Herpetological Conservation and Biology 10(2):740–752.
Submitted: 27 January 2015; Accepted: 2 April 2015; Published: 31 August 2015.

LIFE HISTORY AND DEMOGRAPHIC DIFFERENCES BETWEEN CAVE AND SURFACE POPULATIONS OF THE WESTERN SLIMY SALAMANDER, *PLETHODON ALBAGULA* (CAUDATA: PLETHODONTIDAE), IN CENTRAL TEXAS

STEVEN J. TAYLOR[1], JEAN K. KREJCA[2], MATTHEW L. NIEMILLER[1], MICHAEL J. DRESLIK[1], AND CHRISTOPHER A. PHILLIPS[1,3]

[1]Illinois Natural History Survey, Prairie Research Institute, University of Illinois at Urbana-Champaign, 1816 S Oak St., Champaign, Illinois 61820, USA, e-mails: sjtaylor@illlinois.edu, mniemill@illinois.edu, dreslik@illinois.edu
[2]Zara Environmental, LLC, 1707 W FM 1626, Manchaca, Texas 78652, USA, e-mail: jean@zaraenvironmental.com
[3]Corresponding author, e-mail: chrisp@inhs.illinois.edu

Abstract.*—The Western Slimy Salamander (*Plethodon albagula*) in central Texas is known from both surface and cave environments. Threshold species, such as *P. albagula*, may be excellent candidates to study potential differences in life-history traits during the evolutionary transition from surface into subterranean habitats. We conducted a 29-mo mark-recapture study of a surface and a cave population in Bell County, Texas, USA, to determine whether these populations differed in body size, growth rate, age at sexual maturity, and life span. We employed a growth model to estimate growth rate, age at sexual maturity, and life span, and an open population model to estimate population size, density, catchability, and survival rates. Salamanders were smaller on average and reached a smaller maximum size in the surface population compared to the cave population, which was skewed toward larger, older individuals. Growth trajectories were similar between populations, but the cave population reached sexual maturity faster (0.9–1.4 y) than the surface population (1.5–2.2 y). Survival rates were similar between populations. Although population size estimates were 10 times higher for the surface compared to the cave population, densities were similar between sites suggesting that habitat availability alone could explain population size differences. *Plethodon albagula* exhibits plasticity in growth, body size, and development, which may be adaptive and a function of extreme variation in surface environmental conditions. Subterranean habitats may be important for the long-term persistence of local populations, which may persist for years in subterranean habitats.

Key Words.—body size; demography; density; Fort Hood; growth; habitat; life span; subterranean; troglophile

INTRODUCTION

Caves are particularly challenging and extreme habitats because of sensory limitations associated with perpetual darkness (Culver 1982; Culver and Pipan 2009). In general, cave ecosystems are also energy limited and nutrient poor, lacking photoautotrophic primary production and typically limited influx of allochthonous organic matter (Culver 1986; Poulson and Lavoie 2000; Culver and Pipan 2009). These constraints are thought to have driven a suite of life-history adaptations in subterranean organisms, such as prolonged life spans, delays in sexual maturity, slower growth and metabolism, and decreased fecundity (Culver 1982; Hüppop 2000). Species with delayed sexual maturity typically also exhibit low fecundity, and high adult, but low juvenile survival (Stearns and Koella 1986). All of these traits have been documented in subterranean organisms (Culver 1982) and may skew populations toward larger and older individuals (Poulson 1963; Hüppop 2012).

Only 10 of the approximately 655 species of salamanders have successfully colonized and obligately inhabit cave systems (Goricki et al. 2012). These troglobionts exhibit varying degrees of adaptation to cave life in life-history traits. For example, the European Cave Salamander (*Proteus anguinus*; i.e., Olm) exhibits a remarkable delay in age at sexual maturity and increase in life span relative to surface relatives (Voituron et al. 2010). Sexual maturity is delayed up to 16 y of age, and some salamanders are known to live at least 50 and perhaps 100+ y (Voituron et al. 2010), one of the longest life spans of all amphibians. However, several other species, including several species in the family Plethodontidae, that use caves on a temporary or semi-permanent basis for reproduction, shelter or foraging are not considered troglobionts (Briggler and Prather 2006; Niemiller and Miller 2009; Goricki et al. 2012). These species lack obvious morphological changes (e.g., degenerate eyes, reduced pigmentation, attenuate limbs) associated with cave life and are often primarily found in surface habitats. The perpetual darkness of caves can represent

an extreme constraint, and, consequently, only those species that possess the necessary morphological, physiological, and behavioral adaptation may persist and exploit subterranean habitats over extended periods of time. These Threshold Species that are comprised of both surface and cave populations are excellent candidates to study changes in life-history traits during the transition from surface into subterranean habitats.

In this study we examine potential differences in life-history traits between a cave and surface population of the Western Slimy Salamander (*Plethodon albagula*), a large woodland salamander (family Plethodontidae) that is a member of the Slimy Salamander (*P. glutinosus*) species complex (Highton et al. 1989; Highton 1995). The species is distributed throughout the Ozark Highlands and Ouachita Mountains, with disjunct populations in the Edwards Plateau region of central Texas (Anthony 2005) where it occurs on damp and wooded hillsides, ravines, and the entrances and twilight zone of caves and mines (Grobman 1944; Taylor and Phillips 2002; Trauth et al. 2004). Using a mark-recapture approach, we ask whether four life-history traits (body size, growth rate, age at sexual maturity, and minimum life span) of *P. albagula* differ between a population restricted to a cave and a nearby surface population in the Edwards Plateau of central Texas. Caves are generally more stable with respect to environmental parameters than comparable surface habitats (Culver and Pipan 2009). Coupled with limited energy availability, we predict that the cave population will have slower growth rates and delayed age at sexual maturity compared to the surface population. Salamanders are often the top predators in subterranean ecosystems (Huntsman et al. 2011; Goricki et al. 2012). In the Edwards Plateau, few predators large enough to consume adult *P. albagula* exist in caves, potentially skewing the cave population toward larger and older size classes relative to the surface population. Furthermore, we investigated population size differences between cave and surface populations, with the prediction that cave population will be smaller due to limited resources and habitat availability.

MATERIALS AND METHODS

Study system.—Populations of the Western Slimy Salamander, *Plethodon albagula*, inhabit mesic woodlands and ravines throughout their distribution (Trauth et al. 2004; Anthony 2005). In Texas, *P. albagula* occurs along the Edwards Plateau and is disjunct from the main distribution of the species by 450 km (Baird et al. 2006), with the northern limit reaching Fort Hood in Bell and Coryell counties. At Fort Hood, populations are known from several caves, sinks, and at one spring run (Taylor and Phillips 2002; Baird et al. 2006). The taxonomic status of the Texas populations has been the subject of debate (see Baird et al. 2006), but most authors follow the arrangement of Highton et al. (1989), who grouped the Edwards Plateau populations with populations from the Ozark Plateau and Ouachita Mountains of Missouri, Arkansas, and northeastern Oklahoma as *P. albagula*. This arrangement is also supported by mtDNA data (Baird et al. 2006). Within the Edwards Plateau, populations from Bell and Coryell counties (Fort Hood Military Reservation) are further isolated from other Edwards Plateau populations to the south by about 80 km. Many individuals from Bell and Coryell populations are either completely black or have greatly reduced white spotting compared to other Edwards Plateau populations (Baird et al. 2006). In addition, Baird et al. (2006) demonstrated that the Bell, Coryell, Travis, and Williamson county populations form a well-supported mtDNA lineage distinct from other Edwards Plateau populations and Ozark/Ouachita populations.

Study sites.—We surveyed for salamanders at two localities located 1.4 km apart in Bell County, Texas, USA, at Fort Hood. Bear Springs is composed of two primary springs and associated spring runs (Fig. 1). The west spring branch is approximately three times as long as the east spring branch. Wildlife and cattle use the springs as a water source. The study was confined to the region indicated by dashed lines in Fig. 1a, with a search area of 311.5 m^2.

Estes Cave is a narrow, vertical pit, approximately 10 m deep and 1–3 m in diameter (Fig. 2). In Estes Cave, the study area included detailed inspection of the floor and walls of the cave, with an estimated search area, including cave walls, of 62.2 m^2. The area of the floor where almost all of the salamanders were found is 8.2 m^2. It was not practical for more than one researcher to search the cave because of the constricted width of the pit. The cave entrance occurs within a remote wooded plateau, and is inconspicuous and difficult to find. Entering the cave requires vertical rope techniques, and the site functions as a pitfall trap for a variety of animal life, but, in addition to *P. albagula*, other predators were occasionally observed in the bottom of the pit, including snakes and frogs. The site is infrequently visited by humans. Both sites were chosen based on prior observations of high salamander numbers (Taylor and Phillips 2002).

Sampling and data collection.—The field team surveyed both sites on an approximately bi-monthly basis during a 3-y period between February 2004 and June 2006, representing a total of 15 surveys. Searchers used time and area constrained visual encounter surveys (VES; Heyer et al. 1994). At Bear Springs, the spring runs were divided into seven segments (Fig. 1). During each survey, we searched each segment by lifting rocks,

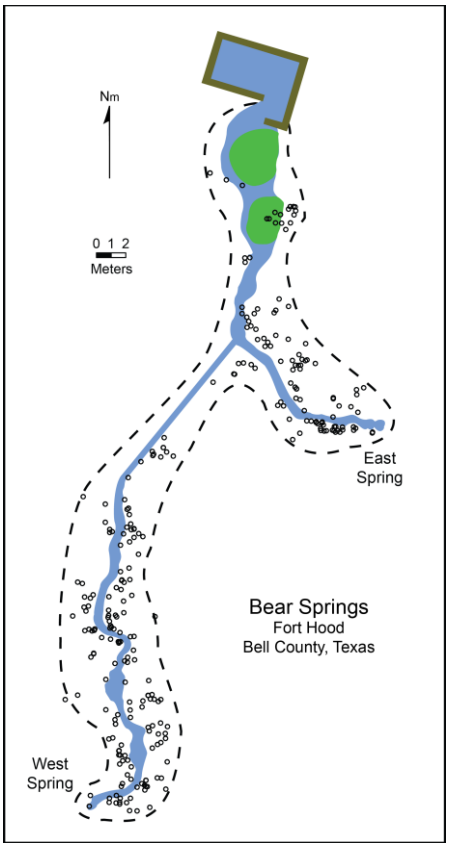


FIGURE 1. Survey sites for *Plethodon albagula* in terrestrial habitat around springs and spring runs at Bear Springs, Bell Co., Texas, at Fort Hood. Green areas near man-made pool with retention wall indicate watercress (*Nasturtium officinale*), open circles represent all locations of salamander captures and dashed line represents boundary of search area.

logs and other cover and marking the location of each salamander with a wire flag. At Estes Cave, we searched all human accessible habitats within the cave, including ledges and crevices along the sides of the pit (Fig. 2). Lifted cover was returned to its original position to minimize habitat disturbance. At least two researchers were present each survey at Bear Springs, with sampling effort ranging 1.5–6.1 person hours for each survey (mean of 4.3 person hours). A single researcher searched Estes Cave, with sampling effort ranging 0.3–1.0 person hours for each survey (mean of 0.6 person hours).

We made a concerted effort to capture each salamander encountered. We placed each captured salamander into a moist zip-lock bag until processing. We measured snout-vent length (SVL) and total length (TL) to nearest 0.1 mm using digital calipers. We also attempted to determine the sex of salamanders by the presence of a mental gland in males and the presence of developing ova visible through the body wall in females. Salamanders not captured previously were uniquely

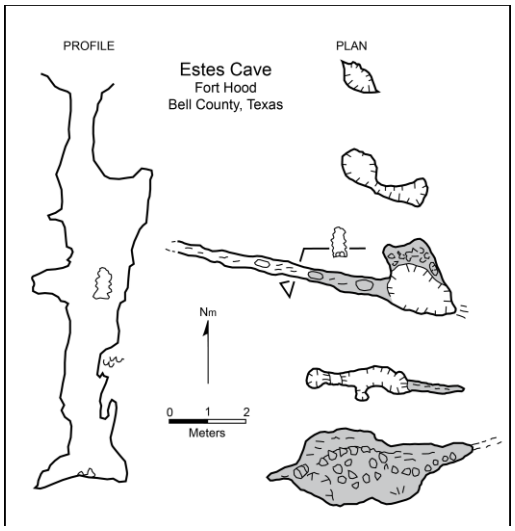


FIGURE 2. Survey sites for *Plethodon albagula* in Estes Cave (profile at ½ scale), Bell Co., Texas, at Fort Hood. Survey areas at the bottom and two ledges, shaded in gray. No *P. albagula* were seen on the walls of the cave (excluding ledges).

marked using different color combinations of visible implant elastomer (Northwest Marine Technology Inc., Shaw Island, Washington, USA). We also batch marked salamanders by clipping one toe using the marking system of Medica et al. (1971). After marking, each salamander was returned to its original capture location.

Body size distribution.—We tested for overall differences between populations in body size using a *t*-test, assuming unequal variances. To test for difference in the distributions of body size we constructed histograms based on SVL for each population then tested the composition of size classes using a χ^2 goodness-of-fit test for a uniform and Poisson distribution. Finally, to determine if the size structure between Bear Springs and Estes Cave differed we used a Kolomogorov Cumulative Probability test (Zar 1996). These statistical tests were conducted in the R statistical computing environment (v3.0.2; R Core Team 2013) with $\alpha = 0.05$.

Catchability, survival rates, and population size.—We used the package RCapture (Baillargeon and Rivest 2007) implemented in R to estimate population size, capture probabilities and survival rates by fitting a Jolly-Seber open population model following the loglinear approach of Cormack (1985, 1989) for the 15 survey events (February 2004 - July 2006). An open population model was most appropriate for this mark-recapture dataset for several reasons. First, the length of study (29 mo) and estimated growth rates (see Results) suggest both birth and death likely contribute to a lack of closure. Second, immigration and emigration likely

TABLE 1. Age-specific and mark-recapture analogues of individual growth models used in this study for *Plethodon albagula* captured from Estes Cave and Bear Springs in Bell Co., Texas, at Fort Hood. Parameters are: t – age (in years or days), L_t – size at age t, k – characteristic growth rate, A_∞ – asymptotic size, b –proportion of growth remaining toward A_∞ at t_0 , m – shape parameter for the Richard's function and the slope of growth for the Weibull and Stannard functions. For the Schnute models, a – the constant relative rate of growth, b – incremental relative rate, τ_1 – first specified age, τ_2 – second specified age, y_1 – size at age τ_1, and y_2 – size at age τ_2, and K, which is a function of τ_1 and τ_2.

Model	Age-Specific	Mark/Recapture
von Bertalanffy	$L_t = A_\infty\,(1 - be^{-kt})$ (Bertalanffy 1957)	$L_R = A_\infty - (A_\infty - L_C)e^{-k\Delta t}$ (Fabens 1965)
Logistic	$L_t = \frac{A_\infty}{(1 + be^{-kt})}$ (Verhulst 1838)	$L_R = \frac{A_\infty L_C}{(L_C + (A_\infty - L_C)e^{-k\Delta t})}$ (Schoener and Schoener 1978)
Weibull	$L_t = A_\infty - be^{-kt^m}$ (Weibull, 1951)	$L_R = \frac{A_\infty}{\left(\left(1 + e^{\frac{k\Delta t}{m}}\right)\left(-1 + \frac{L_C}{A_\infty}\right)^{-m^{-1}}\right)^m}$ This Paper
Gompertz	$L_t = A_\infty\, e^{-be^{-kt}}$ (Gompertz 1825)	$L_R = A_\infty \left(\frac{L_C}{A_\infty}\right)^{e^{-k\Delta t}}$ (Dodd and Dreslik 2008)
Richards	$L_t = A_\infty\,(1 - be^{-kt})^{\frac{1}{(1-m)}}$ (Richards 1959)	$L_R = A_\infty \left(1 + \left(\left(\frac{L_C}{A_\infty}\right)^{\left(\frac{1}{m}\right)} - 1\right)e^{-k\Delta t}\right)^m$ (Dodd and Dreslik 2008)
Stannard	$L_t = A_\infty(1 + e^{-(\frac{b*k*t}{m})^{-m}})$ (Stannard *et al.*, 1985)	$L_R = A_\infty + (L_C - A_\infty)e^{-k\Delta t^m}$ This Paper
Schnute	$L = \left({y_1}^b + ({y_2}^b - {y_1}^b)\frac{1 - e^{-a(t-\tau_1)}}{1 - e^{-a(\tau_2-\tau_1)}}\right)^{\frac{1}{b}}$ (Schnute 1981)	$L_R = \left({L_C}^b e^{-a\Delta t} + {A_\infty}^b(1 - e^{-a\Delta t})\right)^{(1/b)}$ (Baker et al. 1991)

occurs in both study populations. We evaluated two open population models: one that allowed capture probabilities to vary between survey events, and another that held capture probabilities equal across surveys. Because of a limited number of recaptures for many surveys resulting in poor estimates for demographic parameters, particularly at Bear Springs (see Results), we reduced the capture history matrix from 15 survey events to five primary capture periods by pooling data of individual survey events into sets of three surveys each (i.e., every three surveys were considered a pooled survey period for this analysis). The function periodhist was used to pool capture histories for every three surveys into a single entry such that a value of 1 was assigned for an individual caught at least once during the three surveys and a value of 0 if it was not captured during any of the three surveys. We evaluated model fit via Akaike's Information Criterion (AIC). We also estimated salamander density based on the population size estimates for both populations.

Growth rates, age at sexual maturity, and longevity.—We chose seven growth models used in the study of ectotherms and evaluated our data using their respective mark-recapture analogues (Table 1). For the Stannard and Weibull models, we followed the methods of Fabens (1965) for reparameterizing growth equations into mark-recapture analogues using Wolfram Mathematica 10.0 (Wolfram Research, Champaign, Illinois, USA). Mark-recapture analogues of individual growth models included a time interval between captures and respective sizes at capture. We conducted non-linear regressions in R using the minpack.lm package (Elzhov et al. 2013) on all the models listed above for

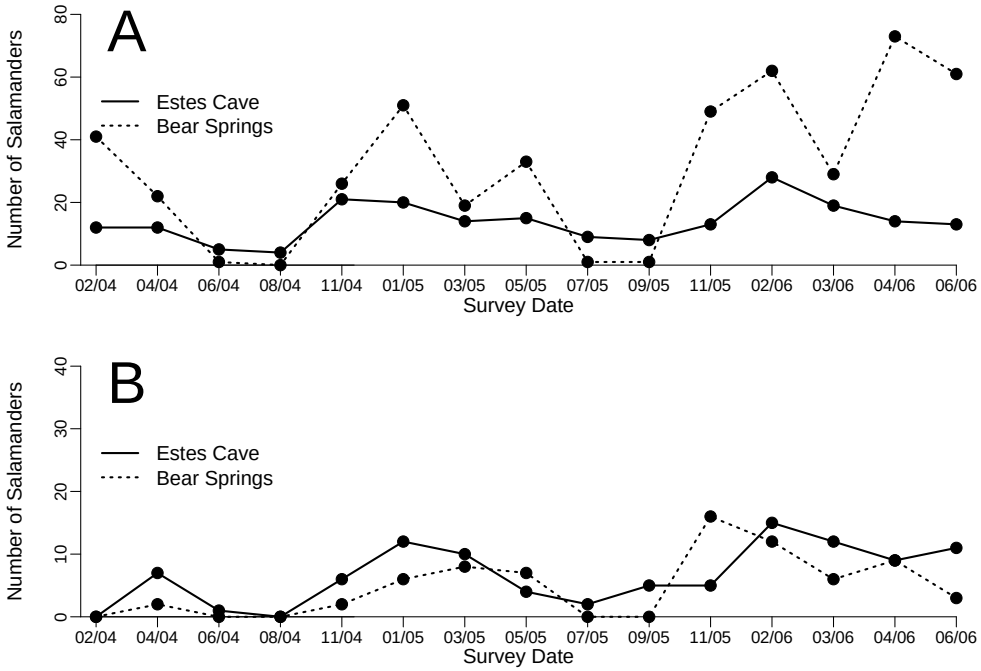


FIGURE 3. Numbers of *Plethodon albagula* observed (A) and recaptured (B) over 15 surveys at Bear Springs (dashed) and Estes Cave (solid) in Bell Co., Texas, USA, at Fort Hood from February 2004 to June 2006.

the entire dataset (Estes Cave and Bear Springs combined). We then determined which growth model fit the entire dataset best using an information theoretic (Burnham and Anderson 1988) approach with the R package AICcmodavg (Mazerolle 2014). Once the best-fit model was selected, we then conducted a secondary analysis where we tested various parameterizations of the model to examine if model fit was improved by fixing asymptotic size, and if there were site-specific effects on parameters. To fix asymptotic size, we averaged the 10 largest individuals from Estes Cave (75.5 cm SVL), Bear Springs (69.4 mm SVL), and overall (72.4 cm SVL). To account for site effects, we dummy coded site into two binary variables: for Estes Cave (S_1), we coded 1 for salamanders from Estes Cave and 0 for animals not from Estes Cave, and the same was done for Bear Springs (S_2). For models that included site specific effects, we replaced each parameter with a term ($S_1X_{Estes} + S_2X_{Bear}$), where X is the parameter of interest. For example, with asymptotic size considering only Estes Cave, the component S_2A_{Bear} reduces to zero. We again performed model selection and considered our confidence set as all the models having a $\Delta AIC_C < 2.0$. We then plotted the best-fit models for graphical comparisons of growth up to age 12, by rooting the curves with a hatchling size of 18.1 mm SVL.

RESULTS

We made 676 salamander captures at Bear Springs (469 salamanders) and Estes Cave (207 salamanders), representing 395 and 108 unique individuals, respectively. We observed a high of 73 salamanders at Bear Springs on 25 April 2006; whereas, we did not find any salamanders on 24 August 2004 (Fig. 3a). We observed only one salamander on three occasions: 29 June 2004, 26 July 2005, and 26 September 2005. The maximum number of salamanders we observed was 28 at Estes Cave on 1 February 2006; whereas, we observed a minimum of five salamanders on 29 June 2004 (Fig. 3a). Recapture rates of unique salamanders were 13.9% and 49.0%, respectively at Bear Springs and in Estes Cave. We recaptured a maximum of 16 salamanders at Bear Springs 30 November 2005, and a minimum of 15 recaptured salamanders in Estes Cave 1 February 2006 (Fig. 3b). At Bear Springs, we captured 340 salamanders only once, 36 salamanders twice, and 19 salamanders three times. In Estes Cave, we captured 55 salamanders once, 32 twice, 10 three times, five salamanders four times, three five times, one six times, one seven times, and one 10 times. The longest time period between captures for a single salamander was 761 days at Bear Springs and 776 days in Estes Cave.

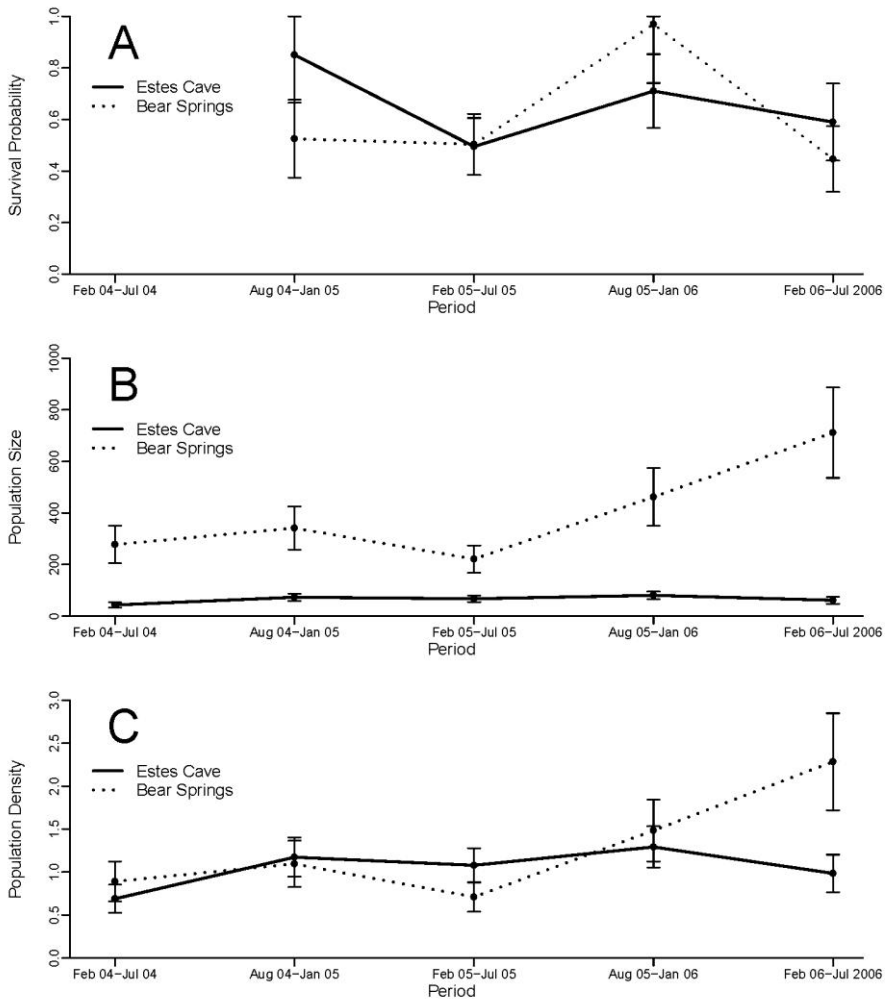


FIGURE 4. Survival probability (A), population size (B), and population density (C) estimates for the Bear Springs (dashed) and Estes Cave (solid) populations of *Plethodon albagula* in Bell Co., Texas, USA, at Fort Hood based on an open population model assuming equal capture probabilities among survey periods.

Catchability, survival rates, and population size.— For the Bear Springs population, an open population model with equal capture probabilities among surveys was the best-fit model (deviance = 21.83, df = 21, AIC = 111.46) compared to a model that assumed unequal capture probabilities among surveys (deviance = 21.62, df = 19, AIC = 115.26). Under the best-fit model, capture probabilities were estimated at 22.3 ± 5.3%. For the Estes Cave population, an open population model with equal capture probabilities among surveys also was the best-fit model (deviance = 24.50, df = 21, AIC = 104.22) compared to a model that assumed unequal capture probabilities among surveys (deviance = 24.42, df = 19, AIC = 108.14). Under the best-fit model, capture probabilities were estimated at 49.0 ± 8.8%.

Survival rates were similar between the Bear Springs and Estes Cave populations throughout the study (Fig. 4a). At Bear Springs, survival probability estimates were greatest (0.97 ± 0.23) during the August 2005 - January 2006 period but then dropped to a low of 0.45 ± 0.13 during the February 2006 to July 2006 period. Survival probabilities peaked at Estes Cave during the August 2004 to January 2005 period (0.85 ± 0.19) and then dropped to a low of 0.49 ± 0.11 during the February 2005 to July 2005 period.

Population size estimates were nearly an order of magnitude greater for the Bear Springs population compared to the Estes Cave population (Fig. 4b). At Bear Springs, population size estimates for individual survey periods ranged 221–712, peaking during the

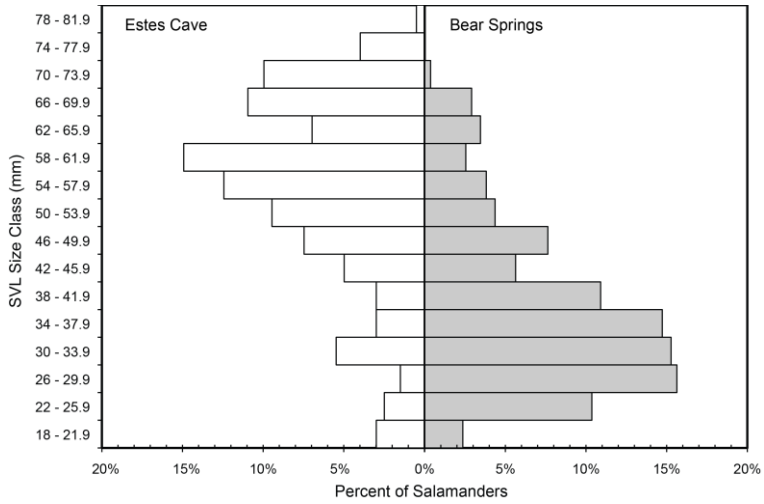


FIGURE 5. Pooled size-frequency distribution of body size (SVL) in mm for *Plethodon albagula* at Bear Springs and Estes Cave in Bell Co., Texas, USA, at Fort Hood.

February 2006 to July 2006 period. However, variance around these estimates was considerably larger than estimates for Estes Cave during the same time periods. Population size increased over the final three time periods at Bear Springs during the study due to a large number of new arrivals (either by immigration or recruitment from smaller size classes) into the population during the August 2005 to January 2006 (248 ± 64 individuals) and February 2006 to July 2006 (505 ± 112) periods. The total population size at Bear Springs over the entire study period was 1,276 ± 224 individuals. In contrast, population size in Estes Cave remained stable over the study period, ranging from 43–80 individuals (Fig. 4b). The total population size in Estes Cave over the entire study period was 157 ± 16 individuals. Mean salamander densities ranged 0.71–2.29 salamanders per m^2 at Bear Springs and 0.61–1.14 salamanders per m^2 in Estes Cave during the study period (Fig. 4c). However, salamanders were nearly always found on the floor of the pit in an area of 8.2 m^2, where estimated densities may reach up to 9.76 salamanders per m^2.

Body size.—Salamanders from Bear Springs averaged 38.6 ± 0.52 (± SE) mm SVL; whereas, those from Estes Caves averaged 54.1 ± 1.03 mm SVL. Salamanders from Bear Springs were significantly smaller than salamanders from Estes Cave (t_{stat} = 13.42, df = 308, P < 0.001). Size-frequency distributions were constructed for each population using data pooled from 2004 to 2006. The size frequency distribution for Bear Springs was skewed toward smaller individuals more so than expected for either a uniform (χ^2 = 398.07, df = 15, P < 0.001) or Poisson (χ^2 = 469.78, df = 15, P < 0.001) distribution. The opposite was observed for Estes Cave, where distributions were skewed toward larger individuals more so than expected for either a uniform (χ^2 = 87.08, df = 15, P < 0.001) or Poisson (χ^2 = 3124.30, df = 15, P < 0.001; Fig. 5) distribution. The size distribution of the Estes Cave population is skewed toward larger individuals compared to the Bear Springs population (D_{max} = 0.517, P < 0.001). Just 13% of the individuals in the Bear Springs population were mature, compared to 60% in Estes Cave.

Growth rates, age at sexual maturity, and longevity.—Growth models for the Estes Cave and Bear Springs populations were based on capture data from 37 and 47 salamanders, respectively. Of the seven growth models tested on the combined dataset, the mark-recapture analogue of the Schnute model (Baker et al. 1991, eq. 11) was the best fit and had the highest support (Table 2). For the parameterizations of the Schnute model, the top four models all had varying degrees of fixed asymptotic sizes, whether by site or overall (Table 3). Fixing asymptotic sizes as such suggests mark-recapture intervals for the larger size classes were sparse in our dataset. The top two models had ΔAIC_C < 2 and were selected for interpretation (Table 3). The cumulative Akaike Weight for the top two models was 0.51 (Table 3). The first model used fixed site-specific asymptotic sizes and a characteristic growth rate and inflection point parameter that were not affected by site (Table 3; Fig. 6). The second model had site-specific characteristic growth rates and a fixed asymptotic size and inflection point parameter that were not affected by site (Table 3; Fig. 6). Parameter estimates for both models show a high degree of variation (Table 4; Fig. 4), but it appears the inflection point parameter is similar for both models (Table 4). When examining the

TABLE 2. Model selection table for seven competing mark/recapture growth models on the combined dataset of *Plethodon albagula* captured from Estes Cave and Bear Springs at Fort Hood, Texas.

Model Class	-2LL	*K*	AICc	ΔAIC_C	w_i	Likelihood
Schnute	-266.84	4	542.19	0.00	1.00	1.0
Von Bertalanffy	-274.60	3	555.50	13.32	0.00	780.6
Weibull	-274.39	4	557.29	15.11	0.00	1910.3
Gompertz	-277.98	3	562.27	20.08	0.00	22925.4
Richards	-277.98	4	564.47	22.28	0.00	68871.7
Stannard	-277.98	4	564.47	22.29	0.00	69216.9
Logistic	-306.15	3	618.61	76.42	0.00	3.93E+16

TABLE 3. Model selection table for 10 reparemetrizations of the Schnute mark-recapture growth model (Baker et al. 1991, eq. 11) for *Plethodon albagula* captured from Estes Cave and Bear Springs at Fort Hood, Texas. The parameters are asymptotic size (*A*), characteristic growth rate (*k*), and relative location of the inflection point (*b*). F is used when *A* was freely estimated, X when *A* was fixed, S refers to when a single parameter was used, and G refers to when the site effect was included.

Model	*A*	*k*	*b*	-2LL	*K*	AICc	ΔAIC_C	w_i	Likelihood
1	X-G	S	S	-266.25	3	538.81	0.00	0.36	1.00
2	X-S	G	S	-266.04	4	540.58	1.77	0.15	2.42
3	X-G	G	G	-265.48	5	541.73	2.92	0.08	4.31
4	X-S	S	S	-267.78	3	541.87	3.06	0.08	4.62
5	F-G	S	S	-265.66	5	542.08	3.28	0.07	5.16
6	F-S	G	S	-265.66	5	542.09	3.28	0.07	5.16
7	F-S	S	S	-266.84	4	542.19	3.38	0.07	5.42
8	F-S	S	G	-265.78	5	542.34	3.53	0.06	5.84
9	X-S	S	G	-267.3	4	543.11	4.31	0.04	8.63
10	F-G	G	G	-265.13	7	545.74	6.94	0.01	32.14

characteristic growth rates, it appears that salamanders from Bear Springs grow to a smaller size when examining the first model or at a faster rate to a similar size when examining the second model (Fig. 6; Table 4). Clearly, there are some site-specific differences in the growth pattern; however, we lack enough data points along the growth trajectory to better tease out if the differences are ascribed to asymptotic size, characteristic growth rate, or both. Based on the top model (Fig. 4), time to sexual maturity for males was estimated at 1.4 y (CI: 0.2–4.0 y) for the Estes Cave and slightly slower at 2.2 y (CI: 0.5–5.9 y) for Bear Springs, corresponding to the size of the smallest sexually mature male observed (53.5 mm). For females, time to sexual maturity was estimated at 0.9 y (CI: 0.2–2.9 y) and also slower for Bear Springs at 1.5 y (CI: 0.3–4.2 y), based on the size of the smallest mature female observed (49.6 mm). The largest individuals captured at Estes Cave and Bear Springs were 80.1 and 73.2 mm SVL, respectively. Minimum life span could not be reliably estimated for either population, as the growth trajectories reach an asymptote before encompassing the maximize body size observed in either population. However, it is likely that salamanders live > 10 y in each population.

DISCUSSION

Mean body size was greater for the cave population at Estes Cave compared to the surface population at Bear Springs. The Estes Cave population was skewed toward a preponderance of larger, mature individuals; whereas, the Bear Springs population was skewed toward an increased number of smaller, younger individuals. Variation in body size-age structure between these populations may be the result of differential regulation by a number of ecological processes, including competition, maturation, reproduction, predation, cannibalism, and climate adaptation. Although understanding the roles of these processes and their interactions on the regulation and dynamics of surface and subterranean populations of *P. albagula* is beyond the scope of the current study, we briefly speculate on potential mechanisms operating in these populations.

Differences in levels of competition for resources between size classes operating within the surface and cave population may explain differences in body size distributions in these populations. If there are large enough differences in competitiveness between adults and juveniles, this may result in large amplitude cycles that are driven by competition (de Roos et al. 2003a). Adults may be competitively superior to juveniles in the more resource-limited habitats at Estes Cave resulting in

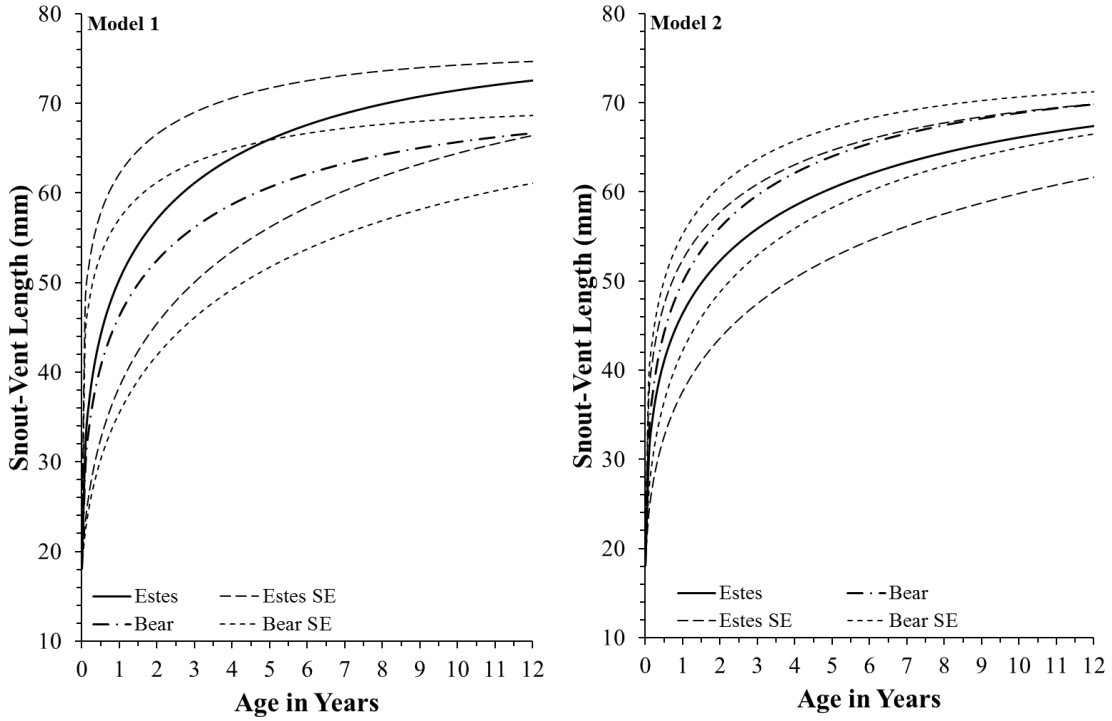


FIGURE 6. Top two growth models for *Plethodon albagula* captured from Estes Cave and Bear Springs in Bell Co., Texas, at Fort Hood based on body size (SVL in mm) and age (in years). Upper and lower confidence intervals (± 1 SE) are shown.

a skew toward larger size classes; whereas, juveniles may be competitively superior to adults at Bear Springs. Predation may also shape the body size distribution of populations if a predator is size-selective, feeding primarily on a particular size of prey (de Roos et al. 2003b). The size of rocks used as cover from mammalian and avian predators may also favor smaller body sizes. Unfortunately, data on predation are unavailable for *P. albagula*, but there is the possibility for differential predation pressures between cave and surface habitats that might drive body size distributions in these populations. Intraspecific predation, or cannibalism, is another possible mechanism regulating population dynamics in populations within different environments (Claessen et al. 2004; Nilsson et al. 2011). Cannibalism of hatchlings or small juveniles at Estes Cave is a possibility, as the stomach contents of one salamander contained the tip of another *P. albagula* tail at Estes Cave in a diet study (Taylor et al. 2007). Anecdotal reports of cannibalism also have been reported for at least one member of the *P. glutinosus* species complex (Powders 1973). The smaller body size at Bear Springs may also be a result of increased metabolism needed in surface habitats, characterized by greater fluctuations in temperature and humidity, as compared to cave habitats. Climatic shifts toward warmer and drier conditions may require an increased metabolic expenditure. Reduced body size in one population of central Texas *Eurycea* is associated with the stress of drought (Bendik and Gluesenkamp 2012), and plasticity of that characteristic is hypothesized to correlate with food availability.

Differences in age at sexual maturity also exist between the surface and cave population at Fort Hood.

TABLE 4. Parameter estimates for the top two Schnute growth model parameterizations for *Plethodon albagula* captured from Estes Cave and Bear Springs at Fort Hood, Texas. The parameters are asymptotic size (*A*), characteristic growth rate (*k*), and relative location of the inflection point (*b*). Asymptotic sizes used were Estes Cave (75.5 cm SVL), Bear Springs (69.4 mm SVL), and overall (72.4 cm SVL).

Parameter	Estimate	Std. Error	*t*	*P*
Fixed Group *A*, Single *k*, *b*				
k	0.145	0.063	2.307	0.024
b	4.950	1.287	3.847	< 0.001
Fixed Single *A*, Group *k* Single *b*				
k_{Estes}	0.095	0.038	2.513	0.014
k_{Bear}	0.145	0.047	3.073	0.003
b	5.386	1.045	5.155	< 0.001

Sexual maturity in Ouachita populations of *P. albagula* in Arkansas occurs between 55–72 mm SVL (Trauth et al. 2004), although Anthony (2005) suggested maturity occurs as small as 50 mm SVL. Sexual maturity in the two populations studied at Fort Hood likely occurs between 50–55 mm SVL, based on the size of the smallest male (53.5 mm) and female (49.6 mm) observed during this study. Age at sexual maturity has not been previously reported for *P. albagula*. Sexual maturity can be reached in 1.5 y for females and 2.2 y for males of the surface population at Bear Springs, which is slightly slower than salamanders at Estes Cave (0.9 y for females and 1.4 y for males). We could not obtain reliable estimates of minimum life span in either population.

Although not a strictly subterranean species, *P. albagula* in our study appears to exhibit plasticity in growth, body size, and development. Plasticity in response to biotic and abiotic variation is common in amphibians for a wide range of traits, from behavior to morphology to life history (Relyea 2001; Urban 2010; Urban et al. 2014). Plasticity in *P. albagula* at Fort Hood may be adaptive and a function of extreme fluctuations in surface environmental conditions, particularly temperature and moisture, which occur in the central Texas region. Many cave-dwelling organisms, including salamanders, have evolved slower development, longer life spans, and other life-history trait changes relative to their surface counterparts, likely in response to limited food resources and the stability of habitats in many subterranean ecosystems (Culver 1982; Niemiller and Poulson 2010; Voituron et al. 2010; Venarsky et al. 2012; Fenolio et al. 2014). Subterranean habitats, such as Estes Cave, have higher environmental stability and potentially reduced predation compared to surface habitats. Daily mean temperatures at Fort Hood varied up to 17.8° C during the study period (http://www.wunderground.com/. Accessed 19 October 2014); whereas, temperatures deep within caves tend to vary less than surface temperatures, generally approaching annual temperatures above ground (Wigley and Brown 1976). However, our study suggests that individuals in the Estes Cave population grow faster than individuals in the surface population at Bear Springs. Though food availability was not quantified, we noted that Estes Cave was rich with fresh organic debris, nutrients, and invertebrate biomass that either wash or fall into the cave. *Plethodon albagula* appears to be a top predator in this ecosystem. The potentially higher influx of energy into this cave ecosystem and greater prey availability compared to other caves, in addition to higher environmental stability, may explain faster growth rates observed in this population relative to Bear Springs.

Temperature and moisture variation likely were major drivers of *P. albagula* abundance in surface habitats at Bear Springs. During periods of hot and dry weather when temperatures could reach in excess of 100° F (i.e., June into October annually), salamander abundance was extremely low (Fig. 3a), with only three salamanders found during the four surveys conducted in the summers of 2004 and 2005. The low abundance of salamanders observed during the summer surveys contrasts starkly to the number of salamanders observed during surveys that occurred during the late winter and spring months. We suspect that salamanders migrate horizontally into hillsides or vertically into karst bedrock through cracks and crevices to seek refuge in caves or other connected voids (i.e., the *milieu souterrain superficiel*, Juberthie et al. 1980) during periods of inhospitable conditions only to return during cooler, moister conditions when they can be found under rocks, logs, and, occasionally, in leaf litter. The complexity of the habitat and behavioral response of *P. albagula* to harsh surface conditions likely explains large variance in population size estimates and low detectability at Bear Springs.

In contrast, abundance and estimated population size, albeit low at Estes Cave, remained quite stable throughout the duration of the study, which might reflect the more stable environmental conditions found in the cave. Difference in population size between the cave and surface populations at Fort Hood are clearly related to habitat availability (8.24 m^2 of floors and wall ledges totaling 62.2 m^2 at Estes Cave and 311.5 m^2 at Bear Springs). A more useful comparison is salamander density, which was similar between the two sites when the total area searched was used in calculating densities. However, it is worth noting that almost no salamanders were observed on the walls of Estes Cave. Nearly all salamanders were found on the 8.24 m^2 floor of the pit, where estimated densities approached 10 salamanders per m^2 during the study. Although salamanders likely used other areas of the cave that we could not survey, such high densities suggest that most *P. albagula* may use the cave on a semi-regular to regular basis, possibly as a refuge from inhospitable surface conditions. Higher salamander densities might also reflect the structure of entrance and surrounding landscape (i.e., a pit cave) that funnels organic debris, nutrients, and potential prey into the cave at potentially higher concentrations than the surrounding surface landscape.

From a conservation perspective, caves and associated subterranean habitats, such as epikarst, may be important for the long-term persistence of local salamander populations at Fort Hood in central Texas. Although comparing only one surface and one cave population, our study suggests that *P. albagula* may persist in or use subterranean habitats for multiple years or they may make seasonal migrations into caves and other subterranean voids to seek refuge from inhospitable conditions at the surface during summer months. At Bear Springs, no salamanders were observed during

summer surveys even in microhabitats adjacent to the spring and spring run. Although there is much uncertainty in climate change projections in addition to the difficulty in distinguishing climate change from other interacting factors, such as land-use change, caves and associated subterranean voids in karst areas may become increasingly important habitats for *P. albagula* in the coming years. Thus, conserving caves and the area on the surface around them (including surface and subsurface drainage basins), as well as around springs and spring runs where soil moisture content is higher, may aid in the long-term protection of local populations.

Acknowledgments.—We thank the Texas Nature Conservancy and the Natural Resources Branch of Fort Hood for their cooperation and assistance, and in particular Charles E. Pekins and John D. Cornelius were instrumental in making this project happen. We thank Michael L. Denight (formerly of U.S. Army Engineer Research and Development Center, Champaign, Ilinois, USA) for his contributions to and oversight of this project. We thank the following individuals for assistance with fieldwork: Isabelle-Anne Bisson, Vicki Bump, Kevin Cagle, Amy Fergus, Andy G. Glusenkamp, Liz Guillorn, Jinelle B. Hutchins, Cling King, Christine L. Krejca, Crystal M. LeBoeuf, Timothy G. Marston, Charles E. Pekins, Dave Sperry, Jeremy S. Tiemann, and Chris Taylor. This study was authorized under the University of Illinois IACUC protocol no. 04067 and supported by two grants from the U.S. Army Engineer Research and Development Center to SJT and CAP.

LITERATURE CITED

Anthony, C.D. 2005. *Plethodon albagula*, Western Slimy Salamander. Pp. 788–789 *In* Amphibian Declines: The Conservation Status of United States Species. Lannoo, M.L. (Ed.). University of California Press, Berkeley, California, USA.

Baillargeon, S., and L. Rivest. 2007. Rcapture: loglinear models for capture-recapture in R. Journal of Statistical Software 19:1–31.

Baird, A.B., J.K. Krejca, J.R. Reddell, C.E. Peden, M.J. Mahoney, and D.M. Hillis. 2006. Phylogeographic structure and color pattern variation among populations of *Plethodon albagula* on the Edwards Plateau of central Texas. Copeia 2006:760–768.

Baker, T.T., R. Lafferty, and T.J. Quinn, II. 1991. A general growth model for mark-recapture data. Fisheries Research (Amsterdam) 11:257–281.

Bendik, N.F., and A.G. Gluesenkamp. 2012. Body length shrinkage in an endangered amphibian is associated with drought. Journal of Zoology 290:35–41.

Briggler, J.T., and J.W. Prather. 2006. Seasonal use and selection of caves by plethodontid salamanders in a karst area of Arkansas. American Midland Naturalist 155:136–148.

Burnham, K.P., and D.R. Anderson. 1998. Model Selection and Inference: a Practical Information-Theoretic Approach. Springer-Verlag New York Inc., New York, New York, USA.

Claessen, D., A.M. de Roos, and L. Persson. 2004. Population dynamic theory of size-dependent cannibalism. Proceedings of the Royal Society of London Series B-Biological Sciences 271:333–340.

Cormack, R.M. 1985. Example of the use of GLIM to analyze capture-recapture studies. Pp. 242–274 *In* Lecture Notes in Statistics 29: Statistics in Ornithology. Morgan, B.J.T., and P.M. North (Eds.). Springer-Verlag, New York, New York, USA.

Cormack, R.M. 1989. Loglinear models for capture-recapture. Biometrics 45:395–413.

Culver, D.C. 1982. Cave Life: Evolution and Ecology. Harvard University Press, Cambridge, Massachusetts, USA.

Culver, D.C. 1986. Cave faunas. Pp. 427–443 *In* Conservation Biology, the Science of Scarcity and Diversity. Soulé, M.E. (Ed.). Sinauer Associates, Sunderland, USA.

Culver, D.C., and T. Pipan. 2009. The Biology of Caves and Other Subterranean Habitats. 2nd Edition. Oxford University Press, Oxford, UK.

de Roos, A.M., L. Persson, and E. McCauley. 2003a. The influence of size-dependent life-history traits on the structure and dynamics of populations and communities. Ecology Letters 6:473–487.

de Roos, A., L. Persson, and H.R. Thieme. 2003b. Emergent Allee effects in top predators feeding on structured prey populations. Proceedings of the Royal Society of London Series B-Biological Sciences 270:611–618.

Elzhov, T.V., K.M. Mullen, A.-N. Spiess, and B. Bolker. 2013. Minpack.lm: R interface to the Levenberg-Marquardt nonlinear least-squares algorithn found in MINPACK, plus support for bounds. R package version 1.1-8. URL – http://CRAN.R-project.org/package=minpack.lm.

Fabens, A.J. 1965. Properties and fitting of the von Bertalanffy growth curve. Growth 29:265–289.

Fenolio, D.B., M.L. Niemiller, R.M. Bonett, G.O. Graening, B.A. Collier, and J.F. Stout. 2014. Life history, demography, and the influence of cave-roosting bats on a population of the grotto salamander (*Eurycea spelaea*) from the Ozark Plateaus of Oklahoma (Caudata: Plethodontidae). Herpetological Conservation and Biology 9:394–405.

Goricki, S., M.L. Niemiller, and D.B. Fenolio. 2012. Salamanders. Pp. 665–676 *In* Encyclopedia of Caves.

2nd Edition. White, W.H., and D.C. Culver (Eds.). Elsevier, London, UK.

Grobman, A.B. 1944. The distribution of the salamanders of the genus *Plethodon* in eastern United States and Canada. Annals of the New York Academy of Sciences 45:261–316.

Heyer, W.R., M.A. Donnelly, R.W. McDiarmid, L.C. Hayek, and M.S. Foster (Eds.). 1994. Measuring and Monitoring Biodiversity: Standard Methods for Amphibians. Smithsonian Institution Press, Washington, D.C., USA.

Highton, R. 1995. Speciation in eastern North American salamanders of the genus *Plethodon*. Annual Review of Ecology and Systematics 26:579–600.

Highton, R., G.C. Maha, and L.R. Maxson. 1989. Biochemical Evolution in the Slimy Salamanders of the *Plethodon glutinosus* Complex in the Eastern United States. University of Illinois Biological Monograph 57.

Huntsman, B.M., M.P. Venarsky, J.P. Benstead, and A.D. Huryn. 2011. Effects of organic matter availability on the life history and production of a top vertebrate predator (Plethodontidae: *Gyrinophilus palleucus*) in two cave streams. Freshwater Biology 56:1746–1760.

Hüppop, K. 2000. How do cave animals cope with the food scarcity in caves? Pp. 159–188 *In* Subterranean Ecosystems. Wilkens, H., D.C. Culver, and W.F. Humphreys (Eds.). Ecosystems of the World, Volume 30. Elsevier, Amsterdam, The Netherlands.

Hüppop, K. 2012. Adaptation to low food. Pp. 1–9 *In* Encyclopedia of Caves. Culver, D.C., and W.B. White (Eds.). 2nd Edition. Elsevier, Amsterdam, The Netherlands.

Juberthie, C., B. Delay, and M. Bouillon. 1980. Extension du milieu souterrain en zone non-volcanic: description d'un nouveau milieu et son peuplement par les coléoptères troglobies. Mémoires de Biospéologie 7:19–52.

Mazerolle, M.J. 2014. Package AICcmodavg. R package version 2.0-3. URL – http://cran.rproject.org/web/packages/AICcmodavg/AICcmodavg.pdf.

Medica, P.A., G.A. Hoddenbach, and J.R. Lannom, Jr. 1971. Lizard Sampling Techniques. Rock Valley Miscellaneous Publications No. 1.

Niemiller, M.L., and B.T. Miller. 2009. A survey of the cave-associated amphibians of the eastern United States with an emphasis on salamanders. Pp. 249–256 *In* Proceedings of the 15th International Congress of Speleology. White, E.B. (Ed.). International Union of Speleology, Kerrville, Texas, USA.

Niemiller, M.L., and T.L. Poulson. 2010. Subterranean fishes of North America: Amblyopsidae. Pp. 169–280 *In* The Biology of Subterranean Fishes. Trajano, E., M.E. Bichuette, and B.G. Kapoor (Eds.). Science Publishers, Enfield, New Hampshire, USA.

Nilsson, K.A., S. Lundback, A. Postavnicheva-Harri, and L. Persson. 2011. Guppy populations differ in cannibalistic degree and adaptation to structural environments. Oecologia 167:391–400.

Poulson, T.L. 1963. Cave adaptation in amblyopsid fishes. American Midland Naturalist 70:257–290.

Poulson, T.L., and K.H. Lavoie. 2000. The trophic basis of subsurface ecosystems. Pp. 231–249 *In* Subterranean Ecosystems. Wilkens, H., D.C. Culver, and W.F. Humphreys (Eds.). Ecosystems of the World, Volume 30. Elsevier, Amsterdam, The Netherlands.

Powders, V.N. 1973. Cannibalism by the Slimy Salamander, *Plethodon glutinosus* in eastern Tennessee. Journal of Herpetology 7:139.

R Developmental Core Team. 2013. R: a Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

Relyea, R.A. 2001. Morphological and behavioral plasticity of larval anurans in response to different predators. Ecology 82:523–540.

Stearns, S.C., and J.C. Koella. 1986. The evolution of phenotypic plasticity in life-history traits: predictions of reaction norms for age and size at maturity. Evolution 40:893–913.

Taylor, S.J., and C.A. Phillips. 2002. A Survey of *Plethodon* sp. (Plethodontidae) Salamander Populations in Caves and Sinkholes at Fort Hood, Texas. Illinois Natural History Survey, Center for Biodiversity Technical Report 2002(12), Champaign, Illinois, USA.

Taylor, S.J., C.A. Phillips, and J.K. Krejca. 2007. Prey of the cave and surface populations of *Plethodon albagula* (Plethodontidae) at Fort Hood, Texas. Illinois Natural History Survey, Center for Biodiversity Technical Report 2007 (48), Champaign, Illinois, USA.

Trauth, S.E., H.W. Robison, and M.V. Plummer. 2004. The Amphibians and Reptiles of Arkansas. University of Arkansas Press, Fayetteville, Arkansas, USA.

Urban, M.C. 2010. Microgeographic adaptations of spotted salamander morphological defenses in response to a predaceous salamander and beetle. Oikos 119:646–658.

Urban M.C., J.L. Richardson, and N.A. Freidenfelds. 2014. Plasticity and genetic adaptation mediate amphibian and reptile responses to climate change. Evolutionary Applications 7:88–103.

Venarsky, M.P., A.D. Huryn, and J.P. Benstead. 2012. Re-examining extreme longevity of the cave crayfish *Orconectes australis* using new mark-recapture data: a lesson on limitations of iterative size-at-age models. Freshwater Biology 57:1471–1481.

Voituron, Y., M. Fraipont, J. Issartel, O. Guillaume, and J. Clobert. 2010. Extreme lifespan of the human fish

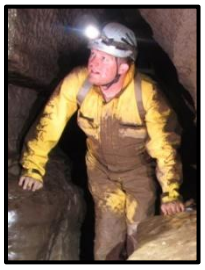
(*Proteus anguinus*): a challenge for ageing mechanisms. Biology Letters 7:105–107.

Wigley, T.M.L., and Brown, M.C. 1976. The physics of caves. Pp. 329–358 *In* The Science of Speleology. Ford, T.D., and Cullingford, C.H.D. (Eds.). Academic Press, London, UK.

Zar, J.H. 1996. Biostatistical Analysis. 3rd Edition. Prentice Hall, Upper Saddle River, New Jersey, USA.

STEVEN J. TAYLOR is a Biologist at the Illinois Natural History Survey (University of Illinois) where his work focuses on biology, conservation and management in caves, karst, and other subterranean environments. He obtained a Ph.D. in Zoology from Southern Illinois University at Carbondale. In addition to salamanders, he has worked broadly in caves in the Western Hemisphere, working with a variety of invertebrates, as well as studies of bats. In addition to cave and karst systems, he is interested in natural history, conservation and management, especially relating to invertebrates, in a variety of terrestrial and freshwater systems. Steve is active internationally, serving on the IUCN Cave Invertebrate Specialist Group, the steering committee for the National Cave and Karst Management Symposium, and in various other capacities. (Photographed by Charles E. Pekins).

JEAN K. KREJCA has a Bachelor's degree in Zoology from Southern Illinois University, and a Ph.D. in Evolution, Ecology, and Behavior from the University of Texas at Austin. Since 1991, she has worked as a cave biologist and her experience in that area spans across the United States as well as Mexico, Belize, Thailand, China, Malaysia and the Philippines. In 2003, she co-founded Zara Environmental LLC where she continued her endangered species work from independent consulting and expanded her work to include regional HCP's (Section 10(a)(1)(A) permits), litigation support, USFWS consultations, and performing custom research projects. The Zara team she supports includes species specialists (mussels, birds, herps), groundwater and geology specialists, and field crews. In addition, she has been involved with a variety of public outreach efforts such as public talks, field trips, and cave biology photography. She is an avid cave explorer, and enjoys the challenges of caving expeditions in remote places.. (Photographed by Steven J. Taylor).



MATTHEW L. NIEMILLER earned his B.S. and M.S. in Biology from Middle Tennessee State University and Ph.D. in Ecology and Evolutionary Biology from the University of Tennessee and is currently a postdoctoral researcher at the Illinois Natural History Survey (University of Illinois). His research interests focus on the evolution, ecology, and conservation of subterranean biodiversity as well as herpetofauna in the eastern United States. He is coeditor of The Amphibians of Tennessee and The Reptiles of Tennessee, lead author of Cave Life of TAG, and has published more than 50 articles on cave life and herpetofauna. (Photographed by Alfred Crabtree).

MICHAEL J. DRESLIK is currently an Academic Professional at the Illinois Natural History Survey (INHS), University of Illinois Urbana-Champaign, Illinois where he began working in 2004. He has an A.S. from Lake Land College (1992), a B.S. from Eastern Illinois University (1994), an M.S. Eastern Illinois University (1996) examining the ecological of the River Cooter (*Pseudemys concinna*), and a Ph.D. from University of Illinois Urbana-Champaign (2005) on the ecology and conservation of the Eastern Massasauga (*Sistrurus catenatus*). After completing his doctorate, he was hired at the INHS for an environmental planning and assessment contract with the Illinois Tollway. Dr. Dreslik serves on recovery teams for the Illinois Department of Natural Resources, served in an advisory capacity to the Illinois Endangered Protection Species Board, provides advice on the conservation of the Eastern Massasauga to the USFWS, and coordinated the update to the amphibian and reptile portion of the Illinois Wildlife Action Plan. He is an adjunct in the Department of Natural Resources and Environmental Sciences at the University of Illinois and advises graduate students. (Photographed by Jen Mui).

CHRISTOPHER A. PHILLIPS is a Research Program Leader with the Illinois Natural History Survey in Champaign, Illinois. He received his B.Sc. from Eastern Illinois University (1983) and his Ph.D. from Washington University in St. Louis (1989). His main research focus concerns how populations of amphibians and reptiles have arrived at their current spatial distributions and how they maintain (or fail to maintain) these distributions. He approaches this topic in two ways, indirectly through the use of molecular markers, and directly through field observations, field manipulations, and laboratory experiments. Over the past five years, his research focus has expanded to include the importance of infectious disease in the distribution and abundance of amphibians and reptiles. Christopher is a member of the IUCN's Amphibian Specialist Group and Viper Specialist Group. He has published over 60 peer-reviewed articles and one book. (Photographed by Steven J. Taylor).