Title: Variation in abundances of *Eurycea sosorum* and *Eurycea waterlooensis* (Plethodontidae: Hemidactyliini: *Eurycea*: Notiomolge), with examination of influences of flow regime and drought

Laurie A. Dries

Abstract

Eurycea sosorum and *Eurycea waterlooensis* are federally recognized as imperiled; *E. sosorum* is listed as endangered; *E. waterlooensis* is a candidate for endangered status. Both are perennibranchiate salamander species endemic to the habitats within and beneath a cluster of springs along the Balcones Fault of the Edwards Aquifer, collectively known as Barton Springs. Threats to these species include habitat loss and fragmentation due to modification of natural flow regimes of these springs (*e.g.*, dams, impoundment) for commercial and recreational uses. Additionally, increasing withdrawal of groundwater from the Edwards Aquifer threatens the quantity and quality of water emanating from Barton Springs. Evaluating effects of anthropogenic threats on these salamanders requires an understanding of the relationship between habitat variation arising from threats and salamander abundance and. In this paper I use salamander census and habitat quality data to examine variation in salamander abundance within and among springs sites and over 8 – 17 years, in the context of variation in habitats, specifically flow regime modification and drought. Populations of *E. sosorum* and *E. waterlooensis*, varied in size within and among spring sites, as did habitat. There are more salamanders during periods of higher discharge from Barton Springs (< 25 cfs) and in sites where natural flow regime has been partially reconstructed. *Eurycea sosorum* is found in significantly higher abundances, with increased reproduction and recruitment, in sites with habitat consisting of clean, rocky substrate in flowing water (mean 0.57 ft./sec.), with low sediment depth (< 0.7 in.) and cover. Abundance of subterranean *E. waterlooensis* in surface habitats is low, but is positively correlated with abundance of *E. sosorum*, suggesting similarity of habitat requirements. Periods of drought are accompanied by decreases in flow velocity, but also biologically significant decreases in dissolved oxygen and increases in water temperature. *Eurycea sosorum* experiences steep reductions in abundance and curtailment of reproduction and recruitment; *E. waterlooensis* largely disappears from surface habitat. Flow regime alteration and groundwater withdrawal magnify the severity of droughts that threaten both species, continued efforts to fully restore natural flow regimes could potentially help mitigate detrimental effects of drought.

Introduction

Eurycea sosorum and *Eurycea waterlooensis* are perennibranchiate salamander species whose known habitats are within and beneath a cluster of springs along the Balcones Fault of the Edwards Aquifer, collectively known as Barton Springs (Sweet 1982, Chippindale *et al*. 1993, Hillis *et al*. 2001). Both species are federally recognized as imperiled; *E. sosorum* is listed as endangered (U.S. Dept. of the Interior 1997); *E. waterlooensis* is a candidate for endangered status (U.S. Dept. of the Interior 2002). Typically, endangered species have small population sizes or small ranges (Munton 1987, Mace and Kunin 1994, Mace and Kershaw 1997, Manne *et al*. 1999, Abrams 2002), both of which are true for Barton Springs' *Eurycea*. Maximum observed abundances are small enough (1900 for *E. sosorum* and 43 for *E. waterlooensis*) for both species to be considered at risk of extinction by several rules-of-thumb (Muller 1950, Bell 1983, Lynch and Gabriel 1990, Lynch 1996, Maynard Smith 1998). *Eurycea sosorum* and *E. waterlooensis* also have very small ranges (Chippindale *et al*. 1993, Hillis *et al*. 2001); the four springs in which they are found are located within 1200 feet (350 meters) of one another, adjacent to or within Barton Creek, in Zilker Park, Austin, Texas (Fig. 1). The species are sympatric (Chippindale *et al*. 1993, Hillis *et al*. 2001), they occupy the same cluster of springs, and are syntopic, their ranges can overlap. This segregation of epigean and subterranean habitat within spring sites has been documented in other Edwards Aquifer *Eurycea* (*E. neotenes* and *E. tridentifera*: Sweet 1984, *E. nana* and *E. rathbuni*: Bishop 1941, Russell 1976, Longley 1978, Chippindale 1995). Epigean *E. sosorum* is found in abundance in surface habitat and utilizes subterranean habitat for reproduction and retreat (Chippindale *et al*. 1993, Hillis *et al*. 2001, City of Austin 2010), while very few subterranean *E. waterlooensis* are found at the surface (Hillis *et al*. 2001, City of Austin 2010). Each species has morphological characteristics reflecting adaptation to epigean or subterranean habitat such as image-forming lenses in the eye of *E. sosorum* (Chippindale *et al*. 1993), and their lack in subterranean *E. waterlooensis* (Hillis *et al*. 2001). *Eurycea* found in Barton Springs have been recognized for decades as distinct from perennibranchiate *E. nana* found 30 miles to south (Bryce and Flury specimens collected in 1946, Sweet 1982, Chippindale *et al*. 2000, Hillis *et al*. 2001, Bendik 2006).

Thus, the entire ranges of both species lies within a city with a rapidly growing human population (790,390 U.S. Census data 2011), leading to increasing urban development of the Edwards Aquifer and consequent degradation in quality and quantity of groundwater feeding Barton Springs (citations). In addition, Barton Springs has been used for site of commercial and recreational purposes since the 19th century (Pipkin 1995, reviewed in Limbacher and Godfrey 2007, Austin History Center archive photographs). The springs have been modified to facilitate those uses, resulting in loss and fragmentation of habitat. While these factors have been recognized as major threats to the persistence of both species, (U.S. Fish and Wildlife Service 1997, 2001), an complete understanding of how these threats affect Barton Springs' *Eurycea* is hampered by lack of scientific information on natural history of both species. Strategies for protection and management of these species have been based on inferences drawn from other *Eurycea* species.

All *Eurycea* species are members of Plethodontidae, an evolutionary clade of lungless brook salamanders. All of the species of brook salamanders (~240) are associated with streams and surrounding riparian habitats (Petranka 1998). Most *Eurycea* have biphasic life cycles where aquatic juveniles metamorphose into semi-aquatic or terrestrial adults (Duellman and Trueb 1994; Petranka 1998), utilizing aquatic habitat for at least some portion of their life. This

is in contrast with several other closely related salamander groups that inhabit ponds, swamps, sloughs, and lakes (Fig. 2).

The Edwards Aquifer of the Edwards Plateau region of central Texas contains a monophyletic group (*Paedomolge*, Hillis *et al*. 2001) of solely aquatic, perennibranchiate ("always gilled") *Eurycea* species (Chippindale *et al*. 2000). There are numerous intermittent and perennial springs throughout the Edwards Aquifer that harbor endemic epigean and subterranean *Eurycea* species (Sweet 1978; Chippindale *et al*. 1993; Chippindale *et al*. 2000; Hillis *et al*. 2001; Bendik 2006). Since the regional climate is generally arid, these springs and spring-fed streams are the only sites where presence of flowing water is reliable. And Barton Springs is one cluster of the few perennial springs in the Edwards Aquifer (Brune 1975, 1981).

Edwards Aquifer spring-fed surface streams ebb and flow with climatically driven variation in amount and distribution of recharge to ground waters (Brune 1981). Thus, resident perennibranchiate *Eurycea* experience natural contractions and expansions of surface habitat (Sweet 1982, Hubbs 1995), and occasional inundation by floods. These conditions are thought to have favored the evolutionary loss of metamorphosis and consequent dependence on epigean and/or subterranean spring-fed streams throughout the life span of central Texas *Eurycea* (Bruce 1976, Sweet 1977, 1982; Chippindale *et al*. 2000). Natural variation in amount of water flowing into the surface of springs is thought to play a role in the evolution of life histories of Edwards Aquifer *Eurycea* species (Bruce 1976, Sweet 1982). Reliable patterns of flow variation may provide signals of impending habitat contractions and expansions, and could influence a variety of characteristics in perennibranchiate *Eurycea* species, from timing of reproduction to movement between epigean and subterranean habitat (Levins 1968, Schmidt-Nielsen 1975, Sweet 1982, Pianka 1983, Tumlison and Cline 1997, Bonett and Chippindale 2006).

Existing knowledge of life history, and evolutionary ecology of Barton Springs' *Eurycea* is limited; much of information about life history and behavior comes from salamanders in captivity and two experiments conducted by Gillespie (2011) on wild-caught salamanders. Gillespie's work (2011) included examination of sensory modalities of response to potential predators and temporal variation in diet. She demonstrated that wild-caught *E. sosorum* reduce activity in response to visual and bioelectric cues of predatory largemouth bass (*Micropterus salmoides*) and red crayfish (*Procambarus clarkii*), but did not respond to olfactory cues. Gillespie (2011) also expanded the suite of known prey items of *E. sosorum* (predominantly *Hyalella azteca* amphipods, chironomid larvae, ostracods and isopods; Bogart 1967, Chippindale *et al*. 1993, Chamberlain and O'Donnell 2001) to include planarians (*Dugesia* sp.) and mayfly larvae (Baetidae). This study also showed that planarians form the largest proportion of the diet of wild *E. sosorum*, followed by amphipods and chironomid larvae, but diet varies temporally with relative abundances of potential prey items. Data collected from captive populations of both species maintained by the City of Austin have identified courtship behavior, size at sexual maturity, duration of embryonic development and juvenile growth, fecundity, and life span (Chamberlain and O'Donnell 2001). Captive *E. sosorum* engage in courtship that includes the tail-straddling walk, chin rubbing, and chin slapping (Chamberlain and O'Donnell 2001), as described by Arnold (1977) for other plethodontids. Median fecundity of captive *E. sosorum* females is ~ 20 eggs, with hatching success of ~ 40%, which is similar to captive *E. nana* (Navar *et al*. 2007). Eggs are a few millimeters in diameter and deposited singly on substrate to which they adhere, which is also seen in other *Eurycea* species (Duellman and Trueb 1986, Nelson 1993). In captivity, such substrate is mostly moss and plastic plants, although rocks are not available in every aquarium. All eggs of captive Barton Springs' *Eurycea* were deposited in

flowing water because all aquaria have some degree of constant water flow (D. Chamberlain personal communication). Many other *Eurycea* species also deposit eggs in flowing water (Fries 2002, Petranka 1998), which presumably maximizes diffusion of oxygen through the egg capsules (citation). Less than 10 eggs have been seen in the wild. Those found in surface habitat were loose in leaf litter, moss, or on exposed substrate, and they did not have developing embryos (City of Austin staff personal observations). The rarity of eggs in surface habitats suggests egg deposition occurs predominantly underground, which is consistent with other perennibranchiate *Eurycea* (Nelson 1993, Tumlison *et al*. 1990, Fries 2002, Roberts *et al*. 1995). Embryonic development takes 3-4 weeks, hatchlings are small (~ 10mm) and often with incomplete development of limbs and yolk sacs. Survival of captivity juvenile *E. sosorum* is roughly 0.60 of hatched eggs, conferring average female reproductive success of 0.7 offspring per clutch, which is considerable higher than juvenile survivorship of wild *E. neotenes* of 0.10 (Bruce 1976). Captive-bred *E. sosorum* reach sexual maturity in about 11 months at 1.7- 2 inches (43-50 mm) total length (0.9-1.0 inches, 24 - 27 mm SVL). Captive-bred *Eurycea waterlooensis* grow to sexual maturity in about 18 - 23 months at 1.9 - 2.1 inches (48-55 mm) total length. Adults of both species continue to grow after sexual maturity but much more slowly, reaching ~ 3 inches (76 mm) total length. Longevity data from captive-reared and wild-caught juvenile *E. sosorum* and *E. waterlooensis* indicate that these salamanders can live at least 15 years. Longevity in the wild is unknown.

Eurycea sosorum salamanders are found in epigean habitat at the four springs of Barton Springs, Parthenia Spring in Barton Springs Pool (hereafter "Parthenia"), Eliza Spring, Old Mill/Sunken Garden Spring (hereafter “Old Mill”), and Upper Barton Spring (Chippindale *et al*. 1993; City of Austin 2004, 2005, 2006, 2007). *Eurycea waterlooensis* is predominantly a subterranean species, spending most of its life in the aquifer (Hillis *et al*. 2001). These salamanders are found in small numbers in the surface habitats of Parthenia, Old Mill, and Eliza Spring where *E. sosorum* is found. It has not been found at intermittent Upper Barton Spring. The four springs of Barton Springs are hydrologically connected via the subterranean conduits of the underlying karst aquifer (Brune 1981, Slade *et al*. 1986, Hauwert *et al*. 2004, Hauwert 2009). In the past, there were surface connections among springs via outflow streams that converged with Barton Creek. While subterranean connections remain, surface habitats have been isolated by construction of dams, amphitheaters, and a floodwater diversion culvert, and the interment of outflow streams. No surface migration routes from Parthenia to other springs exist today; marginal migration routes exist between Eliza, Old Mill, and Upper Barton springs (Fig. 1). Water flow from Parthenia and Eliza Spring is perennial; surface habitats have not gone dry, according to recorded human history (Brune 1975, 1981).

Barton Springs Pool contains the largest area of potential habitat (~15,000 sq. ft.). The natural habitat of Parthenia Spring is composed of crevices, fissures, and small natural caves (< 5-foot diameter) in the limestone rock (~6,000 sq. ft.) where groundwater issues from the aquifer. An additional 11,000-square-foot area along the northern margin of Barton Springs Pool was designated as salamander habitat (USFWS 1998) and is a manmade shelf of compacted caliche, gravel, and cobble known as the “beach”. The beach was originally cut out of the creek bank and flattened to create a wading area for recreation in the 1930s. Area in which the majority of salamanders are found are at and immediately downstream of the caves. Parthenia Spring is submerged under unnaturally deep water (3-17 feet) by the upstream and downstream dams across Barton Creek creating Barton Springs Pool.

Eliza Spring is a small spring pool of roughly 800 square feet, surrounded by a concrete amphitheater. The floor of the spring pool is a layer of concrete overlying natural habitat and artificially raising the elevation of surface habitat ~ 1 foot. Groundwater exits the aquifer beneath the concrete and reaches surface habitat through 15, 1-foot openings around the perimeter of the spring pool, and 7, 10-inch diameter holes through the concrete. In the early 1930s, the outflow stream was confined to a buried pipe that carried water into Barton Springs Pool, but that connection was eliminated with the construction of a floodwater bypass culvert in 1974. Presently, outflow from the spring pool is carried through the buried pipe into the culvert and on to Barton Creek downstream of Barton Springs Pool. Groundwater flow into Eliza Spring varies with aquifer conditions and apparently does not cease, as water was present in natural surface habitat during the drought of the 1900s. Since 1998, water flow in unnatural surface habitat on top of the concrete has been managed by obstructing outflow to maintain wetted habitat under all natural aquifer conditions. Consequently, surface habitat has been submerged under 2 to 7 feet of water periodically until 2003, when target managed water depth was decreased to approximately foot.

Salamander habitat in Old Mill Spring ranges from approximately 1300 to 1700 square feet composed of a spring pool and outflow stream. Wetted surface habitat contracts with decreasing discharge and, based on anecdotal accounts, the spring pool may have gone dry in the 1800s. The first permanent alterations to this spring occurred in the 1800s with the construction of Paggi's Mill, which partially obstructed outflow to the natural stream. In 1937, under the auspices of the National Youth Administration, an amphitheater was built on top of the Old Mill walls, which replaced the gates with a wall and eliminated the stream by diverting outflow into a buried pipe, which connects to Barton Creek downstream of all three of the other spring sites. Elevation of surface habitat was raised 5 to ten feet with the addition of deep layer of rock sometime in the last few decades. All of these changes resulted in unnaturally deep water in salamander habitat under non-drought conditions. The elevated substrate resulted in apparent loss of wetted surface habitat in the last decade (D.A. Chamberlain pers. communication 2004). Currently, removal of some of the excess rock has lowered substrate roughly 5 feet, allowing for continuously wetted habitat in the spring pool since 2003. A stream has been partially reconstructed, creating additional wetted habitat in all aquifer conditions except extreme drought. Construction of this stream also restored the surface connection between the spring and Barton Creek.

Upper Barton Spring is the smallest site. The average size of the surface habitat is 493 square feet, and can be as large as 880 square feet under high aquifer conditions. Water flow at the surface is intermittent; it disappears when Barton Springs' discharge drops below 40 ft^3/s. The site lies in the flood plain on the southeast bank of Barton Creek and has no artificial impoundments or permanent structures around it. Only *E. sosorum* has been found at this site; the first sighting occurred on April 1, 1997.

Evaluating potential effects of anthropogenic threats to these species requires basic ecological and population dynamic information on these species, which is lacking. Gillespie (2011) presented evidence of climatic environmental features correlated with salamander abundance. She demonstrated that much of the variability in abundance of young adult and adult *E. sosorum* could be explained by patterns of rainfall over the recharge zone of Barton Springs 7 to 12 months earlier. Rainfall recharging the aquifer influences a suite of interconnected characteristics of groundwater in Barton Springs, *i.e.*, discharge, flow velocity, water temperature, dissolved oxygen, turbidity (Mahler *et al*. 2006). The identification of rainfall and

other climatic factors correlated with subsequent variation in Barton Springs' *Eurycea* populations increases our understanding of indirect, longer-term influences of watershed-scale factors. But, we still lack a clear understanding of which aspects of habitat within Barton Springs directly affect resident salamander populations.

In general, suitable habitat for *E. waterlooensis* and *E. sosorum* appears to be areas of flowing groundwater associated with subterranean and epigean habitats, respectively. Habitats with flowing water and rocky substrates have networks of clean interstitial spaces, which are typical of habitats occupied by other karst-associated perennibranchiate *Eurycea* species (Randolph 1978; Tumlinson *et al*. 1990; Petranka 1998, Barr and Babbitt 2002; Bonett and Chippindale 2006, Bowles *et al*. 2006, Pierce *et al*. 2010). It has been posited that this type of habitat also provides protection from predators, abundant invertebrate prey, and constantly renewing dissolved oxygen. In the past, *E. sosorum* has been reported as abundant in submerged leaves (J. R. Reddell personal communication to P. Chippindale reported in Chippindale et al. 1993), moss (Dee Ann Chamberlain personal communication 2002), and plants (Andrew H. Price, personal communication 2005). *Eurycea nana*, sister species to *E. sosorum*, is reported to be found in rocks, logs, and vegetation (Tupa and Davis 1976, Thaker *et al*. 2006, Epp and Gabor 2008), and *Spyrogyra* sp. algal mats (Najvar 2001, personal communication 2011). This suggests that there is variation in optimal microhabitat among Notiomolge *Eurycea*, or optimal microhabitat is unavailable to species in sites modified by human activities.

There are no published studies of the microhabitats in which in *E. sosorum* is found, or the relationship between water chemistry, flow velocity, spring discharge and salamander abundance. Identification and description of microhabitats in which Barton Springs' *Eurycea* are found when all types are available would be a significant advance in understanding precisely what constitutes good habitat. Furthermore, examination of variation in microhabitat among spring sites and with aquifer conditions would contribute to a more integrated understanding of how we expect natural and anthropogenic environmental variation to affect Barton Springs' *Eurycea* and over what time frames. Yet, no studies to date have described variation in average annual abundance of juveniles, young adults, and adults, or examined recruitment in wild populations of either species in all spring sites for entire periods of record.

My objective in this paper is to begin to address the lack of scientific information. I use data from 8 to 17 years of monitoring to ask several questions about salamander populations and habitat. Specifically, I ask 1) do salamander abundance and density vary among and within spring sites, 2) is there evidence of reproduction and recruitment within spring sites, 3) which microhabitat characteristics are correlated with salamander abundance, and 4) does salamander abundance vary with discharge and water chemistry, particularly during drought? I also ask if habitat management since federal listing of *E. sosorum* is correlated with change in salamander abundance. I use the information to discuss variation in populations of *E. sosorum* and *E. waterlooensis*, and how surface habitat quality may affect both species.

Materials and Methods

Barton Springs' *Eurycea* abundance data have been collected in all spring sites by City of Austin staff roughly 12 times per year from 1993 through 2011 for *E. sosorum*, and from 1998 through 2011 for *E. waterlooensis*. Initial year of data collection varies among spring sites, with Parthenia Spring surveys initiated in 1993, Eliza and Old Mill springs in 1995, and Upper Barton Spring in 1997. Data collected before 1998 classify all perennibranchiate salamanders found as

E. sosorum because Eurycea *waterlooensis* was not discovered until 1998 (subsequently described in Hillis *et al*. 2001).

Annual survey number and frequency have varied over time. Target frequency of each site was one each month, but, actual number of surveys varied and intervals were irregular prior to 2003. From 2003 through 2011, surveys were conducted every thirty days or multiple thereof to facilitate use of times series statistical analyses. Since Upper Barton Spring flows intermittently, there are gaps in survey data corresponding with dry surface habitat. All surveys were conducted during daylight hours of a single day except two surveys of Parthenia Spring, which were conducted at night. Surveys of Parthenia Spring require SCUBA to search substrate because the spring has been submerged under several feet of water since the construction of permanent dams in 1929. Eliza and Old Mill springs have variable water depths; some surveys required SCUBA while others only required snorkeling; since 2003 all but four surveys were conducted by snorkeling. Upper Barton Spring water depth was always shallow enough to searched substrate by wading except during floods. Surveys of Parthenia and Upper Barton springs are not conducted when it is inundated by floodwater from Barton Creek because underwater visibility is typically nil and current velocity is too fast to ensure safety of surveyors. Generally, floodwater does not inundate Eliza and Old Mill Spring, although floodwater can reach Eliza Spring if the gates in the downstream dam of Barton Springs Pool are closed.

Surveys conducted from 1993 to 2003 were rapid scans of some or all of surface habitat in all spring sites. Prior to 2003, more than one spring site may have been surveyed in a single day; since 2003, only one spring site was surveyed per day to allow for more exhaustive searching of habitat. From 1993 through 1998, surveys of Parthenia Spring were of 1 x 1 meter squares every 10 feet along six transects across fissures and caves where groundwater exits the aquifer. From 1999 through 2001, survey method in Parthenia Spring was changed to searches of contiguous habitat areas at the caves and sporadic searches of fissures. From 2002 through June 2003, salamander abundance was estimated by rapid scan of disjunct areas at the spring mouths. From 1995 to June 2003, surveys of Old Mill and Eliza springs generally consisted of scan and/or targeted searches of the entire wetted habitat in the spring pool or a smaller contiguous area. When a surface outflow stream was present at Old Mill Spring, it was also searched for salamanders. Total wetted area in Eliza Spring varied with water depth, which was not recorded for some surveys in 2001 and 2002. Consequently, total survey area is unknown for some dates.

In 2003, I changed survey design and method. From July 2003 through 2010 salamander abundance was estimated in all spring sites using the drive survey method (Rasmussen and Doman 1943, Gilbert and Grieb 1957) of all of wetted surface habitat in Eliza, Old Mill, and Upper Barton springs, and large, contiguous areas of Parthenia Spring. In Parthenia Spring, areas associated with caves were always surveyed, while fissures were surveyed as time and staffing permitted. Only the upstream most section of the "beach" (Beach 1) has been included in salamander monitoring. It was surveyed regularly from 1993 to 2001, and in 2010. The modified drive method consisted of observers oriented in a line perpendicular to the current, moving in concert from downstream to upstream, removing all loose substrate and replacing it behind the line. This creates a moving, 6 to 10-inch strip of coverless habitat that these salamanders are reticent to cross. Each salamander crossing coverless habitat from upstream to downstream was added to the cumulative number; any salamander returning to upstream habitat from behind the line was subtracted. When observers were in close proximity to aquifer

openings, salamanders observed moving forward and retreating into the aquifer were added to the total.

Since 1998, each *Eurycea* salamander counted was identified to species. Since, *E. waterlooensis* was not discovered until 1998; salamanders encountered during surveys from 1993 through 1997 were assumed to be *E. sosorum*. Each salamander found was categorized by total body length (TL) according to two categories from 1998 through June 2003, < 1 inch (25.4 mm) and ≥ 1 inch (25.4 mm). From 2003 through 2010, each was categorized according to three categories, < 1 inch, 1-2 inches (25.4-50.0 mm), and ≥ 2 inches (50 mm). Total length categories were converted to snout-vent length (SVL) according the following equation:

SVL (mm) = 3.171 + 0.476*TL (mm).

This equation is based on linear regression ($p<0.0001$, $r^2=0.91$) of unpublished City of Austin data collected in 2003 from 208 wild *E. sosorum*. The snout-vent length categories were then compared to SVLs reported for juvenile and sexually mature *E. sosorum* museum specimens (Chippindale *et al*. 1993), and size at first reproduction and approximate growth of captive-bred salamanders (Chamberlain and O'Donnell 2001, 2002). This resulted in three categories of life stage, juvenile (<15.3 mm SVL), young adult (15.3-27.0 mm SVL), and adult (≥ 27.0 mm SVL). These categories are consistent with life-stage/size relationships for *E. nana* (Najvar 2001), sister species to *E. sosorum* (Hillis *et al*. 2001, Chippindale et al. 1993, Bendik 2006), and *E.* "*neotenes*" of Lamb and Turtle Creek springs (Bruce 1976), now recognized as *E. latitans* (Bendik 2006, Chippindale *et al*. 2000). I applied the same procedure to assign life stage to *E. waterlooensis* because the size/age relationship is similar to *E. sosorum* (Hillis *et al*. 2001, City of Austin unpublished. Lastly, type of microhabitat in which each salamander was found was noted (under rock, in plants, moss, algae, or leaf litter, or no cover).

Each spring site was divided into sections, within which substrate habitat characteristics were measured. Percent of habitat area composed of rocks, plants, moss, algae, and leaf letter was estimated visually and verified using a grid overlaid on photographs. In each section in each spring, we collected five measurements of sediment depth to the nearest millimeter and visually estimated percent of substrate with overlying layer of sediment. We also estimated percent by volume of sediment composed of sand. We measured water depth to the nearest millimeter in five random locations in each section of each spring, except Parthenia Spring. Water in Parthenia Spring is unnaturally deep (5–20 feet) because the downstream dam is used to keep it relatively constant for recreational users. So, water depth was not measured during these surveys. Since 2003, total dissolved gas pressure, partial pressure of dissolved oxygen, water temperature, and barometric pressure measured near a spring mouth in each site using a saturometer (Common Sensing, Model TBO-F). Dissolved carbon dioxide concentration was measured using Winkler titration. During low discharge conditions, dissolved oxygen concentrations (DO) decreased to levels of concern for *E. sosorum* (Woods *et al*. 2010) in Eliza Spring in 2008 and in Old Mill Spring in 2006 and 2008. Consequently, DO was artificially increased in these sites by water recirculation and/or aeration. Hence, the data collected during these periods are higher than natural concentrations. Prior to 2003, measurements of dissolved oxygen in Parthenia, Eliza, Old Mill, and Upper Barton springs, were sporadic and obtained using Hydrolab datasonde (model #). I also used U.S. Geological Survey estimates of aquifer discharge from Barton Springs (all flowing springs combined) to categorize climate condition as drought or non-drought and examine potential correlations with salamander abundance. Finally,

from 2008 through 2011, site-specific discharge was measured in Eliza, Old Mill, and Upper Barton springs during each survey using a Marsh-McBirney flow meter.

I generated descriptive statistics for salamander abundance and density of *E. sosorum* and *E. waterlooensis* for each year of record for each site. *Eurycea waterlooensis* are seen in very small numbers and infrequently in the surface spring, which limited most statistical analysis to simple, descriptive methods. The *Eurycea sosorum* data sets are larger and more salamanders are found in general, it was feasible to use statistical tests to compare variables among and within sites. I used all of the data for Parthenia Spring (1993 – present) to compare numbers of salamanders among survey sections because of obvious, large differences in habitat characteristics, e.g., water depth, flow rate, anthropogenic disturbance from recreation. I chose to exclude data from prior to 2003 from many analyses because data collection methods varied, which could confound causes underlying results. Because data collection methods and survey frequency changed in 2003, I chose to exclude earlier data from many analyses. Since the nature of drive surveys alters distribution of animals within the surveyed, measurements of density can vary if total area surveyed varies, and thus not necessarily reflect intraspecific competition. This potential problem was mitigated in Eliza and Old Mill springs by surveying all of wetted surface habitat. This problem could not be avoided in Parthenia Spring because exhaustive searches of all of surface habitat were not possible with the resources available. Densities calculated for this study are not meant to indicate actual spatial distribution of salamanders.

I examined potential differences in these variables within sites and in severe drought ($\leq$ 25 ft^3/s total Barton Springs' discharge) *versus* non-drought (> 25 ft^3/s) conditions. I used this threshold because it is biologically relevant. When the discharge of the Barton Springs complex is below 40 ft^3/s, surface habitat of Upper Barton Spring and adjacent Barton Creek are dry. This represents loss of surface connection of this site with the perennial springs, and signals when retreat underground may begin to affect interspecific interaction between *E. sosorum* and *E. waterlooensis*. In addition, the surface habitat in old Mill Spring contracts and the outflow stream ceases to flow, and habitat in Eliza Spring would be dry if water depth were not managed. At $\leq$ 25 ft^3/s, dissolved oxygen in Parthenia declines to below 5 mg/L (Mahler *et al*. 2010). Because Barton Springs' discharge measured and reported by the U. S. Geological Survey is that of all flowing springs sites combined, it is directly correlated with site-specific discharges. I used the combined spring discharge data a proxy in statistical analyses of all sites except where noted because they are used to guide various conservation management activities, from onsite maintenance of Barton Springs Pool to regulation of groundwater removal from the aquifer.

All data were tested for statistical assumptions of typical parametric *t*-tests, ANOVA, and linear regression (Sokal and Rohlf 1995, Zar 1984). Most of the data did not meet requisite assumptions of normality and homogeneity of variances. In addition, salamander abundance and some habitat data within sites are also serially auto-correlated. Therefore, I did not test for deterministic trends in salamander abundance or water chemistry here. Time series analyses of *E. sosorum* data from Eliza and Parthenia Spring are presented elsewhere (Gillespie 2011, Bendik and Turner 2011). I used non-parametric tests because although the probability of Type II error is increased (accepting the null when it is false), their power and reliability are not as compromised when assumptions are violated as in parametric tests (Tukey 1962, Seaman and Jaeger 1990, Potvin and Roff 1993). I used non-parametric Mann-Whitney *U* and Kruskall-Wallis tests to detect differences in salamander abundance and density within and among sites. I used non-parametric Pearson Rank correlations to test for variation in habitat variables and relationships with salamander abundance and density within sites. I also used Pearson Rank

Correlation to test for recruitment within sites by asking if abundance of younger salamanders is correlated with older salamanders 2, 3, and 4 months in the future. These time lags are consistent with development and growth observed in captive *E. sosorum*. Metric measurements were converted to inches after statistical analyses. I used StatView software (SAS Institute 1992-1998) for analysis of all data. Significance thresholds used were at $\alpha = 0.05$, unless otherwise noted.

Results

Variation in salamander abundance among and within spring sites

Abundance and density of both species of salamander vary over time among sites (Figs. 4-8, Tables 1). Total abundances and densities of both species differ significantly among sites (*E. sosorum* abundance: H=141.8, p<0.0001, density: H=182.3, p<0.0001; *E. waterlooensis* abundance: H = 34.7, p<0.0001, density: H=70.2, p<0.0001). Highest to lowest average abundances of *E. sosorum* were found in Eliza, Parthenia, Old Mill, and Upper Barton Spring, in descending order. *Eurycea sosorum* abundance and density in Old Mill Spring is significantly lower than in Eliza and Parthenia Springs (abundance: Kruskal-Wallis $H = 37.53$, $p < 0.0001$; density: $H = 133.02$, $p < 0.0001$; Fig. 5, Tables 2,3). While salamander abundance is lowest in Upper Barton Spring (Fig. 6), density is not significantly different than in Old Mill Spring ($U = 4811$, $z = -1.629$, $p < 0.0001$; Table 3). Average annual abundances range across several orders of magnitude for *E. sosorum* and reached record highs in all sites in 2008.

Eurycea waterlooensis abundance is significantly positively correlated with *E. sosorum* abundance ($\rho = 0.505$ $z = 4.628$, $p < 0.0001$). Abundance and density of *E. waterlooensis* are significantly higher in Old Mill Spring relative to Eliza and Parthenia Springs (abundance: $H = 36.10$, $p < 0.0001$; density: $H = 32.96$, $p < 0.0001$; Fig. 7, Tables 4, 5). Ranges of *E. waterlooensis* abundance in all sites are small relative to *E. sosorum* (Tables 2 and 3). Salamanders of this species were found frequently in Old Mill Spring (Table 5) over the period of record, while they were not found regularly in Eliza or Parthenia Spring until 2003 (Table 4). There is no significant difference in abundance of these salamanders in Old Mill Spring before and after 2003 ($U = 1536$, $z = -0.082$, $p = 0.935$). Abundances in Eliza and Parthenia Spring are significantly higher since 2004 (Eliza abundance: $U = 1332.5$, $z = -3.950$, $p < 0.0001$; Parthenia abundance: $U = 2207$, $z = -1.855$, $p = 0.0005$).

Abundance of *E. sosorum* varied within sites over the period of record. Abundance in Eliza Spring was significantly lower from 1995 - 2002 than from 2003 - 2010 ($U = 150.5$, $z = -9.667$, $p < 0.0001$), which corresponds with before and after reconstruction of some natural features of aquatic habitat (City of Austin 2005, 2006; Fig. 4a). Abundance in Parthenia Spring increased significantly after changes in management of Barton Springs Pool associated with federal listing of *E. sosorum* (U.S. Fish and Wildlife Service 1998) ($U = 1{,}765.5$, $z = -3.281$, $p = 0.001$). Abundance is significantly higher from 2006 - 2010, relative to 1998 - 2005 ($U = 2158.5$, $z = -2.871$, $p_{\alpha=0.025} = 0.004$; Fig. 5a). These periods correspond with before and after habitat reconstruction in Parthenia Spring in 2004-2005. There is no significant difference in *E. sosorum* abundance in Old Mill Spring for these time periods (abundance: $U = 388.5$, $z = -0.310$, $p_{\alpha=0.05} = 0.756$; density: $U = 376.50$, $z = -0.465$, $p_{\alpha=0.05} = 0.641$).

Reproduction and recruitment within spring sites

There is evidence of sporadic reproduction of *E. sosorum* in all spring sites for the periods of record (Fig. 8). Timing and amount of reproduction are not constant and do not

follow terrestrial seasons (Fig. 8). In Parthenia and Eliza springs, juvenile abundance is positively correlated with adult abundance 3 months earlier (Parthenia: $\rho = 0.534$, $z = 3.291$, $p = 0.001$; Eliza: $\rho = 0.381$, $z = 2.771$, $p < 0.0056$). In Old Mill Spring, adult abundance is negatively correlated with juvenile abundance 3 months later ($\rho = -0.686$, $z = 4.394$, $p < 0.0001$). Few juveniles had been found in Upper Barton Spring until 2008, but there is no statistical evidence of a consistent pattern of reproduction. The number of adults is not correlated with number of juveniles three months later for the period of record ($\rho = 0.053$, $z = 0.268$, $p = 0.79$).

There is evidence of recruitment in Parthenia, Eliza, and Old Mill springs during some time periods (Fig. 8). From 2003 -2010, juvenile abundance is significantly positively correlated with young adult abundance three months later in these three springs (Eliza: $\rho = 0.721$, $z = 5.395$, $p<0.000$, Fig. 8a; Parthenia: $\rho = 0.509$ $z = 3.135$, $p_{\alpha=0.05} = 0.0017$, Fig. 8b; Old Mill: $\rho = 0.663$ $z = 2.901$, $p_{\alpha=0.05} = 0.005$, Fig. 8c). In Parthenia Spring, there is no significant relationship among juvenile abundance and "adult" (> 1in. TL) abundance 3 months later from 1993 – 1997, ($\rho = -0.085$, $z = -0.583$, $p_{\alpha=0.05} = 0.5596$), but this relationship is statistically significant after 1997 ($\rho = 0.467$, $z = 2.723$, $p_{\alpha=0.05} = 0.0065$). Young adult abundance is positively correlated with adult abundance two months later in Eliza ($\rho=0.342$, $z=2.512$, $p=0.012$) and Parthenia ($\rho = 0.507$ $z = 2.999$, $p_{\alpha=0.05} = 0.0027$); and three months later in Old Mill ($\rho = 0.669$ $z = 3.068$, $p_{\alpha=0.05} = 0.003$). There are no statistically significant correlations among size classes of salamanders in Upper Barton Spring for the period of record (Fig. 8d). Number of juveniles is not correlated with young adults three months later ($\rho=0.255$, $z=1.145$, $p_{\alpha=0.05}=0.25$), neither is number of young adults correlated with adults three months later ($\rho=-0.061$, $z=-0.311$, $p_{\alpha=0.05}=0.76$).

Reproduction and recruitment of *E. waterlooensis* are difficult to discern based on abundance of salamanders observed in surface habitat (Fig. 9). Reproduction does occur because juveniles are seen in surface habitat of all three perennial spring sites, typically when there are higher numbers of juvenile *E. sosorum* ($\rho = 0.633$, $z = 7.443$, $p < 0.0001$). Based on visual examination of graphs of abundance (Fig. 9) there does not appear to be recruitment in the *E. waterlooensis* populations of any site. There are no statistically significant correlations among size classes in any site.

Microhabitat, flow regime, and salamander abundance

Abundance of *E. sosorum* varies significantly among potential cover microhabitat within sites. The vast majority of salamanders have been found in the interstitial spaces of clean, rocky substrate (98% in rock, 1.7% in moss + plants + algae, 0.2% leaf litter, 0.1% no cover). Salamander abundance and density in Eliza Spring are significantly positively correlated with flow velocity, and negatively correlated with percent sediment cover and water depth (Table 6). Significantly larger numbers of salamanders were found after a more natural flow regime was restored in 2003 ($U = 152$, $z = -7.348$, $p < 0.0001$), relative to 1998 to 2002. Percent sediment cover is positively correlated with water depth; as water depth decreases, percent sediment cover also decreases.

In Parthenia Spring, mean sediment depth was significantly less in two sections of deeper habitat in front of the caves after habitat reconstruction (2006-2010) than before (2003-2005)(Little Main: $U = 153.0$, $z = -2.730$, $p = 0.006$; Side Spring: $U = 158$, $z = -2.192$, $p = 0.03$). From 1993 to the present in Parthenia Spring, more *E. sosorum* were found in habitat in deeper water in front of the caves than in fissures in shallower water ($H = 213.18$, $p_{\alpha=0.05} < 0.0001$).

In Old Mill Spring, *E. sosorum* abundance is also significantly positively correlated with flow velocity ($\rho = 0.787$, $z = 5.944$, $p < 0.0001$) and water depth ($\rho = 0.528$, $z = 5.944$, $p < 0.0001$), and negatively correlated with sediment depth ($\rho = -0.366$, $z = -2.761$, $p = 0.0058$) and percent sediment cover ($\rho = -0.413$, $z = -2.802$, $p = 0.0051$). These variables are correlated with one another; flow velocity is negatively correlated with sediment depth ($\rho = -0.486$, $z = -2.477$, $p_{\alpha=0.01} = 0.013$), percent sediment cover ($\rho = -0.529$, $z = -2.181$, $p_{\alpha=0.01} = 0.03$), and water depth ($\rho = -0.340$, $z = -2.095$, $p_{\alpha=0.01} = 0.036$). In Upper Barton Spring, salamander abundance is not significantly correlated with flow velocity, water depth, sediment depth, or percent sediment cover, and none of the habitat characteristics are significantly correlated with one another

Discharge, water chemistry, and drought

In general, *E. sosorum* and *E. waterlooensis* abundances vary with discharge from Barton Springs; total from all springs ranges from ~ 10 - 120 cubic feet per second (cfs). Discharge differs among spring sites; the largest volumes of water issue from Parthenia Spring (75-90%). Site-specific discharges from Eliza and Old Mill springs vary from 1 - 12 cfs and 0 - 12 cfs, respectively. Upper Barton Spring discharge ranges from 0 – 3 cfs.

From 1993 to the present, total abundance of salamanders in Parthenia Spring is significantly negatively correlated with Barton Springs' discharge ($\rho = -0.262$, $z = -2.048$, $p = 0.04$), but is significantly *positively* correlated with discharge 6 months earlier ($\rho = 0.500$, $z = 3.042$, $p < 0.0023$). The relationship between discharge and abundance is statistically significant for juveniles ($\rho = 0.484$, $z = 2.947$, $p_{\alpha=0.0125} < 0.0032$) and all adults combined (≥ 1")($\rho = 0.504$, $z = 3.067$, $p_{\alpha=0.0125} < 0.0022$). From 2003 to the present, young adult and adult abundances are significantly correlated with a six-month lag in discharge (young adult: $\rho = 0.467$, $z = 2.838$, $p_{\alpha=0.0125} = 0.0045$; adult: $\rho = 0.422$, $z = 2.568$, $p_{\alpha=0.0125} = 0.012$). There are no similar significant correlations for any of the other spring sites.

While there have been several periods of low discharge since 1993, there was only one period of severe drought during which total Barton Springs' discharge was ≤ 25 cfs from June 2008 to October 2009. Parthenia and Eliza Spring remained wet with detectable water flow for the entire period. Mean water flow velocity in Eliza Spring was significantly lower ($U = 36.50$, $z = -2.960$, $p = 0.0031$) during the drought (0.29 ±0.05 s.e.) than before (0.85 ft/sec. ± 0.17 s.e.). There was water in surface habitat in the spring pool of Old Mill Spring, but there was no detectable discharge and the stream was dry. Upper Barton Spring had gone dry 30 days earlier.

The drought's effects on surface habitat were evident in the reduction of dissolved oxygen in all sites, increases in water temperature in Eliza and Old Mill Springs (Tables 7,8,9). Dissolved oxygen was significantly lower in Eliza and Parthenia springs during the 2008 - 2009 drought than in the previous 5 years (2003 - 2008) (Eliza: 2003-2008: $U = 28.0$, $z = -4.733$, $p < 0.0001$; Parthenia: $U = 13.0$, $z = -4.556$, $p < 0.0001$; Table 7) and the previous twelve months (May 2007- May 2008) (Eliza: $U = 0.0$, $z = -3.766$, $p = 0.0002$; Parthenia: $U = 0.0$, $z = -3.554$, $p = 0.0004$). There is no significant difference in DO in Old Mill Spring for either of those comparisons (pervious 5 years: $U = 20.0$, $z = -0.485$, $p = 0.6274$; preceding 12 months: $U = 175$, $z = -0.139$, $p = 0.889$)(Table 9). However, dissolved oxygen was augmented in Old Mill Spring during the majority of the 2008-2009 drought to protect salamanders, effectively reducing sample size of natural concentrations to 3 measurements. In addition, a less severe drought in 2006 also required augmentation of DO because its concentration dropped to below 2.0 mg/L while Barton Springs' discharge remained above 25 cfs. When data from the 2006 and 2008 droughts are combined, there is a significant difference in DO concentration ($U = 447.5$, z = -

4.674, $p < 0.0001$). Approximately 1 month before Barton Springs' discharge dropped to 25 cfs, Upper Barton Spring surface habitat had contracted down to a 1-foot square puddle with a dissolved oxygen concentration of 1.6 mg/L.

Mean water temperature was significantly higher during the drought in Eliza ($U = 328.0$, $z = -3.225$, $p = 0.00$), Old Mill ($U = 802$, $z = -2.141$, $p < 0.0001$), and Parthenia ($U = 230.5$, $z = -3.715$, $p = 0.0002$). Mean flow velocity in Eliza Spring during drought (0.32 ft./s. ± 0.19 S.D., 0.06 s.e.) was significantly lower than during non-drought (0.85 ft./s. ± 0.58 S.D, 0.12 s.e.; $U = 46.5$, $z = -3.038$, $p = 0.002$).

There were significantly fewer *E. sosorum* salamanders in Eliza and Old Mill springs during the drought than in the preceding twelve months (Eliza: $U = 46.0$, $z = -2.147$, $p = 0.032$, Fig. 10a; Old Mill: $U = 5.0$, $z = -3.444$, $p = 0.0006$, Fig. 11). In Eliza Spring, juvenile and adult abundances were significantly lower during the drought (juvenile: $U = 172.0$, z =z –2.662, $p = 0.0078$; Adult: $U = 131.5$, $z = -3.286$, $p = 0.001$; Fig. 10a), while young adult abundance was not ($U = 268.5$, $z = -0.960$, $p = 0.337$). Abundances of young adults and adults in the year following the drought did not differ significantly from during the drought (young adult: $U = 46.0$, $z = -1.609$, $p = 0.11$; adult: $U = 49.0$, $z = -1.442$, $p = 0.15$), but juvenile abundance was significantly *lower after* the drought than before ($U = 31.5$, $z = -2.413$, $p = 0.016$).

In Parthenia Spring, there was no significant difference between abundances during the drought and the previous year ($U = 40.0$, $z = 0.0$, $p > 0.99$), nor was there a difference among abundances before, during, and after the drought (abundance: $H = 0.825$, $p = 0.66$; Fig. 10b).

Discussion

There is significant variation in abundances of *E. sosorum* and *E. waterlooensis* among and within spring sites. In general, abundance of *E. sosorum* has increased significantly since 2003 in all spring sites except Old Mill, where it has not increased but also has not decreased. *Eurycea sosorum* abundance in Upper Barton is low on average, with densities similar to those in Old Mill Spring. Abundance varies directly with discharge from this spring as lower discharge causes surface habitat contraction and disappearance. The fate of resident salamanders during periods when surface habitat is dry is unknown. But, within a couple of weeks of return wetted surface habitat apparently healthy adult and young adult salamanders have been found (City of Austin data L. Dries pers. obs.). Those salamanders may have migrated to one of the perennial sites, although of 48 salamanders marked in 2007, none appeared in any other spring when Upper Barton Spring went dry in 2008, and only four (8%) were seen again in Upper Barton Spring when flow returned in 2009 (City of Austin 2010, 2011). There is no evidence of recruitment in Upper Barton Spring, but, juveniles have been found, and in record high abundance in 2008. *Eurycea waterlooensis* has been seen more frequently and in higher numbers in Eliza and Parthenia Spring since 2003, and continues to been seen regularly in Old Mill Spring. It has yet to been observed in Upper Barton Spring, although whether its subterranean range extends to this spring site is unknown.

There is evidence of reproduction and recruitment of E. *sosorum* in the three perennial spring sites. Juvenile abundance is positively correlated with subsequent young adult and adult abundances at time lags are consistent with growth rates in captivity. In addition, the positive correlation of adult abundance with juvenile abundance 3 months later suggests that increases in adult abundance may be useful indication of onset of a period of reproduction. In general, periods of reproduction and recruitment are not seasonal *per se*, but vary with aquifer discharge; reproduction and recruitment decrease or disappear during severe drought.

Factors other than increases in population size could have contributed to observed increases in *E. sosorum* abundance within sites. Migration of salamanders among sites or between epigean and/or subterranean microhabitats within sites or change in survey method could underlie the increases in abundance within each site. The presence of obvious periods of reproduction and recruitment of juveniles into the adult populations of Eliza, Old Mill, and Parthenia Spring, indicates that real biological processes are the major drivers of increases in populations. Moreover, there is evidence of reproduction and recruitment in Parthenia Spring since 1998, which is before survey method changed.

The vast majority of Barton Springs' *Eurycea* salamanders (98%) were found in rocky substrate in all springs. Although, common use of other microhabitat has been reported by others, the results presented here suggest that these salamanders prefer clean, rocky substrate if it is available, rather than moss, plants, algae, or leaf litter. This is consistent with microhabitats where many other perennibranchiate *Eurycea* are found (Tupa and Davis 1976, Randolph 1978, Sweet 1982, Tumlison *et al*. 1990; Petranka 1998, Barr and Babbitt 2002; Bonett and Chippindale 2006, Bowles *et al*. 2006, Pierce *et al*. 2010). Interestingly, *E. sosorum* is not commonly found in abundance in green filamentous algae, as has been reported for closely related *E. nana* (Najvar 200x). However, the dominant green, filamentous algae in Barton Springs are *Cladophora* sp., and the algae in which *E. nana* is typically found in abundance are *Spyrogyra* sp. or *Lyngbya* sp. (P. Najvar personal communication). During the recent drought, the predominant filamentous algae have been *Spyrogyra* sp. and more *E. sosorum* has been found in there than in the past, but this is still a very small proportion of salamanders.

In Eliza Spring, there were dramatic changes in habitat associated with reconstruction of more natural flow regime in surface habitat in 2003 and 2004 (City of Austin 2004, 2005). Large obstructions to outflow from the spring pool were permanently removed, resulting in generally shallower water, and faster water flow. Increased flow velocity was accompanied by decreases in sediment depth and the extent of substrate covered with a thick layer of sediment. In 2004 and 2005 there were similar efforts to enhance water flow in Parthenia spring by removing accumulated sediment and rock from fissures and cave mouths. Sediment suspended in the groundwater and surface water settles in Parthenia Spring during periods of high aquifer discharge (Mahler and Lynch 1999, Mahler *et al*. 1999) and floods; large amounts of gravel and rock are also deposited with Barton Springs Pool during floods.

Since habitat reconstruction in Eliza Spring, salamander density is positively correlated with flow velocity, and negatively correlated with water depth and sediment cover. In Parthenia Spring, fewer salamanders are found in fissures compared with sections in front of the spring mouths, which is consistent with the sediment depth results; sediment depth has not changed in the fissures, while it has decreased in two areas in front of spring mouths.

The negative correlations between salamander density and percent sediment cover suggests that one of the benefits of flowing water is less of substrate area is covered in sediment. The pattern of correlations among flow velocity, sediment cover, water depth, and sediment depth in Eliza Spring are consistent with typical interactions in stream systems. Shallower water flows faster, faster water flow flushes out excess sediment and helps prevent its deposition (Leopold *et al*. 1992), all of which help create clean interstitial spaces in rocky substrate that can be inhabited by aquatic flora and fauna (Hynes 1972, Nowell and Jumars 1984, Giller and Malmqvist, Poff and Ward 1989, Poff *et al*. 1990, Vogel 1994). Mean values of sediment and water depth became more typical of shallow, flowing streams in which the majority of *Eurycea* species are found (Wells 2007, Petranka 1998).

Eurycea sosorum abundance varies among the deeper and shallower habitat locations within Parthenia Spring. Within the natural habitat, more salamanders were found in sections in front of the small caves where the majority groundwater issues from the aquifer. This isn't simply an artifact of the drive survey method because of the architecture of the fault system in and the direction of the drive. The shallower survey sections are located on the upstream part of the system, on top of a rimrock ledge littered with small fissures. These fissures carry groundwater toward an abrupt drop off that leads to the relatively larger cave openings at the bottom of a rimrock ledge. These deeper sections are surveyed before or at the same time as shallow habitat, and salamanders counted are those that move from upstream to downstream, away from caves and fissures. Greater abundance of salamanders in deeper water near the caves in Parthenia is a real phenomenon.

The occurrence of more salamanders in deeper water (10-17 feet) in Parthenia Spring may seem contradictory to results from Eliza Spring. However, the water current issuing from the caves is readily detectable by humans as stronger than water flowing in fissures, suggesting the relationship may be driven by flow velocity and the resulting effects on substrate condition rather than water depth. Since *E. sosorum* and *E. waterlooensis* are stream-adapted salamanders, water velocity is likely to be the more critical proximate factor. Flow velocity varies with water depth, but the degree to which that affects salamander abundance is also driven by volume and rate of water discharge from a particular spring. Parthenia Spring is much, much larger than Eliza Spring, emitting up to 10 times the water flow. Water velocity at the spring mouths in Parthenia Spring is likely similar to or higher than in Eliza Spring, even when submerged under several feet of water. In addition, occupation of habitat closer to the surface of the water in Parthenia Spring puts salamanders in closer proximity to swimmers and other recreational users, and may experience more harassment from unnatural habitat disturbance.

As would be expected for a stream-adapted species, *E. sosorum* abundance is correlated with these factors. Higher abundances occur when flow velocity is faster, and sediment cover, and sediment and water depths are lower. After habitat reconstruction, *E. sosorum* abundance and density increased by several orders of magnitude, and have remained significantly higher to date, despite the recent severe drought. Although no flow velocity data were collected in Parthenia Spring, sediment depth was significantly less after these efforts in some areas, and *E. sosorum* abundance increased significantly by 2006. *Eurycea waterlooensis* has been seen more frequently after the temporary or permanent flow regime reconstructions in Parthenia and Eliza Spring, respectively.

All of the results of examinations of microhabitat indicate that *E. sosorum* fares better in habitats with briskly flowing water (~ 0.5 – 1 ft./s.) and less sediment-laden, rocky substrate. This is consistent with a preference for flowing water (Thaker *et al*. 2006) of 0.39 ft/sec in *E. nana* (Fries 2002). The benefits of flowing water to *E. sosorum* are not surprising considering the evolutionary history of central Texas perennibranchiate *Eurycea*. The entire clade consists of species that evolved and reside in spring-fed streams (Sweet 1977, 1982, 1984, Wiens *et al*. 2003, Hillis *et al*. 2001, Chippindale *et al*. 2001, Petranka 1998, Bowles *et al*. 2006). Higher flow velocities of streams and rivers are the dominant features distinguishing them from lakes and ponds (Leopold *et al*. 1992). Flowing water influences every part of the aquatic ecosystem (Wetzel 2001; Giller and Malmqvist 1998), from the amount of sediment (Nowell and Jumars 1984) and type of algae (Poff *et al*. 1990, Reiter and Carlson 1986) to the community of invertebrates and vertebrates (Vogel 1994). Faster, unidirectional water flow naturally favors growth of tightly attached algae (Stevenson 1983, Korte and Blinn 1983, Fritsch 1929), favors a

diversity of stream-adapted invertebrates (Hynes 1972), and helps maintain high water quality (Spellman and Drinan 2001). Moreover, periodic disturbance imposed by variation in water flow also plays a critical role in stream ecosystems (Resh *et a*. 1988). Unfortunately, imperiled *E. nana* and *E. sosorum* are limited to habitats whose flow regimes have been altered by dams or other impoundments. Long-term effects of Alteration of flow regime on the San Marcos River of central Texas decreased the frequencies of small and large floods, resulting in a shift in the dominant species from endemic specialists to generalists (Perkin and Bonner 2010). Permanent loss of natural flow regimes of Barton Creek and Barton Springs *Eurycea* may inhibit the ability of endangered endemic species to recover.

Barton Springs' *Eurycea* abundance varies within discharge from Barton Springs, which ranges ~ 10 - 125 cfs (citation). Six-month lag in discharge with salamander abundance is consistent with the 10-11 month lag in rainfall and salamander abundance, and synchronicity of total salamander abundance and increases in discharge documented by Gillespie (2011). Although water can travel quickly through karst aquifers, a single, average rainfall after a period of drought rarely results in immediate large increases in Barton Springs' discharge. It appears that it takes several months for rainfall to produce enough recharge water to the aquifer to result in biologically significant increases in discharge.

The severe drought of 2008-2009 resulted in reduced Barton Springs' discharge to 13 cfs, a level not seen since the drought of record in the 1950s (Smith and Hunt 2010). Parthenia Spring had higher flow than Eliza Spring, followed by Old Mill Spring, where surface habitat was reduced to a stagnant pool with undetectable flow velocity and therefore, discharge was at or near zero. Reduction in discharge was accompanied by significant increases in water temperature in the three spring sites, and decreases in flow velocity in Eliza and Old Mill Spring, thus, inhibiting processes and flow regime conditions that foster higher concentrations of dissolved oxygen (Levine 1978, Lampert and Sommer 1997, Giller and Malmqvist 1998, Wetzel 2001). Since dissolved oxygen and temperature can influence every aspect of the aquatic community (Cushing and Allan 2001; Giller and Malmqvist 1998 references therein; Wetzel 2001 and references therein), drought-related reductions in spring discharge can have strong effects on resident flora and fauna.

These changes are of biological significance to resident *E. sosorum*. Dissolved oxygen decreased in all sites to concentrations that are of concern for *E. sosorum*. Woods *et al*. 2010 showed that in metabolic responses of *E. nana* and *E. sosorum* to a range of dissolved oxygen concentrations are similar. They demonstrated that neither species habituates to low DO by reducing metabolic rate; metabolic rates increase until salamanders are approaching death. They demonstrated that 28-day dissolved oxygen concentrations of 4.5 mg/L, 4.2 mg/L, 3.7mg/L, and 3.4 mg/L result in mortality of 5%, 10%, 25%, and 50% of adult *E. nana*. Chronic 60-day exposure to 4.44 mg/L dissolved oxygen compromised growth of juvenile *E. nana*. Mean DO concentrations in Eliza Spring and Old Mill Spring during drought were below the growth inhibition and LC_5 thresholds (4.3 mg/L and 4.26 mg/L, respectively). Moreover, minimum DO concentrations in Eliza Spring (3.9 mg/L) dropped below the LC_{10} threshold, and the minimum in Old Mill Spring (1.04 mg/L) dropped below the LC_{50}. Fortunately, DO augmentation was implemented immediately after these concentrations were measured.

Variation in water temperature in the perennial springs of the Edwards Aquifer is typically less than in other surface waters (Brune 1981, Sweet 1982, Groeger *et al*. 1997), although it is not constant in Barton Springs (Mahler *et al*. 2010, Gillespie 2011). Increases in water temperature have detrimental effects on other Edwards Aquifer perennibranchiate *Eurycea*

(Norris *et al*. 1963, McAllister and Fitzpatrick 1989, Berkhouse and Fries 1995) and it is reasonable to assume that Barton Springs' *Eurycea* could be similarly affected.

Thus, it should be no surprise that Barton Springs' *Eurycea* abundance was significantly lower during the drought. No *E. waterlooensis* were seen in any spring site during the drought. There were substantial decreases in *E. sosorum* of all size classes in all sites. The *E. sosorum* population in Old Mill was more severely affected by drought than those in Eliza and Parthenia Springs. There were 11 consecutive months during the 2008 - 2009 drought, when no salamanders of either species were found. During the less severe drought of 2006, there were 6 consecutive months of zero salamander abundance. This coupled with the dissolved oxygen concentrations during these droughts, suggests that when dissolved oxygen is below 4.0 mg/L and adult abundance is at or near zero, there is no reproduction, and hence no recruitment.

Eurycea sosorum abundance in Parthenia Spring decreased during the drought, but not as drastically as in Old Mill Spring. There were few juveniles and no evidence of recruitment during the drought, even though dissolved oxygen was the highest of all three sites and never dropped to concentrations of concern.

Abundance in Eliza Spring remained the highest of the three sites throughout the drought. We have some evidence from this site that salamanders retreated to inaccessible areas during the worst of the drought. In the month before rainfall broke the drought, only 27 young adult and 14 adult *E. sosorum* were seen in Eliza Spring. Six weeks after the rainfall, these abundances increased to 230 young adults, and 154 adults, which is too short a time for reproduction and recruitment to have occurred. In eight weeks, juveniles appeared in very low abundance, 12. Clearly, these salamanders went somewhere, but, whether they retreated to subterranean habitat or the inaccessible outflow pipe from the spring pool is unclear. Water flow is faster in the pipe and there is a vent to the atmosphere, so dissolved oxygen was likely higher than in the spring pool. However, condition of subterranean habitat is less certain. Regardless of where surviving salamanders retreated, comparison of November abundances with 2008 pre-drought highs of 256 adults, 535 young adults, and 568 juveniles shows a 98% decrease in juveniles, a 57% decreased in young adults, and a 40% decrease in adults.

The very small numbers of juveniles during the drought suggest that adult reproduction was very low, which is consistent with theoretical and empirical demonstrations of resource allocation for long-lived animals (Pianka 1983, Harris and Ludwig 2004, Takahashi and Pauley 2010). Adults that will have more than one lifetime opportunity to reproduce are expected to allocate metabolic energy to survival alone when environmental conditions are poor (Pianka 1983). Barton Springs' *Eurycea* are long-lived and reproduce more than once in a lifetime. The lack of constant, year-round reproduction, and extremely low abundance of juvenile *E. sosorum* during drought suggests that in the wild these salamanders suspend reproduction under adverse environmental conditions.

It is clear that drought imposes direct detrimental effects on survival, reproduction, and recruitment of *Eurycea sosorum*. It is also apparent that abundances and population sizes can increase rapidly when environmental conditions are good. What isn't clear is what triggers these bouts of reproduction and recruitment leading to the increases. In the fourteen months since the end of the 2008-2009 drought, *E. sosorum* and *E. waterlooensis* abundances have not returned to pre-drought levels. In Eliza Spring, juvenile abundance is *lower* after the drought then during; In Old Mill Spring, maximum number of salamanders seen after the drought, was 4; and in Parthenia Spring, abundances did not change after the drought. It may be that adult *E. sosorum* have not reached a level of metabolic energy where reproduction is favored, even though

dissolved oxygen concentration returned to pre-drought concentrations. While this confirms the positive relationship between dissolved oxygen and discharge, it also suggests that indirect effects of lower dissolved oxygen on the ecosystem may persist after a drought. It also suggests that there may be other drought-related factors that affect salamanders, such as water temperature dips associated with winter rains (Gillespie 2011). The effects of frequent, repeated, extended drops in Barton Springs' discharge during severe droughts (Smith and Hunt 2010) on *E. sosorum* and *E. waterlooensis* may be dependent on not only the duration and frequency of low discharge, but also the duration of intervening non-drought conditions.

Conclusions

Populations of *E. sosorum* and *E. waterlooensis* vary within and among spring sites, as do ecological conditions. In general, there are more salamanders during periods of average or higher Barton Springs' discharge. Average abundance of *E. sosorum* increased in Parthenia and Eliza Spring after partial restoration of natural flow regimes. *Eurycea sosorum* prefers clean, rocky substrates in quickly flowing water and little sediment. Since 2003, there have been bouts of reproduction and recruitment in Eliza, Parthenia, and Old Mill Spring, and there have also been periods of drought during which there was little reproduction and recruitment. During droughts, dissolved oxygen is lower and water temperature is higher, both critical factors known to affect *E. sosorum*, *E. nana*, and other central Texas perennibranchiate *Eurycea*. Despite the recent severe drought, Eliza Spring remains the best habitat and harbors the largest and most robust *E. sosorum* salamander population, which likely has the best potential to weather adverse conditions. Since *E. waterlooensis* resides in subterranean habitat of the Barton Springs complex and has been observed in surface habitat of the three perennial springs, Eliza, Parthenia, and Old Mill, it is difficult to infer the status of the populations and the species. Lack of information on life history characteristics in wild populations further hampers assessment of reproduction and recruitment. However, *E. waterlooensis* depends on the same groundwater that feeds surface habitats of Barton Springs. Efforts to protect the quantity and quality of this groundwater associated with *E. sosorum* will also protect subterranean habitat for *E. waterlooensis*. What isn't clear is the natural degree of overlap of preferred microhabitats and resultant interspecific competition. Moreover, how anthropogenically derived increases in habitat overlap would affect both species is unknown.

The results presented here suggest two anthropogenic factors that impose significant threats to persistence of Barton Springs' *Eurycea*, alterations of natural flow regimes of the springs, and drought. While rainfall is the climatic cause of drought, the effects on Barton Springs' discharge are magnified by withdrawal of groundwater from the outlying watershed. By the 1950s, ~ 1 cfs of groundwater was regularly extracted from the Barton Springs Zone of the Edwards Aquifer upstream of Barton Springs, resulting in a low discharge from combined Barton Springs of 9.6 cfs during the drought of record in the late 1950s (Smith and Hunt 2010). As of today, demand for groundwater has increased to levels that threaten to cause cessation of flow from Barton and other Edwards Aquifer springs during droughts (Bowles and Arsuffi 2006). The effects of drought are magnified by dams, amphitheaters, and other impoundment structures (Giller and Malmqvist 1998) at Eliza, Parthenia, and Old Mill springs. Conservation of Barton Springs' *Eurycea* requires consideration of the evolutionary adaptations of each species, how anthropogenic changes impose selection countering those adaptations (contemporary evolution *sensu* Stockwell *et al*. 2003) and whether the species can adapt before they go extinct. Given the suite of characteristics that change with flow regime alteration, and

the positive response of *E. sosorum* to partial restoration, continued efforts to reverse the effects of dams could not only improve habitat, it could potentially help mitigate the effects of drought.

Literature Cited

Abrams, P.A. 2002. Will small population sizes warn us of impending extinctions? The American Naturalist 160(3):293-305.

Arnold, S.J. 1977. The evolution of courtship behavior in New World salamanders with some comments on Old World salamandrids. Pp. 141-183 In: The Reproductive Biology of Amphibians, Tayler, D.H., and Guttman, S.I., editors. Plenum Press, New York, New York, USA.

Baker VR. 1977. Stream-channel response to floods, with examples from central Texas. GSA Bulletin. 88: 1057-1071.

Barr, G.E., and Babbitt, J.K. 2002. Effects of biotic and abiotic factors on the distribution and abundance of larval two-lined salamanders (*Eurycea bislineata*) across spatial scales. Oecologia 133:176-185.

Bendik, N.F. 2006. Population genetics, systematics, biogeography, and evolution of the southeastern central Texas *Eurycea* clade Blepsimolge (Plethodontidae). M.S. Thesis. University of Texas at Arlington.

Bendik, N.F., and Turner, M.T. 2011.

Berkhouse, C.S., and Fries, J.N. 1995. Critical thermal maxima of juvenile and adult San Marcos salamanders (*Eurycea nana*). The Southwestern Naturalist 40(4):430-434.

Bishop, S.C. 1941. Notes on salamanders with descriptions of several new forms. Occasional Papers of the Museum of Zoology, University of Michigan (451:6-9.

Blum JL. 1960. Alga populations in flowing waters. Special Publications of the Pymatuning Laboratory of Field Biology 2: 11-21.

Bogart, J.P. 1967. Life history and chromosomes of some of the neotenic salamanders of the Edwards Plateau. M.S. Thesis. University of Texas at Austin, Austin, Texas. USA.

Bonett, R.M., and Chippindale, P.T. 2006. Streambed microstructure predicts evolution of development and life history mode in the plethodontid salamander *Eurycea tynerensis*. BMC Biology 4:6.

Bowles, B.D., Sanders, M.S., and Hansen, R.S. 2006. Ecology of the Jollyville Plateau Salamander (*Eurycea tonkawae*: Plethodontidae) with an assessment of the potential effects of urbanization. Hydrobiologia 553:111-120.

Bowles, D.E, and Arsuffi, T.L. 2006. Karst aquatic ecosystems of the Edwards Plateau region of central Texas, USA: A consideration of their importance, threats to their existence, and efforts for their conservation. Aquatic Conservation: Marine and Freshwater Ecosystems: 3(4): 317-329.

Bruce, R.C. 1976. Populations structure, life history and evolution of paedogenesis in the salamander *Eurycea neotenes*. Copeia 1976:242-249.

Brune, G. 1975. Major and historical springs of Texas. Texas Water Development Board Report 189, Austin, Texas, USA.

Brune G. 1981. Springs of Texas, Volume 1. Gunnar Brune, Inc., Fort Worth, Texas, USA. publisher,

Chamberlain, D.A., and O'Donnell, L. 2001. Captive breeding report....

Chippindale, P.T., Price, A.H., and Hillis, D.M. 1993. A new species of perennibranchiate salamander (*Eurycea*: Plethodontidae) from Austin, Texas. Herpetologica 49: 248-259.

Chippindale, P.T. 1995. Evolution, phylogeny, biogeography, and taxonomy of central Texas cave and spring salamanders, *Eurycea* and *Typhlomolge*. Ph.D. dissertation. University of Texas at Austin.

Chippindale, P.T., Price, A.H., Wiens, J.J., and Hillis, D.M. 2000. Phylogenetic relationships and systematic revision of central Texas hemidactyliine plethodontid salamanders. Herpetological Monographs 14: 1-80.

City of Austin. 1997. Barton Creek Report. Technical Report CM-97-01. Watershed Protection Department, City of Austin.

City of Austin. 2002. City of Austin's captive breeding program for the Barton Springs and Austin Blind Salamanders, annual report. Watershed Protection Department, City of Austin.

City of Austin. 2004. Endangered Species Act section 10(a)(1)(B) permit for the incidental take of the Barton Springs Salamander (*Eurycea sosorum*) for the operation and maintenance of Barton Springs Pool and adjacent springs permit #PRT-839031. Annual Report 1 October 2002 - 30 September 2004. Watershed Protection Department, City of Austin.

City of Austin. 2005. Endangered Species Act section 10(a)(1)(B) permit for the incidental take of the Barton Springs Salamander (*Eurycea sosorum*) for the operation and maintenance of Barton Springs Pool and adjacent springs permit #PRT-839031. Annual Report 1 October 2004 - 30 September 2005. Watershed Protection Department, City of Austin.

City of Austin. 2006. Endangered Species Act section 10(a)(1)(B) permit for the incidental take of the Barton Springs Salamander (*Eurycea sosorum*) for the operation and maintenance of Barton Springs Pool and adjacent springs permit #PRT-839031. Annual Report 1 October 2005 - 30 September 2006. Watershed Protection Department, City of Austin.

City of Austin. 2007. Endangered Species Act section 10(a)(1)(B) permit for the incidental take of the Barton Springs Salamander (*Eurycea sosorum*) for the operation and maintenance of Barton Springs Pool and adjacent springs permit #PRT-839031. Annual Report 1 October 2006 - 30 September 2007. Watershed Protection Department, City of Austin.

City of Austin. 2010. Biological Assessment Barton Springs Flood Debris Removal and Bypass Repairs, Austin, Texas. Report Prepared for U.S. Army Corps of Engineers Ft. Worth District Office. Watershed Protection Department, City of Austin.
Cushing, C.E., and Allan, J.D. 2001. Streams: Their Ecology and Life. Academic Press, San Diego, California, USA.

Duellman, W.E., and Trueb, L. 1994. Biology of Amphibians. The Johns Hopkins University Press, Baltimore, MD, USA.

Environmental Protection Agency (EPA). 1988. A portion of the Austin-area Edwards Aquifer in parts of Hays and Travis Counties, Texas; Sole source aquifer, final determination. Federal Register 53(109): 20897.

Epp, K.J., and Gabor, C.R. 2008. Innate and learned predator recognition mediate dby chemical signals in *Eurycea nana*. Ethology 114:607-615.

Fries, J.N. 2002. Upwelling preferences of captive adult San Marcos salamanders. North American Journal of Aquaculture 64:113-116.

Fritsch, F.E. 1929. The encrusting algal communities of certain fast flowing streams. New Phytologist 28:165-196.

Gilbert, P.F., and Grieb, J.R. 1957. Comparions of air and ground deer counts in Colorado. Journal of Wildife Management 21:33-37.

Giller PS, Malmqvist B. 1998. The Biology of Streams and Rivers. Oxford University Press, Oxford, UK.

Gillespie, J.H. 2011. Behavioral ecology of the endangered Barton Springs Salamander (*Eurycea sosorum*) with implications for conservation and management. Ph.D. dissertation. University of Texas at Austin.

Gordon ND, McMahon TA, Finlayson BL, Gippel CJ, Nathan RJ. 2004. Stream hydrology: an introduction for ecologists. Chichester (WS): John Wiley & Sons Ltd. 429 p.

Groeger, A.W., Brown, P.F., Tietjen, T.E., and T.C.kelsey. 1997. Water quality of the San Marcos River. Texas Journal of Sciences 49:279-294.

Harris R.N., Ludwig P.M. 2004. Resource level and reproductive frequency in female four toed salamanders, *Hemidactylium scutatum*. Ecology 85(6):1585-1590.

Hauwert, N. M. 2009. Groundwater flow and recharge within the Barton Springs Segment of the Edwards Aquifer, southern Travis County and northern Hays Counties, Texas. Ph.D. Dissertation. University of Texas at Austin, Austin, Texas. USA.

Hauwert, N.M., Johns, D.A., Hunt, B., Beery, J., Smith, B., and Sharp, J. 2004. Flow Systems of the Edwards Aquifer Barton Springs Segment Interpreted from Tracing and Associated Field Studies: Proceedings from Edwards water resources in central Texas, retrospective and prospective symposium of the South Texas Geological Society and Austin Geological Society, 2004 May 21. San Antonio, Texas, USA.

Hillis, D.M., Chamberlain, D.A, Wilcox, T.P., and Chippindale, P.T. 2001. A new species of subterranean blind salamander (Plethodontidae: Hemidactyliini: *Eurycea*: *Typhlomolge*) from Austin, Texas, and a systematic revision of Central Texas paedomorphic salamanders. Herpetologica 57: 266-280.

Hubbs, C. 1995. Springs and Spring runs as unique aquatic systems. Copeia 1995(4): 989-991.

Hynes, H.B.N. 1972. The Ecology of Running Waters. University of Toronto Press, Toronto, Ontario, CAN.

Klein RD. 1979. Urbanization and stream quality impairment. Water Resources Bulletin 15:948-963.

Korte, V.L., and Blinn, D.W. 1983. Diatom colonization on artificial substrate in pool and riffle zones studied by light and scanning electron microscopy. Journal of Phycology 19:332-341.

Lampert, W., and Sommer, U. 1997. Limnoecology. Oxford University Press, New York, New York, USA.

Leopold, L.B., Wolman, M.G., and Miller, J.P. 1992. Fluvial Processes in Geomorphology. Dover Publications, New York, New York, USA.

Levine, I.N. 1978. Physical Chemistry. University of Brooklyn: McGraw-Hill Publishing, New York, New York, USA.

Levins. R. 1968. Evolution in Changing Environments: Some Theoretical Explorations. Princeton University Press, Princeton, New Jersey, USA.

Limbacher, L., and Godfrey, A. 2008. Barton Springs Pool Master Plan: Concepts for Preservation and Improvement. City of Austin, Parks and Recreation Department. http://www.ci.austin.tx.us/parks/bspmasterplan.htm.

Longley, G. 1978. Status of *Typhlomolge* (= *Eurycea*) *rathbuni*, the Texas Blind Salamander. Endangered Species Repor 2, U. S. Fish and Wildlife Service, Albuquerque, New Mexico, USA.

Lynch, M. 1996. A quantitative-genetic perspective on conservation issues. In: Conservation Genetics: Case Histories From Nature. Avise, J.C. and Hamrick, J.L., editors. Chapman and Hall, New York, New York. pp. 471-501.

Mace, G.M, and Kunin, W. 1994. Classifying threatened species: means and ends [and discussion]. Philosophical Transactions of the Royal Society London, Series B. 344:91-97.

Mace, G., and Kershaw M. 1997. Extinction risk and rarity on an ecological timescale. pp. 130-149 in: The Biology of Rarity. Kunin, W. and Gaston, K., editors. Chapman and Hall, London, UK.

Mahler, B.J., and Lynch, L. 1999. Muddy waters: temporal variation in sediment discharging from a karst spring. Journal of Hydrology 214:165-178.

Mahler, B.J, Lynch, L., and Bennett, P.C. 1999. Mobile sediment in an urbanizing karst aquifer:implications for contaminant transport. Environmental Geology 39(1):25-38.

Mahler, B.J., Garner, B.D., Musgrove, M., Guilfoyle, A.L., and Rao, M.V. 2006. Recent (2003-05) Water quality of Barton Springs, Austin, Texas, with emphasis on factors affecting variability. U.S. Geological Survey Scientific Investigations Report. 2006:5299.

Mahler, B.J., Bourgeais, R., Musgrove, M., and Sample, T.L. 2010. The relation between dissolved oxygen and other physicochemical properties in Barton Springs, central Texas. Geological Society of American Abstract 58-9. http://gsa.confex.com/gsa/2010AM/finalprogram/abstract_181980.htm

Manne, L.L, Brooks, T.M., and Pimm, S.L. 1999. The relative risk of extinction of passerine birds on continents and islands. Nature. 399:258-261.

Maynard Smith, J. 1998. Evolutionary Genetics. Oxford (UK): Oxford University Press. 330p.

McAllister, C.T., and Fitzpatrick, L.C. 1989. The effect of thermal acclimation on oxygen consumption in the salamander, *Eurycea neotenes*. Journal of Herpetology 23(4):439-442.

Muller, H.J. 1950. Our load of mutations. American Journal of Human Genetics. 2:111-176.

Munton, P. 1987. concepts of threat to the survival of species used in Red Data Books and similar compilations. In: The Road to Extinction. Fitter, R. and Fitter, M., editors. Gland: IUCN.

Najvar, P.A. 2001. The effects of diel water quality fluctuations on reproduction and growth in the San Marcos Salamander. M.S. Thesis, Southwest Texas State University, San Marcos, Texas, USA.

Najvar, P.A., Fries, J.N, and Baccus, J.T. 2007. Fecundity of San Marcos salamanders in captivity. The Southwestern Naturalist 52(1):145-147.

Nelson, J.M. 1993. Population size, distribution, and life history of *Eurycea nana* in the San Marcos River. M.S. Thesis, Southwest Texas State University, San Marcos, Texas, USA.

Norris, jr. W.E., Grandy, P.S., and Davis, W.K. 1963. Comparative studies of the oxygen consumption of three species of neotenic salamanders as influenced by temperature, body size, and oxygen tension. Biological Bulletin 125(3):523-533.

Nowell, A.R.M., and Jumars, P.A. 1984. Flow environments of aquatic benthos. Annual Review of Ecology and Systematics 15: 303-328.

Perkin, J.S., and bonner, T.H. 2011. Long-term changes in flow regime and fish assemblage composition in the Guadalupe and San Marcos Rivers of Texas. River Research and Applications 27(5):566-579.

Petranka, J.W. 1998. Salamanders of the United States and Canada. Smithsonian Institution Press, Washington, D.C., USA.

Pianka, E.R. 1983. Evolutionary Ecology. 3rd edition. Harper and Row, Inc. New York, New York, USA.

Pierce BA. 1985. Acid tolerance in amphibians. Bioscience 35: 239-243.

Pierce, B.A, Christiansen, J.L., Ritzer, A.L., and Jones, T.A. 2010. Ecology of Georgetown salamanders (*Eurycea naufragia*) with the flow of a spring. The Southwestern Naturalist 55(2):291-297.

Pipkin, Turk. 1993. Barton Springs Eternal: the Soul of a City. Softshoe Publishing, Hill Country Foundation, Austin, Texas, USA.

Poff, N.L., Voelz, N.J., and Ward, J.V. 1990. Alga colonization under four experimentally-controlled current regimes in a high mountain stream. Journal of the North American Benthological Society 9: 303-318.

Poff, N.L., and Ward, J.V. 1989. Implications of streamflow variability and predictability for lotic community structure: a regional analysis of streamflow patterns. Canadian Journal of Fisheries and Aquatic Sciences 46: 1805-1818.

Potvin, C., and Roff, D.A. 1993. Distribution-free and robust statistical methods: viable alternatives to parametric statistics. Ecology 74:1617-1628.

Randolph, D.C. 1978. Aspects of the larval ecology of five plethodontid salamanders of the western Ozarks. The American Midland Naturalist 1978: 141-159.

Rasmussen, D.I., and Doman, E.R. 1943. Census methods and their application in the management of mule deer. Transactions of the North American Wildlife Conference 8:369-380.

Reiter, M.A., and Carlson, R.E. 1986. Current velocity in streams and the composition of benthic algal mats. Canadian Journal of Fisheries and Aquatic Sciences 43:1156-1162.

Resh, V,H., Brown, A.V., Covich, A.P., Gurtz, M.E., Li, H.W., Minshall, G.W., Reice, S.R., Sheldon, A.L., Wallace, J.B., and Wissmar, R.C.. 1988. Role of disturbance in stream ecology. Journal of the North American Benthological Society 7: 433-455.

Roberts, D.T., Schleser, D.M., and Jordan, T.L. 1995. Notes on the captive husbandry and reproduction of the Texas Salamander *Euryce neotenes* at the Dallas Aquarium. Herpetological Review 26:23-25.

Russell, W.H. 1976. Distribution of Troglobitic salamanders in the San Marcos Area, Hays County, Texas. In: Texas Association of Biological Investigation, Troglobitic *Eurycea*, Austin, Texas. USA.

SAS Institute, Inc., Cary North Carolina, USA. Statview Software, Version 5.0.1, Copyright 1992-1998.

Seaman, Jr., J.W., and Jaeger, R.G. 1990. Statistical dogmaticae: a critical essay on statistical practice in ecology. Herpetologica 46:337-346.

Slade, Jr., R., Dorsey, M., and Stewart, S. 1986. Hydrology and water quality of the Edwards Aquifer associated with Barton Springs in the Austin area, Texas. U.S. Geological Survey Water-Resources Investigations Report 86-4036.

Smith, B., and Hunt, B. 2010. A comparison of the 1950s drought of record and the 2009 drought, Barton Springs segment of the Edwards Aquifer, Central Texas: Gulf Coast Association of Geological Societies Transactions 60:611-622.

Sokal, R.R., and Rohlf, F.J. 1995. Biometry: the Principles of Statistics in Biological Research. W.H. Freeman and Company, New York, New York, USA.

Spellman, F.R., and Drinan, J.E. 2001. Stream Ecology and Self-purification: an Introduction. Technomic Publishing Co., Inc. Lancaster, Pennsylvania, USA.

Stevenson, R.J. 1983. Effects of current and conditions simulating autogenically changing microhabitats on benthic diatom immigration. Ecology 64:1514-1524.

Stockwell, C.A, Hendry, A. P., and Kinnison, M. T. 2003. Contemporary evolution meets conservation biology. TRENDS in Ecology and Evolution. 18(2):94-101.

Sweet, S.S. 1977. Natural metamorphosis in *Eurycea neotenes*, and the generic allocation of the Texas *Eurycea* (Amphibia: Plethodontidae). Herpetologica 33:364-375.

Sweet, S.S. 1978. The evolutionary development of the Texas *Eurycea* (Amphibia: Plethodontidae). Ph.D. Thesis. Berkeley (CA): University of California.

Sweet, S.S. 1982. A distributional analysis of epigean populations of *Eurycea neotenes* in central Texas, with comments on the origin of troglobitic populations. Herpetologica 38: 430-444.

Sweet, S.S. 1984. Secondary contact and hybridization in the Texas cave salamanders *Eurycea neotenes* and *E. tridentifera.* Copeia 1984: 428-441.

Takahashi, M.K., and Pauley, T.K. 2010. Resource allocation and life history traits of *Plethodon cinereus* at different elevations. American Midland Naturalist 163(1):87-94.

Thaker, M., Gabor, C.R., and Fries, J.N. 2006. Sensory cues for conspecific associations in aquatic San Marcos salamanders. Herpetologica 62(2):151-155.

Tukey, J.W. 1962. The future of data analysis. Annals of Mathematical Statistica 33:1-67.

Tumlison, R., and Cline, G.R. 1997. Further notes on the habitat of the Oklahoma Salamander, *Eurycea tynerensis*. Proceedings from the Oklahoma Academy of Science 77:103-106.

Tumlison, R., Cline, G.R., and Zwank. P. 1990. Surface habitat associations of the Oklahoma Salamander (*Eurycea tynerensis*). Herpetologica 46:169-175.

Tupa, D.D., and Davis, W.K. 1976. Populations dunamics of the San Marcos Salamander, *Eurycea nana* Bishop. Texas Journal of Sciences 27:179-195.

U.S. Department of the Interior. 1997. Endangered and threatened wildlife: final rule to list the Barton Springs Salamander as endangered. Federal Register. 62:23377-23392.

U.S. Department of the Interior. 2002. Endangered and threatened wildlife and plants; Review of species that are candidates or proposed for listing as endangered or threatened; Annual notice of findings on recycled petitions; Annual description of progress on listing actions. Federal Register 67(114): 40657-40679.

U.S. Fish and Wildlife Service. 1998. Endangered Species Act section 10(a)(1)(B) permit for the incidental take of the Barton Springs Salamander (*Eurycea sosorum*) for the operation and maintenance of Barton Springs Pool and adjacent springs. Permit #PRT-839031.

U.S. Fish and Wildlife Service and National Marine Fisheries Service. 1998. Endangered species consultation handbook: procedures for conducting consultation and conference activities under section 7 of the Endangered Species Act.

U.S. Geological Survey. 1990. Water Resources Data. Texas, Water Year 1990: U. S. Geological Survey Water-Data Report TX 90.

Vogel, S. 1994. Life in Moving Fluids: the Physical Biology of Flow. Princeton University Press, Princeton, New Jersey, USA.

Wells, K.D. 2007. The Ecology and Behavior of Amphibians. University of Chicago Press, Chicago, Illinois, USA.
Wiens, J.J., Chippindale, P.T., and Hillis, D.M. 2003. Why are phylogenetic analyses misled by convergence? A case study in Texas cave salamanders. Systematic Biology 52(4):501-514.

Woods, H.A., Poteet, M.F., Hitchings, P.D., Brain, R.A, and Brooks, B.A. 2010. Conservation physiology of the plethodontid salamanders *Eurycea nana* and *Eurycea sosorum*: Response to declining dissolved oxygen. Copeia 2010(4): 540-553.

Wetzel RG. 2001. Limnology: Lake and River Ecosystems. 3rd edition. Academic Press, San Diego, California, USA.

Woodruff CM, Abbott PL. 1979. Drainage-basin evolution and aquifer development in a karstic limestone terrane, south-central Texas, USA. Earth Surface Processes 4:319-334.

Woods HA, Poteet MF, Hitchings PD, Brain RA, Brooks BW. 2010. Conservation physiology of the plethodontid salamanders *Eurycea nana* and *E. sosorum*: Response to declining dissolved oxygen. Copeia 2010: 540-553.

Zar, J.H. 1984. Biostatistics. Prentice-Hall, Englewood Cliffs, New Jersey, USA.

Table 1. Mean, standard deviation (S.D.), and standard error (s.e.) of *E. sosorum* and *E. waterlooensis* salamander abundance and density in each spring site for the period of record are listed below. Minimum (Min.) and Maximum (Max.) salamander abundance and number of surveys (N) are also listed.

	Abundance (#)					**Density (#/sq. ft.)**				
	Mean	**S.D.**	**s.e.**	**Min-Max**	**N**	**Mean**	**S.D.**	**s.e.**	**Min-Max**	**N**
Eurycea sosorum										
Eliza (1995-2011)	190.5	255.4	20.6	0-1234	154	0.35	0.34	0.03	0-1.54	103
Parthenia (1993-2011)	44.5	59.3	4.5	1-447	171	0.03	0.03	0.002	0.0-0.18	154
Old Mill (1998-2011)	15.4	19.7	1.7	0-97	134	0.02	0.02	0.002	0-0.09	134
Upper Barton (1997-2011)	8.0	12.9	1.3	0-100	92	0.02	0.02	0.002	0-0.15	92
All Sites Combined All Years	72.1	158.1	6.4	0-1234	551	0.09	0.21	0.009	0-1.54	483
Eurycea waterlooensis										
Eliza (1998-2011)	0.76	1.8	0.16	0-12	128	0.001	0.003	0.0003	0-0.02	89
Parthenia (1998-2011)	0.29	0.74	0.07	0-5	113	0.0001	0.0003	0.00003	0-0.001	98
Old Mill (1998-2011)	3.6	7.6	0.68	0-43	125	0.003	06	0.001	0-0.03	25
Upper Barton (1998-2011)	0	0	0	0	83	0.02	0.02	0.002	0-0.15	83
All Sites Combined (1998-2011)	1.3	4.4	0.21	0-43	449	0.001	0.004	0.0002	0-0.032	395

Table 2. Descriptive statistics of *E. sosorum* abundance and density in Eliza and Parthenia Spring for each year of record are listed below. n/a indicates that density cannot be calculated because exact area surveyed was not recorded. Changes in habitat management associated with federal protection of *E. sosorum* were implemented in 1997. Habitat reconstruction in Eliza Spring occurred from 2003-2004, in Parthenia Spring from 2004-2005.

	Abundance (#)						**Density (#/sq ft)**			
Year	**Mean**	**S.D.**	**s.e.**	**N**	**Min.**	**Max.**	**Mean**	**S.D.**	**s.e.**	**N**
Eliza										
1995	20.3	7.14	3.57	4	12	29	0.026	0.009	0.005	3
1996	7.7	8.19	2.47	11	1	23	0.01	0.009	0.003	10
1997	25.8	12.51	5.11	6	13	44	0.01	n/a	n/a	1
1998	14.9	5.16	1.72	9	8	23	n/a	n/a	n/a	
1999	6.6	4.04	1.35	9	1	13	n/a	n/a	n/a	
2000	1.6	2.68	0.85	10	0	8	n/a	n/a	n/a	
2001	4.1	2.36	0.83	8	1	7	n/a	n/a	n/a	
2002	4.5	2.45	0.87	8	2	8	n/a	n/a	n/a	
2003	39.8	44.24	14.0	10	3	148	0.04	0.06	0.02	10
2004	350.6	124.1	46.9	7	233	601	0.44	0.16	0.06	7
2005	369.6	197.2	62.4	10	151	673	0.44	0.25	0.08	10
2006	453.4	169.5	53.6	10	216	738	0.57	0.21	0.07	10
2007	437.0	166.7	50.3	11	280	701	0.55	0.21	0.06	11
2008	703.4	347.4	100.3	12	231	1234	0.88	0.43	0.13	12
2009	163.6	114.3	36.1	10	35	405	0.20	0.14	0.05	10
2010	155.6	88.7	31.4	8	53	360	0.18	0.12	0.04	8
2011	152.1	63.7	20.1	10	49	226	0.19	0.08	0.025	10
Parthenia										
1993	18.2	6.9	3.1	5	11	27	0.038	0.014	0.006	5
1994	15.2	7.8	2.2	12	3	28	0.031	0.016	0.005	12
1995	16.0	12.0	-	13	1	40	0.033	0.025	0.007	13
1996	21.4	12.6	3.2	16	7	45	0.044	0.026	0.007	16
1997	19.7	17.1	6.5	7	4	44	0.041	0.035	0.013	7
1998	29.6	10.6	3.4	10	10	42	0.059	0.012	0.007	3
1999	57.2	21.9	6.9	10	17	82	0.037	0.014	0.005	10
2000	17.7	14.1	4.7	9	3	42	0.012	0.009	0.003	9
2001	10.7	3.1	1.2	7	6	15	0.007	0.002	0.001	7
2002	22.0	8.1	2.7	9	5	32	n/a	n/a	n/a	n/a
2003	46.1	29.5	10.4	8	11	100	0.023	0.010	0.005	5
2004	37.2	38.9	13.0	9	5	127	0.015	0.016	0.005	9
2005	111.0	84.5	32.0	7	16	236	0.042	0.032	0.012	7
2006	86.9	124.6	41.5	9	1	300	0.034	0.045	0.015	9
2007	27.8	16.0	6.5	6	9	55	0.011	0.007	0.003	6
2008	177.6	110.6	36.9	9	76	447	0.081	0.042	0.014	9
2009	28.7	22.5	8.5	7	5	73	0.010	0.010	0.004	7
2010	54.9	33.8	11.9	8	13	111	0.013	0.006	0.002	8

Table 3. Descriptive statistics of *E. sosorum* abundance and density in Old Mill and Upper Barton Spring for each year of record are listed below. n/a indicates that density cannot be calculated because exact area surveyed was not recorded. Changes in habitat management associated with federal protection of *E. sosorum* were implemented in 1997. Habitat reconstruction in Eliza Spring occurred in 2003, in Parthenia Spring from 2004-2005.

	Abundance (#)						**Density (#/sq ft)**			
Year	**Mean**	**S.D.**	**s.e.**	**N**	**Min.**	**Max.**	**Mean**	**S.D.**	**s.e.**	**N**
Old Mill										
1997	39.6	23.3	11.7	4	8	60	0.058	0.037	0.019	4
1998	27.9	18.1	6.0	9	4	51	0.027	0.021	0.007	9
1999	5.9	4.4	1.5	9	0	13	0.004	0.003	0.001	9
2000	2.0	2.6	0.9	8	0	7	0.002	0.004	0.001	8
2001	27.6	17.6	5.6	10	8	56	0.031	0.023	0.007	10
2002	19.1	9.5	3.2	9	4	33	0.016	0.010	0.003	9
2003	27.6	18.8	5.9	10	1	52	0.021	0.014	0.004	10
2004	42.8	16.9	5.7	9	6	67	0.032	0.013	0.004	9
2005	13.4	6.7	2.4	8	7	23	0.007	0.003	0.001	8
2006	0.8	1.3	0.4	9	0	3	0.001	0.001	0.0003	9
2007	6.5	4.4	1.8	6	1	14	0.005	0.003	0.001	6
2008	32.5	38.2	13.5	8	0	97	0.026	0.030	0.011	8
2009	0.9	2.1	0.6	12	0	7	0.001	0.001	0.0004	12
2010	1.5	1.2	0.4	11	0	4	0.001	0.001	0.0002	11
Upper Barton										
1997	5.8	5.3	2.4	5	1	14	0.013	0.012	0.005	5
1998	1.9	1.3	0.4	9	0	4	0.004	0.003	0.001	9
1999	1.0	10.6	0.3	6	0	2	0.002	0.001	0.001	6
2000	5.0	3.5	2.0	3	3	9	0.011	0.008	0.004	3
2001	5.4	5.0	1.6	10	0	14	0.012	0.011	0.004	10
2002	5.0	3.6	1.1	10	0	12	0.011	0.008	0.003	10
2003	2.9	1.9	0.6	9	0	5	0.006	0.004	0.001	9
2004	7.3	4.5	1.6	8	1	14	0.016	0.010	0.004	8
2005	4.4	3.1	1.4	5	1	9	0.010	0.007	0.003	5
2007	5.3	5.1	1.7	9	0	13	0.010	0.010	0.003	9
2008	20.3	12.5.	6.3	4	3	30	0.051	0.036	0.018	4
2009	9.0	9.9	7.0	2	2	16	0.013	0.012	0.009	2
2010	28.1	27.0	8.1	11	4	100	0.043	0.042	0.013	11

Table 4. Descriptive statistics of *E. waterlooensis* abundance and density in Eliza and Parthenia, Spring for each year of record are listed below. n/a indicates that density cannot be calculated because exact area surveyed was not recorded. Changes in habitat management associated with federal protection of *E. sosorum* were implemented in 1997. Habitat reconstruction in Eliza Spring occurred in 2003, in Parthenia Spring from 2004-2005.

	Abundance (#)						**Density (#/sq ft)**			
Year	**Mean**	**S.D.**	**s.e.**	**N**	**Min.**	**Max.**	**Mean**	**S.D.**	**s.e.**	**N**
					Eliza					
1998	0	0	0	5	0	0	0	0	0	5
1999	0	0	0	9	0	0	0	0	0	9
2000	0	0	0	10	0	0	0	0	0	10
2001	0	0	0	8	0	0	0	0	0	8
2002	0	0	0	8	0	0	0	0	0	8
2003	0	0	0	10	0	0	0	0	0	10
2004	1.1	1.1	0.4	7	0	3	0.001	0.001	0.001	7
2005	0.9	1.7	0.6	9	0	5	0.001	0.005	0.001	10
2006	3.7	4.5	1.7	10	0	12	0.005	0.006	0.002	10
2007	1.2	1.1	0.4	10	0	3	0.002	0.001	0.0005	11
2008	1.0	4.5	0.4	12	0	4	0.001	0.002	0.001	12
2009	0.1	0.3	0.1	10	0	1	0.0001	0.0004	0.0003	10
2010	0	0	0	8	0	0	0	0	0	8
					Parthenia					
1998	0.2	0.5	0.2	10	0	1	0.0003	0.0005	0.0003	2
1999	0	0	0	10	0	0	0	0	0	10
2000	0	0	0	9	0	0	0	0	0	9
2001	0	0	0	7	0	0	0	0	0	7
2002	0.3	0.5	0.2	9	0	1	n/a	n/a	n/a	n/a
2003	0.6	0.9	0.3	8	0	2	0.0003	0.0004	0.0002	5
2004	0.1	0.3	0.1	9	0	1	0.00005	0.0002	0.00005	9
2005	0.1	0.4	0.1	7	0	1	0.00005	0.0001	0.00005	7
2006	0.3	0.7	0.2	9	0	2	0.0001	0.0003	0.0001	9
2007	0.7	0.8	0.3	6	0	2	0.0003	0.0004	0.0002	6
2008	0.2	0.7	0.2	9	0	2	0.0001	0.0003	0.0001	9
2009	0.1	0.4	0.1	7	0	1	0.00003	0.0001	0.00003	7
2010	1.1	2.0	0.8	7	0	5	0.0003	0.0004	0.0002	7

Table 5. Descriptive statistics of *E. waterlooensis* abundance and density in Old Mill and Upper Barton Spring for each year of record are listed below. n/a indicates that density cannot be calculated because exact area surveyed was not recorded. Changes in habitat management associated with federal protection of *E. sosorum* were implemented in 1997. Habitat reconstruction in Eliza Spring occurred in 2003, in Parthenia Spring from 2004-2005.

	Abundance (#)						**Density (#/sq ft)**			
Year	**Mean**	**S.D.**	**s.e.**	**N**	**Min.**	**Max.**	**Mean**	**S.D.**	**s.e.**	**N**
					Old Mill					
1998	1.2	1.1	0.5	5	0	2	0.001	0.001	0.0004	5
1999	0.3	1.0	0.3	9	0	3	0.0003	0.001	0.0003	9
2000	0.5	0.8	0.3	8	0	2	0.001	0.001	0.0004	8
2001	9.1	12.4	3.9	10	0	37	0.008	0.009	0.003	10
2002	9.1	6.5	2.2	9	1	21	0.007	0.005	0.002	9
2003	15.5	15.3	4.8	10	0	43	0.012	0.011	0.004	10
2004	8.8	5.3	1.8	9	0	16	0.007	0.004	0.001	9
2005	1.5	1.8	0.6	8	0	5	0.001	0.001	0.0005	8
2006	0.4	0.7	0.2	9	0	2	0.0003	0.001	0.0002	9
2007	0.2	0.4	0.2	6	0	1	0.0001	0.0003	0.0001	6
2008	1.8	2.4	0.9	8	0	6	0.001	0.002	0.001	8
2009	0	0	0	12	0	0	0	0	0	12
2010	0.1	0.3	0.1	11	0	1	0.00005	0.0002	0.00005	11
					Upper Barton					
1998-2010	0	0	0	83	0	0	0	0	0	83

Table 6. Spearman Rank correlation coefficients (ρ) and significance values (p**)** of habitat and *E. sosorum* density in Eliza Spring from July 2003 through December 2010 are presented below. Mean ± Standard Deviation of each variable is also listed. Water and sediment depth are listed in inches, velocity in feet per second.

Variable Mean ± SD	Salamander Density 348.9 ± 274.5	Sediment Depth 0.68 ± 0.51 in.	% Sediment Cover 36.2 ± 23.2
Flow Velocity 0.57 ± 0.55 ft./sec.	ρ=0.067 p= 0.016	ρ=-0.058 p= 0.581	ρ= 0.320 p= 0.002
Water Depth 15.2 ± 8.3 in.	ρ=-0.305 p=0.024	ρ= 0.219 p= 0.002	ρ= 0.471 p=0.0003
% Sediment Cover 36.2 ± 23.2	ρ=-0.166 p= 0.011	ρ= 0.173 p= 0.002	.

Table 7. Mean, standard deviation (S.D.), and standard error (s.e.) of dissolved oxygen (DO) abundance and density of each size class of *E. sosorum* in Eliza Spring from 2003 – 2010 before the severe drought, during, and after the drought. Totals and values for each size class are included. Minimum (Min.) and Maximum (Max.) salamander abundances and dissolved oxygen concentrations are also listed.

	Abundance (#)						Density (#/sq ft)		
Eliza	**Mean**	**S.D.**	**s.e.**	**N**	**Min.**	**Max.**	**Mean**	**S.D.**	**s.e.**
No Drought 7/03-5/08									
Total	430.7	281.9	39.5	51	29	1234	0.54	0.36	0.05
Juvenile	116.7	124.7	17.5	51	0	568	0.16	0.16	0.02
Young Adult	177.2	123.1	17.4	50	14	535	0.22	0.16	0.02
Adult	130.9	88.4	12.5	50	2	365	0.16	0.11	0.02
DO	5.08	0.88	0.14	39	4.35	7.64	n/a	n/a	n/a
H_2O Temp.(C°)	21.0	0.57	0.06	78	19.0	22.1	n/a	n/a	n/a
Drought 6/08-9/09									
Total	253.4	211.1	58.55	13	35	642	0.32	0.26	0.07
Juvenile	47.23	59.8	16.6	13	3	195	0.06	0.08	0.02
Young Adult	151.0	125.7	34.9	13	17	374	0.19	0.16	0.04
Adult	48.9	27.4	7.6	13	14	91	0.06	0.03	0.01
DO	4.30	0.34	0.10	12	3.88	5.03	n/a	n/a	n/a
H_2O Temp.(C°)	21.5	0.17	0.05	15	21.2	21.8	n/a	n/a	n/a
No Drought 10/09-12/10									
Total	193.2	115.1	36.4	10	53	405	0.23	0.15	0.05
Juvenile	9.9	7.9	2.5	10	0	24	0.01	0.01	0.003
Young Adult	85.4	70.5	22.3	10	15	230	0.10	0.09	0.03
Adult	87.7	47.5	15.0	10	22	168	0.10	0.06	0.02
DO	6.48	0.78	0.25	10	5.6	8.12	n/a	n/a	n/a
H_2O Temp.(C°)	20.6	1.11	0.31	13	18.4	21.9	n/a	n/a	n/a

Table 8. Mean, standard deviation (S.D.), and standard error (s.e.) of dissolved oxygen (DO) abundance and density of each size class of *E. sosorum* in Parthenia Spring from 2003 – 2010 before the severe drought, during, and after the drought. Totals and values for each size class are included. Minimum (Min.) and Maximum (Max.) salamander abundances and dissolved oxygen concentrations are also listed.

	Abundance (#)						Density (#/sq ft)		
Parthenia	**Mean**	**S.D.**	**s.e.**	**N**	**Min.**	**Max.**	**Mean**	**S.D.**	**s.e.**
No Drought 7/03-5/08									
Total	72.6	78.2	12.2	41	1	300	0.029	0.03	0.005
Juvenile	26.1	25.7	4.0	41	0	102	0.010	0.010	0.002
Young Adult	34.6	42.6	6.7	40	0	175	0.014	0.016	0.003
Adult	11.7	16.2	2.6	40	0	58	0.005	0.006	0.001
DO	6.02	0.71	0.11	41	4.57	7.44	n/a	n/a	n/a
H_2O Temp.(C°)	21.1	0.55	0.07	70	19.1	22.0			
Drought 6/08-9/09									
Total	116.1	136.5	43.2	10	5	447	0.054	0.057	0.018
Juvenile	45.5	66.6	21.1	10	0	204	0.020	0.027	0.009
Young Adult	55.0	58.3	18.4	10	3	199	0.027	0.027	0.008
Adult	11.9	13.0	4.1	10	0	36	0.005	0.006	0.002
DO	4.57	0.32	0.10	10	4.13	5.00	n/a	n/a	n/a
H_2O Temp.(C°)	21.4	0.52	0.14	15	19.6	21.8	n/a	n/a	n/a
No Drought 10/09-12/10									
Total	49.5	32.1	10.2	10	13	111	0.010	0.006	0.002
Juvenile	14.3	13.2	4.2	10	2	41	0.003	0.002	0.001
Young Adult	24.4	14.4	4.5	10	4	51	0.006	0.003	0.001
Adult	9.9	7.1	2.2	10	1	22	0.002	0.001	0.0005
DO	6.40	0.52	0.16	10	5.80	7.24	n/a	n/a	n/a
H_2O Temp.(C°)	20.4	1.02	0.32	10	18.7	21.7	n/a	n/a	n/a

Table 9. Mean, standard deviation (S.D.), and standard error (s.e.) of dissolved oxygen (DO) and abundance and density of each size class of *E. sosorum* Old Mill Spring during drought and non-drought. The droughts of 2006 and 2008 are pooled. Minimum (Min.) and Maximum (Max.) salamander abundances, dissolved oxygen concentrations, and water temperatures are also listed.

	Abundance						**Density (#/sq ft)**		
Old Mill	**Mean**	**S.D.**	**s.e.**	**N**	**Min.**	**Max.**	**Mean**	**S.D.**	**s.e.**
Droughts 10/05-10/06, 6/08-9/09									
Total	4.1	14.4	2.9	25	0	71	0.003	0.013	0.003
Juvenile	1.2	4.7	0.9	25	0	23	0.001	0.004	0.001
Young Adult	2.2	7.7	1.5	25	0	38	0.002	0.007	0.001
Adult	0.7	2.1	0.4	25	0	10	0.001	0.002	0.0004
DO	4.26	2.12	0.41	27	1.04	9.07	n/a	n/a	n/a
H_2O Temp.(C°)	21.6	3.2	0.62	27	10.8	30.2	n/a	n/a	n/a
No Drought 7/03-9/05, 11/06-5/08, 10/09-12/10									
Total	21.8	23.6	3.6	43	0	97	0.016	0.018	0.003
Juvenile	5.4	7.3	1.1	43	0	24	0.004	0.006	0.001
Young Adult	9.7	11.8	1.8	43	0	45	0.007	0.009	0.001
Adult	6.1	6.6	1.0	43	0	22	0.004	0.005	0.001
DO	5.83	0.65	0.07	83	4.3	7.56	n/a	n/a	n/a
H_2O Temp.(C°)	20.8	1.2	0.13	82	11.4	21.9	n/a	n/a	n/a