

Barton Springs and Austin blind salamander capture-recapture study: interim report

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Abstract

Here we present results from the first comprehensive summary of capture-recapture monitoring data for Barton Springs and Austin blind salamanders (Eurycea sosorum and E. waterlooensis, respectively). Using capture-recapture represented a marked change in our approach to studying and understanding the wild populations of these unique and endangered animals. We used photographic identification in lieu of physically tagging salamanders to generate capturehistories and estimate survival, temporary emigration, and abundance. Salamanders were captured, photographed, and assessed for gravidity over a four-year period (ca. 2014–2018). We measured the length of each salamander to get a better understanding of age structure and sexual maturity, as well as account for differences in detection between size classes. Only a small fraction of salamanders were Austin blind salamanders (1.2% of all observations; n = 46), all of which were immature individuals. The bulk of our data came from Barton Springs salamanders at Eliza Spring (89% of observations, n = 3458) where we had our most intensive survey effort and highest recapture rates. We found that gravidity had a weak, positive correlation with flow and there was also a weak seasonal pattern, but some gravid Barton Springs salamanders were encountered during all seasons. In 2018 we observed a large increase in population size of Barton Springs salamanders at all sites, driven by reproduction and recruitment. During the same period, we also observed an uptick in abundance of Austin blind salamanders, which suggests both populations may be responding to similar environmental cues. Survival and reproduction were positively associated with spring-flow. These observations lend further support to the hypothesis that spring-flow dynamics are a critical external driver of salamander population dynamics in the Barton Springs ecosystem. Based on high estimates of temporary emigration, a large proportion of the population of Barton Springs salamanders was often underground and unavailable for capture. This indicates that surface abundance is not a good approximation of population size and supports other observations that this species is not primarily a surfacedweller, as was once thought. Movements between the surface and subsurface appear to have a large effect on the number of individuals that can be observed during any given period. These results have important implications for species conservation and recovery goals because extinction threat cannot be assessed based on surface abundance alone.

Introduction

Background

Barton Springs and Austin blind salamanders (Eurycea sosorum and Eurycea waterlooensis, respectively) are permanently aquatic plethodontid salamanders endemic to four springs that collectively make up Barton Springs in Austin, Texas (Figure 1). Located in the City of Austin's (City) Zilker Park near downtown Austin, three of these springs (Parthenia, Eliza, and Sunken Gardens) have been impounded or otherwise modified by humans beginning in the late 1800's. A fourth spring (Upper Barton) flows intermittently and is the only outlet that has not been impounded. Parthenia Spring is in what is now Barton Springs Pool, a popular swimming area that was formed by the damming of Barton Creek in 1929. Due to their limited distributions and ongoing threats to their persistence, both Barton Springs and Austin blind salamanders are listed as endangered under the Endangered Species Act (62 FR 23377-23392; 78 FR 51278-51326). The City's operation and maintenance of Barton Springs Pool as a recreational facility imposes incidental take of Barton Springs and Austin blind salamanders. As such, the City must have a 10(a)(1)(B) incidental take permit issued by the U.S. Fish & Wildlife Service (Service) to allow for continued operation of the pool. In 1998, the Service issued a 10(a)(1)(B) permit to the City and approved the Habitat Conservation Plan (HCP). In 2013, the City renewed their permit and amended their HCP to include Austin blind salamanders (among other changes).



Figure 1. Location of the four major springs of the Barton Springs group.

Population Monitoring by the City

In this report, we describe the first comprehensive effort to estimate population size and demographic rates using capture-recapture data collected as part of a continuous monitoring program. Continuous population monitoring is one of several conservation measures of the City's HCP. The goal of monitoring is to gather information about populations of the covered species at different points in time to gauge their status, assess population viability and determine what factors govern population dynamics (Dries et al. 2013, U.S. Fish and Wildlife Service 2005, 2016). Monitoring makes it possible to detect departures from some desired state and

measure the effects of perturbations such as natural disturbance or habitat management (Williams et al. 2002, Conroy and Carroll 2009).

The City began monitoring salamander populations in 1993 (reviewed in Dries et al. 2013 and Devitt 2016). To date, monitoring has consisted primarily of counts, where the number of individual salamanders found is used as an index of population size. An index of population size is typically a field measure (e.g., a count) that contains information about the relative size or density of the population (Williams et al. 2002). Count data have formed the basis of most of our knowledge about wild populations of Barton Springs and Austin blind salamanders (Chippindale et al. 1993, City of Austin 1997, Hansen 1999, Hillis et al. 2001, Bendik and Dries 2018, Dries and Colucci 2018). In general, abundances of Barton Springs salamanders fluctuate widely near the spring outlets, and these dynamics have been linked to changes in spring-flow rates and sedimentation (Bendik and Dries 2018, Dries and Colucci 2018). The counts are uncorrected for detection error so changes in abundance may be a reflection of movement of the population between the surface and subsurface or a consequence of differential survival and recruitment for Barton Springs salamanders.

A common assumption of count-based methods is that all individuals in a population are equally detectable over space and time, and that counts are directly proportional to population size. Counts do not represent a complete census, however, because they do not account for unobserved animals. In most cases, counts represent some unknown fraction of the population (Pollock et al. 1990) and can be insufficient for inferring population trends if they do not account for detection error (Yoccoz et al. 2001, Schmidt 2003; but see Royle 2004, Kéry and Royle 2016). Alternatively, population dynamics can be examined using state-space models of count data (de Valpine and Hastings 2002, Ives et al. 2003). In lieu of direct estimates of detection error, these models make assumptions about the form of detection error and allow for improved estimation of a population size index (Kéry and Schaub 2012). These models have been used to document density-dependent and density-independent drivers of population change in Barton Springs salamanders (Bendik and Dries 2018). However, state-space models cannot accurately estimate population size without direct estimates of detection error (Kéry and Schaub 2012). Estimating detection error is therefore key to estimating population size, as well as other demographic parameters (see below), and aids understanding of how environmental conditions relate to population dynamics.

Demographic Parameters

Capture-recapture models account for imperfect detection of individuals and provide estimates of demographic parameters and vital rates, e.g., migration and survival (Otis et al. 1978, Lebreton et al. 1992, Williams et al. 2002). The estimation of these parameters is based on probabilistic events that make up the capture history of an individual. Many different models are available for capture-recapture estimation (Otis et al. 1978, Pollock et al. 1990). These models are generally classified as either closed-population models, which assume the population has a constant size throughout the sampling period, or open-population models, which allow for additions or deletions from the population through, birth, death, or migration during the sampling interval (Otis et al. 1978, Pollock et al. 1970).

Two types of models have been developed to analyze data from open-population capturerecapture studies. Cormack-Jolly-Seber (CJS) models permit the estimation of survival and capture probabilities, conditional on the number of animals released during each sampling interval (Cormack 1964, Jolly 1965, Seber 1965). Jolly-Seber (JS) models are unconditional, modeling initial captures of unmarked animals in addition to the history of marked animals (Jolly 1965, Seber 1965), allowing for estimation of abundance and/or recruitment in addition to survival and detection probability. The JS model assumes that the probability of detection is equal for all individuals in the population, and that emigration is permanent (Pollock et al. 1990). Any violation of these assumptions may result in biased parameter estimates, especially with respect to population size and recruitment (Kendall et al. 1995).

To address the possibility of temporary migration, Pollock (1982) proposed a more flexible approach combining aspects of both closed and open-population models. He suggested a sampling design (referred to as the "robust design") consisting of primary sampling events separated by intervals that are long enough (e.g., months or years) to assume that the population is open to gains and losses. Within each primary sampling event, a series of secondary, short-term sampling sessions is performed (e.g., over consecutive days), during which the population is assumed closed. A series of models under the robust capture-recapture sampling design have been developed (Kendall et al. 1995, 1997) including methods which relax the assumption of equal detection probability and allow for temporary emigration (Kendall and Bjorkland 2001, Schwarz et al. 2007).

Relating Capture-Recapture Data to Salamander Ecology

Estimates of migration of interest for understanding the life history, abundance, home range and geographic distribution of Barton Springs salamanders. Sweet (1978) initially suggested Barton Springs salamanders were troglobites and that individuals present at the surface were discharged from the spring. Opposing this idea in the formal species description, Chippindale et al. (1993) thought that Barton Springs salamanders were primarily surface-dwellers also capable of living below ground. This led to the assumption that low abundance at the surface meant that Barton Springs salamanders were "particularly subject to" extinction (City of Austin 1997). Since that time, new populations have been discovered throughout the Barton Springs recharge and contributing zones (watersheds that drain into the aquifer feeding the springs), expanding the known range of the species far beyond the type locality at Barton Springs (McDermid et al. 2015, Devitt and Nissen 2018). These newer localities include subterranean sites (a monitoring well and a cave), indicating that some populations of Barton Springs salamanders may be entirely subterranean. Additionally, eggs are almost never observed at the surface, despite many exhaustive searches (Bendik and Dries 2018), suggesting Barton Springs salamanders reproduce underground and therefore require subterranean habitat to complete their life cycle. Nevertheless, Barton Springs salamanders extensively use surface habitat where it is available near spring outlets, where they occasionally occur in great numbers (e.g., > 300; Bendik & Dries 2018; Dries & Colucci 2018). However, their abundance at the surface also fluctuates by orders of magnitude and occasionally reaches zero, or nearly so (Bendik and Dries 2018). This indicates that either surface populations are occasionally extirpated and recolonized from subterranean populations or that migration into the aquifer is occurring. Complete extirpation without migration into the

aquifer would suggest that the surface habitat is a population sink (unable to be maintained without immigration; Pulliam 1988) and that surface populations are a dead-end in terms of species persistence, which would have important consequences for population management and species recovery (U.S. Fish and Wildlife Service 2005). Estimating temporary emigration from capture-recapture data will indicate whether salamanders are likely to leave the surface and later return. The presence of temporary migrants would be indicative of a population that extends beyond the spring outlets and into the subterranean habitat, rather than a population that only persists at the surface with one-way immigration from the aquifer. Migration may also occur between sites, and this can also be tested with the capture-recapture data.

Survival and recruitment will also influence the abundance of salamanders observed at the surface. While counts provide an indication of when recruitment occurs at the surface (because we can assume that small juvenile salamanders are new recruits), changes in abundance of larger size classes may occur due to growth, differential survival, and/or movement. Using capture-recapture data, we can test whether changing environmental conditions, such as spring-flow, are affecting survival, temporary emigration, or both. Ultimately this allows us to understand some of the mechanisms of how surface abundance changes and what factors are responsible.

In addition to estimating demographic parameters from capture-recapture data, we also examined patterns relating to population age-structure (based on size distributions) and reproductive state (gravidity). Abundance and recruitment appear to be non-seasonal for Barton Springs salamanders based on count data (Bendik and Dries 2018), but patterns of gravidity have never been examined in the wild for either Barton Springs or Austin blind salamanders. Size distribution data for Jollyville Plateau salamanders (*E. tonkawae*), a close relative, revealed a seasonal pattern, suggestive of differences in movement patterns between newly-recruited salamanders and older individuals (Bendik 2017). We are therefore interested in examining whether there are similar patterns in the size structure for Barton Springs and Austin blind salamanders.

Aims and Scope

We performed capture-recapture surveys at all four spring sites to better understand the population ecology of Barton Springs and Austin blind salamanders. In this report, we present the first comprehensive analysis of these data, collected from 2014–2018. Previous presentations of these data consisted of yearly summaries for permit reports, including periodic estimates of abundance or summaries of our observations (City of Austin 2016, 2017). Here, our aim is to provide an up-to-date summary of our efforts for the capture-recapture study and summarize what we have learned about the life history and population ecology of Austin blind and Barton Springs salamanders. We present capture-recapture summaries for all sites and species, but, because of low recapture rates, the bulk of our inferences and demographic parameter estimates are from a robust-design study at Eliza Spring for Barton Springs salamanders. Using the Eliza data, we provide estimates of demographic parameters, including estimates of abundance for all periods and size classes of Barton Springs salamanders. We also explore factors that govern variation in detection probability, provide estimates of survival and temporary emigration, and examine environmental factors that influence the presence of salamanders at the surface.

Methods

Study Sites

Parthenia Spring

Parthenia Spring emerges from caves and fissures from within the bed of Barton Creek at Barton Springs Pool and is confined by upstream and downstream dams spanning Barton Creek. The survey area includes the loose gravel and cobble in front of several large spring outlets, with a depth of up to 5 m (Figure 2).



Figure 2. Aerial view of the central portion of Barton Springs Pool showing the location of the survey area.

Sunken Gardens Spring

Sunken Gardens Spring (also called Old Mill Spring) emerges on the south side of Barton Creek, downstream of Barton Springs Pool, and is contained by a masonry wall/amphitheater constructed in 1937 (Figure 3). The maximum water depth is ca. 1 m, where the springs bubble up from the bottom of a spring pool. Water flows through a slightly elevated, narrow constriction into a fast-moving spring run. Surveys from 2009–2016 have found very few salamanders at this site (most surveys found ≤ 1 individual, which were usually in the spring run).



Figure 3. Sunken Gardens (Old Mill) spring pool.

Upper Barton Spring

Upper Barton Spring emerges directly adjacent to Barton Creek on the south side, upstream of Barton Springs Pool (Figure 4). It is an intermittent spring, ceasing to flow when the combined discharge from Barton Springs is below approximately 40 ft³/s. Upper Barton Spring contains a large, discrete spring orifice which flows in opposite directions to reach Barton Creek. The survey area consists of the first 12 m downstream and 7.5 m upstream from the main spring opening (linear length of stream channel along the wetted channel center measured from the spring orifice) and spanning the width of the wetted channel.



Figure 4. Upper Barton Spring (center) and Barton Creek (top left).

Eliza Spring

Eliza Spring is a concrete-encased, spring-fed pool (Figure 5). During most of our study, the spring pool emptied directly into a pipe, representing a point of no return for salamanders that ventured too far downstream. During the last year of our study, the pipe was replaced by an overland stream terminating at a concrete tunnel (another point of no return).



Figure 5. Eliza Spring before (A) and after (B) overland stream reconstruction. The orange arrow in panel A indicates the location of the outflow pipe.

Data Collection

Capture-Recapture Sampling Schemes

We performed surveys using two different capture-recapture sampling schemes. At Parthenia, Sunken Gardens, and Upper Barton springs, we performed quarterly surveys to collect data compatible with open-population models. A robust design was not performed at these springs because each spring had challenges that could prevent enough data for the robust design to produce an accurate analysis. At Parthenia Spring, the logistical constraints imposed by the deeper water made the robust-design data more challenging. At Sunken Gardens counts were typically low (single digits) prior to this study (City of Austin 2009, 2010, 2011, 2013). Previous capture-recapture work using batch marks at Upper Barton Spring (City of Austin 2009, 2010, 2011, 2013) also suggested that recaptures would be very low, which can result in poor fit or nonsensical results in capture-recapture models due to data sparsity.

Because Eliza Spring typically has the largest abundances and the site is logistically suitable for capturing and photographing many salamanders, it was the focus of our most intense survey efforts. There, data collection followed a robust-design sampling scheme (Pollock 1982) to allow for more precise estimates of abundance. The hierarchical sampling strategy at Eliza Spring consisted of three consecutive surveys performed within a one-week sampling period, followed by a longer interval (typically 3 months, but ranging from approximately 2–6 months) before the next sampling event, from October 2014 through November 2018. We assumed the population was demographically closed (no births, deaths or migration) within each sampling period, and demographically open between each period.

Field Methods

Within the boundaries of each survey area, surveyors lifted all available cover objects (typically, gravel and cobble-sized rocks) using a drive survey, attempting to capture all observed salamanders using small hand nets or net bags. Salamanders were then temporarily held in a

flow-through mesh container to await processing. While observers attempted to capture all salamanders seen, some were missed. Misses were categorized by species and the following size classes: $\leq 25 \text{ mm}, 25-50 \text{ mm}, \geq 50 \text{ mm}$ (i.e., approximately < 1", 1-2", > 2"), or "small", "medium" and "large" salamanders, corresponding to the following life stages: small juveniles, large juveniles and small adults, and large adults, respectively. Surveys were performed on a quarterly basis each year, although occasionally surveys were missed due to inclement weather or site conditions.

Captured salamanders were photographed in a transparent water-filled tray against a 5 mm grid using a Nikon DSLR and macro lens with two flashes. Salamanders were assessed for gravidity by visually checking for yolked oocytes (the candling method; Gillette and Peterson 2001). Gravid females were considered sexually mature. Otherwise, individuals were not sexed due to the difficulty of candling for determining presence or absence of testes.

Prior to each survey, we photographed ten sampling quadrats (0.25 m^2) evenly spaced through the center of the survey area. Each quadrat was visually assessed for embeddedness, estimated visually by superimposing a 100-cell grid over the photograph. Cells were classified as embedded if they met the following conditions: 1) consisted of 50% or more coverage of fine sediments (silt, sand and clay), and 2) gravel or cobble-sized rocks were covered or partially covered by these fine sediments. We excluded areas without suitable rock cover for salamanders in calculations of embeddedness. We summed the number of embedded cells and divided by the total to generate a percent embeddedness value for each grid. These values were then averaged across all grids for each survey.

Additionally, we performed a visual estimate (count) of the number of centrarchids (sunfishes and/or bass), cyprinids (minnows), *Astyanax mexicanus* (Mexican tetras), *Gambusia affinis* (mosquitofish), and any other fishes observed (this excluded secretive fish such as darters). The goal was to provide a qualitative snapshot of the density and diversity of fish.

We recorded cumulative survey effort (time), weather conditions, spring discharge, and dissolved oxygen measured using a Hydrolab MS5 minisonde. Portable flow meters and water quality sondes were used to collect these data in Upper Barton, Eliza, and Old Mill springs; spring-flow and dissolved oxygen from Parthenia Spring are reported from data collected by the USGS (https://waterdata.usgs.gov/tx/nwis/dv/?site_no=08155500).

Differences in water depth necessitated slightly different survey techniques at each site, but the same general drive-survey approach was used for Eliza, Parthenia and Upper Barton. At Sunken Gardens, we combined a drive-survey approach with a timed search (1 hour, 2 surveyors within the spring pool; 30 minutes within the stream). Table 1 summarizes the differences in methods between sites, and their physical characteristics.

Sample Site	Survey Period (<i>n</i> samples)	Survey Method	Sampling Scheme	Survey Area	Survey Depth (maximum)
Parthenia (BSP)	2016–2017 (8)	SCUBA, mesh bag capture	Single event, open population	65 m ²	5 m
Eliza	10/2014–2018 (16*)	Snorkel, hand net capture	Robust-design	74 m ²	0.25 m
Sunken Gardens	2016–2018 (12)	SCUBA/snorkel, hand net	Time-constrained single event, open population	140 m ²	1 m
Upper Barton	12/2013–2018 (22)	Wading, hand net	Single event, open population	40 m ²	0.1 m

Table 1. Survey methods and site details.

*the number of primary samples

Data Processing

We measured the body length and total length for all individuals captured to the nearest 0.1 mm using ImageJ (Rasband 1997). For capture-recapture, photographs were cropped to contain just the head, and we used program Wild-ID to identify unique individuals (Bolger et al. 2012). We then used the R statistical software environment (R Core Team 2019) to generate a matrix of capture histories from Wild-ID output. For E. tonkawae, a species with similar pigmentation, photographic identification using these methods was more accurate than colored elastomers (Bendik et al. 2013). One limitation is that small juveniles cannot be reliably tracked using photographs over periods greater than a month or two because of changes in pigmentation during growth (Bendik et al. 2013). For this reason, we excluded data from individuals < 22.5 mm in body length, the approximate size for a mature adult (Chippindale et al. 1993), for the robustdesign analyses. For assessments of body size and gravidity, we collapsed data from multi-event surveys at Eliza Spring to one observation per individual. In the event of multiple observations of the same individual, we calculated the average size, and considered an individual to be gravid if it was noted as being gravid at least once during the same period (i.e., we assumed a falsenegative observation of gravidity was more likely than a false-positive). To facilitate comparisons of the number of recaptures among size, we calculated the number of captures and recaptures for Eliza using data from only the first (of three) secondary survey sessions.

Statistical Analyses

Abundance and Detection Probability

We used closed-population models to obtain estimates of within-period detection probability as well as population size for Barton Springs salamanders at Eliza Spring. These estimates do not rely on information between periods, negating the problem of individual growth changing natural marks and confounding photographic identification, which is of concern for small juveniles. During long intervals (e.g., periods > 1 month) between recaptures, growth of small juveniles is rapid, and their pigment patterns change, making it very difficult to identify recaptures using the photographic identification technique. Using this approach, rather than a complete-data approach

(i.e., estimating all Jolly-Seber parameters at once; Kendall et al. 1995), allows us to estimate abundance for all size classes.

We tested if body size, gravidity, and sedimentation affected within-period detection probability. Body size can influence detection because larger animals may be easier to see (and therefore capture) than smaller ones or may respond differently to the effects of the survey. Gravidity may influence detection, for example, if their proclivity for engaging in mating behavior influences how well they "hide" at the surface and how they respond to disturbance from the survey. Sedimentation may have a direct effect on observers, making it more difficult to see salamanders, although this effect should be the strongest on the first secondary survey day, as sediment is cleared out as the survey progresses.

We used a categorical body length variable for each size class. Using body size categories gives a straightforward way for us to estimate abundance by size class, and to relate our results to previous studies that relied on the same discrete size classes (Bendik and Dries 2018, Dries and Colucci 2018). We used the method described by Royle (2009) to model individual detection probability (p_i) as a function of size class and to estimate population size, N. This method uses Bayesian estimation with data augmentation to facilitate estimation of N, which we calculated for each period and size class. A fixed number of all-zero capture histories are added to the data set which is then modeled as a zero-inflated version of the complete-data model (Royle 2009, Kéry and Schaub 2012). First, we modeled individual detection probability (p_i) among k periods and t surveys as

$logit(p_{k,t,i}) = \alpha_{k,t} + \beta_{sizeclass}$

where $\alpha_{k,t}$ and $\beta_{sizeclass}$ represent fixed effects for time and size class, respectively. The β for the smallest size class was fixed at zero, such that each β indicates the difference with the smallest size (on the logit scale). Similarly, we examined the effects of gravidity on detection, and calculated abundances explicitly for gravid animals. We included a term for size to isolate the effect of gravidity from body size, as these are correlated (Spearman's $\rho = 0.28$). For all models with gravidity, we excluded immature individuals (< 22.5 mm) from the data set; therefore, only the largest two size classes were included. We assumed that the categorical distributions of unobserved individuals (for size and gravid status) was the same as the observed individuals. We later compared the estimated abundances of gravid individuals to spring-flow using simple linear regression.

Effects of gravidity may be confounded with sex effects; except for gravid status, we did not identify the sex of each salamander. So, we also compared the effect of gravidity on detection to the effect of ever being gravid ("ever-gravid"), as a better surrogate for female identification. A stronger effect (i.e., either more negative or more positive) of ever-gravid individuals could suggest that gravid status is indicating a sex effect, because sex would be more accurately identified within the data. A weaker effect would indicate that the ever-gravid classification dilutes the effect of gravidity, presumably because the true effect relates to the actual gravid status of an individual. However, the overall difference in sample size between groups is relatively small (19% gravid vs. 25% ever-gravid), so it is possible that only a small difference between coefficients is evident.

Finally, we tested whether sediment deposition (embeddedness) influenced detection probability. Substrate data collection was initiated in 2016, so we performed this analysis on a subset of the full data (n = 10 periods). As above, detection was modeled using a logistic function:

$$logit(p_{k,t,i}) = \alpha_{k,t} + \beta_{sizeclass} + \beta_0 * embeddedness_k.$$

Survival, Temporary Emigration and Migration Between Sites

We used robust design models to estimate survival and temporary emigration rates for Barton Springs salamanders at Eliza Spring. Temporary emigration occurs when individuals in a population are temporarily unavailable for capture—for example, when an animal within the sampled population has moved out of the sampling area but later returns. Some plethodontid salamander populations exhibit high levels of temporary emigration because a large proportion may be beneath the forest floor, whereby only a few individuals are available for capture at a given time (Bailey et al. 2004, Price et al. 2012).

By quantifying temporary migration, we can measure the prevalence of subterranean migration and the factors that influence it. The bottom of the Eliza Spring pool was filled with concrete in the early 1900's, except for formed outlets to convey the spring upwellings, so most of the baselevel substrate is impenetrable by salamanders except through those outlets. Therefore, based on the physical conditions at our study site, all migrants that eventually can return to the surface must retreat below ground, and this rate can be approximated by estimates of temporary emigration from capture-recapture data. However, our inference is limited to individuals that can be reliably identified based on their pigmentation patterns (see above).

We first fit a variety of models without covariates to determine the optimal structure for capture and recapture probabilities. We then modeled temporary-emigration and survival parameters either as fully time-varying (this assumes for each survey interval, survival and migration can change) or as a function of spring discharge and the change in spring discharge between periods as

$$logit(\theta_k) = \alpha + \beta_1 * inst_flow_k + \beta_2 * \Delta flow_k$$

where α and β are fixed effects representing the intercept and slopes (respectively) of the relationship between the survival or emigration parameters (θ) and streamflow covariates.

We used spring-flow (i.e., discharge) as a covariate because it is a dominant environmental driver in the Barton Springs system. It can affect the timing of reproduction in Barton Springs salamanders (Bendik and Dries 2018) and is correlated with various aspects of water quality (e.g., Mahler & Bourgeais 2013) that are important to the ecology and physiology of neotenic *Eurycea* (Fries 2002, Woods et al. 2010, Crow et al. 2016). Increases in flow may help flush additional animals to the surface via drift, but flow may also prompt compensatory movement back into the spring outlets, influencing the rate of temporary migration. Permanent migration back into the aquifer in response to discharge may also be reflected in the apparent survival parameter, which we refer to simply as "survival" in this document. Survival is "apparent" because the fate of each animal that permanently leaves the study area cannot ultimately be known without auxiliary information (e.g., from radio telemetry) (but see Schaub & Royle

2014). Thus, the survival parameter cannot help us distinguish between mortality and permanent emigration. In general, increasing flow is thought to be beneficial to Barton Springs salamanders, particularly recovering from drought conditions (Dries and Colucci 2018), so our expectation is that discharge may have a positive influence on actual survival, but high flow could prompt migration underground, producing an overall negative effect on apparent survival if migration is permanent. Thus, we do not have a strong a priori hypothesis for the direction of the effect of these discharge covariates. We used the instantaneous flow rate of the mean daily discharge from Barton Springs (obtained from https://waterdata.usgs.gov/tx/nwis/dv/?site_no=08155500). Change in flow (Δ flow) was calculated using the difference between the first and last day of the survey interval.

Higher discharge is also correlated with increased sedimentation (Mahler and Lynch 1999), which has negative effects on the number of salamanders observed at the surface (Bendik and Dries 2018). For this reason, we also quantified the amount of fine sediment deposition on habitat within Eliza Spring (see above). Ultimately, we excluded sediment cover as a covariate in this analysis because it was strongly correlated with discharge (Pearson's correlation: t = 5.92, df = 8, p-value = 0.00035, $\rho = 0.90$), and strongly correlated variables in a linear model will confound interpretation of the parameter estimates (Dormann et al. 2013).

We fit closed capture-recapture models using MCMC methods in MultiBUGS v1.0 (Goudie et al. 2017). Example BUGS code is provided in Appendix I. Convergence was checked by visually examining trace-plots. We fit the robust design data using maximum likelihood methods, as implemented in program MARK v. 9.0 (White 2015) and used Akieke Information Criterion corrected for small sample sizes (AICc) to compare the relative strength of each model. AICc is the most common form of multi-model inference used in capture-recapture studies. Where applicable, we used standard robust design model constraints to ensure parameter identifiability. This includes equating the last two temporary migration parameters when survival is fully time varying, and equating the last two capture probability estimates, when recapture probability is also estimated. Finally, we also quantify the amount of migration between sites by testing for the presence of salamanders that were recaptured at a different spring site.

Results

Summary of Site and Survey Conditions

We performed a total of 90 surveys from 2013 through 2018. Average survey times varied greatly by site (Table 2), probably due to the number of salamanders we captured and site conditions (e.g., turbidity).

Table 2. Summary of capture-recapture survey effort by site.

Site	Survey Days	Average Survey Time (person-minutes)	Average Time/m ² (min)		
Parthenia	12	245	3.75		
Eliza	46	1109	14.9		
Old Mill	12	157	1.12		
Upper Barton	20	278	6.95		



Species BASS (MICROPTERUS) CICHLIDAE OTHER FISH POECILIIDAE (GAMBUSIA) SUNFISH (LEPOMIS

Figure 6. Summary of fish data at Parthenia (A), Sunken Gardens (B) Upper Barton (C) and Eliza (D) springs. "Other fish" at Upper Barton Spring were mostly identified as either Texas or blacktail shiners (cyprinids). Darters were present at some sites but were not included in counts. Note each y-axis has a different scale.

The results of fish surveys are summarized in Figure 6. The assemblage of fish species observed at Parthenia spring was the most diverse, with sunfishes, bass and Rio Grande cichlids being the most abundant. Most fish observed within Eliza Spring and Old Mill were *Gambusia affinis*.

Occasionally cyprinid fish were observed at these sites as well. Cyprinids, namely Texas and blacktail shiners, were the most prevalent at Upper Barton Spring (denoted as "other fish").

Embeddedness was consistently the greatest at Sunken Gardens (Figure 7). Sunken Gardens also had the lowest measured value for dissolved oxygen (Figure 8). Measured spring-flow (i.e., discharge) values at Eliza and Sunken Gardens were similar and tended to follow a similar pattern of total discharge measured by the USGS (Figure 9). Spring-flow measured at Upper Barton was always the lowest and peaked in 2017, unlike the other sites which had peak flow values in 2016. This may be due to the influence of Barton Creek or measurement error at low flow values.



Figure 7. Percent embeddedness at Parthenia (A), Sunken Gardens (B) Upper Barton (C) and Eliza (D) springs. Values were averaged among all quadrats for each survey. Embeddedness was not quantified for Sunken Gardens in 2018 because moss obscured the substrate in most samples.



Figure 8. Dissolved oxygen measurements (mg/L) at Parthenia (A), Sunken Gardens (B) Upper Barton (C) and Eliza (D) springs from 2016–2018. Daily mean values of dissolved oxygen are shown for Parthenia spring as measured by the USGS; the remaining values are grab samples collected at the time of each survey.



Figure 9. Spring-flow measurements (ft³/s) at Barton Springs. The top three plots show spring-flow measured during surveys. The lower plot shows the combined spring-flow of Parthenia, Eliza and Old Mill springs as calculated by the USGS. Most of the water for the Barton Springs complex issues from Parthenia Spring. Upper Barton Spring was noted as dry on 8 August 2018. Note each y-axis has a different scale.

Austin blind Salamanders

Austin blind salamanders represented 1.2% (46 of 3940 individuals) of the total number of individual salamanders observed during this study. Low sample sizes precluded statistical comparisons, so we present data summaries only. Most individuals were small juveniles (Figure 10) observed at Eliza Spring (Figure 11), none were gravid, and we did not document any recaptures between periods. Some individuals identified as *E. waterlooensis* may have been hybrids (Figure 12). Similarly, some individuals identified as Barton Springs salamanders may have also been hybrids, which is supported by results from recent genetic work (City of Austin 2018). We did not attempt to separate individuals by their putative hybrid status (i.e., to put them into a third group), but judgements were made to determine which species to assign the identification to. It is possible that hybrids exhibit different behaviors and demographic rates

compared to pure individuals, but without a consistent and reliable way to identify each individual, this will remain a source of "noise" in our data with respect to characterizations of each species.



Figure 10. Body size histogram (body length) for all Austin blind salamanders photographed from 2014 through 2018.



Figure 11. Total observations of Austin blind salamanders by date at all sites. No individuals were recaptured. Most Austin blind salamanders were observed in Eliza Spring (43 out of 46). We did not observe any Austin blind salamanders at Upper Barton Spring.



Figure 12. Comparison of hybrid and "pure" Austin blind and Barton Springs salamanders. A-Barton Springs salamander; **B** & C-putative hybrids; **D**-Austin blind salamander. Individuals B and C were included in the *E. waterlooensis* data summary.



Figure 13. Number of captures and recaptures of Barton Springs salamanders during each survey at Parthenia (A), Sunken Gardens (B) Upper Barton (C) and Eliza (D) springs. Captures and recaptures for Eliza were calculated using data from only the first of three secondary survey sessions to facilitate comparison with the other sites. Surveys with zero captures are not shown (see Figure 15).



Figure 14. Body size histogram for all Barton Springs salamanders recaptured between periods at Eliza Spring from 2014 through 2018. The red line indicates the size cutoff for individuals included in the robust-design analysis.



Figure 15. Number of observations of Barton Springs salamanders during each survey at Parthenia (A), Sunken Gardens (B), Upper Barton (C) and Eliza (D) springs. Total count includes individuals that were tallied as "missed" as well as photographed salamanders during each survey event. Note each y-axis has a different scale.

Barton Springs Salamanders

Barton Springs salamanders represented 98.8% of the total number of salamanders observed during this study. We captured 3,894 salamanders (excluding within-period recaptures), 89% of which were from Eliza Spring (from both increased survey efforts and higher abundances). Very few salamanders were recaptured at Parthenia, Sunken Gardens and Upper Barton spring, whereas recaptures were encountered during every Eliza Spring survey, even after accounting for the higher survey efforts at Eliza (Figure 13). Ultimately, no statistical population modeling was performed for Parthenia, Sunken Gardens or Upper Barton springs because of these challenges. No salamanders were recaptured at a site different from the site of origin. Thus, we found no evidence of migration, although samples sizes were low for three of the four sites. The smallest salamander that was recaptured between periods was 10.5 mm in body length, and 17.3 mm total length. Individuals < 15 mm body length were excluded from the robust-design analysis (determined a priori), which corresponded to the 5th percentile of size for individuals recaptured between periods (Figure 14). The total number of observed salamanders, resulting from the sum of "missed" salamanders plus those captured and photographed are comparable to naïve counts as used previously (e.g., in Dries et al. 2013, Bendik and Dries 2018, Dries and Colucci 2018). A total of four surveys resulted in no salamander observations, one at Parthenia, two at Sunken Gardens, and one at Upper Barton (excluding dry periods) (Figure 15). Gravid females represented 6% of our observations. The smallest gravid individual was 21.2 mm, although 90% of gravid individuals were 26.8 mm or larger (Figure 16). The proportion of gravid individuals also increased with body size (Figure 16). Gravidity within the Barton Springs salamander population appears to peak between October and March, although gravid individuals may be encountered year-round (Figure 17). Gravidity was not observed without error, as 17% of gravid individuals noted as gravid were also recorded as being non-gravid at another time during the same survey period (i.e., within a week). It is possible some individuals laid their eggs between observations, but mismatches were evenly split between whether they were observed as gravid or non-gravid at first observation.



Figure 16. Body size histogram (body length) for all Barton Springs salamanders photographed at Parthenia (A), Sunken Gardens (B), Upper Barton (C) and Eliza (D) springs. Note that each y-axis has a different scale.



Figure 17. Total number of gravid individuals observed by site and season for all surveys. Numbers above bars represent percent of gravid individuals observed out of all individuals greater than 24 mm body length.

Abundance and Detection Probability

We estimated abundance (Figure 18, Figure 19) and detection probabilities (Figure 20) using closed-population models from 15 primary sampling periods (May 2016 was an incomplete survey and was excluded from capture-recapture analyses). We found that two largest size classes were more likely to be detected compared to the smallest size class ($\beta_{\text{large v. small}} = 0.41$, 95% CRI = 0.25–0.59; $\beta_{\text{medium v. small}} 0.47$, 95% CRI = 0.35–0.58). The average detection probability for a single survey at Eliza, excluding the effects of size and conditional on an individual being present in the study area, was 35%. The average probability of detecting an individual at least once during a 3-day survey period was 72%, indicating that our survey technique was relatively efficient at sampling the Barton Springs salamander population at Eliza Spring. These results were also consistent with self-reported misses (where salamanders escaped capture). On average, 32% of small individuals were reported as "missed", whereas 14% and 20% of medium and large individuals were reported as missed (across all surveys and sites

where n > 10). The average percentage of all salamanders missed was 19% of the total salamanders observed.

Our analysis indicated that gravidity had a positive effect on detection rates ($\beta_{\text{gravid}} 0.27, 95\%$ CRI = 0.04–0.51), although because size is positively correlated with both detection and gravidity, there was a weak negative association between the coefficients for size and gravidity during each MCMC iteration. In other words, there is some confounding between these parameters, making it difficult to test for the effect of gravidity, completely independent of size. The effect of ever-gravid was slightly weaker than the base gravid effect ($\beta_{\text{evergravid}} 0.19, 95\%$ CRI = -0.016–0.40), which gives some indication that the effect of gravidity is not simply a surrogate for a sex effect. There was a positive, but weak, statistical relationship between the proportion of gravid individuals and average spring-flow (p = 0.06; adjusted $R^2 = 0.17$; Figure 21).

Using a subset of the full data, we did not find strong evidence that embeddedness influenced detection probabilities. The mean estimate of the slope for the effect of sediment on detection was 0.23, but the 95% CRI for this estimate was wide and spanned zero (-0.36, 0.80).

The distribution of size classes throughout the study was variable and did not appear to be correlated to season (Figure 19). For example, of four surveys occurring in late winter (February and March), there were no consistencies in which size class was most abundant—small juveniles were most abundant during the winter of 2017 and 2018, while the other two size classes each were most abundant for 2015 and 2016.

Total abundance during the three-year period varied from 93–820 (Figure 19). The highest abundances of salamanders during our study occurred in the first three quarters of 2018 at Eliza Spring, and this pattern was consistent among species and across sites (Figure 11, Figure 13 & Figure 19). Counts within Parthenia Spring were also highest during this same period (data not shown).



Size Class < 25 mm 25-50 mm > 50 mm

Figure 18. Estimated surface abundance of Barton Springs salamanders at Eliza Spring from October 2014 through November 2018 by size class with 95% credible intervals.



Figure 19. Estimates total surface abundance (with 95% credible intervals) of Barton Springs salamanders at Eliza Spring from October 2014 through November 2018.



Figure 20. Estimates of mean detection probability (probability of capture, conditional on the salamander being present in the study area) for each secondary survey event at Eliza, excluding the effects of covariates. Alternating shaded and non-shaded regions represent primary sampling periods.



Figure 21. Proportion of gravid salamanders vs. mean spring-flow at Eliza Spring with trendline and standard error (shaded region).

Survival and Temporary Emigration

Models including flow covariates (instantaneous flow rate and change in flow) as a function of survival (φ) outperformed models that included only time variation in parameters (Table 3) and models that included covariates on temporary emigration (γ " and γ '). Additionally, models where capture (p) and recapture probability (c) were equivalent outperformed models where recapture probability was estimated separately. Because instantaneous flow rates and change in flow can be temporally correlated, we also added year as a grouping factor on survival, although this still performed more poorly compared to models including covariates (Table 3). We excluded the year effects model and the fully time-varying model from our model-averaged estimates because of problems with extrinsic non-identifiability (boundary estimates) on several survival parameters.

Table 3. Table of model selection results based on AICc for the top seven models. φ = apparent survival; γ'' = unavailable at the surface | present during the last survey; γ' = unavailable at the surface | unavailable during the last survey; p = capture probability; c = recapture probability. (t) represents full time variation (excepting constraints) for survival and migration parameters whereas (t, t) represents within and between period variation for detection probabilities.

Model	AICc	Delta	AICc	Num.	Deviance	-2log(L)
		AICc	Weights	Par		
$\varphi(\text{inst_flow x } \Delta \text{flow}) \gamma''(t) \gamma'(t) p = c(t,t)$	10676.72	0.00	0.64	76	11653.9	10521.2
$\varphi(\Delta \text{flow}) \gamma''(t) \gamma'(t) p = c(t,t)$	10680.29	3.57	0.11	74	11661.7	10529.0
$\varphi(\text{inst}_flow + \Delta flow) \gamma''(t) \gamma'(t) p = c(t,t)$	10680.45	3.73	0.10	75	11659.7	10527.1
$\varphi(\text{year}) \gamma''(t) \gamma'(t) p = c(t,t)$	10680.62	3.91	0.09	75	11659.9	10527.2
$\varphi(t) \gamma''(t) \gamma'(t) p = c(t,t)$	10682.43	5.71	0.04	84	11642.8	10510.2
$\varphi(\text{inst}_flow) \gamma''(t) \gamma'(t) p = c(t,t)$	10683.18	6.47	0.03	74	11664.6	10531.9
$\varphi(t) \gamma''(t) \gamma'(t) p(t,t) c(t,t)$	10687.97	11.25	0.00	99	11616.7	10484.0

Monthly survival rates ranged between 0.83 and 0.98 (Figure 22), which corresponds to yearly survival rates between 0.11 and 0.78. Most estimates of temporary emigration were above 0.50 (Figure 22), indicating that a large portion of the population is often unavailable for capture at any given time. However, estimates had low precision for the latter three periods (in 2018). This period also coincided with a large population boom and decline (Figure 19).

Typical recaptures were not observed for at least one period before being observed again, which is consistent with the high estimates of temporary emigration. The median time for between-period recaptures was 105 days. In some cases, individuals were not observed for several survey periods before being recaptured (Figure 23). For example, 18% of recaptured individuals (n = 66) were not seen for more than one year at some point during the study, and 13 individuals had at least a two-year stint between observations.



Figure 22. Model-averaged estimates of (monthly) apparent survival (A), and the probabilities of temporary emigration for moving away (B) and remaining away (C) between survey periods. Dates of the x-axis correspond to estimates for the time interval ending at that date.



Figure 23. Histogram of the maximum number of days between two successive capture events, out of all individuals that were recaptured at least once.

The most optimal model for survival included an interaction between instantaneous flow and the change in flow during the survey interval (Table 3). This model predicts that when flow is increasing or unchanged between periods, survival has a positive relationship with flow rate (Figure 24). That is, higher rates of discharge from the spring result in higher survival of salamanders. However, the predicted relationship reverses when flow decreases. When flow decreases between intervals, higher flow rates are negatively associated with survival (Figure 24).



Figure 24. Predicted survival vs. instantaneous flow rates (inst_flow) under different scenarios of changing flow rate (Δ flow ft³/s). Predicted values are shown for the range of flow rates observed during the study (Δ 14 ft³/s = 1 standard deviation). Note each y-axis has a different scale.



Figure 25. Scatterplot of change in spring-flow rate (Δ flow) vs. instantaneous flow rate (inst_flow) for each survey. Each quadrant indicates a different combination of flow conditions and relationship with survival. Values shown were z-scored by subtracting the mean and dividing by the standard deviation, such that values of 0 correspond to the mean and values of -1 and 1 correspond to one standard deviation above and below the mean.

Figure 25 shows the relationship between the measured covariate values and their associated survey period, which helps illustrate several important points to consider when interpreting these results. First, not all combinations of flow conditions were sampled evenly (i.e., the number of samples varies by each quadrant in Figure 25). For example, flow can only increase so much during "low flow" (top left quadrant in Figure 25) before it becomes "high flow" (top right quadrant in Figure 25). Second, flow conditions are also temporally correlated to some degree, but were modeled as independent samples. This results in an artificial inflation of sample size and can affect our inference. However, to the extent that an arbitrary grouping of year represents this temporal correlation of conditions, the flow covariate model still performed better (Table 3). Additionally, it is also important to note that models without the interaction term (Table 3) were also competitive (e.g., Δ AIC values < 10; Burnham and Anderson 2002). In each case, Δ flow had a negative relationship with survival, while instantaneous flow was positively correlated with survival (coefficient values not shown).

Discussion

For more than 20 years the City has relied on counts to makes inferences about population health and dynamics, life history, and ecology of the salamanders that inhabit Barton Springs (Hansen

1999, City of Austin 2011, Dries et al. 2013, Bendik and Dries 2018, Dries and Colucci 2018). Using capture-recapture methods, where individuals can be observed over time and observations can be corrected for detection error, we have been able to expand our knowledge of these species beyond what has been possible using count-based methods. Robust-design data collected at Eliza Spring allowed us to report for the first time estimates of population size, survival and temporary emigration for Barton Springs salamanders. In some cases, lack of recaptures yielded results similar to counts. However, even in those cases, examination of each individual has provided additional information beyond just enumeration (e.g., reproductive status, body size), and the lack of recaptures also provides some clues about the ecology of these animals.

Austin blind salamanders were infrequently observed at the surface and were never recaptured. These salamanders are subterranean specialists (troglobites), and therefore their uncommon occurrence at the surface is not unusual (Hillis et al. 2001). Furthermore, all individuals observed were sexually immature (< 60 mm total length; Hillis et al. 2001). One possible explanation for the lack of occurrence of adults at the surface may be that juveniles are flushed to the surface by water currents, whereas adults may be able to actively avoid the surface because they are stronger swimmers. Juveniles may drift "downstream" with the current because of high flows, or as an active dispersal mechanism, as similar patterns have been observed in stream-dwelling salamanders (Stoneburner 1978, Bruce 1986, Fenolio et al. 2014, Bendik et al. 2016). At the same time, adults may actively avoid the surface because predation risk is probably higher for pale, blind animals. It has been speculated that Austin blind and other related blind salamanders may be able to detect light, despite the lack of an image forming lens in their eyes (Hillis et al. 2001). The most recent observation of an adult Austin blind salamander was at Upper Barton Spring shortly after dark on November 16, 2013 (TJD personal observation; photo voucher TNHC 92949). Thus, it could be that adults only forage on the surface at night, when sighted predators are less of a threat. Whatever the mechanism, their relatively low abundances and strong size bias towards juvenile Austin blind salamanders at the surface is consistent with previous observations (Hillis et al. 2001). The lack of recaptures of Austin blind salamanders may be a function of their low numbers and small size. Juvenile Barton Springs salamanders had a statistically lower chance of being recaptured, and the same probably holds true for Austin blind salamanders. Austin blind salamanders may also have lower survival at the surface, which may explain their low observed abundances as well as their low recapture rates. Alternatively, they may not inhabit the surface for long before returning underground, which would also negatively affect their recapture rate.

The relative frequency of Austin blind salamanders compared to Barton Springs salamanders was very small, but also consistent with previous observations. For example, Hills et al. (2001) note that visual encounter surveys from 1998–2000 documented 1535 salamanders, only 1.1% of which were Austin blind salamanders, similar to our observations (1.2%). One difference between these and previous observations is Austin blind salamanders have been most abundant at Sunken Gardens Spring (Hillis et al. 2001, City of Austin 2003) whereas most of our observations were at Eliza Spring. This may be a consequence of habitat changes at Sunken Gardens. For example, the spring pool was gradually excavated from 2005–2012 to lower the level of the pool bottom, and several changes have been made to the outflow configuration

(Robinson 2019). These changes may have been detrimental to Austin blind salamanders (such as lower survival at the surface) or made it more difficult for them to be observed (e.g., more likely to move downstream, or less likely to enter the habitat from the aquifer). Alternatively, some change may have occurred in the aquifer affecting the abundance, distribution and/or dispersal of Austin blind salamanders, reducing their frequency at the surface.

For Barton Springs salamanders, Eliza and Parthenia springs continue to be the sites that exhibit the highest densities, which is consistent with previous data (Dries et al. 2013, Bendik and Dries 2018, Dries and Colucci 2018). Surveys resulting in zero salamander observations also continue to occur periodically at Parthenia, Upper Barton and Sunken Gardens springs. Site-specific differences in salamander presence and abundance may be partly attributed to differences in flow regime characteristics (Dries and Colucci 2018) and other environmental conditions at each site. For example, we observed differing levels of embeddedness and different fish assemblages at each site. Additionally, aquifer flow routes can differ between sites, which may influence the probability and magnitude of immigration to the surface. For example, the groundwater basin for Upper Barton Spring is small compared to the others and receives a large portion of recharge from an urbanized area (Hauwert et al. 2004a, Hunt et al. 2019). Additionally, Sunken Gardens Spring receives a larger share of water from the saline zone within the aquifer (Hauwert et al. 2004a, Hunt et al. 2019). Eliza and Parthenia springs have the most similar source-water profiles based on dye-trace data and water chemistry (Hauwert et al. 2004a, 2004b, Hunt et al. 2019), and typically exhibit the highest densities of salamanders (Dries and Colucci 2018). The lack of migration between sites, indicated by a lack of between-site recaptures, also suggests that the spring populations are isolated from each other. Site-specific similarities or differences in population size are therefore not mitigated by migration but are likely a consequence of their unique surface and subterranean habitat characteristics.

Peak abundances for both Austin blind and Barton Springs salamanders occurred in 2018. This population boom (or "bonanza"; Morris and Doak 2002) followed an extended period of high spring-flow in 2016 and 2017. If population booms occur at the same time for both species, this could be in response to the same environmental conditions that promote reproduction and migration to the surface. Both species occur not just at the springs, but within the aquifer; Austin blind salamanders are presumably obligate aquifer-dwellers (Hillis et al. 2001) whereas Barton Springs salamanders are abundant near spring outlets (this study; Bendik and Dries 2018, Dries and Colucci 2018), but have also been found in wells (McDermid et al. 2015, TJD, pers. obs.) and within the stream in Blowing Sink Cave (Bendik et al. 2013, Devitt and Nissen 2018), each of which are more than 200 feet below ground. Pulses in relative abundance of juveniles tend to occur following periods of high flow (Bendik and Dries 2018). Similarly, the population boom we observed starting in February 2018 coincided with high flows extending through the previous year. The exact timing of these events seems to vary, but the peak lagged correlation is 9 months, based on small juvenile count data (Bendik and Dries 2018). Bendik and Dries (2018) postulated that salamanders may be exhibiting an increase in reproduction in response to greater food availability, as energy enters the aquifer from recharging creeks in the form of particulate and dissolved organic matter and travels up through the food chain. In a study of cave-dwelling salamanders in the eastern U.S., salamander density and biomass has been shown to increase in

response to the experimental addition of organic carbon into the ecosystem (Huntsman et al. 2011). The hypothesis linking organic matter to secondary production in Barton Springs salamanders gains some support from our finding that gravidity was positively associated with spring-flow. However, these population booms tend to occur as spring discharge is declining from a peak, rather than when discharge is increasing or steady at high levels. Thus, another explanation is that salamanders move out of perched voids and other habitats within the Edwards Aquifer as the water table drops, possibly resulting in increased chances of finding mates (if individuals were widely dispersed), dispersal in response to higher densities, or both. The presence of perched reservoirs within the aquifer are plausible based on temporal patterns of recharge and discharge within the Barton Springs segment (Wong et al. 2012), and these areas may be habitat for salamanders when they are filled with water.

In addition to associations between reproduction and spring-flow, there was also a strong statistical relationship between spring-flow and survival. Flow rate and change in the flow were important predictors in models explaining apparent survival, compared to models without covariates. Based on results from the top model, changes in apparent survival in response to spring-flow depended on whether flow was increasing or declining. Low flow rates were typically associated with lower apparent survival, except when flow had a large decline (from high values). Although, even in this case, predicted values of survival were higher for high-flow conditions on the decline compared to low-flow conditions on the incline (compare values along y-axis in Figure 24). This may mean that mortality was higher, or that individuals permanently migrated back into the aquifer (or downstream) at a higher rate, under stable or increasing lowflow conditions. Several competing models included flow covariates but no interaction term, suggesting that simpler explanations to the relationship between flow and survival are plausible. In these cases, changing flow had a negative relationship with survival, and instantaneous flow had a positive relationship. As noted in the results, the small number of surveys and the lack of independence in the analysis of flow data could affect this conclusion. In general, our prediction of a positive relationship between survival and spring-flow has some support from the data. Additionally, there is some indication that the relationship between survival (which includes both mortality and permanent migration) and spring-flow is not linear.

At this point, we can only speculate as to the mechanism of why spring-flow and changes in this rate would affect salamander mortality or migration. Spring-flow is correlated with several other physical and chemical characteristics of the springs and salamander habitat. For example, flow and dissolved oxygen concentrations broadly follow a very similar pattern (Mahler and Bourgeais 2013), and dissolved oxygen is important for salamander survival. However, we did not observe flow rates low enough to decrease dissolved oxygen to critical levels that would begin to affect predicted survival rates according to a laboratory study on a related species, *Eurycea nana* (< 4.5 mg/l; Woods et al. 2010). Spring-flow may be associated with food availability at the surface or in the aquifer and these questions are the subject of ongoing investigations, although data are not available yet. Spring-flow was positively correlated with embeddedness, which can limit the available space for salamanders to find cover at the surface. In general, higher spring-flow increases sedimentation (Mahler and Lynch 1999), which has negative effects on salamander counts at the surface, presumably because it reduces their

available cover (Bendik and Dries 2018). However, if there is density-dependent competition for space (i.e., cover), we would expect this to reduce apparent survival, which is the opposite of what we observed. If the apparent survival pattern we observed is a consequence of permanent migration rather than mortality, it could be that high flow rates make returning to the aquifer (permanently) more difficult because of water velocities through underground conduits. During these conditions, salamanders may be more likely to remain in and around the surface (i.e., including accessible near-subterranean habitats associated with the "superpopulation") simply because of physical constraints of their habitat. However, we did not observe this pattern with temporary emigration, which would be expected if flow velocities were affecting the ability of salamanders to move underground. Without knowledge of the structure of this habitat, flow velocities within migration pathways, and/or direct movements and swimming performance of salamanders, this is highly speculative. Spring-flow is not strictly seasonal, and patterns of abundance do not seem to follow any seasonal patterns either (this study; Bendik and Dries 2018). Other central Texas Eurycea exhibit stronger seasonal patterns in population dynamics than we observed (e.g., Pierce et al. 2014), although this could be related to the stronger effects season has on patterns of spring-flow at smaller springs (Bendik 2017). Collectively, our observations and statistical results add further support to the hypothesis that spring-flow dynamics are an important (if not the most important) aspect of this ecosystem that influences the population dynamics of Barton Springs salamanders at Barton Springs.

The conditions that promote temporary movements underground or to the surface at Eliza Spring remain unclear. Neither flow covariates were supported as explanatory variables for either temporary emigration parameters, although these were important for survival. Simulation studies of robust-design models have shown that it can be difficult to estimate the probability of staying away from the site (γ '), as it can have problems with identifiability and is correlated with estimates of survival (φ) (Rankin et al. 2016, Gibson et al. 2018). It may be useful to explore questions of identifiability in the future using simulations based on the parameter values observed in this study, to better understand the consequences of different parameterizations.

One long-standing question regarding the ecology of Barton Springs salamanders has been whether they are primarily surface-dwellers or a subterranean species that gets flushed out to the surface (Sweet 1978, Chippindale et al. 1993). At the time the species was federally listed, and the HCP was in development, biologists believed that small numbers (e.g., a maximum of 45 during surveys from 1993 through 1996 in Barton Springs Pool) observed at the surface meant that Barton Springs salamanders were "particularly subject to" extinction (City of Austin 1997). Similarly, Dries and Colucci (2018) note that the "maximum observed abundance…is small enough for this species to be considered at risk of extinction by several rules-of-thumb." These statements imply that Barton Springs salamanders are viewed as a predominantly surfacedwelling species, a view initially espoused by Chippindale et al. (1993) in the species description.

Our results indicated that, on average, more than half of the population associated with the surface is underground, and unavailable for capture, at any given time. The presence of a "superpopulation" of salamanders consisting of individuals that move between the surface and subterranean "near-surface" areas is demonstrated by the high performance of models that

included temporary emigration compared to those that did not (Appendix I). Some individuals were also not seen for long periods of time (> 1 y), suggesting that salamanders may travel into the aquifer and return to the surface of Eliza Spring much later. Without robust-design data for the remaining sites, it is not possible to exclude other hypotheses, for example, that migration is unidirectional from the subsurface to the surface, effectively making these surface habitats a population sink. Recapture rates were very low at these sites, suggesting that when relative abundances were zero, extirpation (from the surface) and recolonization (from the aquifer) could have been occurring. For example, no recaptures were encountered after a zero-count at Upper Barton in late 2016, and none were observed prior to, or between, zero counts for a two-year period at Sunken Gardens (see Figure 13 & Figure 15). Based on VIE batch marks at Upper Barton spring from a previous study, salamanders were recaptured from before a dry spell at that site, indicating that some individuals do return to the surface, although the recapture frequency was low (City of Austin 2009, 2010, 2011, 2013).

Other ecological data indicate the use of subterranean habitat by Barton Springs salamanders. The lack of observations of eggs in surface habitats (e.g., under rock substrates) during this study, and the sparsity of those observations over the course of 25 years of surveys at Barton Springs is clear evidence that these salamanders must spend some portion of their life cycle underground to reproduce. Additionally, given the distance from the springs that subterranean observations of Barton Springs salamanders have been made (up to at least 300 feet underground, miles from any springs; McDermid et al. 2015, Devitt and Nissen 2018), some individuals probably never occupy surface habitat. The presence of hybrid individuals at the surface also suggests use of subterranean habitat by Barton Springs salamanders. Given that adult Austin blind salamanders are very rarely observed at the surface, mating between species probably takes place within the aquifer. Based on these observations and our results, we conclude that, for populations near the springs, both surface and subterranean habitats are extensively used, and that subterranean habitat is required to complete their life cycle. Thus, Barton Springs salamanders are not strictly subterranean dwellers (although some populations may be) that are only flushed out to the surface, nor are they primarily surface-dwellers.

Having a large proportion of the population away from the surface and unavailable for capture poses a challenge for understanding extinction risk, which is important for endangered species conservation, management, and recovery. For example, population viability analyses (PVA) (e.g., as required by the Recovery Plan; U.S. Fish and Wildlife Service 2016) require estimates of population size or other vital rates and their and temporal variability (Morris and Doak 2002), each of which can only be obtained for near-surface populations and are partly confounded with movement below ground. For example, the result of a PVA based only on surface population size would lead to an overestimate of extinction risk. While smaller populations are at higher risk of extinction, a decreasing surface population decline. Thus, assessments of population viability would need to take these factors into consideration. However, for Barton Springs and Austin blind salamanders that have cryptic life histories, acquiring the data needed for such an analysis is not practical at this time. Rather than a relying on the outcome of PVAs, focusing on population representation, resiliency, and redundancy ("the three Rs") may provide a more

flexible, efficient framework for evaluating species recovery (Shaffer and Stein 2000, Wolf et al. 2015).

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Appendix I- Example BUGS code for closed-population models

```
#code adapted from Kéry and Schaub (2012) chapter 6.
model {
  # Priors
    for(k in 1:n.per) {
      for (s in 1:3) { #size classes
    omega[k,s] ~ dunif(0, 1)
                     }
    for (j in 1:T) {
    alpha[k,j] <- log(mean.p[k,j]/(1-mean.p[k,j]))</pre>
    mean.p[k,j] ~ dunif(0,1)
    }#j time
    }#k periods
    for (n in 2:3) {
    beta[n] \sim dnorm(0, 0.001)
    } # n size groups
    beta[1] <- 0 #corner constraint</pre>
  # Likelihood
     # size[i] ~ dcat(pi[period[i],1],pi[period[i],2],pi[period[i],3]) #This
might work in OpenBUGS, but JAGS does not like this formulation.
      for (i in start[1]:end[1]) {
       size[i] ~ dcat(pi1[])
      }
      for (i in start[2]:end[2]) {
       size[i] ~ dcat(pi2[])
      }
      for (i in start[3]:end[3]) {
       size[i] ~ dcat(pi3[])
      }
      for (i in start[4]:end[4]) {
       size[i] ~ dcat(pi4[])
      }
      for (i in start[5]:end[5]) {
       size[i] ~ dcat(pi5[])
      }
      for (i in start[6]:end[6]){
       size[i] ~ dcat(pi6[])
      }
      for (i in start[7]:end[7]) {
       size[i] ~ dcat(pi7[])
      }
      for (i in start[8]:end[8]){
       size[i] ~ dcat(pi8[])
      }
      for (i in start[9]:end[9]) {
       size[i] ~ dcat(pi9[])
      }
      for (i in start[10]:end[10]) {
```

```
size[i] ~ dcat(pi10[])
      }
      for (i in start[11]:end[11]) {
       size[i] ~ dcat(pi11[])
      }
      for (i in start[12]:end[12]) {
       size[i] ~ dcat(pi12[])
      }
      for (i in start[13]:end[13]) {
       size[i] ~ dcat(pi13[])
      for (i in start[14]:end[14]) {
       size[i] ~ dcat(pi14[])
      }
      for (i in start[15]:end[15]) {
       size[i] ~ dcat(pi15[])
      }
    for (i in 1:n.ind) {
    z[i] ~ dbern(omega[period[i],size[i]])
    for (j in 1:T) {
    y[i,j] ~ dbern(p.eff[i,j])
    p.eff[i,j] <- z[i] * p[i,j]</pre>
    p[i,j] <- 1 / (1 + exp(-lp[i,j]))
    lp[i,j] <- alpha[period[i],j] + beta[size[i]] #combination of time and</pre>
size class effect
    } #j is for n occasions
    } #i is for n individuals
  #Derived Parameters
    #Period-specific total abundances
    for (l in 1:n.per) {
    Nper[1] <- sum(z[start[1]:end[1]]) # # Derived quantities</pre>
    } #l is for n periods
    #Size+period-specific total abundances
    for (i in 1:n.ind) {
    #size is assigned whether z = 1 or not, so must condition on z = 1,
otherwise sum of size equals size of augmented data
     s1[i] <- equals(size[i],z[i]) #if z is 1, animal is real; if size =1,</pre>
then s1 = 1
      s2[i] \le equals(size[i],(z[i]*2))#if z is 1, animal is real (and 1*2 = )
size 2), then s2 = 1, else 0
      s3[i] <- equals(size[i],(z[i]*3))</pre>
     }
      for (l in 1:n.per) {
         N[1,1] <- sum(s1[start[1]:end[1]]) #sum each size class for size-
specific estimate of N for each period
         N[1,2] <- sum(s2[start[1]:end[1]])</pre>
         N[1,3] <- sum(s3[start[1]:end[1]])</pre>
      } #l is for n periods }
```

Appendix II- Robust-Design Model Selection Results

		Delta	AICc	Model	Num.		
Model	AICc	AICc	Weights	Likelihood	Par	Deviance	-2log(L)
$\varphi(\text{inst}_f\text{low x } \Delta f\text{low}) \gamma''(t) \gamma'(t) p = c(t,t)$	10676.72	0.00	0.64	1	76	11653.9	10521.2
$\varphi(\Delta flow) \gamma''(t) \gamma'(t) p = c(t,t)$	10680.29	3.57	0.11	0.1672	74	11661.7	10529.0
$\varphi(\text{inst}_f\text{low} + \Delta \text{flow}) \gamma''(t) \gamma'(t) p = c(t,t)$	10680.45	3.73	0.10	0.154	75	11659.7	10527.1
$\varphi(\text{year}) \gamma''(t) \gamma'(t) p = c(t,t)$	10680.62	3.91	0.09	0.1402	75	11659.9	10527.2
$\varphi(t) \gamma''(t) \gamma'(t) p = c(t,t)$	10682.43	5.71	0.04	0.057	84	11642.8	10510.2
$\varphi(\text{inst}_f\text{low}) \gamma''(t) \gamma'(t) p = c(t,t)$	10683.18	6.47	0.03	0.039	74	11664.6	10531.9
$\varphi(t) \gamma''(t) \gamma'(t) p(t,t) c(t,t)$	10687.97	11.25	0.00	0.0036	99	11616.7	10484.0
$\varphi(t) \gamma''(t) \gamma'(.) p = c(t,t)$	10703	26.31	0	0	73	11686.5	10553.8
$\varphi(\text{inst}_f\text{low} + \Delta f\text{low}) \gamma''(t) \gamma'(\text{inst}_f\text{low} + \Delta f\text{low}) p = c(t,t)$	10703.49	26.80	0	0	65	11703.6	10570.9
$\varphi(t) \gamma''(t) \gamma'(t) p(t) c(t)$	10720.68	43.98	0	0	69	11712.5	10579.8
$\varphi(t) \gamma''=\gamma'(.) p=c(t,t)$	10730.12	53.43	0	0	72	11715.7	10583.0
$\varphi(\text{inst}_f\text{low} + \Delta \text{flow}) \gamma'' (\text{inst}_f\text{low} + \Delta \text{flow}) \gamma'(t) p = c(t,t)$	10733.52	56.82	0	0	65	11733.6	10601.0
$\varphi(.) \gamma''(.) \gamma'(.) p = c(t,t)$	10801.26	124.56	0	0	48	11836.5	10703.9