterion (AIC) (Akaike 1973). AIC provides a reliable decision criterion for model selection for both nested and non-nested models (Schmidt and Anholt 1999, Burnham and Anderson 2002).

Program MARK (White and Burnham 1999) is a freeware application designed to estimate survival probabilities from MR data. In addition to the most commonly used MR metrics (Lebreton and others 1992), MARK allows users to incorporate covariates, often environmental factors such as precipitation, into the design matrix of the models (Cooch and White 2006). In the case of taxa like amphibians, whose survival is intimately coupled with environmental conditions, incorporating environmental factors into the models can provide better estimates for survival. For many rare or threatened species, little information exists about the species life history and survival estimates are paramount for developing well-informed conservation plans.

The Houston toad (*Bufo houstonensis*) is a good example of an imperiled species, and is currently the focus of a habitat conservation plan, yet survivorship remains enigmatic. *Bufo houstonensis* (Sanders 1953) has been listed as endangered for over three decades and is currently limited to 9 Texas counties (Dixon 2000, Gaston et al. 2001). The Houston toad is restricted to areas with deep sandy soils and is commonly associated with pine or mixed-oak woodlands (Brown 1971). The largest remaining pockets of viable Houston toad habitat are in Bastrop County and currently there are two large tracts of land, Bastrop State Park (BSP) and the Griffith League Ranch (GLR) that contain relatively large breeding populations (Hatfield et al. 2004). These areas are separated by a minimum distance of 2.2 km. *Bufo houstonensis* has been the focus of a MR study at BSP since 1990 (Price 2003) and at the GLR since 2000. These studies provided survivorship estimates for three life stages: 1) egg to emergent metamorph (4.73%) (Greuter 2004), 2) emergent metamorph to 13 weeks post-emergence (84.6%) (Greuter 2004), and 3) annual adult female survivorship (20.2% per year) (Hatfield et al. 2004). Adult male survivorship for this species has not been reported. While females appear to be limiting in populations of *B. houstonensis* (Price 2003), estimates for male survival are still needed in order to better understand the dynamics of the species. Caswell (2001) emphasized the need for estimates of survival for both sexes in order to better model the dynamics of sexually reproducing organisms.

This study used an information-theoretic approach to model selection to choose models that best fit an MR dataset for male *B. houstonensis* captured from 2001 – 2005 at the GLR. Under this philosophy, statistical inference requires rigorous attention to selecting the candidate set of models. Based on the known biology of the Houston toad, the set of candidate models chosen examined the effects of time and / or precipitation on the probability of survival.

Methods

Description of study site and field methods

The GLR is a 1,948 ha property, owned by the Boy Scouts of America, located in Bastrop County within the Lost Pines region of Texas. The majority of the property (over 90%) is underlain with deep sandy soils and there are 17 semi-permanent or permanent ponds on the property. *Bufo houstonensis* was originally detected on the property during the early 1980s (A. Price, pers comm, 2002), but a monitoring program was not established until the BSA acquired the property in 2000. In 2000, audio surveys established the distribution of *B. houstonensis* on the property and based on these results, a trapping design was developed. Due to limited initial funding, the traps were placed at the GLR during two consecutive years. In 2001, eight aluminum flashing drift fences, along with pitfall traps, were placed on the property to begin a monitoring project for the Houston toad. In 2002, an additional 10 drift fence / pitfall trap arrays were placed on the property. The final trapping design consisted of 19 traps: 13 Y-shaped drift fences (each arm of the Y was 15 m) with one 19-liter pitfall trap at the point of intersection and identical buckets at the end of each arm and 6 linear drift fences (one 45 m, two 61 m, and three 76 m) with 19-liter pitfalls placed every 15.25 m. In addition to the drift fence arrays, funnel traps were placed alongside the arms of each Y-array and covered with pieces of flashing for shading. Each pitfall trap was fitted with a predator-exclusion-device (Ferguson and Forstner 2006), which also shaded the buckets.

Traps were checked every morning beginning on 12 March 2001 and ending 30 June 2004, with the exception of 1 August 2003 through 9 August 2003, and 20 August 2003 through 1 September 2003 when the traps were closed in order to prevent trap mortalities due to excessive temperatures (greater than 37^{o} C). Likewise, the traps were closed as a result of exceptional rainfall in July 2002 (a total of seven non-consecutive days). Standard measurements were taken for all vertebrate taxa. Each adult *B. houstonensis* received a passive integrated transponder (PIT) (Camper and Dixon 1988). In 2003, Greuter (2004) marked a cohort of emerging *B. houstonensis* metamorphs with a single toe clip. All organisms were released near their capture site shortly after collection. Tissue samples were taken from every individual and are retained at the tissue collection at Texas State University at San Marcos. Dead specimens, and vouchers, when relevant, were deposited in either the Texas Co-operative Wildlife Collection at Texas A & M University, College Station, Texas, or the Museum at Texas Tech University, Lubbock, Texas.

In addition to trapping, nightly surveys were conducted at each of the 17 ponds in 2001 – 2005 at the GLR during the breeding season of *B. houstonensis*, which extends from mid-February to mid-April (Hillis et al. 1984) with the peak of activity occurring in mid-March. Any *B. houstonensis* captured were measured, marked, and released at the point of capture within minutes.

Recaptured individuals were identified using a Power Tracker II (AVID®, Microchip I. D. Systems, Folsom, LA) each time they were captured. Capture histories were established for every individual on a yearly basis and were recorded in the format required for program MARK (Cooch and White 2006). Due to a small sample size, too few data were available for a finer temporal resolution. Capture histories for these data had 5 time periods (e.g., 00110, which represents an individual captured for the first time in 2003, recaptured in 2004, and not seen in 2005). The number of individuals initially captured per year as well as between-year return rate was recorded. Goodness-of-fit tests were used to determine if there were statistical differences ($\alpha = 0.05$) in number of individuals captured per year.

Rain gauges were placed at the GLR on 5 June 2001 and precipitation was recorded daily until the traps were closed on 30 June 2004. Missing data and the 2005 precipitation were obtained from the nearest weather station, which was located approximately 16 km NW from the GLR in Elgin, Texas (National Climatic Data Center: station ID 41280).

Model selection procedure

Using a model selection approach based on information theoretic methods, program MARK (White and Burnham 1999) was used for estimating the probability of survival (φ) and probability of recapture (p) for adult male *B. houstonensis*. Methods used for analyses followed Cooch and White (2006). Two explanatory factors were used to explore variation in φ and p: time and precipitation. Time was considered as variable across all years or constant among years for both φ and p. Total yearly precipitation for the current year (*cp*) or the previous year (*pp*) were used as covariates to determine if the amount of rainfall during the present or previous year affected φ, p, or both. Covariates were standardized to prevent convergence problems in the log-likelihood function (A. Breton, pers. comm). Based on these factors, 16 candidate models were created which explored the effects of time and / or precipitation on the estimates of φ and p.

Each candidate model represented a different, biologically-relevant, *a priori* hypothesis (Table 3.1). For example, model $\varphi_t\ p_t$ represented the Cormack-Jolly-Seber (CJS) model, which was used as the base model for analyses. The CJS model is fully time-dependent for both φ and p (i.e., different estimates were obtained for each year for each parameter). Whereas $\varphi_{cp}\ p.$ represented a model where survivorship is affected by the covariate *cp* and p remained constant across the years.

The amount of support for each of the 16 candidate models was evaluated using a correction factor for AIC (AIC_c), which protects against over-fitting the models, especially with small samples (Hurvich and Tsai 1989). The model with the lowest AIC_c was considered to be the best approximating model. If the difference in AIC_c (ΔAIC_c) between the best fit model and each competing model was < 2.0, then the models were considered to be statistically indistinguishable (Simonoff 2003). Models were ranked from 1 – 16, based on AIC_c scores with 1 being the best model and 16 being the least supported model. Point estimates, standard errors, 95% confidence intervals were recorded for φ and p for each model.

Results

Capture results

From 2001 through 2005, 225 (199 M : 26 F) individual adult *B. houstonensis* were captured and marked at the GLR (Table 3.2). More males were captured at ponds than in the traps, while more females were captured in traps than at the ponds (refer to Chapter IV). The most male toads were captured in 2005, after the traps were closed, while the most females were captured in 2004 (Table 3.2). We did not recapture any females among years. Males were not captured in equal frequencies across years (χ^2 = 51.2663, P < 0.001). There was not a statistical difference in the number of females captured across years (χ^2 = 9.2381, P = 0.055).

Twenty-one of the 199 (10.5%) adult males were recaptured among years (Table 3.2). The majority of males were only recaptured the year immediately following initial capture: 1 male captured in 2001 was recaptured in 2002, 6 captured in 2002 were recaptured in 2003, 5 captured in 2003 were recaptured in 2004, and 4 captured in 2004 were recaptured in 2005. Two males were known to survive at least 3 years and one was

Table 3.1. Candidate models and model selection results used for estimating φ and *p* of 172 adult male *B. houstonensis* captured at the Griffith League Ranch, Bastrop County, Texas, from 2001 – 2005. Models are listed by most supported to least supported based on AIC_c scores. *t* represents time-specific estimates (one estimate available for each time period), **.** indicates estimates were constant across time, *pp* is a covariate representing the total precipitation for the previous year and *cp* is a covariate representing the total precipitation for the current year.

#	Model	AIC_c	ΔAIC_c	AIC_c Weights
1	$\varphi_{\cdot}\ p_{\cdot}$	128.4419	0	0.15953
2	$\varphi_{pp}\ p_{\cdot}$	129.1640	0.7221	0.11118
3	$\varphi_{\cdot}\ p_{pp}$	129.3960	0.9541	0.099
4	$\varphi_{cp}\ p_{cp}$	129.7178	1.2759	0.08429
5	$\varphi_{cp}\ p_{pp}$	129.8434	1.4015	0.07916
6	$\varphi_{t}\ p_{pp}$	129.8893	1.4474	0.07736
7	$\varphi_{t}\ p_{cp}$	129.8893	1.4474	0.07736
8	$\varphi_{\cdot}\ p_{cp}$	129.9428	1.5009	0.07532
9	$\varphi_{cp}\ p_{\cdot}$	130.5413	2.0994	0.05584
10	$\varphi_{pp}\ p_{cp}$	131.0126	2.5707	0.04412
11	$\varphi_{pp}\ p_{pp}$	131.0707	2.6288	0.04285
12	$\varphi_{cp}\ p_{t}$	131.5835	3.1416	0.03316
13	$\varphi_{t}\ p_{\cdot}$	132.6805	4.2386	0.01916
14	$\varphi_{\cdot}\ p_{t}$	132.9572	4.5153	0.01669
15	$\varphi_{pp}\ p_{t}$	132.9572	4.5153	0.01669
16	$\varphi_{t}\ p_{t}$	134.3587	5.9168	0.00828

Table 3.2. Number of Houston toads captured per year at the Griffith League Ranch, Bastrop County, Texas, from 2001 – 2005. *Initial males* and *Initial Females* represent the number of new individuals captured each year. *Recaptured males* is the number of males marked in prior years recaptured during that year. During the study period, females were not recaptured across years.

Year	Initial Males	Recaptured Males	Initial Females
2001	11	0	2
2002	69	1	7
2003	35	7	6
2004	18	6	9
2005	66	7	2

at least four years old. Two were initially captured in 2003, not seen in 2004, and recaptured in 2005. One was initially captured in 2002 and subsequently recaptured in 2003, 2004, and 2005. Each male was recaptured at the same pond (or at a trap within 50 m of the pond) where it was initially captured.

The between-year return rates of males varied across years. The proportions surviving to the next year were: 0.11 (2001-2002), 0.17 (2002-2003), 0.29 (2003-2004, including the two individuals recaptured in 2005), and 0.28 (2004-2005).

Model selection and parameter estimates

Based on ΔAIC_c, models 1 – 8 were supported (Table 3.1). The most parsimonious model ($\varphi. p.$) had the lowest AIC_c (128.4419), however, seven other models also had a $\Delta AIC_c < 2.0$, therefore none could be distinguished as the best approximating model. Models 9 – 11 were reasonably supported ($2.0 < \Delta AIC_c < 3.0$). Models with p_{cp} (models 4, 7, 8, 10) and p_{pp} (models 3, 5, 6, 11) were reasonably well supported by the data (Tables 3.3 and 3.4). Only six of the eight models associating *cp* or *pp* with φ were supported – models 12 ($\varphi_{pc}\, p_t$) and 15 ($\varphi_{pp}\, p_t$) were not ($\Delta AIC_c = 3.1416$ and 4.5153, respectively) (Table 3.3).

Survival estimates of male *B. houstonensis* varied among the plausible models (estimates along with their standard errors and 95% confidence intervals are listed in Table 3.3). In the most parsimonious model (model 1, $\varphi. p.$) the estimate of φ was 0.270 (95% CI: [0.15, 0.437]). Both models 3 and 8 estimated constant φ across all time periods and the estimates were 0.243 (95% CI: [0.124, 0.422]) and 0.244 (95% CI: [0.097, .490]), respectively. Survival estimates for models containing φ_{cp} (models 4, 5,

Table 3.3. Estimates for φ in Houston toads, based on models supported by using information theoretic approach using program MARK. t represents time-specific estimates (one estimate available for each time period), **.** indicates estimates were constant across time, *pp* is a covariate representing the total precipitation for the previous year and *cp* is a covariate representing the total precipitation for the current year..

#	Model	Year	Estimate	SE	LCI	UCI
1	$\varphi_{\cdot}\ p_{\cdot}$	all	0.270	0.074	0.150	0.437
2	$\varphi_{pp}\ p_{\cdot}$	2001-2002	0.266	0.076	0.145	0.438
		2002-2003	0.242	0.072	0.128	0.409
		2003-2004	0.236	0.072	0.123	0.405
		2004-2005	0.408	0.173	0.145	0.736
3	$\varphi_{\cdot}\ p_{pp}$	all	0.243	0.077	0.124	0.422
4	$\varphi_{cp}\ p_{cp}$	2001-2002	0.191	0.040	0.125	0.280
		2002-2003	0.184	0.040	0.118	0.275
		2003-2004	0.422	0.220	0.111	0.810
		2004-2005	0.143	0.050	0.070	0.270
5	$\varphi_{cp}\ p_{pp}$	2001-2002	0.191	0.049	0.113	0.306
		2002-2003	0.185	0.050	0.106	0.302
		2003-2004	0.413	0.214	0.111	0.799
		2004-2005	0.145	0.060	0.062	0.303
6	$\varphi_{t}\ p_{pp}$	2001-2002	0.100	0.095	0.014	0.467
		2002-2003	0.143	0.050	0.070	0.271
		2003-2004	0.411	0.204	0.117	0.785
		2004-2005	0.208	0.083	0.089	0.413
7	$\varphi_{t}\ p_{cp}$	2001-2002	0.100	0.095	0.014	0.467
		2002-2003	0.143	0.050	0.070	0.271
		2003-2004	0.411	0.204	0.117	0.785
		2004-2005	0.208	0.083	0.089	0.413
8	$\varphi_{\cdot}\ p_{cp}$	all	0.244	0.103	0.097	0.490
9	$\varphi_{cp}\ p_{\cdot}$	2001-2002	0.272	0.083	0.142	0.459
		2002-2003	0.273	0.085	0.140	0.464
		2003-2004	0.266	0.101	0.116	0.500
		2004-2005	0.275	0.101	0.122	0.506

Table 3.4. Estimates for *p*, in Houston toads, based on models supported by using information theoretic approach using program MARK. *t* represents time-specific estimates (one estimate available for each time period), **.** indicates estimates were constant across time, *pp* is a covariate representing the total precipitation for the previous year and *cp* is a covariate representing the total precipitation for the current year..

Model #	Model	Year	Estimate	SE	LCI	UCI
1	$\varphi_{\bullet}\, p_{\bullet}$	all	0.585	0.191	0.232	0.868
2	$\varphi_{pp}\, p_{\bullet}$	all	0.572	0.191	0.225	0.860
3	$\varphi_{\bullet}\, p_{pp}$	2002	0.731	0.303	0.117	0.982
		2003	0.738	0.306	0.113	0.984
		2004	0.502	0.211	0.162	0.840
		2005	0.786	0.315	0.086	0.993
4	$\varphi_{cp}\, p_{cp}$	2002	NE	NE	NE	NE
		2003	NE	NE	NE	NE
		2004	0.359	0.205	0.089	0.763
		2005	NE	NE	NE	NE
5	$\varphi_{cp}\, p_{pp}$	2002	NE	NE	NE	NE
		2003	NE	NE	NE	NE
		2004	0.366	0.208	0.091	0.770
		2005	NE	NE	NE	NE
6	$\varphi_{t}\, p_{pp}$	2002	NE	NE	NE	NE
		2003	NE	NE	NE	NE
		2004	0.385	0.215	0.095	0.788
		2005	NE	NE	NE	NE
7	$\varphi_{t}\, p_{cp}$	2002	NE	NE	NE	NE
		2003	NE	NE	NE	NE
		2004	0.385	0.215	0.095	0.788
		2005	NE	NE	NE	NE
8	$\varphi_{\bullet}\, p_{cp}$	2002	0.611	0.297	0.119	0.948
		2003	NE	NE	NE	NE
		2004	0.539	0.214	0.178	0.864
		2005	0.701	0.435	0.038	0.993
9	$\varphi_{cp}\, p_{\bullet}$	all	0.583	0.192	0.229	0.868

and 9) varied from 0.143 – 0.422 and did not increase with increasing rainfall. Plausible models that included φ_{pp} (2, 10, and 11) had higher estimates for φ when compared to models including φ_{cp} and these estimates varied from 0.232 – 0.408, once again, the estimates did not increase with increasing precipitation. Models 6 and 7 estimated φ for each time period without including an environmental covariate. The estimates for these models were identical within five decimal places and varied from 0.1 – 0.411, with the highest survivorship being between 2003 and 2004 (Table 3.3).

The estimates for probability of recapture also varied among the competing models (estimates and associated data are listed in Table 3.4). Several parameters were not estimable in models 4 – 7, due to the small sample size (Table 3.4). The most parsimonious model (model 1) estimated p as 0.5849 (95% CI: [0.232, 0.868]). Of the remaining models with 4 estimable parameters, p varied from 0.50 – 0.78. Models 3 and 8, which held φ constant (φ.) and included p_{pp} or p_{cp} as a covariate had estimates of p between 0.50 and 0.79 and the estimates did not increase with increasing precipitation. When p was held constant across all years, (models 2 and 9, not including the highest ranked model) the estimates were 0.57 and 0.58, respectively. None of the models that include p_t were included in the set of plausible models.

Discussion

Capture results

During this five year study very few male and no female *B. houstonensis* were recaptured. From 2001 – 2004, the pitfall traps were checked daily and from 2001 – 2005, nightly surveys were conducted at the ponds at the GLR during the breeding season. At first glance, these numbers are low, however, the BSP site showed similar trends from 2001 – 2004 (currently, 2005 data from BSP are not available). While more toads were captured at BSP (233 M : 65 F) than at GLR (133 M : 24 F), toad abundance at BSP was at the nadir of the 14 year study. Male recapture rates were higher at BSP in 2002 (BSP: 12%, GLR: 2%), similar in 2003 (BSP: 19%, GLR: 18%) and were higher at the GLR in 2004 (BSP: 19%, GLR: 24%). Few females were recaptured at BSP: two in 2001, one in 2002, none in 2003, and two in 2004 (Price 2003) and no females were recaptured at the GLR. The low return rates of females at both locations indicate that females either do not return to the same breeding location or they may not breed in consecutive years. The results from the GLR, taken in this context, seem to represent an accurate snapshot of the dynamics of a small, but representative, group of *B. houstonensis* in Bastrop County from 2001 – 2005.

At the GLR, every recaptured male returned to the same breeding pond where they were initially captured, without exception. All but two males were recaptured at the same location the year after its initial capture. Two males that were initially captured in 2003 were not seen in 2004 and were recaptured at the initial capture location in 2005. In 2004, these males did not breed, emigrated to another breeding location, or were not captured. Given the behavior of the other recaptured males, it seems that the latter two are the most likely, however, 2004 was a dry year and these males may not have bred as a result of unfavorable environmental conditions. Two individuals marked as post metamorphic juveniles in 2003 (Greuter 2004) were recaptured at their nascent pond as adult males in 2005. They appeared to be first year breeders (SUL 59.3 mm and 57.4 mm) indicating that maturation may take longer than 1 year for males.

Model selection

Model selection procedures identified eight models with essentially equal support. The first was the most parsimonious model (model 1, $\varphi. p.$), which assumed the probabilities of survival and recapture were constant across years. The other seven models included precipitation (either *cp* or *pp*) as a covariate. Based on these results, there is evidence for constant survival and recapture in male *B. houstonensis* during the study period, and there is also evidence that both φ and p are dependent on precipitation, which is intuitive, because *B. houstonensis*, like the majority of amphibians (Duellman and Trueb 1994), still relies on available water to complete its life cycle.

The small sample size limited the ability to draw precise conclusions regarding the effect of specific levels of precipitation on both survival estimates and probability of recapture. Gross inferences can be made based on the plausible models that included precipitation. After the breeding season, *B. houstonensis* is thought to spend the majority of the time underground, presumably to avoid desiccation during the hot Texas summers (daily temperatures in excess of 30°C from early July – mid September). This behavior is common in burrowing bufonids as it reduces rates of cutaneous water loss due to higher moisture content in the soils than on the surface (Hoffman and Katz 1989, Schwarzkopf and Alford 1996). Dry years would decrease the amount of available soil moisture and would therefore increase mortality in the population during the following year (as reflected in models containing φ_{pp}). The same logic applies to the probability of recapture as well. Precipitation events at the beginning of the calendar year (models with p_{cp}) should positively influence p as the microclimate will be more favorable for toads. Therefore, the effects of precipitation cannot be eliminated and will be examined in more detail as more data are accumulated for *B. houstonensis* at the GLR.

Survival estimates

Historically, return rates between subsequent sampling periods were used as estimates of the minimum survival rate. Return rates were used to determine minimum survival probabilities for several species of *Bufo*: *B. hemiophrys* (32.7%) (Kelleher and Tester 1969), *B. woodhousei* (22.5%) (Clarke 1974) and *B. w. fowerli* (Volpe 1960). The return rates for *B. houstonensis* varied between 2 – 24%. This method underestimates survival probabilities (Nichols and Pollock 1983) because the number of individuals recaptured during any time period is the result of two events: the probability of surviving and the probability of being recaptured, given the individual is alive (Lebreton et al. 1992). The method used in this study (White and Burnham 1999) takes the probability of recapture into account and also allowed the inclusion of environmental covariates to estimate φ, as well as the variability surrounding the estimate.

Estimated probabilities of survival for models that included precipitation varied from 0.1 – 0.4, with the majority of the estimates being between 0.19 and 0.30 (Table 3.3). These estimates of φ are within the range of previously reported values for species of *Bufo* (Duellman and Trueb 1994, Schmidt and Anholt 1999). Although these models were supported (Table 3.1), the 95% confidence intervals were wide (Table 3.3), therefore strong conclusions regarding the precision of the point estimate cannot be made. Precipitation is obviously important to the survival of amphibian species and the effects of specific levels of precipitation on survivorship may become clearer with a larger sample size.

The best supported model (model 1, $\varphi.\, p.$) estimated yearly survival of males at 0.270, which is slightly higher than the estimate of the mean φ reported for females (0.2022, $\sigma^2 = 0.0194$) by Hatfield et al. (2004) from the BSP site. The dataset used to estimate female survivorship was much larger than dataset from the GLR and it is reasonable to assume that the results reported by Hatfield et al. (2004) were not affected by low sample size problems.

Compared to the point estimate for females, it is likely that the point estimate for model 1 is high. During the active period (i.e., breeding season), males are more visible to predators than females because they call from the pond's edge to attract mates and also, males return to the breeding ponds multiple times during the breeding season. This male-specific behavior should increase mortality in the males. Conversely, females visit the pond once per season, deposit eggs, and return to the upland habitat (refer to Chapter II), which should lower the risk of predation and mortality. Also, females mature later than males (Quinn and Mengden 1984), which causes the sex ratio to be male-biased (refer to Chapter IV) and selection should drive the sex ratio towards parity (Wilson 1975), which would also favor adult male survival being lower than females'.

There is evidence for the effects of precipitation on survivorship of adult male *B. houstonensis*, however, due to the variability surrounding those estimates, particularly robust statements cannot be made about these effects. This is not a failure of the method, but a result of sampling a population that is at its lowest abundances during the last 15 years (Price 2003). Our future research includes using these estimates to build a mathematical simulation model of the population dynamics of the Houston toad. Given the breadth of knowledge regarding the survivorship of this species (Greuter 2004, Hatfield et al. 2004), we can use the data presented here as a stepping stone for evaluating and estimating male survivorship. Furthermore, male survivorship is a prime candidate for sensitivity analysis (a technique which allows uncertain parameters values to be refined through simulation (Grant et al. 1997)). These data are a small, but essential, step forward towards learning about the complete life history of the endangered Houston toad.

CHAPTER IV

A POSSIBLE CAUSE FOR THE SEX RATIO DISPARITY IN THE ENDANGERED HOUSTON TOAD (*BUFO HOUSTONENSIS*)

Introduction

Anurans exhibit several different temporal breeding strategies, from continuous year-round breeding to short, seasonal breeding lasting anywhere from a few days to a few weeks per year (Wells 1977). Demographic parameters (i.e., population size and sex ratios) of species with short breeding seasons are difficult to ascertain because the adults are above ground for such a limited time. The functional sex ratio (FSR) is the proportion of adult males to adult females that are alive within a population (Gibbons 1990). The FSR is difficult to estimate for short term breeders, especially in species where males congregate at a breeding area and vocalize to attract females. Males are thus concentrated at breeding areas and more accessible to researchers, whereas females make less frequent and shorter trips to breeding areas (Duellman and Trueb 1994), and as a result are less likely to be captured. As a result of this breeding strategy, the adult sex ratio at any given time at a breeding pond will most likely be male-biased. The individuals at breeding ponds function under an operational sex ratio (OSR), which is the ratio of potentially mating males to receptive females located at the breeding areas at any given time (Emlen 1976). For many anuran species, the OSR changes through the season (Eggert and Guyétant 2003). Male generally arrive at the ponds earlier in the season and their vocalizations lure females to the ponds (Duellman and Trueb 1994), causing the OSR to shift from strongly male-biased closer to parity. Females of many anuran species may not breed every year and therefore short-term research efforts focused specifically on the breeding areas would be able to accurately estimate the OSR, but the estimates of the FSR may remain unknown.

Accurate estimates of both the FSR and OSR are important because of the potential influence of the sex ratio on population dynamics (Gibbons 1990). Wilson (1975) showed that an equal sex ratio (1 M : 1 F) was evolutionarily stable. Whereas, a biased sex ratio lowers the effective population size (N_e), which is the number of individuals actually contributing to reproduction in the population (Freeman and Herron 1998). There are several biological reasons sex ratios can be biased: 1) sex ratios can be intrinsically biased because of unequal sex ratio at birth, 2) differential mortality between the sexes, 3) differential migration rates between the sexes, and 4) differential maturation rates (Wilson 1975, Gibbons 1990). Delayed maturation is common in turtles (Ernst et al. 1994) and Gibbons (1990) stated that differential maturation was the most important factor affecting the FSR in turtles, yet few studies have explored the effects of this life history characteristic in anurans.

Researcher bias and / or sampling error may artificially skew sex ratio estimates in either direction (Gibbons 1970). Different types of sampling methods (i.e., pitfall traps, hand captures, etc…) can produce skewed sex ratio estimates and may not accurately reflect natural conditions (Ream and Ream 1966, Dodd 1991). It is paramount to distinguish between a perceived sex ratio bias (i.e., from sampling error or collection bias) and an intrinsic bias, especially for species possessing life history characteristics that may lead to otherwise undetected intrinsic biases. Distinguishing between intrinsic versus sampling biases increases our ability to evaluate natural population processes.

The endangered Houston toad, *Bufo houstonensis*, is an excellent model species to examine the sex ratio of anurans with delayed maturation. Data gathered from a captive study (Quinn and Mengden 1984), demonstrate male *B. houstonensis* mature in one year while females mature in two years, and as a consequence of this the adult sex ratio has the potential to be naturally skewed.

Reproductive activity for *B. houstonensis* extends from late January through early May (Hillis et al. 1984), yet, *B. houstonensis* does not breed continuously throughout the season, instead activity is confined to 3 – 5 day spurts (Price 2003). Male toads assemble at ponds (either ephemeral or permanent) and attract females through chorusing. Within a given season, individual males will return to the same pond and females rarely visit a breeding site more than once (Jacobson 1989). In between these short breeding periods, and after the reproductive season is finished, adult Houston toads are rarely seen above ground. Both Hillis et al. (1984) and Price (2003) reported male-biased sex ratios for populations of *B. houstonensis* in Bastrop County, Texas, the largest remaining refugium for *B. houstonensis*. Both of these studies were limited to individuals collected at breeding ponds, where a higher number of males are expected, due to their breeding strategy.

Bufo houstonensis has been the focus of an extensive 4-year study encompassing both breeding pond surveys and drift fence-pitfall traps placed throughout Houston toad habitat at the Griffith League Ranch (GLR) in Bastrop County, Texas (Forstner and

Ahlbrandt 2003). This provides the first opportunity to test sex ratios based on both breeding pond and upland habitat captures of *B. houstonensis*. The objectives of this study were: 1) to estimate the OSR and FSR of *B. houstonensis* captured at the GLR, and 2) to explore causes of sex ratio biases using field data and a computer simulation model which examined the effect of differential ages at first reproduction on the adult sex ratio.

Methods

Study system

The GLR is a 1,948 ha property owned by the Boy Scouts of America (BSA) in Bastrop County, Texas. The GLR was historically pine and mixed hardwood forest, but three large tracts of approximately 200 ha each were cleared for cattle grazing early in the 20th century. *Bufo houstonensis* were originally detected on the property during the early 1980s (Andrew Price, pers. comm.). Audio surveys conducted since 2000 have documented *B. houstonensis* choruses at 12 of the 17 ponds on the property.

Field methods

Demographic data were collected from 71 pitfall traps associated with 18 drift fences in 3 habitats on the GLR (Fig. 4.1). Traps were checked every morning (year-round) from 12 March 2001 – 30 June 2004. Snout-urostyle length (SUL), head width (HW), and weight were recorded for all anurans. Each adult *B. houstonensis* received a passive integrated transponder (PIT) (Camper and Dixon 1988). All organisms were released near their capture site shortly after collection.

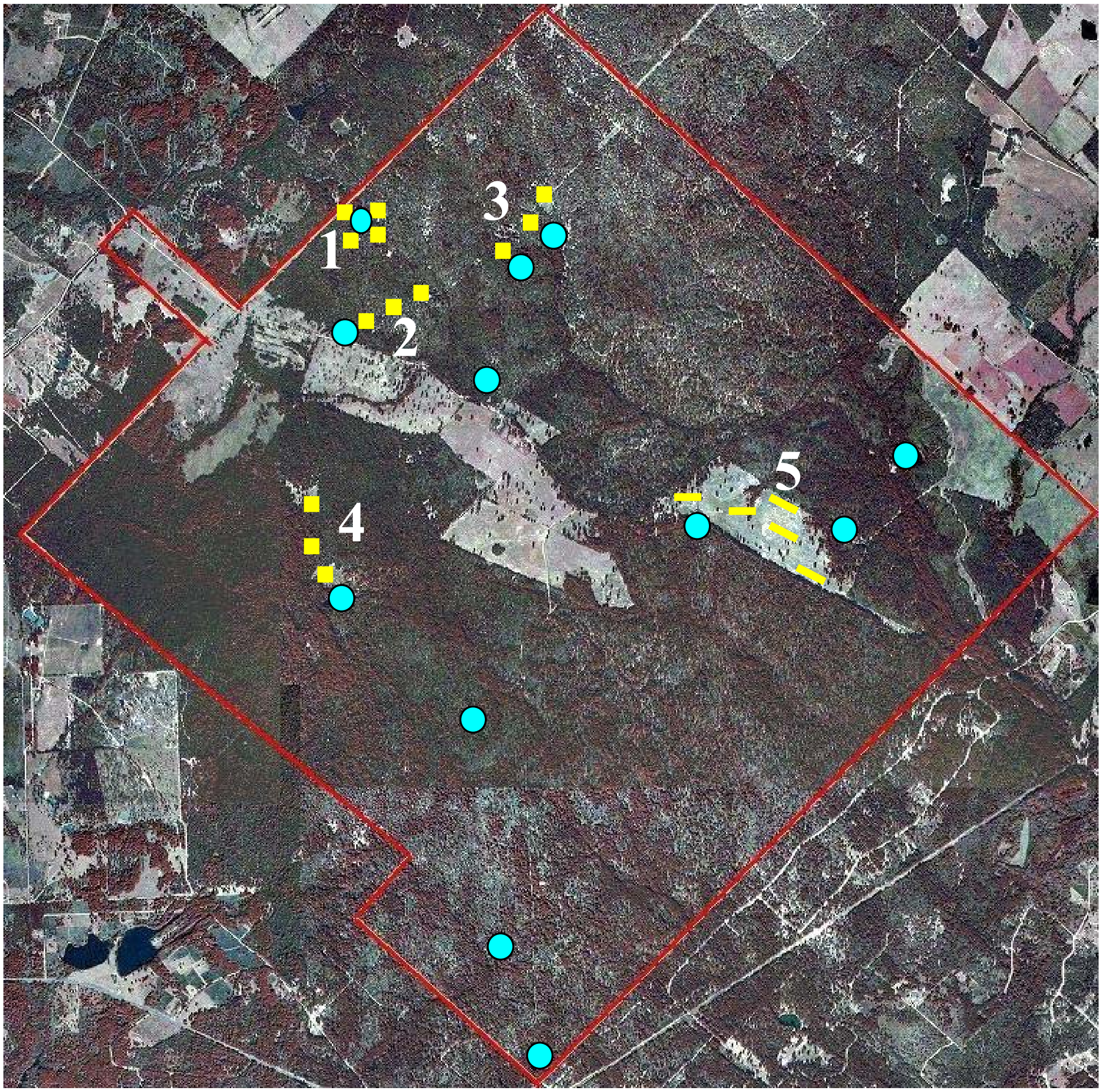

Fig. 4.1. Map of the trapping design on the Griffith League Ranch. Circles represent ponds where Houston toads have either chorused or bred. Boxes represent Y-shape drift fence arrays. Lines represent linear drift fence arrays. Numbers represent the numbers used for the treatment groups of the traps.

Nightly surveys were conducted at each of the 17 ponds at the GLR during the breeding seasons of 2001 – 2004 (Jackson et al. 2006). Any *B. houstonensis* captured were measured, marked, and released at the spot of capture within 10 minutes.

Statistical analyses

The total number of *B. houstonensis* was separated by sex and capture method (pitfall traps or hand captured at breeding ponds, henceforth traps and ponds respectively). Using a χ^2 test corrected for 1 df, we tested for significant differences in the numbers captured per method for each sex independently. A 2x2x4 contingency table was created using the collection method (ponds or traps), sex, and year to determine if trap type and sex were conditionally independent given the year. A Cochran-Mantel-Haenszel (CMH) statistic was calculated (Agresti 1996) to determine if the conditional odds ratio ($\theta_{\mathrm{TRAP.SEX(year)}}$) for each partial table was 1.0 (H_0: $\theta_{\mathrm{TRAP.SEX(2001)}} = \ldots \theta_{\mathrm{TRAP.SEX(2004)}} = 1$). Rejecting the null would indicate there is not conditional independence among traps and sex for each year. A Breslow-Day (BD) statistic (Agresti 1996) tested that the odds ratio between trap type and sex was the same across all years (H_0: $\theta_{\mathrm{TRAP.SEX(2001)}} = \ldots \theta_{\mathrm{TRAP.SEX(2004)}}$). If H_0 for the BD is not rejected, a common odds ratio for sex vs collection method can be estimated for all years. Tables were analyzed using PROC FREQ in SAS.

The number of times each individual was captured per year was analyzed to determine the percentages of individuals that visited the breeding areas once or more than once.

Sex ratios were established for the individuals captured, separated by year by sampling method (pitfall traps or hand captures at breeding ponds). Each observed ratio was tested for differences from unity (1M : 1F) using a χ^2 test corrected for 1 degree of freedom. Sex ratios established from the trapping data and breeding pond data were tested for significant differences from parity as well as from each other using a χ^2 test corrected for continuity.

Simulation model

We wanted to determine quantitatively how the adult sex ratio of *B. houstonensis* was affected by delayed maturation. In order to examine the hypothesis that the bias in the adult sex ratio is a result of delayed maturation, a simulation model was created using STELLA® v7 (isee Systems, Lebanon, New Hampshire).

The model was represented mathematically as a discrete-time compartment model with a 1-year time step. Recruitment (R) into the terrestrial life stages was the driving variable (see Grant et al., 1997 for specific definitions of variable types) of the model and was parameterized as constant, adding the same number of new individuals to the system at the beginning of each time step. The sex ratio was assumed equal at parturition since gender is genetically determined in toads (Duellman and Trueb 1994) and there is currently no reason to suspect an unequal sex ratio at birth in *B. houstonensis*. Sexually immature individuals were assumed to have equal mortality rates regardless of their future gender (Gibbons 1990). The state variables represented the four terrestrial life stages of an anuran: post-metamorphic juveniles (PMJ), sexually mature adult males (AM), immature females (IF), and sexually mature adult females

(AF). Since male *B. hosutonensis* mature in one year (the length of the time step), we did not include a state variable to represent juvenile males. After the first time step, 50% of the individuals in the PMJ state variable were transferred to the AM state variable and the other half went into IF. Immature, one-year old, females should die at a different rate compared to year-old adult males in their cohort. Current data indicate juvenile and adult *B. houstonensis* do have different mortality rates (Greuter 2004, Hatfield et al. 2004). Per-capita mortality (*k*) for the IF state variable was a constant, which was re-parameterized for each simulation – *k* was calculated and immature females died at that rate at every time step. A conservative assumption of this model was that the annual adult per capita mortality for both the AM and AF state variables was the same (0.8 as reported for *B. houstonensis* (Hatfield et al. 2004)). The state variables were calculated as follows:

$$\boldsymbol{PMJ_{t+1} = PMJ_t + \left(R - PMJ_t\right)\Delta t}$$

$$\boldsymbol{AM_{t+1} = AM_t + \left(0.5PMJ_t - 0.8AM_t\right)\Delta t}$$

$$\boldsymbol{IF_{t+1} = IF_t + \left(0.5PMJ_t - (k * IF_t) - (IF_t - (k * IF_t))\right)\Delta t}$$

$$\boldsymbol{AF_{t+1} = AF_t + (IF_t - (k * IF_t) - 0.8AF_t)\Delta t}$$

where Δt represents the change in time. The age at first reproduction was based on maturation data from a captive population with males maturing in one year and females maturing in two (Quinn and Mengden 1984). Data are not available for natural estimates of *k* in *B. houstonensis*, so we chose six mortalities (0.01, 0.1, 0.25, 0.5, 0.75, or 0.8) that represented a wide range of possible values including setting *k* equal to adult mortality (0.8). Six simulations were run, one at each different value of *k*. The length of each simulation was 10 years. Adult sex ratios (M/F) were calculated. The resulting sex ratios were tested for differences from unity using a χ^2 test corrected for continuity.

Results

Between 12 March 2001 and 31 August 2004, a total of 157 (133M : 24F) distinct, individual adult *B. houstonensis* was captured at the GLR. Significantly more males were captured at ponds than in the traps (88 ponds : 45 traps, $\chi^2 = 13.26$, $P = 0.0003$) while more females were captured at the traps than in ponds, however, the difference was not significant (16 traps: 8 ponds, $\chi^2 = 2.04$, $P = 0.1532$).

The CMH test from the 2x2x4 table indicated the odds of capturing males and females were different and varied by trapping method (CMH = 6.98, P=0.0083). The BD test ($\chi^2 = 1.97$, P=0.5782) indicated a common odds ratio could be estimated across all years. The odds of capturing a female in a trap were 3.53 greater than capturing a female in a pond. The odds of capturing a male in a trap was 0.2833 compared to capturing males while chorusing at the breeding ponds.

Females were never captured more than once per year, however, 21% of the males were captured more than once per year. In 2001, only 1 male out of the 11 captured was captured more than once. In 2002, 14% of the individuals were captured more than once while in 2003 and 2004, 29% and 33% were recaptured during the season. In 2003, 12 individuals were captured between 2 and 5 times, and in 2004 eight individuals were captured between 2 and 3 times.

Sex ratios varied by collection methods and across years (Table 4.1). Collection at the breeding ponds yielded 96 (88M : 8F) toads from 800 person hours (4 years of

Table 4.1 Individual *B. houstonensis* captured at the Griffith League Ranch (GLR) from 2001 – 2004. Sex ratios (SR, M:F) were established per year based on sampling method (toads captured in pitfall traps or at breeding ponds). Sex ratios were tested for differences from parity using χ^2 goodness of fit tests corrected for continuity.

	Traps				Ponds (OSR)				Overall (FSR)			
Yr.	M	F	SR	*P*	M	F	SR	*P*	M	F	SR	*P*
2001	4	2	2:1	0.68	7	0	--	--	11	2	5.5:1	0.03
2002	21	3	7:1	<0.001	48	4	12:1	<0.001	69	7	9.9:1	<0.001
2003	13	4	3.3:1	0.05	22	2	11:1	<0.001	35	6	5.8:1	<0.001
2004	7	7	1:1	--	11	2	5.5:1	0.0265	18	9	2:1	0.12
Total	45	16	2.8:1	<0.001	88	8	11:1	<0.001	133	24	5.5:1	<0.001

surveys, 25 surveys per year, 4 hours per survey, 2 researchers per night). An additional 61 toads (45M : 16F, 17,157 trap nights), were captured at drift fence-pitfall traps. Overall, the yearly sex ratios were significantly male-biased except for 2004 (Table 4.1). Sex ratios established for individuals captured in the traps were not significantly different from parity in 2001, 2003, and 2004, while significantly more males were captured in the traps in 2002 (Table 4.1). Sex ratios established for individuals captured at the breeding ponds were all significantly male-biased. The sex ratio established from toads captured at the breeding ponds (11M: 1F) was significantly different from the sex ratio of the trapping results (2.8M : 1F, $\chi^2 = 15.1$, $P = 0.0001$).

The results of the simulations are shown in Fig. 4.2. The model stabilized two time steps (2 years) after female maturation. When the age at first reproduction of females was 2 years, the adult sex ratio was not significantly different from parity at the three lowest values of k (0.01, 0.1, and 0.25) ($P > 0.15$), however, at higher values of k (0.5, 0.75, 0.8), the adult sex ratio was significantly biased ($P < 0.001$). The sex ratios from the simulation for $k = 0.5$ and $k = 0.75$ were 2M : 1F and 4M : 1F, respectively. When k was equal to adult mortality (0.8) the final sex ratio was 5M : 1F and was significantly different from unity ($P < 0.0001$)

Discussion

The sex ratio for the overall sample of *B. houstonensis* collected at the GLR was significantly male-biased (Table 4.1). However, trapping methods significantly affected the sex ratio estimates. Previous studies on *B. houstonensis* also reported male-biased sex ratios (Hillis et al. 1984, Price 2003), however, in those studies, toads were only

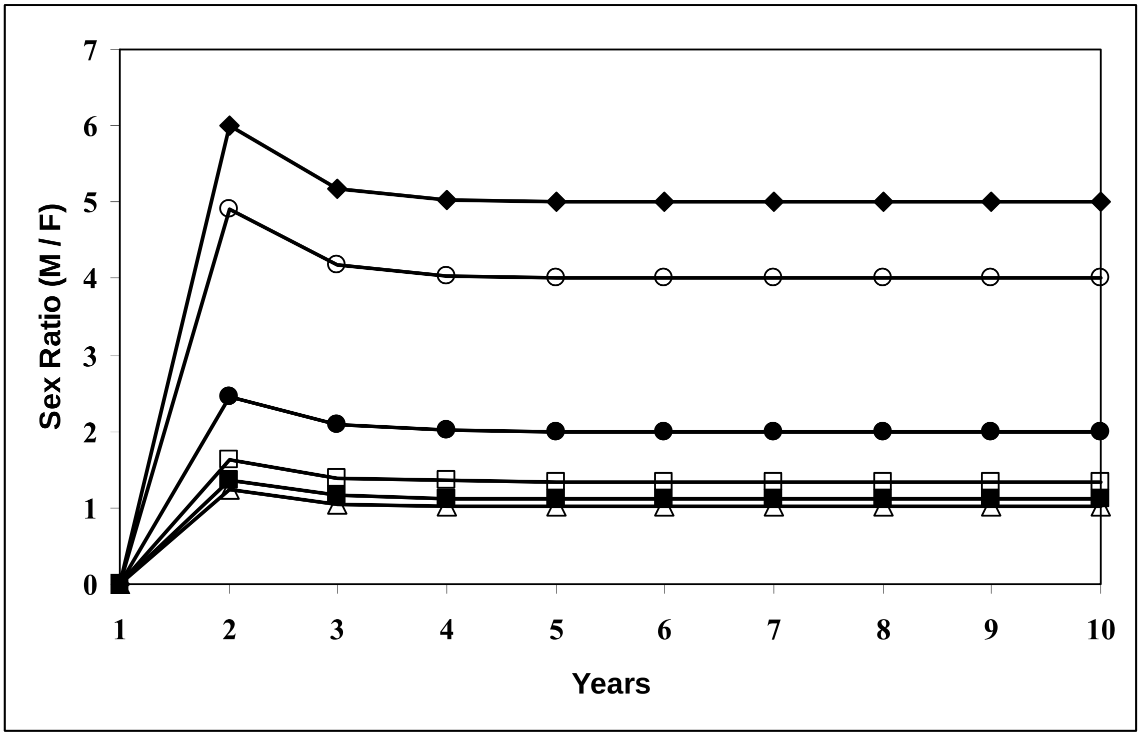

Fig. 4.2. Sex ratios resulting from a 10-year simulation using a model created to examine the effects of 5 levels of yearly mortality (*k*) on female *Bufo houstonensis* that mature in either 2 (a) or 3 (b) years. Open triangles represent $k = 0.01$, closed squares represent $k = 0.1$, open squares represent $k = 0.25$, closed circles represent $k = 0.5$, open circles represent $k = 0.75$, and closed diamonds represent $k = 0.8$, which was the mortality used for adult *B. houstonensis*.

collected at chorusing ponds, and our breeding pond results were similar. The captures at the breeding ponds represent the OSR, which can over-estimate males in the population (Emlen 1976). Our results indicate that in order to accurately estimate the FSR of *B. houstonensis*, multiple sampling techniques are required. In fact, the odds of catching females in traps were over 3 times greater than the odds of capturing a female at the pond. The overall sex ratio (Table 4.1) represents our estimate of the FSR for the population at the GLR. Yearly estimates of the FSR varied, but more males were always captured. In 2004, we captured double the number of males than females, but the small sample size prevented strong statistical inference. Females were never captured more than once during a breeding season (year), however, males were captured more frequently. If a large number of males visited a breeding area more than once during a season, then this suggests a possible female-biased FSR because the same males would be mating with different females. At the GLR, this was not the case. The majority of males were captured at the ponds only once per season, indicating that many males were attempting to breed – this result, coupled with the small number of females we captured, indicates a skewed FSR.

Sampling bias can easily skew sex ratio estimates (Ream and Ream 1966, Dodd 1991) and we tried to mitigate these biases through year-round sampling and multiple collection techniques. Our sampling efforts were constant across the years, with the exception of 2001, when we started the study. Sampling began shortly after the peak of the breeding season that year. The OSR estimated for toads captured at the breeding ponds are undoubtedly an artifact of the breeding strategy of *B. houstonensis* and may not reflect the FSR. The FSR incorporated both sampling methods and should more accurately reflect the true sex ratio of the population. Females of many species of anurans do not breed in consecutive seasons (Duellman and Trueb 1994). However, the sampling efforts at the GLR were continuous for four years, sufficient time to capture females that did not breed every year. Based the attempts to mitigate sampling error and results from the multiple collection techniques across four years, it is likely that there at least some biological bias in the sex ratio of *B. houstonensis*.

Gibbons (1990) stressed how delayed maturation affected the FSR of turtle populations. The difference in maturation time in turtles is often several years (Ernst et al. 1994), however, the delay in anurans is considerably less (Duellman and Trueb 1994), so the effect may not be as pronounced The results of our simulation model indicate that delaying maturation by a single year can skew the sex ratio significantly. Within a given cohort of *B. houstonensis*, males join the breeding population a year before females, which biologically skews both the FSR and OSR. The amount of bias depends on the mortality of the year-old juvenile females. These results emphasize the coupled nature of delayed maturation with differential mortality. If juvenile female mortality (*k*) is equal to adult male mortality (in this case assumed to be the same as reported for adult female *B. houstonensis* (0.8, Hatfield et al. (2004)), the sex ratio of the breeding population (FSR) would be 5M : 1F. The higher the value of *k*, the more biased the FSR (Fig. 4.2). Small values of *k* did not significantly bias the sex ratio. Other species of *Bufo* have low juvenile survivorship (Zug and Zug 1979) and it is unlikely that immature *B. houstonensis* are any different. The field data indicate the majority of males do not visit a breeding area more than once per year and this likely further skews the OSR at the ponds, and this bias would not be as apparent from the trap captures.

Evolutionarily, females benefit by delaying maturation because fecundity is positively correlated with size in toads – larger toads are generally older (Reading 1986). In *B. houstonensis*, under ideal conditions, females in captivity matured later and were larger than males (Quinn and Mengden 1984). The trade-off, however, based on the results of the simulations from this study, is fewer females reaching sexual maturity, especially if the mortality of juvenile females is high. A male-biased sex ratio results in a smaller N_e (Freeman and Herron 1998), which will decrease genetic variation more rapidly than a population with a sex ratio at parity (Wilson 1975). The loss of variation can be detrimental to small populations and this effect is further exacerbated for species living in fragmented habitats (Soulé 1986). In the case of the Houston toad, where migration among patches is extremely limited, and in the majority of instances likely impossible due to urban development, a male-biased sex ratio will be a natural, intrinsic property of the dynamics of smaller and more isolated populations, therefore further increasing the importance of each individual female. This dramatically affects management applications as strategies that maximize female survival are revealed as critical to Houston toad recovery.

CHAPTER V

PROJECTING POPULATION DYNAMICS AND PROBABILITY OF EXTINCTION OF THE ENDANGERED HOUSTON TOAD: AN INDIVIDUAL-BASED APPROACH

Introduction

Current abundance of the endangered Houston toad (*Bufo houstonensis*) is at a 15-year low (Price 2003), this study), with their geographic distribution limited to a nine-county area in Texas (Dixon 2000, Gaston et al. 2001). The two main breeding populations are found in Bastrop County (Fig. 5.1), one in Bastrop State Park (BSP, 2207 ha) and the other on the Griffith League Ranch (GLR, 1,948 ha), which are separated by a straight-line distance of 2200 m. Since risk of extinction for small, isolated populations is particularly high (MacArthur and Wilson 1967, Krebs 2001), there are valid concerns about the fate of the Houston toad populations at these two locations, and as an extant species

Simulation models often are used to project future dynamics of populations of threatened and endangered species (Vos et al. 2001, Mooij and DeAngelis 2003) and to estimate risk of population extinction (Boyce 1992, Krebs 2001). Hatfield et al. (2004) used the program RAMAS Metapop (Akçakaya 2002) to conduct a population viability analysis (PVA) for the Houston toad population at BSP. Only the dynamics of females were modeled because they are thought to be the limiting sex (Hatfield et al. 2004). Caswell (2001) emphasized the necessity for two sex models, if the assumption of

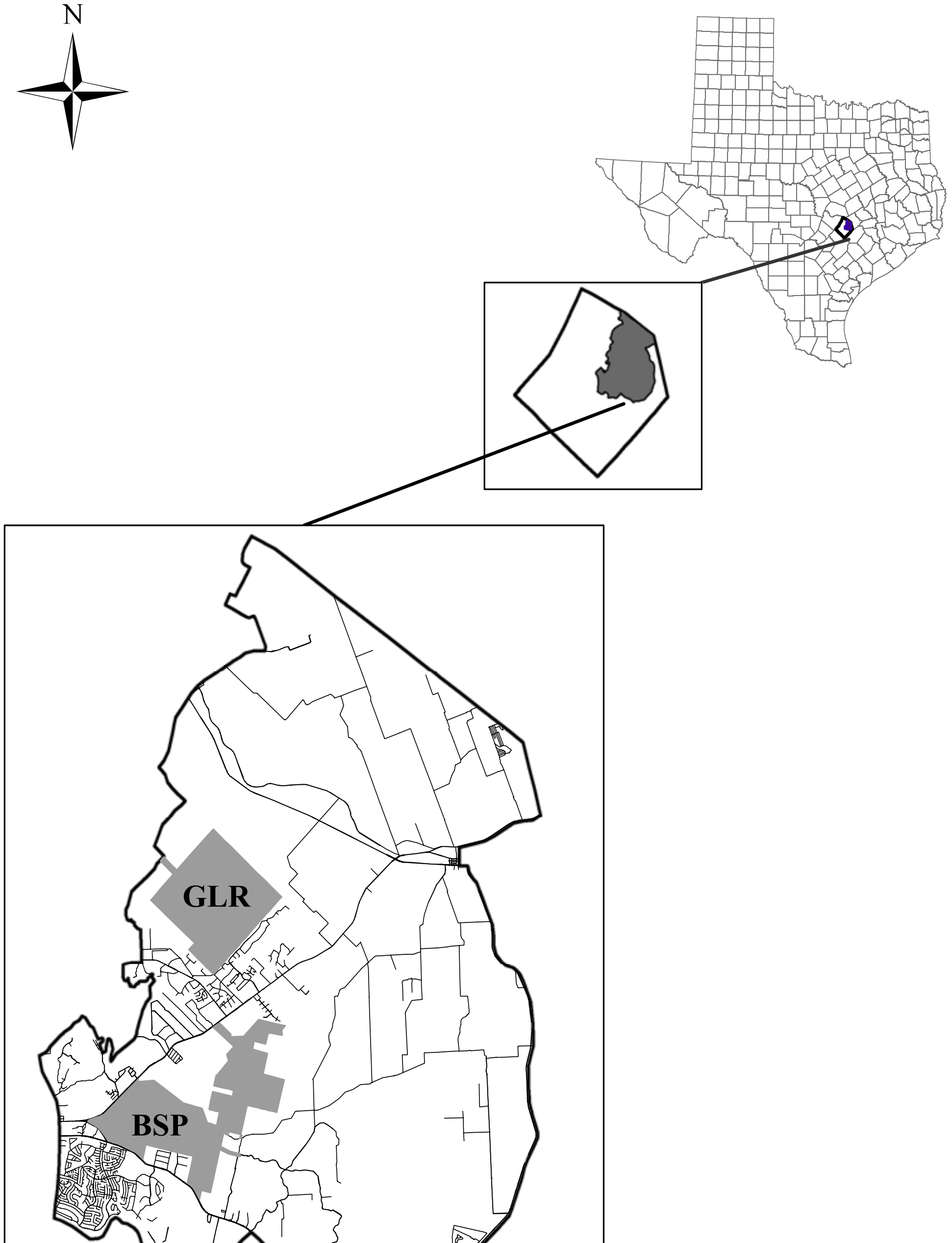

Fig. 5.1. Map identifying the critical habitat region of the Houston toad in Bastrop County (gray area, middle). The lower left map represents the critical habitat region for Houston toads. Bastrop State Park (BSP) and the Griffith League Ranch (GLR) are the two areas currently thought to have the largest remaining groups of Houston toads. Lines within the critical habitat region represent roads (bottom left).

dominance (e.g., female dominance indicates every female is able to mate) is not met. While females are limiting in Houston toads (Chapter IV), the assumption of dominance has not been tested in the field, so a two-sex model is a more conservative approach (Caswell 2001). No projections have been made for the Houston toad population on GLR.

Two important considerations in projecting the dynamics of endangered species are (1) the large variability in estimates of demographic parameters (i.e., φ, Chapter III) (Anderson and Burnham 1999, Williams et al. 2002) and (2) the risk of extinction due to environmental stochasticity (Krebs 2001) associated with small populations. In addition to the generic problems of sampling small populations, data on juvenile stages of many pond-breeding anurans, like the Houston toad, are particularly difficult to obtain due to their small size and cryptic nature.

In this chapter, I describe development, evaluation, and application of a simulation model to project dynamics and probability of extinction of the endangered Houston toad population located at the GLR in Bastrop County, Texas. I also examine the sensitivity of model projections to uncertainty in the estimates of key demographic parameters.

Background information

Population demography

The breeding season of *B. houstonensis* extends from late January to late May with the majority of the activity occurring from the middle of March to the middle of April. Breeding activity is not continuous and occurs in 3-5 day periods, depending on weather conditions (Chapter II). Males congregate at ponds and chorus to attract females. After the breeding season, adults are thought to be dormant until the next year. Adult males can breed multiple times per year and return to the same breeding site every year (Hillis et al. 1984). Females have one clutch per year (Price 2003). Based on data from a captive study, males are sexually mature the breeding season following parturition, while females mature a year later than males (Quinn and Mengden 1984).

Average clutch size in females is 1772 (Kennedy 1962, Quinn and Mengden 1984), however, only about 5% of the eggs survive and emerge from the pond as terrestrial juveniles (Greuter 2004). Juvenile survivorship from emergence to 13 weeks post emergence was estimated at 0.84 (Greuter 2004). Hatfield et al. (2004) projected population dynamics assuming juvenile survivorship of 0.01 and 0.02, but precise survivorship estimates do not exist from 13 weeks post-emergence to sexual maturity. Annual adult survivorship has been calculated for both males (ranging from 0.15 – 0.43, Chapter III) and females (0.2022, (Hatfield et al. 2004)).

Individual behavior/movement

Results from a mark-recapture study (Chapter III) and radio telemetry (Chapter II) indicate adult *B. houstonensis* remain within 200 m of their respective breeding ponds. juveniles emerge from their nascent pond during the middle of April and remain within 50 meters of the pond’s edge for approximately 12 weeks (Greuter 2004), however, after 12 weeks, movement patterns of juveniles remain enigmatic. Many species of pond-breeding anurans remain within 100-200 m of their first breeding pond (not necessarily the natal pond) (Semlitsch 2003). In many anuran populations, genetic exchange in metapopulations occurs from juveniles dispersing across the landscape and populating non-nascent ponds.

Environmental variability

During the main active period of Houston toads (late Feb. – mid-April), minimum daily temperatures range from 4 – 12°C. Precipitation in Central South Texas is highly variable throughout the year, however, Houston toads are highly dependent on precipitation for breeding and movement activity (Chapter II).

Methods

The model was formulated as a spatially-explicit, individual-based, stochastic, simulation model, programmed in VB.NET© (Microsoft, 2003). Below, the model is described following the protocol for individual-based models suggested by Grimm et al. (2006).

Purpose

The purpose of the model is twofold: (1) Project dynamics and probability of extinction over the next 10 years of the Houston toad population located at the GLR in Bastrop County, Texas and (2) Examine the sensitivity of model projections to uncertainty in survival estimates of juveniles, adult females, and adult males.

Classes, state variables, aggregated variables, and scales

The model is composed of two low-level entities (classes): individual toads and habitat patches. Low-level (state) variables describing individual toads include (1) life stage (emergent, juvenile, or adult), (2) age (in years), (3) sex (male or female), (4) status (alive or dead), (5) nascent pond (identification number of habitat patch (ID) in which the individual's nascent pond is located), (6) first breeding pond (ID in which the pond in which the individual first bred is located), (7) current location (ID in which the individual currently is located), (8) distance moved (number of times during its life the individual moved from one habitat patch to another), and (9) breeding status of females (whether or not a female has bred this year (Table 5.1a).

State variables describing individual habitat cells include (1) ID (number), (2) toads (number of toads currently in the patch), (3) clutches (number of egg clutches currently in the patch), (4) ponds (presence or absence), (5) lotic water (presence or absence), (6) single-track dirt roads (presence or absence), (7) residential paved roads (presence or absence), (8) highways (presence or absence), (9) woodland-forest habitat (presence or absence), (10) grassland habitat (presence or absence), (11) shrub-brush habitat (presence or absence), (12) human-developed land (presence or absence), and (13) habitat quality index (HQI: $-1.0 \leq \text{HQI} \leq 1.0$) (Table 5.1b).

Aggregated variables include (1) population (total number of toads currently in the system), (2) juvenile males (total number of juvenile males currently in the system), (3) juvenile females (total number of juvenile females currently in the system), (4) adult males (total number of adult males currently in the system), (5) adult females (total number of adult females currently in the system), (6) sex ratio (number of adult males : number of adult females currently in the system), (7) maximum movement (maximum distance an individual toad moved during a simulation), (8) mean movement (mean number of moves among cells made by toads during a simulation), (9) proportion dispersing (proportion of toads that dispersed from their natal pond during a simulation), and (10) proportion not dispersing (proportion of toads that dispersed from their natal pond during a simulation) (Table 5.1c).

The model simulates system dynamics over a 10-year period in 1,220 3-day time steps. Each of the 3,965 habitat patches represents a 100 m by 100 m area of the 1,948-ha GLR and surrounding area.

Process overview and scheduling

I provide an overview of the sequencing of model calculations in Figure 5.2. After the toad and habitat patch classes have been created, initialization of the system is completed by calculating a habitat quality index for each habitat patch. The simulation then proceeds by iterating (1220 times) through a series of 6 submodels that (1) specify current environmental conditions of the system (temperature, precipitation, and moon phase for the current 3-day period), (2) determine if individual toads should advance to the next stage of maturation (from emergent to juvenile to adult), calculate (3) breeding dynamics, (4) mortality, and (5) movement of individual toads, and (6) update habitat patch state variables and aggregated variables. Within submodels 2 through 5, all ("alive") toads are processed in the order in which they entered the system, and toad state variables are updated as changes occur.

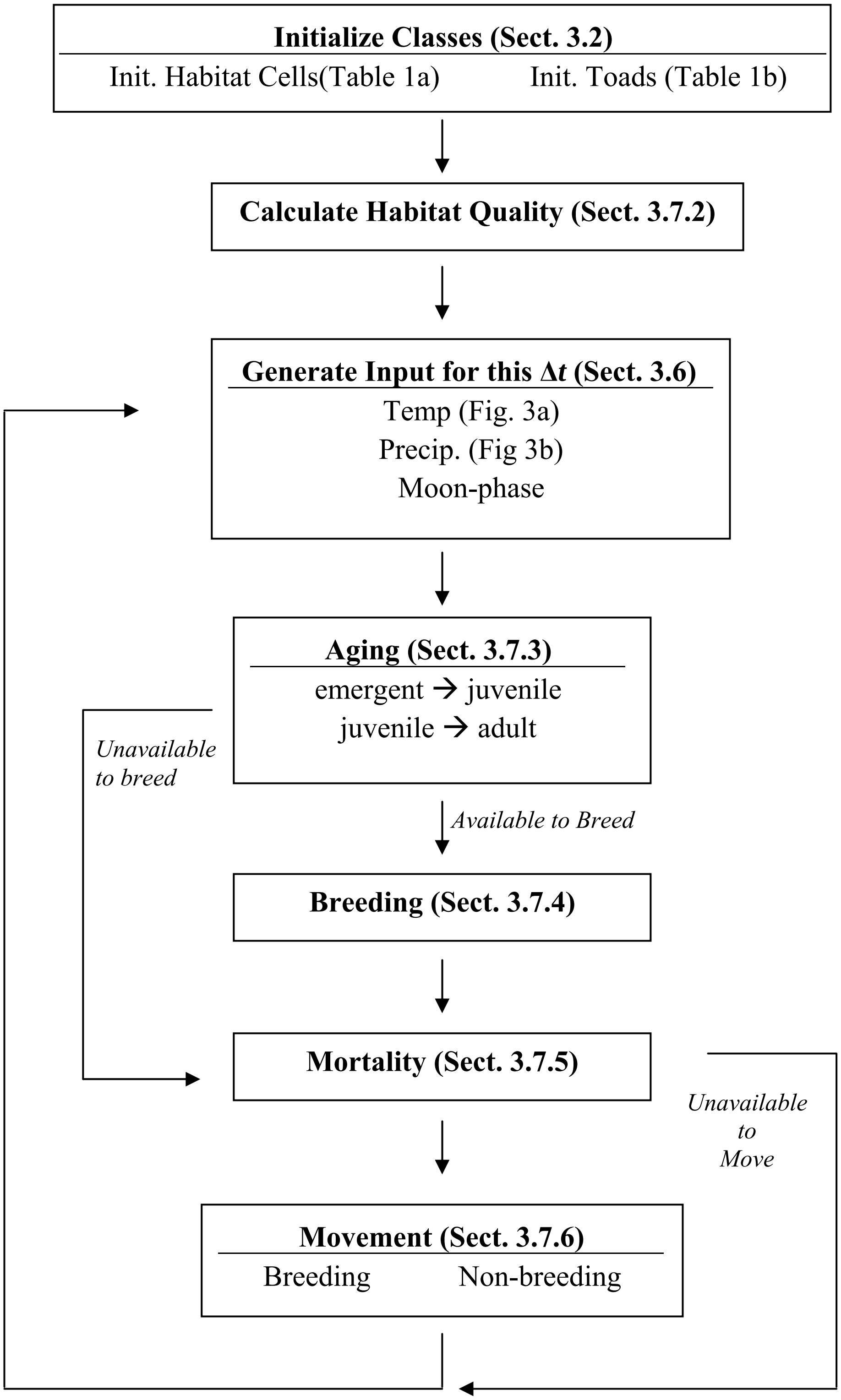

Fig. 5.2. Flow chart of model dynamics. The breeding and movement submodels are conditional on life stage, an individual's location and weather conditions for that specific time period (refer to text for specific rules).

Table 5.1. Summary of (a) low-level (state) variables describing the individual toad entity, (b) low-level state variables describing the habitat cell class, and (c) aggregated variables. See text or details.

a

Individual Toad State Variables
Life stage
Age (years)
Sex
Alive / dead
Fecundity (attribute for females only)
Available to breed (attributes for females only)
No. of cells moved during life
Attributes describing location
Nascent pond (cell #)
First breeding pond (cell #)
Current cell (cell #)

b

Habitat Cell State Variables
Dirt roads
Highways
Park Road
Paved Roads
Total roads
Ponds
Streams
Forests / woodlands
Shrub / brushy cover
Grassland / cropland
Developed land
ID number (Cell #)
Habitat Quality Index
No. of toads
No. of clutches

c

Aggregated Variables
Population size
Juvenile Males
Juvenile Females
Adult Males
Adult Females
Adult Sex Ratio
Maximum Movement
Mean Movement
Proportion Dispersing
Proportion not Dispersing

Design concepts

Emergent properties

Toad population dynamics and structure emerge from the behavior of individual toads. The maturation, breeding, mortality, and movement of individual toads are described empirically.

Sensing

Individual toads know their own life stage, sex, status, nascent pond, first breeding pond, current location, and breeding status, which affect their maturation, breeding, mortality, and movement.

Interaction

Several interactions between toads and their habitat are modeled implicitly. Breeding, mortality, and movement of toads depend implicitly on the land cover state variables of the habitat patches in which they are located. Breeding interactions between male and female toads are modeled explicitly. A male can breed only 1 female during any given time step, and the female must be located within the same habitat patch.

Stochastic processes

Both mortality and movement of toads are probabilistic.

Observation

Maturation (from emergent to juvenile to adult), breeding (season and location), and movement (distance moved, dispersal from natal pond) of individual toads are observed as part of model verification. Population size, structure (proportion of juveniles, adults, males, females), and time to extinction are observed as part of model evaluation and application.

Initialization

The habitat patch class is initialized to represent the GLR during the five-year field study. Landscape attributes were provided as ArcGIS shapefiles by the Land Information Systems Laboratory, Texas A & M University. A grid consisting of 3,965 100 m x 100m cells was overlain on the shapefiles and landscape data were exported to the grid cells using ArcGIS v 9.0 (ESRI, Redlands, CA).

The toad class is initialized with 136 adult toads distributed among the habitat cells corresponding to the locations in which toads were captured during a five-year field study at the GLR. The proportion of all simulated toads in a given habitat patch equals the proportion of all toads that were captured at that site during the field study, and each habitat patch is initialized with 5 males for each female.

Input

Input data include temperature (°C), precipitation (mm), and moon-phase (percent of the moon’s disk illuminated), each averaged over consecutive 3-day periods from 2001 – 2005. Three-day averages were calculated from daily temperature, precipitation, collected from the GLR and moon-phase for the Central Time Zone (US) from 2001 – 2005 obtained online at: http://aa.usno.navy.mil/data/docs/MoonFraction.html. These input data are used to determine, in part, toad breeding and movement.

Submodels

Habitat quality

An index of habitat quality was quantified based on expert opinion using an expert rule based system (Buchanan and Duda 1983). I am unaware of previous quantitative descriptions of habitat requirements for the Houston toad. Four recognized Houston toad experts were asked to score 11 habitat attributes qualitatively on a continuum from extremely favorable to extremely unfavorable for Houston toads. Qualitative scores were quantified on a scale between -1 and +1, with positive values being favorable and negative values being unfavorable, and were averaged across the four experts (Loh et al. 1994, Loh et al. 1996) (Table 5.2a).

Scores were combined iteratively using the EMYCIN algorithm (Buchanan and Duda 1983) to calculate the habitat quality index for each patch. The first iteration of the algorithm generates a score by combining the scores of first (I_A) and second (I_B) habitat characteristics using one of the following equations:

$$\boldsymbol{I_A + I_B - (I_A * I_B) \,|\, I_A > 0, I_B > 0}$$
$$\boldsymbol{I_A + I_B + (I_A * I_B) \,|\, I_A < 0, I_B < 0}$$

$$\boldsymbol{\frac{I_A + I_B}{1 - \min[|I_A|, |I_B|]}, \textit{otherwise}}$$

Table 5.2. (a) Average scores of habitat patch state variables used to calculate the habitat quality state variable (HQI), and (b) weights based on HQI assigned to habitat cells to determine the probability of individual toads moving into an adjacent cell. See text for details.

a

State Variable	Score
Dirt roads	-0.075
Highways	-0.09
Park Road	-0.175
Paved Roads	-0.6
Total roads	-0.6
Ponds	0.99
Streams	0.75
Forests / woodlands	0.9
Shrub / brushy cover	-0.2
Grassland / cropland	-0.8
Developed land	-0.945

b

HQI Values	Patch Weight
HQI ≤ -0.55	0.01
-0.55 < HQI ≤ 0	0.05
0 < HQI ≤ 0.5	0.1
0.5 < HQI ≤ 0.75	0.15
0.75 < HQI ≤ 0.9	0.2
0.9 < HQI	0.99

The second iteration combines the result of the first with score of the third habitat characteristic, and this process continues until all the scores have been included. As scores approach +1, the habitat is more favorable for Houston toads and as the value approaches -1, the habitat is increasingly unfavorable for Houston toads (Loh et al. 1996).

Environmental conditions

This submodel selects or generates the appropriate values for temperature, precipitation, and moon-phase for the current time step (three-day period). For model verification and evaluation, the three-day averages calculated from daily temperature, precipitation, collected from the GLR and moon-phase from 2001 – 2005 were used (Fig. 5.3). For model application (projecting future scenarios), temperature and precipitation values were drawn randomly from historical frequency distributions of the corresponding three-day period of the year based on data from 1964 – 2006. Weather data were taken from the National Climatic Data Center weather station in Elgin, Texas (station number: 412820), located approximately 16 km from the GLR. Moon phase was projected deterministically assuming a 29.5-day lunar cycle.

Maturation

Emergent toads are advanced to juveniles during the 62nd three-day period of each year (beginning of July) (Greuter 2004). Juveniles are advanced to adults during the first three-day period of the year after they reach the age of first reproduction (1 year for males, 2 years for females (Quinn and Mengden 1984)).

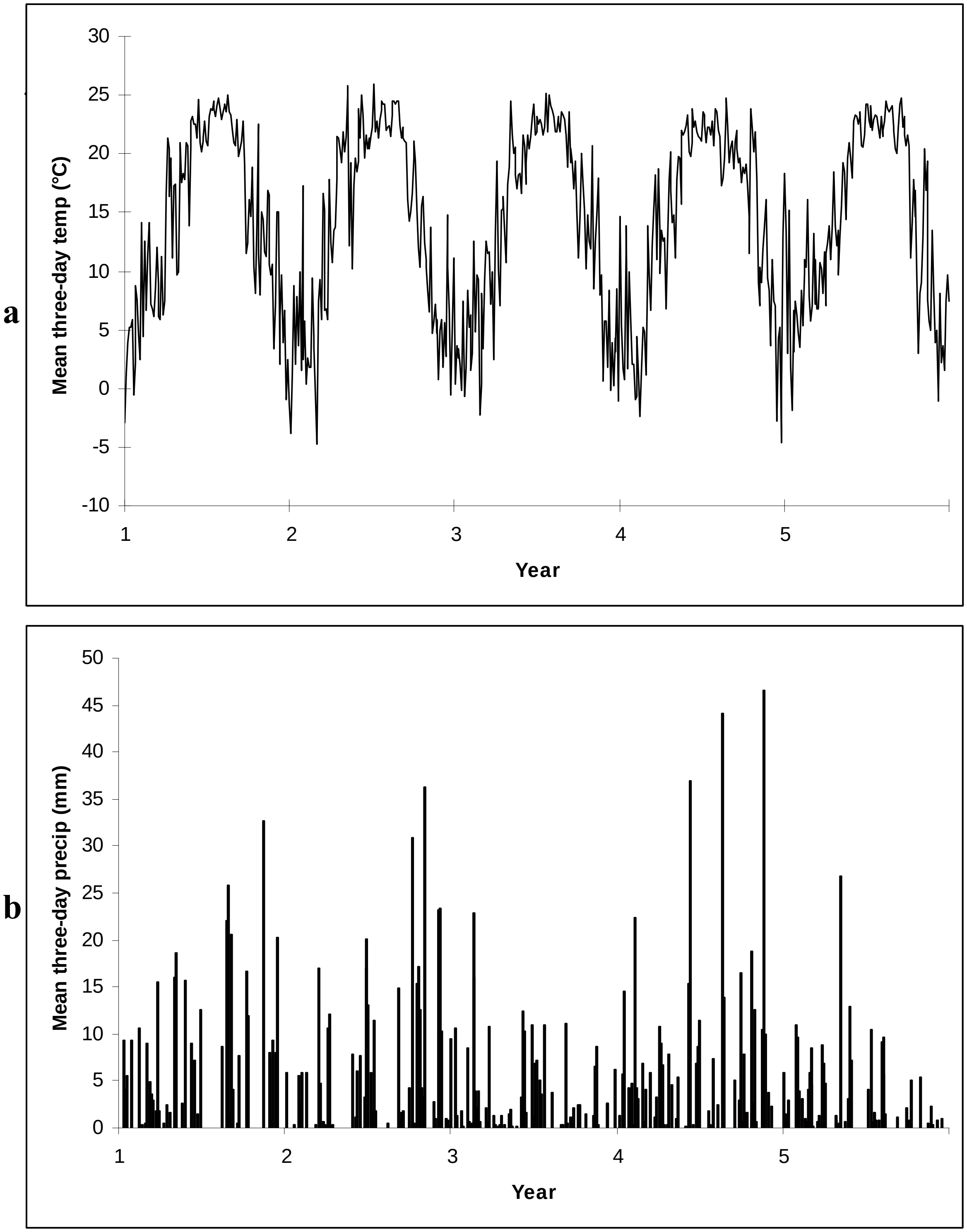

Fig. 5.3. Time series of temperature (C) and precipitation (mm) used as input data for model verification and evaluation. Three-day averages were calculated from daily temperature and precipitation at the GLR from 2001 – 2005.

Breeding

Breeding occurs only between the 10th and the 40th three-day periods of the year (March and April), only during three-day periods in which lag precipitation is greater than or equal to 4 mm, and only in habitat patches with ponds. Any given female can breed only once per year, and any given male can breed only one female per three-day period. Thus the number of females bred during a single three-day period (during the breeding season) within a single habitat patch (with a pond) is equal to the number of females in that patch that have not yet bred during the current year, or the number of males in that patch, whichever is less.

In most anurans, including the Houston toad, about 5% of the average number of eggs actually metamorphose (Semlitsch 2003, Greuter 2004). The aquatic stage (egg and tadpoles) was not modeled explicitly, instead, fecundity (clutch size) was estimated at 89 emergent toadlets per female. The number of clutches per pond is calculated and toads emerge (classified as emergents) on the 36th three-day period of each year (mid-April). The sex ratio is assumed to be 1 M : 1 F at emergence.

Mortality

For adult toads, the probability dying per three-day time step is estimated from annual survival probabilities reported for adult males (0.15, Chapter III) and adult females (0.2022, (Hatfield et al. 2004)). Currently, there are no estimates for juvenile survival, so the probability of juveniles surviving to adulthood is assumed to be 0.01 in order to compare these results to those of Hatfield et al. (2004). Juvenile survivorship was defined as the time from parturition until the males matured, taking into account only 5% of the eggs would metamorphose. These probabilities were converted to three-day probabilities using the following equation:

$$M_{td} = 1 - S^{1/t}$$

where M_{td} is the probability of dying during a given three-day period, S is the survival estimate for the longer time period (e.g., annual survival), and t is the number of three-day periods in the longer time period (for adults, $t = 122$, and for juveniles, $t = 86$). The probability of mortality per three day period for the baseline model is 0.015, 0.013, or 0.0185, for adult males, adult females, and juveniles, respectively.

Movement

Individual toads do not leave a habitat patch that contains a pond, except that juvenile toads must move away from their natal pond during the 62nd three-day period of the year (13 weeks post-emergence). Semlitsch (2003) reported that adult toads tend to stay within 100 – 200 m of their breeding ponds, and that juveniles are the main units of dispersal in many anuran populations. Greuter (2004) reported newly emerged juveniles do not move more than 50 m from the edge of their nascent pond until 13 weeks post emergence.

Movement of individual toads that are not currently in a habitat patch with a pond depends on sex, life stage, breeding condition (if female), season (breeding or non-breeding), and environmental conditions. During the breeding season (10th – 36th three-day period), adult males may move into an adjacent habitat patch if precipitation ≥ 4 mm, the moon-phase is < 50 or > 60, and temperature is > 4°C. Adult females, that are available to breed, may move into an adjacent patch between the 19th and 36th three-day period if precipitation ≥ 4 mm, moon-phase < 50 or > 60 and temperature is > 4°C. Females that are unavailable to breed, juveniles, regardless of sex, and all adults during the non-breeding season may move into an adjacent patch if precipitation is > 4 mm.

If the above conditions are met during any given three-day time period, an individual toad will move into an adjacent habitat patch. The probability of moving into each of the adjacent patches is weighted by the HQI for that patch and calculated as:

$$p_i = \frac{w_i}{\sum_{i=1}^{j} w_i} \tag{3}$$

where p_i is the probability of moving into patch i, w_i is the weighted HQI value (Table 5.2b) for patch i, and j is the total number of adjacent patches.

Update habitat patch state variables and aggregated variables

This submodel updates the number of toads (adult males, adult females, and juveniles) and egg clutches currently in each habitat patch, and all aggregate variables. (Individual toad state variables are updated in the other submodels as changes occur.)

Results

The usefulness of the model was evaluated for projecting dynamics and probability of extinction of the Houston toad population at the GLR in three steps. First, I verified that maturation, breeding, and movement rules included in the model generated the expected temporal and spatial patterns of maturation, breeding, and movement of individual toads. Second, I compared simulated population-level dynamics to field observations at GLR and to patterns reported in the scientific literature. Third, I examined the sensitivity of simulated population size and time to (and probability of) extinction to uncertainty in mortality estimates.

Verification of individual maturation, breeding, and movement rules

Results of 1,000, 10-year, Monte Carlo (replicate stochastic) simulations, each initialized to represent environmental and habitat conditions on the GLR, verified that maturation, breeding, and movement rules for individual toads generated temporal and spatial patterns consistent with the field observations, scientific literature, and expert opinions upon which they were based. That is, simulated individuals matured at the appropriate ages during the appropriate seasons, bred during the appropriate seasons in the appropriate locations, and moved in the appropriate manner relative to temperature, precipitation, and moon phase, and relative to the spatial distribution of habitat patches of different quality .

Comparison of simulated versus observed population-level dynamics

Population-level dynamics resulting from these same 1,000, 5-year, Monte Carlo simulations compared favorably with field observations at GLR and with the scientific literature. The simulated population exhibited seasonal and year-to-year fluctuations typical of those observed in the field (Chapter II) (Fig. 5.4), and the simulated sex ratio

(7.65 M : 1 F) was not statistically significantly different from that observed in the field (5.5 M : 1 F, $\chi^2 = 0.01$, $p = 0.92$, Chapter IV). Population size (≈ 170) and structure (≈ 90% juveniles) also appeared reasonable based on life-history information, although empirical estimates to compare simulated values to are not available.

Mean maximum distance moved by simulated toads (1,565 m, calculated as the Euclidian distance between the center-points of the most distant habitat patches visited) (Table 5.5) was within the range movements (950 – 1,900 m) reported by Price (2003). Field data are not available for the proportion Houston toads that return to their natal pond. The proportion of simulated individuals returning to their natal pond (0.59) was somewhat lower than the proportion reported (0.73) for the closely-related Woodhouse's toad (*B. woodhousei*) (Breden 1987). Simulated patterns of habitat use were qualitatively similar to those reported from radio telemetry studies on the GLR (Chapter II), and to previous studies on *B. houstonensis* (Hillis et al. 1984, Jacobson 1989, Price 2003). Both simulated and unsimulated Houston toads utilized existing drainages and avoided pastoral lands when moving to and from potential breeding sites. Simulated habitat use patterns also appeared reasonable to a recognized Houston toad expert (J. Dixon, Texas A & M University, College Station, Texas), who evaluated them via a Turing test (Turing 1950).

Sensitivity analysis

Sensitivity analysis was based on 1,000, 10-year, Monte Carlo simulations of each of 4 versions of the model. Each version included a different set of estimates for juvenile, adult male, and adult female toad mortalities (Table 5.3). Male survivorship values were taken from the most parsimonious model (model 1, Chapter III). Adult female and juvenile survivorship were taken from Hatfield et al. (2004) in order to facilitate comparison between their model and the one presented here.

For all sensitivity analysis simulations, input data representing temperature and precipitation were stochastic. The temperature and precipitation value for each three-day period of simulated time was drawn randomly from a historical frequency distribution for the corresponding three-day period constructed based on data from the closest weather station to the GLR from 1964 – 2006. Moon phase values were deterministic and were based on the moon phase projections available online at: http://aa.usno.navy.mil/data/docs/MoonFraction.html.

Table 5.3. Four versions of an individual based, spatially-explicit model used to explore the relationship among stage-specific mortality rates and population dynamics of Houston toads. Version 1 represents the baseline model. Numbers in parenthesis indicate survival probabilities (annual for adults, time to maturity for juveniles. Probability of survival was converted into a probability of dying per three-day period using equation 2 in the text.

	Version of the model			
Parameter	**1**	**2**	**3**	**4**
Age at first reproduction (male)	1 year	1 year	1 year	1 year
Age at first reproduction (female)	2 years	2 years	2 years	2 years
Per capita natality of females	89.0	89.0	89.0	89.0
Prob. of adult male mortality	0.0154 (0.15)	0.0154 (0.15)	0.0107 (0.27)	0.0107 (0.27)
Prob. of adult female mortality	0.0130 (0.20)	0.0130 (0.20)	0.0130 (0.20)	0.0130 (0.20)
Prob. of juvenile mortality	0.0185 (0.01)	0.0106 (0.02)	0.0185 (0.01)	0.0106 (0.02)

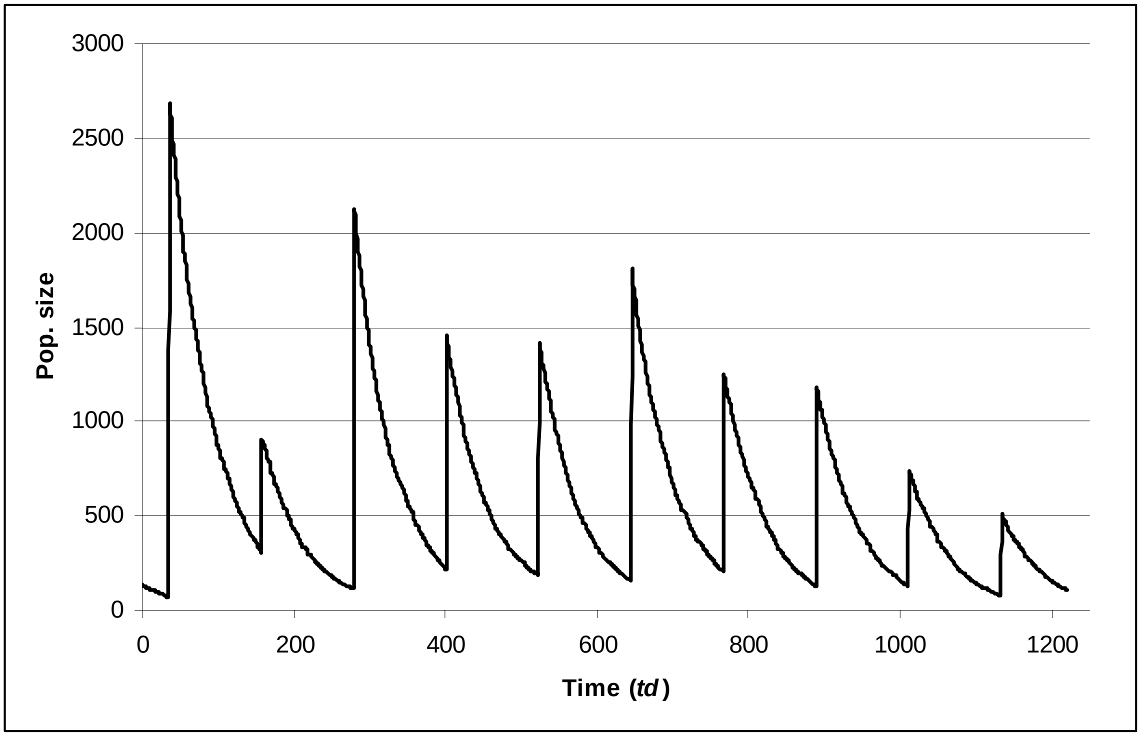

Fig. 5.4. Typical example of population dynamics of *B. houstonensis* generated by the baseline model (Table 3). Time is measured in three day (*td*) periods and the simulation was run for 10 years.

Results suggested that versions 1 and 3 include estimates that are reasonable for Houston toads since the resulting dynamics were similar to those observed at the GLR (Table 5.4, Fig. 5.5a). Versions 2 and 4 of the model include sets of estimates for juvenile, adult male, and adult female toad mortalities that are highly unlikely, since these versions of the model generate unreasonable results (Table 5.4, Fig. 5.5b).

Projecting population dynamics and probability of extinction

I projected population dynamics and time to (probability of) extinction for the Houston toad population at GLR over the next 10 years using versions 1 and 3 of the model. Simulation results suggested the probability of extinction is low. In version 1, 13 of the 1,000 simulations (1.3%) went extinct within 10 years of simulated time. The mean time to extinction was 1,028.23 ± 44.53 (8.4 years ± 0.25 yrs) (95% CI: 931.2, 1125.25), the minimum time was 673 three-day periods (5.5 years), the maximum was 1,204 (9.9 years). In model 3, one repetition went extinct within 10 years of simulated time. The time to extinction was 1,114 time steps (9.13 years).

Some patterns were consistent across all versions. The sex ratios for every model were male-biased, and juveniles made up a large proportion of the population (Table 5.4). The simulated male-biased sex ratio reduced the effective population size considerably. Versions 2 and 4 with higher juvenile survivorship had smaller biases in the sex ratio than versions 1 and 3 with lower juvenile survivorship. As juvenile survivorship increases, more individuals are likely to survive to maturity, which would cause less bias in the adult sex ratio. The proportion of juveniles in the actual population is unknown, but given the high fecundity of females, it is likely that this represents actual conditions as well.

Versions 2 and 4 produced unrealistic results at the population level, with both models generating exponential growth (the mean final population size was 42,581.38 and 43,335.67 for versions 2 and 4, respectively (Table 5.4, Fig. 5.5b)). Due to the size of the simulated landscape (~ 1,940 ha), it is unlikely that many toads could thrive, so to reduce superfluous computing time, a repetition was stopped the time step after the population size reached 30,000 individuals. All of the repetitions for versions 2 and 4 stopped at time step 524 (4.29 years). Based on the field data collected from 2001 – 2005 (Chapter II), the other population-level patterns exhibited in versions 2 and 4 were also unrealistic (Table 5.4) – i.e., it is unrealistic to assume that 40,000+ emergent juveniles were alive on the landscape at the Griffith League Ranch. Versions 1 and 3, however, did produce results comparable to what were observed in the field (Table 5.4,

Table 5.4. Summary of demographic attributes that emerge from the systems level. Population-level criteria used to evaluate the four versions of the model. Simulations were run for 10 years (or until the population reached 30,000 individuals) and 1,000 repetitions were run for each version of the model. Mean values (μ) ± standard error (*SE*), the 95% confidence interval around the mean (*CI*), and minimum (*Min*) and maximum (*Max*) values were recorded for the following variables: final population size (*N*), mean final number of juvenile males and females (*JM*, *JF*, respectively), the mean number of adults (A*M* for males and A*F* for females), and the adult sex ratio (*SR*). calculated from the values reported for *M* and *F*.

		Version of the model			
Var.	**Metric**	**1**	**2**	**3**	**4**
N	μ ± SE	166.88 ± 3.32	42581.38 ± 360.95	209.69 ± 3.76	43335.67 ± 214.4
	CI	159.51, 172.58	41873.08, 43289.68	202.31, 217.07	42914.95, 43756.39
	Min, Max	0, 522	30047, 129970	0, 821	30139, 122500
JM	μ ± SE	70.01 ± 1.49	20500.76 ± 171.92	80.43 ± 1.57	20746.6 ± 102.21
	CI	67.15, 73.02	20163.39, 20838.13	77.35, 83.56	20546.03, 20947.17
	Min, Max	0, 236	14508, 61836	0, 331	11891, 58258
JF	μ ± SE	78.84 ± 1.60	21079.89 ± 178.84	90.65 ± 1.72	21304.25 ± 105.57
	CI	75.70, 81.99	20728.95, 21430.83	87.28, 94.03	21097.09, 21511.41
	Min, Max	0, 250	14758, 64403	0, 377	14652, 60235
AM	μ ± SE	15.14 ± 0.31	658.29 ± 8.37	36.31 ± 0.60	939.1 ± 7.57
	CI	14.53, 15.74	641.87, 674.70	35.13, 37.49	924.25, 953.95
	Min, Max	0, 59	268, 2977	0, 141	514, 4104
AF	μ ± SE	1.97 ± 0.055	342.44 ± 2.85	2.29 ± 0.06	345.72 ± 1.72
	CI	1.86, 2.08	336.85, 348.04	2.18, 2.41	342.35, 349.1
	Min, Max	0, 10	232, 1070	0, 10	195, 969
SR	M : F	7.68 : 1	1.92 : 1	15.86 : 1	2.72 : 1

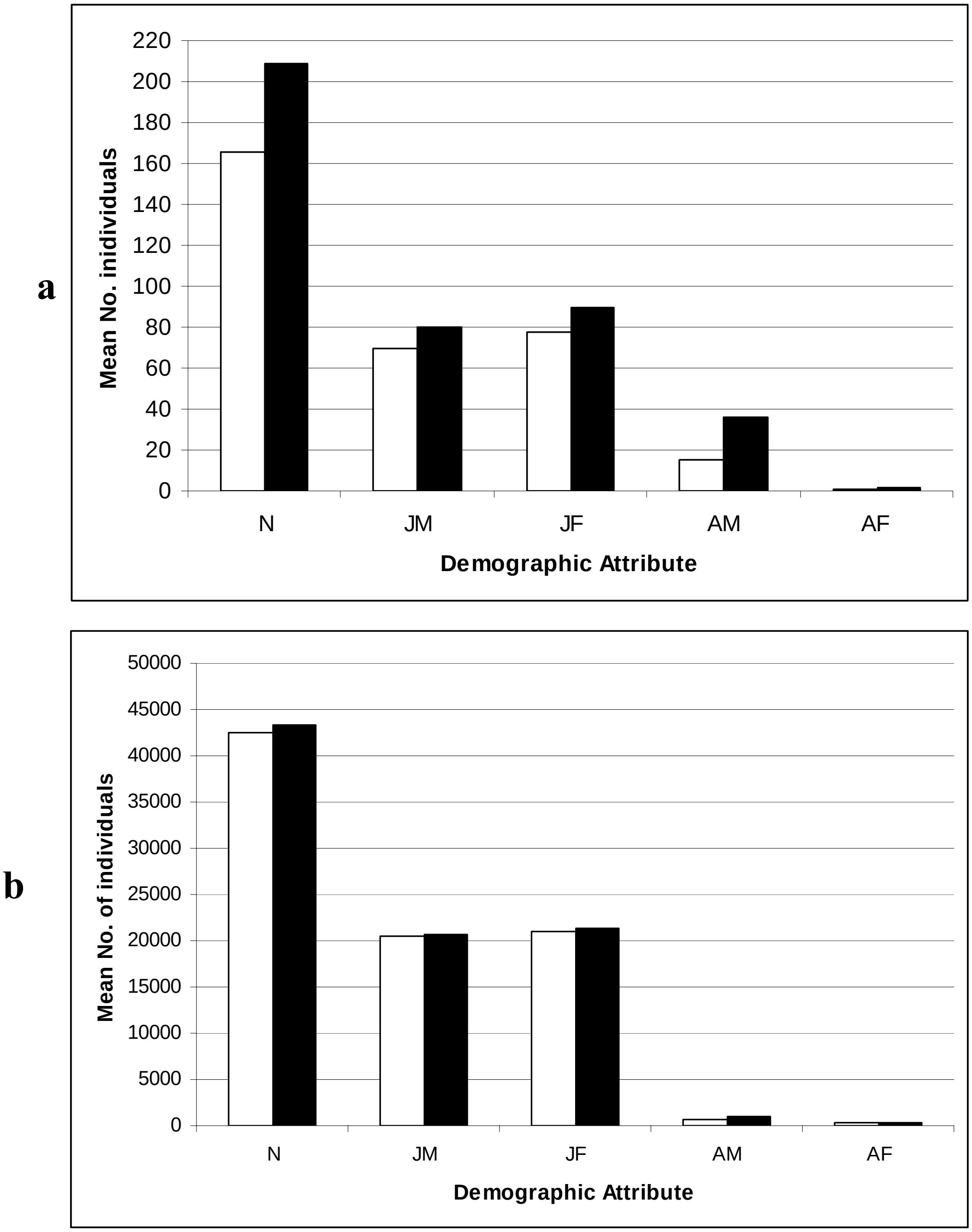

Fig. 5.5. Demographic attributes that emerged from the model (a) of versions 1 (open bars) and 3 (closed bars) and (b) of versions 2 (open bars) and 4 (closed bars) of the model. *N* represents mean final population size, *JM* represents mean final number of juvenile males, *JF* represents the mean final number of females, *AM* represents mean final number of adult males, *AF* represents mean final number of adult females. Standard errors are reported in Table 5.4.

Fig. 5.5a). The mean final population sizes were 166.88 and 209.69 for versions 1 and 3, respectively (Table 5.4, Fig. 5.5a). Juveniles were still a large proportion of the populations, but the numbers were not as unreasonable as models 2 and 4. The average number of males was 15 and 2 for females (Fig. 5.5a). The adult sex ratio for version 1 (7.68 M : 1 F) was significantly different from parity, but only versions 1 and 3 were not significantly different to the 5.5 M : 1 F sex ratio observed in the field (Version 1: $\chi^2 = 0.01$, $p = 0.9203$. Version 2: $\chi^2 = 1.97$, $p = 0.1604$) (Table 4).

Based on the results among these four versions, the model is more sensitive to changes in juvenile survivorship than adult male survivorship. Hatfield et al. (2004) reported that the juvenile life stage is the most critical and these results support their claim.

The mean maximum distance individuals moved during a simulation for version 1 and 3 was 14.27 and 14.60 cells (approximately 1,400 m), while the *MD* for version 2 and 4 was higher, 16.65 and 16.76, respectively (Table 5.5, Figs. 5.6a, 5.6b). Few long range movement data exist for Houston toads, but the average values of all models fall within the range reported by Price (2003), who observed individuals moving up to 1,900 m.

In versions 1 and 3, the proportion returning to the natal pond 0.59, and was 0.84 for versions 2 and 4 (Table 5.5, Fig. 5.6a). Each version of the model did project a large proportion (> 50%) returning to the natal pond, however, since there are not field data to compare these results to, there is still a large amount of uncertainty associated with this system property.

Table 5.5. Summary of movement attributes that emerge at the system-level. Simulations were run for 10 years (or until the population reached 30,000 individuals) and 1,000 repetitions were run for each version of the model. Mean values (μ) ± standard error (*SE*), the 95% confidence interval around the mean (*CI*), and minimum (*Min*) and maximum (*Max*) values were recorded for the following variables: the maximum distance an individual moved during a simulation (*MD*), the proportion of individuals that remained at their natal pond (*PN*), the proportion of individuals that moved away from their natal pond (*PD*), and the average number of cells moved (*NC*).

		Version of the model			
Variables	**Metric**	**1**	**2**	**3**	**4**
MD	μ ± SE	14.17 ± 0.06	16.65 ± 0.06	14.60 ± 0.07	16.76 ± 0.06
	CI	14.06, 14.31	16.53, 16.77	14.47, 14.74	16.64, 16.89
	Min, Max	9.49, 23.60	12.37, 26.17	10, 27.86	13, 26.83
PN	μ ± SE	0.59 ± 0.0008	0.84 ± 0.0003	0.59 ± 0.0006	0.84 ± 0.0003
	CI	0.587, 0.59	0.849, 0.84	0.58, 0.59	0.8408, 0.8421
	Min, Max	0.51, 0.69	0.81, 0.87	0.53, 0.67	0.65, 0.87
PD	μ ± SE	0.41 ± .0008	0.16 ± 0.0003	0.41 ± 0.0007	0.16 ± 0.0003
	CI	0.409, 0.412	0.159, 0.160	0.414, 0.416	0.1579, 0.1592
	Min, Max	0.31, .48	0.13, 0.19	0.33, 0.46	0.13, 0.35
NC	μ ± SE	1.39 ± 0.005	0.6 ± 0.001	1.41± 0.004	0.6 ± 0.0015
	CI	1.39, 1.41	0.60, 0.61	1.40438, 1.42	0.599, 0.6048
	Min, Max	1, 1.86	0.48, 0.75	1.06, 1.82	0.45, 1.3

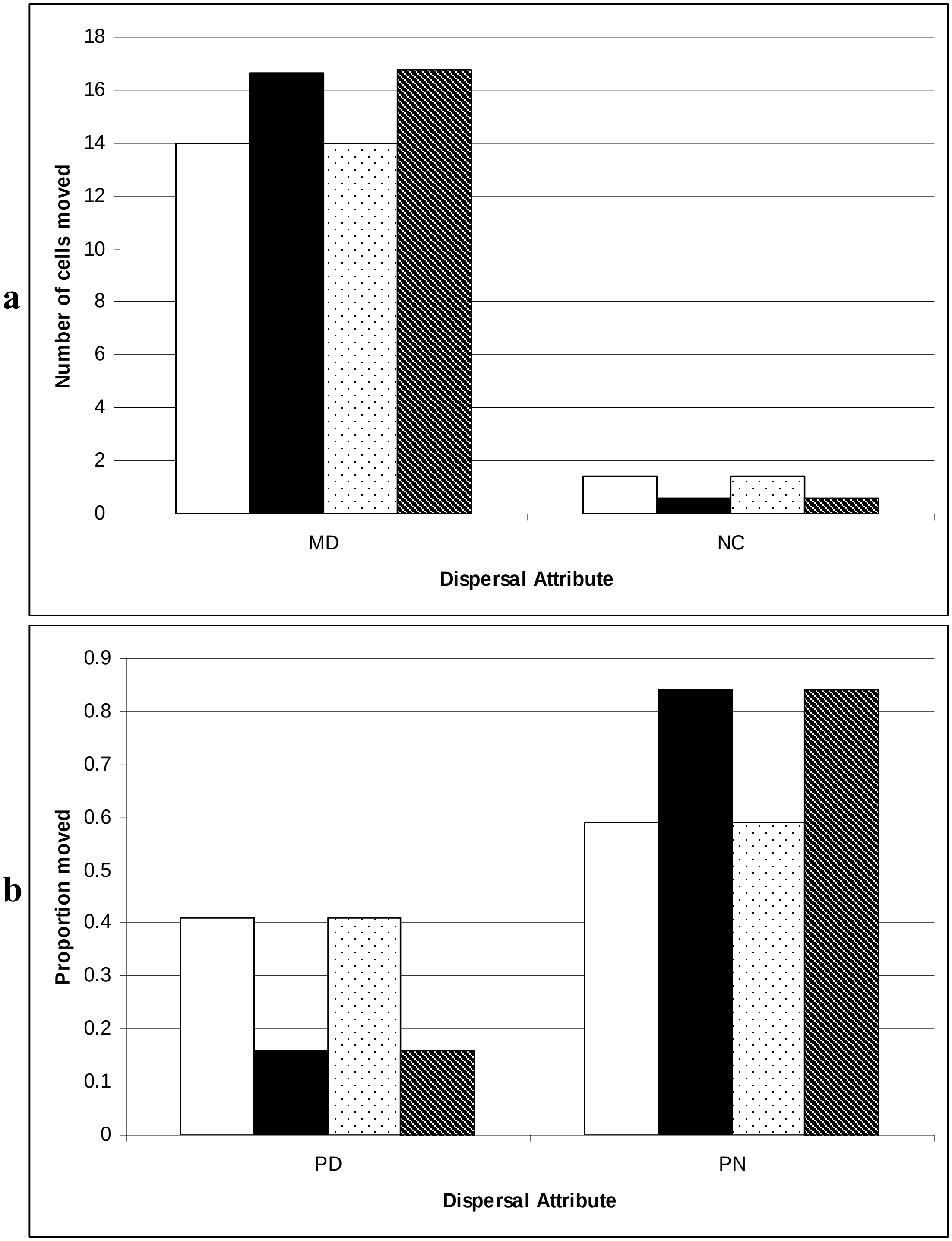

Fig. 5.6. Dispersal attributes used to evaluate the four versions of the model. (a) *MD* represents the average maximum number of cells an individual moved during a simulation, *NC* represents the average number of cells all toads moved during the simulation. (b) *PD* represents the proportion of the population that dispersed from their natal pond, and *PN* represents the proportion that did not disperse. Open bars represent version 1, closed bars represent version 2, dotted bars represent version 3 and cross-hatching represents version 4. Standard errors are reported in Table 5.5.

Discussion

The plausible versions of this model (1 and 3) estimated a low probability (p = 0.013) of Houston toads going extinct at the GLR by 2011 (the model was initialized with data from 2001), under the assumptions used in this model. The simulations also projected relatively low numbers of adults, especially females (Table 5.4, Fig. 5.5a). Further, this model assumed females are available to breed every year, but this may not be the case. If females do not breed every year and they are already at low numbers, this would undoubtedly increase the probability of extinction for the population. The model does project that *B. houstonensis* is at risk, albeit slightly, of extinction in suitable habitat. The GLR is one of two areas in Bastrop County which is large enough to support multiple breeding groups of Houston toads, yet dispersal among potential breeding locations remains unknown. The extent of the *B. houstonensis* metapopulation remains unknown and in order for the conservation of this species to be successful, studies of dispersal among breeding locations needs to be a priority. As previously mentioned, juvenile toadlets are difficult to monitor in the field, but this model can be used to test hypotheses regarding dispersal, by comparing the spatial distribution of actual toads to simulated toads under a variety of dispersal hypotheses, the uncertainty associated with this life history characteristic can be reduced and management strategies based on these results can be more successful.

The model presented in this chapter represents the first individual-based model on the dynamics of the endangered Houston toad. This model differs both in approach from Hatfield et al.'s model (2004). Hatfield et al. (2004) developed a stage-based matrix model (using RAMAS Metapop (Akçakaya 2002)) and modeled the dynamics of female *B. houstonensis*. Their model identified juveniles as the critical life stage of this species and projected lower extinction risks if juvenile survival was 2% rather than 1% (Hatfield et al. 2004). My model was individual-based, spatially-explicit, and included both sexes. The Houston toad exhibits sexual dimorphisms in mortality and the assumption of dominance has not been tested, therefore both sexes should be included in the model (Caswell 2001). Further, the breeding system of the Houston toad includes a spatial component (i.e., they must breed at specific locations on the landscape (i.e., in water), which is not homogenously distributed throughout the habitat) and if males are not present at breeding sites with females, then successful breeding cannot occur and this justifies the inclusion of males in a model of this type.

My model, like Hatfield et al. (2004), was sensitive to changes in juvenile survival rates. Hatfield et al. (2004) did not report final population size for their simulations. In our model, unrealistic results were generated if the probability of juvenile survival was 0.02 (Table 5.4, Fig. 5.5b). This is not to say that juvenile survivorship cannot be as high as 0.02, only that under the assumptions used in this model, it seems unlikely. One difference between this model and Hatfield et al. (2004) is that they incorporated environmental catastrophes, which I purposefully did not do in order to explore the sensitivity of survival estimates without confounding factors. Incorporating catastrophic effects into the model might necessitate juvenile survival be higher for the population to persist.

Versions 1 and 3 produced results that best reflect the toads as they currently exist at the GLR – low numbers and significantly more males than females. There was a significant difference between the mean population sizes between versions 1 and 3 (F = 80.522, $p < 0.001$). The mean number of males and females is relatively low (Table 5.4, Fig. 5.5a), however, simulations were stopped before the cohorts from years 9 (for females) and 10 (for males) would be classified as mature. For example, from version 1, all of the juvenile males (on average about 70, Table 5.4, Fig. 5.5a)) would mature before the next breeding season, which would be about 85 breeding males, which is similar to the numbers captured at the GLR (Chapter II, Fig. 2.3). Likewise, the low number of adult females in the simulated population is also reasonable when compared to the field results (Chapter II, Fig. 2.3). Out of these two versions, when survival for males was higher than females (version 1), the sex ratio was significantly male-biased, indicating that the difference in age at first reproduction coupled with juvenile mortality can cause a bias in the sex ratio even if the limiting sex has a higher probability of survival. The results of the versions 1 and 3 indicate the necessity to gather more data on the juvenile life stage as precise estimates for this species do not currently exist.

In versions 1 and 3, on average, toads moved within the range (950 – 1,900 m) reported by Price (2003). Data do not exist for dispersal from natal ponds for Houston toads, however, in the closely related Woodhouse's toad (*B. woodhousei*) the proportion of individuals returning to the natal pond was 0.73 (Breden 1987). The model does project a large proportion of the population returning to their natal pond (*NP*, Table 5.5), but it is not as high as that reported by Breden (1987). This emergent property of the system is not explicitly modeled and is a result of the movement rules. As more data become available the movement rules can be modified to encompass new information, however, for now, the approach we used for modeling movement can generate similar patterns to those observed in congeneric species.

Ideally, population models would contain exact information about the system-of-interest and be able to project the dynamics with a high degree of confidence. For many rare or endangered species, this is not the case, as precise estimates for many vital life history characteristic remain uncertain (Mooij and DeAngelis 2003). Parameter estimates (i.e., φ, Chapter III) obtained from small populations are generally associated with a large amount of variability (Anderson and Burnham 1999, Williams et al. 2002). Estimating parameters for certain life stages, or life history characteristics, can be further complicated because these data can be challenging to obtain in the field. For example, in many pond breeding anurans, like *B. houstonensis*, juveniles are thought to be the critical life stage as well as the main units of dispersal, yet monitoring juveniles to adulthood is difficult due to their small size and cryptic nature. By not being able to monitor the juveniles, survival estimates during life stage remain uncertain and conservation efforts ultimately suffer. In cases like the Houston toad, where the population is at critically low levels, it is paramount that population models do more than identify “at risk” life stages as the relative amount a specific life stage contributes to future population growth maybe eclipsed by larger scale processes (such as landscape fragmentation). These models must provide a mechanism to explore the relationships between organisms and their environment because ultimately conservation efforts that explicitly model population and landscape-level processes stand to be the most successful (Greenberg and Tanner 2005a).

Spatially explicit, individual-based models (IBMs) provide tools to explore spatial relationships between individual organisms and their environment. IBMs, like the one presented in this chapter, offer a new spectrum of management possibilities as they allow researchers to explore scenarios that they may not be able to examine through field experiments (i.e., develop management strategies based on the results from simulations of large-scale habitat destruction). These models are notoriously data-intensive, but the amount of knowledge that can be gained from the modeling process and the model itself is large as well. While field data may not always be available, recognized experts can always develop hypotheses as to how an ecological process affects a specific species or how an individual would behave under a set of conditions. These testable hypotheses can provide the foundation for successful conservation.

Conservation of any species requires accurate life history and ecological data. For many species, including the Houston toad, these data are either not available or are associated with considerable variability. Models like the one presented in this chapter provide researchers with tools both reduce uncertainty and to hypothesize how individuals interact with their environment. If models are parameterized in such a way that the simulated patterns emerge from, and are not forced by, the model, the results from these simulated experiments can be compared to patterns observed in the real system (i.e., spatial distributions, population-level parameters). As the simulated and observed patterns become similar, researchers will gain insight into the ecological processes that cause the natural patterns. Management based on these results will ultimately aid in these adaptive conservation strategies.

CHAPTER VI

CONCLUSIONS

The likelihood of extinction for *B. houstonensis* at the GLR within the next 10 years appears to be quite small (Chapter V), although the intrinsically male-biased sex ratio is cause for concern because the effective population is much smaller due to the difference in maturation between males and females (Chapter IV). This conclusion assumes no further landscape fragmentation, especially conversion to pastures with non-native grasses, which are not utilizable by Houston toads (Chapter II), or extended droughts since precipitation is intimately tied to both breeding activity and survival (Chapters II and IV, respectively).

These conclusions are based on projections made from a spatially explicit, individual-based, stochastic simulation model used to project population size and structure. The model is based primarily on results of the analyses in Chapters II – IV. Rules for movement and breeding activity were formulated using the capture data and logistic and negative binomial regressions from Chapter II. Survival estimates for adult males were taken from the most parsimonious model used to estimate survivorship (Table 3.3, Chapter III) and from the literature for juveniles and adult females (Hatfield et al. 2004). Age at first reproduction for both males and females was based on the results from a captive-bred study (Quinn and Mengden 1984). The model was verified at the individual-level in terms of movement patterns (Table 5.5, Chapter V) and evaluated at the population level in terms of stage (emergents, juvenile, adults) and sex ratio (Table 5.4, Chapter V).

Overall the results from this work indicate the population is constrained by the landscape, precipitation, and the difference in age at first reproduction. At the GLR, Houston toads appear to be sustaining themselves, and most likely will for the immediate future, but this location is atypical for the agriculturally dominated Bastrop County (i.e., the GLR has 16 ponds and is 87% forested). Rangewide, management and conservation strategies must recognize the effects precipitation have on survival and breeding activity, as well as the impacts of the difference in maturation time, and focus efforts on answering the critical conservation question: how much non-native pastureland is too much to maintain a viable Houston toad population?

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VITA

Todd Michael Swannack was born in Kentucky. A year in the bluegrass state was enough, so he convinced his parents that Texas would be a better place for his siblings to be born. He was right. They rock. He lived in Victoria, Texas until he was 11. He moved to Buda in 1984 and joined the local gang, *The Boys*, in 1985 and has been a member ever since. Watch out for them. They ain't scared. While attending Hays High School, his teachers told him that a big school would eat him up, so, he decided to attend a really big university, obtaining a B. A. in Biology from Texas A & M in May of 1995. He sure showed them. Over the next couple of years, he and a soon-to-be world class doctor traveled across the country with a squirrel and a flamingo. Along the way, they had dinner with the Emmys, went to the Olympics, and managed to get lost any time the doctor let him drive. It wasn't his fault. It was the toxic fumes. After traveling for awhile, he was employed by Origin Systems, where he met the coolest and most creative people on the planet. He entered the graduate program at Southwest Texas State University in 1998, obtaining an M.S. in December 2000. At Southwest, he made good friends, caught some turtles, and was one of the creators of Meat Day. In 2001, he began working with the Houston toad at the Griffith League Ranch. In 2002, he entered the Ph.D. program in the department of Wildlife and Fisheries Sciences at Texas A&M University. At Texas A & M, he achieved one of his personal goals and obtained a Ph.D. in August 2007. His permanent address is 210 Nagle Hall, WFSC, Texas A&M University, College Station, Texas 77843-2258.