**INTRODUCTION**

Spatial distribution and habitat connectivity are important topics of study in amphibians as global extinctions become more apparent. The tendency of amphibians to travel among subpopulations depends on habitat quality and accessibility (Martin et al. 2008; Dancose et al. 2011). Temperate pond-breeding amphibians require both aquatic and upland terrestrial habitats for breeding and foraging activities, respectively (Semlitsch 2000). However, habitat loss and fragmentation of these habitats are major contributing factors to amphibian declines (Davidson et al. 2002; Beebee and Griffiths 2005; Gallant et al. 2007; Collins and Crump 2009). Previous research has found that the wildland-urban interface, where habitat fragmentation often occurs, accounts for 9% of land area in the United States (Radeloff et al. 2005). This human encroachment has left suitable amphibian habitat fragmented throughout the landscape (Lehtinen et al. 1999).

Across mixed landscapes of ephemeral and permanent ponds, the distribution of amphibian populations is dynamic and depends on the volume, geographical location, and distance among water bodies. The success of dispersing individuals, spatial distribution of ponds, and connectivity of breeding sites all contribute to the eventual structure of amphibian populations (Gustafson and Gardner 1996; Semlitsch and Bodie 1998; Marsh and Trenham 2001; Moilanen and Nieminen 2002). There are two basic components to connectivity, structural and functional. Structural connectivity is the spatial connection of habitat types; whereas, functional connectivity describes the utility of the habitat for dispersal across the landscape (Taylor et al. 2006). Managers typically improve structural connectivity (e.g., establishing connections among forest patches) assuming equivalence to functional connectivity (Ribeiro et al. 2011). However, even when habitat preferences are well known, it is important to understand movement patterns of all life stages to improve the functional connectivity for the most actively dispersing life stages.

Several amphibian species in the family Bufonidae exhibit similar spatial habitat use patterns. While most adult individuals remain near a breeding site throughout the year,
juveniles are thought to be the primary units of dispersal among potential breeding sites (Smith and Green 2005; Semlitsch 2008). High breeding site fidelity and low dispersal have been reported in populations separated by tens of kilometers (km) connected by occasional migrants (Smith and Green 2005, 2006). However, because amphibians exhibit a wide range of dispersal abilities and habitat use patterns (Carpenter 1954; Stebbins and Cohen 1995; Dodd and Cade 1998; Wells 2007), it is important to investigate spatial dynamics on a species and life stage specific basis.

The Houston Toad (Bufo [Anaxyrus] houstonensis) is a federally endangered species endemic to east-central Texas (Gottschalk 1970). Since the 1970s, B. houstonensis has been extirpated from at least three of the 12 counties within its historic range (U.S. Fish and Wildlife Service 1984), with populations persisting in isolation (> 40 km from the nearest population) across all but one of the remaining counties (Michael Forstner, unpubl. data). Prior to the Bastrop County Complex Fire of September 2011, the only population not threatened with immediate extinction occurred in the Lost Pines ecoregion in Bastrop County (Brown 1971, 1975; Duarte et al. 2011). B. houstonensis is a habitat specialist that prefers deep sandy soils and forest cover (U.S. Fish and Wildlife Service 1984), and its precipitous decline has been driven largely by habitat loss and degradation (Brown 1971; Brown and Mesrobian 2005; Michael Forstner, unpubl. data).

Few life history data have been collected for this species over the last 60 years, despite its endangered status. Hybridization with Bufo [Anaxyrus] woodhousii and Bufo [Incilius] nebulifer was studied by Brown (1971). Hillis et al. (1984) and Jacobson (1989) addressed population-level behavior and activity; specifically breeding activity with comments on sexual selection and juvenile dispersal. Finally, fluorescent powder has been tested as a tool to quantify juvenile dispersal (Swannack et al. 2006). However, no data have been collected describing the spatial distribution and movement dynamics of either juvenile or adult B. houstonensis. This study represents the first major contribution to our understanding of B. houstonensis spatial dynamics, an essential component of successful recovery and management of this imperiled species.

Here, we describe B. houstonensis movement patterns and spatial habitat use among life stages within the Lost Pines ecoregion. We used audio surveys, pitfall trapping, juvenile emergent observations, and radio telemetry to determine breeding site fidelity, terrestrial movement, and dispersal of adult and juvenile B. houstonensis within and among years. In addition, we collected data to gauge the use of grasslands as travel corridors by B. houstonensis.

Materials and Methods

Study site.—We studied B. houstonensis populations on the Griffith League Ranch (GLR), a 1,948-ha property in Bastrop County, Texas owned by the Boy Scouts of America (BSA). This large tract of land is located within designated critical habitat for B. houstonensis (U.S. Fish and Wildlife Service 1984), and is considered essential for long-term persistence of the species (Hatfield et al. 2004; Duarte et al. 2011). The GLR is primarily a forested ranch, with a canopy dominated by Loblolly Pine (Pinus taeda), Post Oak (Quercus stellata), Blackjack Oak (Q. marilandica), and Eastern Red Cedar (Juniperus virginiana), and an understory dominated by Yaupon Holly (Ilex vomitoria), American Beautyberry (Callicarpa americana), and Farkleberry (Vaccinium arboreum). The GLR supports 17 ponds, with hydroperiods ranging from highly ephemeral (n = 2) to permanent (n = 3). We have observed B. houstonensis at 15 of these ponds since we began monitoring reproduction on the property in 2000, and 11 are known breeding ponds.

Breeding site surveys.—We conducted call surveys between 2001 and 2010 following the protocol detailed in Jackson et al. (2006) to study the use of breeding habitat by adult male and female B. houstonensis during annual courtship. The annual number of call surveys ranged from 19 to 27, depending on B. houstonensis activity levels during their breeding season, between January and June (Table 1). Between 2001 and 2005, and between 2009 and 2010, we measured...
and individually marked *B. houstonensis* during visual surveys at potential breeding ponds, unless individuals were in amplexus. We marked adult *B. houstonensis* using Passive Integrated Transponder (PIT) tags or toe clips (Donnelly et al. 1994). Between 2001 and 2005, we conducted surveys nightly during the breeding season except on nights when weather conditions were hazardous. In 2009 and 2010, we surveyed only on nights when toads were most likely to be active (Kennedy 1962; Hillis et al. 1984; James Dixon, unpubl. data).

**Adult terrestrial movement (drift fence sampling).**—We monitored terrestrial movement in open grassland areas, forested habitat, and along drainages from 2001 to 2004 and 2008 to 2011 using linear and Y-shaped drift fences with pitfall traps and double-opening funnel traps (See Dodd et al. 2007 and Swannack et al. 2007 for design information). In 2001, we installed five linear drift fences (two 121 m and three 153 m) in grasslands parallel to the forest edge, three were 25 m from the forest edge, one was directly adjacent to the forest, and the remaining drift fence was 100 m from the nearest forest edge. We installed additional drift fences to monitor movement within forested habitat, including three additional Y-shaped arrays in 2001, ten Y-shaped arrays in 2002, and nine Y-shaped arrays in 2008. Due to low Houston Toad capture rates in double-opening funnel traps, they were not used with Y-shaped arrays between 2008 and 2011. In 2009, we added seven 15 m linear arrays with double-opening funnel traps (used for a separate study conducted during the same period) centered on each side of the flashing, adjacent and parallel to known breeding ponds. We equipped all traps with predator exclusion devices (Ferguson and Forstner 2006), flotation devices to mitigate mortality during bucket flooding, and sponges to provide a moist environment for amphibians upon capture. The trap locations and breeding sites used during the terrestrial activity monitoring periods are shown in Fig. 1.

We checked traps daily from 12 March 2001 to 30 June 2004, with the exception of seven days in July 2002 and 13 days in August 2003. Between 2008 and 2011, we conducted most of our terrestrial monitoring during the spring, when *B. houstonensis* are most active. In 2008, we trapped from 1 March to 1 May, with the exception of five days in April, from 1 February to 1 May in 2009, from 31 January to 1 May in 2010, and from 13 February to 23 May in 2011, excluding seven days in May.

**Adult terrestrial movement (radio telemetry).**—Between 2003 and 2005, we fitted 21 (16 M : 5 F) *B. houstonensis* with external radio transmitters (model # BD-2, mass: 1.8g, Holohil Systems, Carp, Ontario, Canada). We collected toads for telemetry during the first chorusing event in March and tracked toads up to six weeks. We selected toads based on weight and body condition. We used toads weighing over 20 g to remain within the recommended

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**Table 1.** Number of anuran call surveys conducted on the Griffith League Ranch, Bastrop County, Texas, USA, in seven survey years, and number of unique individual Houston toads (*Bufo [Anaxyrus] houstonensis*) detected at breeding ponds on the property each survey year.

<table>
<thead>
<tr>
<th>Year</th>
<th>Number of surveysa</th>
<th>Number of unique individualsb</th>
</tr>
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<tbody>
<tr>
<td>2001</td>
<td>20</td>
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<td>2002</td>
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<tr>
<td>2010</td>
<td>27</td>
<td>90</td>
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aIncludes number of days each breeding season where all ponds were surveyed on the study site.
bIncludes recaptures from previous years and individuals originally captured in traps.
ratio of transmitter mass to body mass (White and Garrott 1990). We tested three external-fitting techniques for the transmitters, a spandex jacket, stainless steel bead chain, and nylon ribbon (see Swannack 2007 for details). We released all captured and fitted toads at the edge of the pond closest to their initial capture point and located toads again at least once every three days during the life of the transmitter. To determine whether toads were moving during daylight hours, we initially located toads during the day and then located each toad again that night. We tracked each toad until the transmitter fell off or the batteries died.

**Juvenile habitat preference and dispersal.**—In 2002 and 2003, we investigated *B. houstonensis* post-metamorphic habitat use and dispersal rates into upland habitat during their first summer. We identified juvenile toads as being less than 3 cm snout-vent length (SVL). We initially captured toadlets using three semicircle pitfall trap arrays constructed to surround *B. houstonensis* egg strands laid in a breeding pond. The trap arrays were made of flashing and placed 2 m, 5 m, and 8 m from the pond’s edge, with each array extending 1 m into the pond on each side to measure the rate of dispersal from the pond’s edge after metamorphosis and emergence. We positioned covered 2.4 L pitfall traps along each array at 3 m intervals and filled each one with leaf litter and water. We toe-clipped all juveniles captured in the array (Donnelly et al. 1994) and subsequently released them on the opposite side of the flashing.

In 2002, we designed a grid around the natal pond consisting of 13 rows of flags placed every 5 m up to 50 m from the pond’s edge. We surveyed randomly selected flag locations 100
times using a 5 m$^2$ quadrat plot to inspect leaf litter for juvenile *B. houstonensis*. We conducted the surveys within the grid every three days over the course of 13 weeks to document juvenile *B. houstonensis* dispersal rates. No juvenile toads were located within the grid, so in 2003, we redesigned the grid to include 50 artificial refugia randomly constructed within a 250 m radius around the pond. The 1 m$^2$ refugia were dug 15 centimeters (cm) into the ground, lined with rubber pond liner, and filled with leaf litter, water, and sand. Every three days, we inspected refugia for juvenile *B. houstonensis* and sprayed the refugia with 7.5 L of water.

**RESULTS**

**Breeding site fidelity.**—We obtained 380 (358 M : 22 F) unique *B. houstonensis* and 122 (122 M : 0 F) total recaptures from 83 recaptured individuals at ponds on the GLR. Of the 83 recaptured individuals, only one moved between ponds. This adult male moved 150 m to the nearest neighboring pond. The recapture occurred during the following year, and the pond at which it was initially captured was dry at the time of recapture.

**Adult upland habitat use and movement.**—We obtained 120 (85 M : 35 F) unique *B. houstonensis* and 10 (5 M : 5 F) total recaptures in traps on the GLR. In addition, we captured 25 individuals at both traps and ponds (23 M : 2 F). Most recaptures were recorded within 100 m and 100 days of the initial capture (Figs. 2 and 3). The among-trap movement data showed one female moved 60 m over a single night, one male moved 84 m over a single night, and one male moved 680 m over a five month period (minimum straight-line distance). The remaining individuals were recaptured in the same traps. For the trap-pond recapture data, the mean recapture distance for males was 147 ± (SE) 248 m, and movement ranged from 10 m to 777 m (minimum straight-line distance). The two females recaptured moved 46 m and 724 m, respectively (minimum straight-line distance). Between 2001 and 2004, 15 (26% of captures during that time period) *B. houstonensis* were detected in traps 25 m from a forest edge and zero were caught in the central array 100 m into pasture specifically designed to bisect two highly active areas with breeding ponds on either side of the array.

Between 2003 and 2005, we documented 139 locations for radio-telemetered *B. houstonensis*.

**FIGURE. 2.** Documented movement distances for adult Houston Toads (*Bufo Anaxyrus* houstonensis) on the Griffith League Ranch, Bastrop County, Texas, USA between 2001 and 2011. The data include movement among traps and movement between ponds and traps. We used the furthest distance traveled between recaptures for individuals that were recaptured at more than one location. The first four bars represent bins of 25, 50, 75, and 100 m.

**FIGURE. 3.** Number of days between the first and last detection of recaptured adult Houston Toads (*Bufo Anaxyrus* houstonensis) on the Griffith League Ranch, Bastrop County, Texas, USA, between 2001 and 2011. We detected individuals using drift fence trapping from 2001 to 2004, and 2008 to 2011, and call surveys from 2001 to 2010.
(63 in 2003–2004, 76 in 2005). Toads were located on average eight times during the study. One male was only relocated one time before the transmitter had fallen off. Likewise, two males were found six times before the transmitters fell off. The remaining toads were tracked for the life of the transmitter. We observed consistent movement patterns among years. During the breeding season, all males remained within 75 m of their respective breeding pond. All females moved at least 50 m from the pond’s edge within two days of being released. While there were not enough data to determine a home range or gender-specific movements with any degree of statistical accuracy, these data are valuable for qualitative descriptions of the post-breeding behaviors of Houston Toads.

Of the 25 toads transmittered, one was found in a self-made burrow. The remaining 24 were found in cavities under fallen trees, almost exclusively oak trees. Transmittered toads did not move during the day. Toads were observed foraging locally at night (always within 5 m of the refugia), and returned to the same refugia after foraging. Each transmitted toad utilized refugia and made short distance (< 10 m) movements to forage. Longer distance movements (> 10 m) appeared to be driven by rainfall. If toads moved more than 10 m, they would always choose other refugia. In 2005, we recorded one instance of long-distance movement: a male moved 221 m from the site of release over the course of six weeks (from mid-April to early June). Based on eight observations, the male used a water-filled drainage as a travel corridor, never traveling more than 5 m from the drainage. The mean movement of all toads was 74.8 ± (SE) 25.78 m over the course of the study.

**Juvenile terrestrial dispersal.**—We found that post-metamorphic juveniles remained close to the water’s edge (within 12 m) during the first two weeks after emergence (n = 275) and then gradually began dispersing towards the upland forested habitat adjacent to the pond. Thirty-one juveniles were found within 12 to 18 m of the pond after three weeks and 11 juveniles were found 18 to 35 m from the pond after four weeks post-emergence (Fig. 4). Beyond 30 days, five juveniles were found 20 to 35 m from the pond eight weeks post-emergence and four juveniles were found 50 m from the pond 11 weeks post-emergence. General observations regarding

![Figure 4](image-url)
habitat characteristics were made at refugia though we did not quantify microhabitats. However, we did not find any metamorphs in sunny, dry habitats. Every metamorph captured was found in the shade, and always in moist soil.

**Discussion**

Similar to other bufonid species, *B. houstonensis* exhibited movement patterns indicative of strong within-year and among-year breeding site fidelity but with occasional long distance movements (Reading et al. 1991; Bartelt et al. 2004; Smith and Green 2006). All recaptured toads, except one, were at the same pond where we initially captured them during the breeding season. In addition, we found the juveniles within 50 m of their breeding pond within the first three months after emergence. However, we observed four notable long distance movements during separate studies in the summer of 2010. We captured one juvenile 458 m and two juveniles 1,384 m away from the nearest successful breeding pond in 2010 (Donald Brown, unpubl. data). In a separate study of head-starting, the practice of collecting wild egg strands and captive rearing *B. houstonensis* beyond metamorphosis, we accurately tracked a head-started juvenile that dispersed a straight-line distance of 1,340 m over a one month period in 2010 (Vandewege et al. 2012).

Population connectivity could be maintained among close breeding populations through occasional long-distance movements of juveniles and adults, as we observed 15% of recaptured individuals that moved more than 700 m away from their initial point of capture. Both adult and juveniles can disperse distances greater than 1 km. Andrew Price, (unpubl. data) found similar results at the 2,398 ha Bastrop State Park, located 2,200 m south of the GLR. His results from breeding activity monitoring between 1990 and 2002 indicated that breeding site fidelity was high, yet he documented several long-distance movements between breeding ponds. Two males moved 950 m between breeding ponds, three males moved 1,400 m, two males moved 1,600 m, and two males and one female moved 1,850 m. It should be taken into consideration that long distance dispersal is usually underestimated by mark-recapture (Porter and Dooley 1993); thus, we cannot conclude definitively that 1 km is the maximum dispersal distance. The rarity and secretive nature of the species has precluded our ability to collect extensive dispersal data. We were unable to determine distances moved by toads between emergence and maturity. Therefore, we cannot deduce the primary dispersal life stage for *B. houstonensis*, although juveniles are the primary dispersers in other bufonids (Breden 1987; Scribner et al. 1997; Sinsch 1997).

*B. houstonensis* tends to avoid long distance dispersal through grasslands and shows strong preference for forested habitat (Brown 1975; Forstner and Ahlbrandt 2003; Hatfield et al. 2004). Here, we observed no *B. houstonensis* more than 25 m into grasslands, consistent with earlier studies. In a closely related species, *Bufo [Anaxyrus] americanus*, juveniles dispersed shorter distances and exhibited lower survivorship in open fields compared to closed canopy forests (Rothermel and Semlitsch 2002).

To maintain connectivity among forested habitat and facilitate movement among populations, management efforts should concentrate on restoring and improving forested travel corridors to facilitate movement among localized subpopulations.

We infer that breeding sites should be maintained in such a manner that facilitates easy movement to and from breeding ponds for both adult and juvenile life stages. To allow spring breeding connectivity, we recommend that the maximum distance between ponds (ephemeral or permanent) be limited to 1 km because we rarely recorded adult *B. houstonensis* covering distances greater than that. Small, temporary wetlands can be just as important to amphibian conservation as permanent breeding ponds (Semlitsch and Bodie 1998; Brown et al. 2012). In optimal habitat, distance between subpopulations has shown little effect on pond colonization or extinction (Marsh and Trenham 2001); however, in highly disturbed areas, habitat unsuitable for terrestrial movement has been correlated to genetic divergence among subpopulations (Marsh and Trenham 2001). Therefore, both localized management of critical
habitat surrounding breeding ponds and the forested habitat that connects these breeding ponds at the local and regional scales should be considered in order to effectively manage for *B. houstonensis*. The spatial configuration of suitable breeding wetlands required by *B. houstonensis* varies among years and the deleterious effects of pond deletion and habitat fragmentation (either by natural or anthropogenic causes) could play a significant role in population decline.

**Conservation implications.**—The Houston Toad is an amphibian facing a serious extinction threat and understanding movement patterns is critical to their management across heterogeneous landscapes (Gibbs 1998; Semlitsch 2000; Graeter et al. 2008). Our data indicate that individual *B. houstonensis* are not homogenously distributed on the landscape. Rather, adults were captured and observed around localized patches of forested habitat surrounding breeding ponds. The long-term persistence of reproduction and gene flow depends on habitat connectivity (Cushman 2006) among these critical habitat patches.

We have shown that adult *B. houstonensis* are capable of dispersing long distances and other studies have recorded juveniles dispersing more than 1,300 m (Donald Brown, unpubl data; Vandewege et al. 2012). However, movement appears to be restricted to forested habitat and to a greater extent, around breeding ponds as toads were mostly recorded there. Over 8 trapping years we observed Houston Toads in open grasslands only 15 times, despite placing the trapping array to bisect areas between highly active breeding ponds on the forest margins. In addition, we have shown that site fidelity is high at breeding ponds and should be accounted for when managing the size of critical habitat. As critical habitat becomes more fragmented, long-term persistence probabilities will likely decrease for this species. Management efforts should consider a 75 m buffer zone around breeding ponds as the minimum area required for the protection of these critical breeding habitats as both adults and juveniles were most frequently observed in this zone. We refer to this inclusively as breeding habitat, taking into account both the larval aquatic habitat and immediately adjacent uplands supporting it. At a broader spatial extent across a landscape, efforts should also focus on maintaining and restoring forested habitats in increments of 1.5 km surrounding breeding ponds. Our results indicate that the juxtaposition of pond and forest within this radius represents the core of the habitat occupied by the species today. These occupied habitat areas contain the majority of the remaining Houston Toads, provide connectivity among breeding habitats, and act as source areas for dispersal events among populations. Consequently, recovery efforts should also include attempts to establish (or maintain) connectivity among the remaining occupied fragments. Dispersal habitat may be essential to long term persistence of the species; without connectivity, individual populations decline to extinction rapidly (Hatfield et al. 2002). As a result of our evaluation of the maximum dispersal events detected within a single year and genetic connectivity in Bastrop County (Diana McHenry and Michael Forstner, unpubl. data), we consider dispersal habitats to include areas outward from the breeding pond at distances to 5 km.

Drought conditions in Texas during the last five years have been dramatic. Unfortunately, an impact from those conditions was the Bastrop County Complex Fire of September-October 2011. Given the Houston Toad’s apparent strong preference for mature forest, we believe the high intensity fire will have long term negative impacts to the species in what was the last region that retained robust chorusing populations. The species has been in decline in Bastrop County for many years. Choruses of hundreds of individual at a single pond were reported as recently as 1984 (Hillis et al. 1984), while the mean chorus size from 2000 to 2008 was only five males (Gaston et al. 2010). The fire and drought are only part of the ongoing changes to habitat as Bastrop County is currently under tremendous development pressure, particularly in the Lost Pines ecoregion. The human population in Bastrop County increased by 28.5% between 2000 and 2010 (U.S. Census Bureau. 2011. Available from
As the area becomes more urbanized, maintaining connectivity among breeding sites will become increasingly difficult. Maintaining habitat connectivity for future generations is further threatened by the currently unknowable outcomes to the area from the historic wildfires of 2011. The need to design and implement landscape-scale recovery initiatives for *B. houstonensis* cannot be overstated.

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**Literature Cited**


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Donald J. Brown is a Ph.D. candidate in the Biology Department at Texas State University-San Marcos. He is primarily interested in research that contributes to active management of wildlife populations. He is currently investigating the use of fire for managing the Lost Pines ecoregion of Texas, with emphasis on fire as a management tool for recovery of the endangered Houston Toad (*Bufo houstonensis*). (Photographed by Ivana Mali).

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