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THE ECOLOGY AND NATURAL HISTORY OF THE CUMBERLAND DUSKY SALAMANDER (*DESMOGNATHUS ABDITUS*): DISTRIBUTION AND DEMOGRAPHICS

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Abstract.—**Understanding the biology of rare or uncommon species is an essential component of their management and conservation. The Cumberland Dusky Salamander (*Desmognathus abditus*) was described in 2003, but no studies of its ecology, distribution, or demographics have been conducted. The southern Cumberland Plateau is recognized as an under-protected landscape, and recent studies on other stream salamanders suggest that even common species have small population sizes and limited distributions. To describe the ecology of this rare and unstudied species on the southern Cumberland Plateau, we conducted landscape scale occupancy surveys and focused capture-mark-recapture studies on *D. abditus*. We found that *D. abditus* had a limited distribution, and that clusters of populations were split by approximately 85 km. Their distribution coincided with small streams located in coves, and they were locally restricted to small waterfalls and exposed sandstone bedrock. Regional summer survival estimates revealed low bimonthly survival between 0.44–0.51. We found significant ecological differences between the population clusters with temporary emigration being 5.2 times higher in the northern sites relative to the southern sites. Though both population clusters were characterized by low population densities, those in the southern population cluster (0.15–0.56 m^{-2}) were lower than the northern population cluster (0.1–2.09 m^{-2}). *Desmognathus abditus* also occupied habitat on the southern Cumberland Plateau that is distinct from co-occurring species. Their unexplained disjunct distribution, rarity within their distribution, and low survival and density suggest a species in need of monitoring to ensure appropriate conservation actions for the long-term persistence of *D. abditus*.**

Key Words.—amphibian; body condition; Cumberland Plateau; density; geology; habitat; occupancy

INTRODUCTION

Concurrent threats to the long-term persistence of amphibians underscore the need to determine the status and ecology of narrowly distributed species (Stuart et al. 2004; Bury 2006). Recent studies have shown that climate change is likely to negatively impact salamander populations (Walls 2009; Milanovich et al. 2010; Lowe 2012; Caruso et al. 2014; Liles et al. 2017). For species with poor dispersal abilities and limited distributions such as lungless salamanders (Plethodontidae), these effects will be amplified (Smith and Green 2005; Bernardo and Spotila 2006). In other instances, encroaching anthropogenic land-use and forest conversion result in associated population declines (Gibbs 1998; Price et al. 2006; Hof et al. 2011). Furthermore, the threat of emerging diseases and synergistic threats to salamander diversity in North America necessitates that we understand the current distributions to detect changes associated with these threats (Hof et al. 2011; Adams et al. 2013; Martel et al. 2013; Grant et al. 2016). Besides biodiversity declines, amphibians are also important ecologically, serving as both predator and prey, moving energy and resources between terrestrial and aquatic habitats, and helping to retain nutrients (Peterman et al. 2008; Keitzer and Goforth 2013; Milanovich et al. 2015; Trice et al. 2015). Therefore, the loss of amphibians has the potential to transform some ecosystems (Beard et al. 2003; Whiles et al. 2006, 2013; Best and Welsh 2014).

Though the rate of discovery and description of new vertebrate species in the United States has slowed (Costello et al. 2012) revisions to amphibian taxa and new discoveries have elevated some lineages to species (e.g., Highton and Peabody 2000; Camp et al. 2002; Anderson and Tilley 2003; Means et al. 2017; Wray et al. 2017). In these instances, the ecologies of newly elevated species are often assumed to be similar to previously existing species, despite different

Figure 1. Cumberland Dusky Salamander (*Desmognathus abditus*) with a typical morphology (a) and an individual from the southernmost known population in Tennessee (b). (Photographed by Saunders Drukker).

evolutionary histories and geographical distributions (Anderson and Tilley 2003; Camp and Marshall 2006; Alcorn et al. 2013). However, species- and region-specific responses to environmental variables suggest that this assumption is unlikely for all aspects of the ecology of the newly elevated species (Tilghman et al. 2012; Alcorn et al. 2013; Gould et al. 2017). In the worst case, management and conservation needs for elevated species may go unrecognized, or application of existing methods may be ineffective because of these ecological differences (Bickford et al. 2007).

The Cumberland Dusky Salamander (*Desmognathus abditus*; Fig. 1) was described in 2003 by Anderson and Tilley (2003) as an undescribed lineage of the *D. ochrophaeus* complex. Since its description, there have been no other studies of its ecology, and descriptions of the species in recent texts rely on presumed similarity to closely related congeners (e.g., *D. ochrophaeus* or *D. ocoee*; Lannoo 2005; Niemiller and Reynolds 2011). *Desmognathus abditus* also occurs exclusively on the southern Cumberland Plateau of Tennessee, USA, a region for which data on stream-dwelling salamanders is lacking. Two recent surveys on distributions of salamanders in the southern Cumberland Plateau have shown that regional stream-dwelling salamander densities are low and do not share similar patterns with environmental variables as the same species in other ecoregions (Kirchberg et al. 2016; Gould et al. 2017). Specifically, these studies suggest that geographic features associated with plateau topography play a larger role in determining distributions of stream-dwelling salamanders in the Cumberland Plateau ecoregion than does forest cover, a common predictor of stream-dwelling amphibian distributions (Lowe and Bolger 2002; Price et al. 2006; Tilghman et al. 2012).

As an unstudied desmognathan in an understudied and underprotected ecoregion of the southeastern United States (Jenkins et al. 2015), information on the ecology and natural history of *D. abditus* is required to conserve the species. One factor contributing to the lack of knowledge about this species is the difficulty in finding populations (Anderson and Tilley 2003). In this study, we document the distribution and ecology of *D. abditus* in Tennessee on the Cumberland Plateau. Specifically, we address the following questions about *D. abditus*: 1) where is it found, and is its distribution related to specific environmental variables, 2) what are the survival rates and sizes of populations, and 3) what are basic characteristics of the species, including size distributions, breeding phenology, and site fidelity?

Materials and Methods

Distribution surveys.—We conducted occupancy surveys at 71 sites across 10 counties in the southern Cumberland Plateau of Tennessee, USA, from the Tennessee-Alabama state boundary north to the northern boundary of the Catoosa Wildlife Management Area. This region includes all available habitat between contact zones with *D. ochrophaeus* and *D. ocoee* in Franklin, Marion, Grundy, Warren, Van Buren, White, Cumberland, Bledsoe, Sequatchie, and Morgan counties (Fig. 2). We surveyed 50 sites in May-July 2015 and 21 sites in May-July 2016. We selected sites haphazardly to represent well dispersed sites sampling north-south, east-west, plateau-cove, and forest gradients. We identified locations initially using ArcGIS (v10.3) and adjusted in the field for logistics including access. In 2015, we made a priority sites on state-owned property because of limited access to private properties; whereas, we located sites in 2016 primarily on private property. Limited access to private property in 2015 resulted in clumped distribution of sites centered on state-owned properties, and surveys in 2016 were designed to fill in the spatial distribution of our sites.

At each site, we located a 150 m transect along the stream channel (Kroll et al. 2008; Gould et al. 2017). We subdivided transects into 15 5-m plots located 5 m

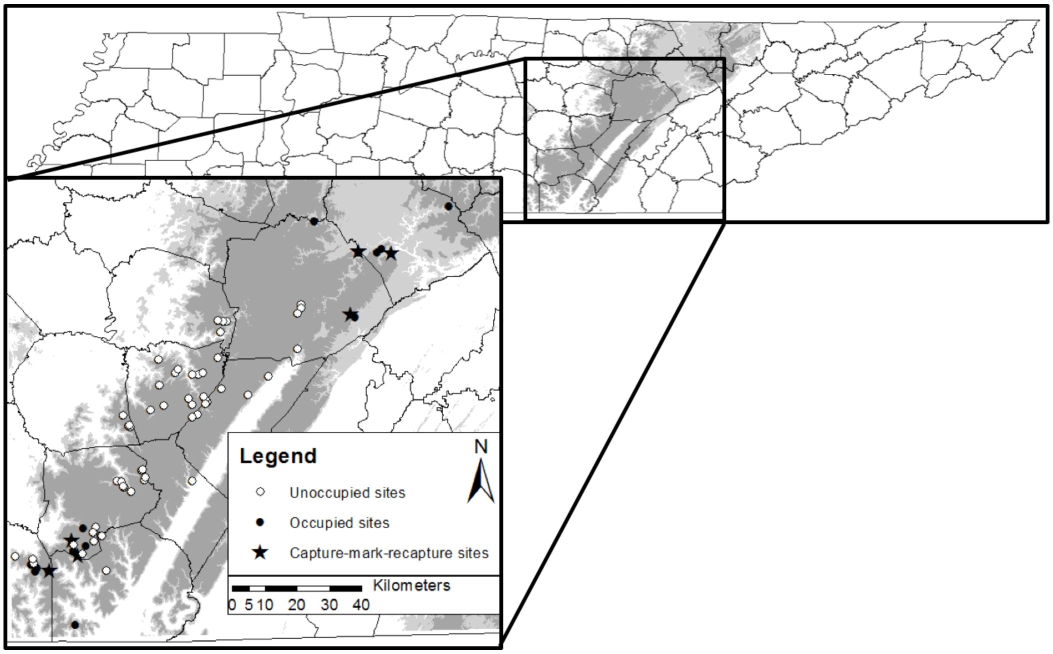

FIGURE 2. Study area for the Cumberland Dusky Salamander (*Desmognathus abditus*) on the southern Cumberland Plateau of Tennessee, USA. Black outlines represent the county boundaries of Tennessee. Dark grey shading represents the top of the Cumberland Plateau at elevations > 500 m above sea level (asl), and white represents the surrounding area at elevations < 350 m asl.

apart. At each plot, we surveyed the stream by lifting rocks and logs and dipnetting through leaves and under banks. We also surveyed both stream banks up to 1 m from the stream edge by lifting rocks and sifting through leaf litter. We identified all captured salamanders to species and life stage (pre- or post-metamorphic), and measured their snout-vent length (SVL), total length (TL), and mass. We also noted any injuries or tail autotomy. We released all individuals at their capture location within 60 min of capture. We repeated surveys on three consecutive days to account for incomplete detection (see modeling approach below).

For evaluation of environmental correlates with the distribution of *D. abditus*, we used geospatial datasets to quantify large-scale predictors of occupancy (Table 1). We used 10 m digital elevation models (Archuleta, C.M., E.W. Constance, S.T. Arundel, A.J. Lowe, K.S. Mantey, and L.A. Phillips. 2017. The National Map Seamless Digital Elevation Model Specifications: U.S. Geological Survey Techniques and Methods. Available at https://doi.org/10.3133/tm11B9. [Accessed 10 December 2015]) and the 2011 National Land Cover Dataset (Homer et al. 2015) to obtain aspect, drainage area, elevation, cove or plateau stream designation, latitude, and watershed-scale forest at each site (Table 1). We used the downstream end of our sampling transect for aspect, elevation, latitude values and to serve as the pour point to delineate watersheds using the hydrology toolset in ArcGIS. We used this watershed delineation to determine the area for which forest land-cover was assessed. Because aspect represented a circular dataset, we converted aspect to degrees from north to represent our hypothesis that northern facing slopes receive less sunlight and remain cooler than southern aspects resulting in higher salamander occupancy. Forested land-uses included hardwoods, mixed forest, and evergreens.

We used pairwise Pearson's correlations to determine if our covariates were correlated. We also quantified the dominant substrate type for inclusion in modeling detection probability. After the third sampling occasion, we qualitatively described the dominant substrate type for the sampled reach as primarily silt/clay, sand, cobble, or bedrock and subsequently assigned a numerical code from 1 to 4 from smallest size to largest size (Wolman 1954).

We developed a mixture model including a process model describing the ecological associations of *D. abditus* and an observation model describing the detection process. The process model included our distribution predictors of aspect, cove, drainage area, elevation, latitude, and forest cover. We converted all predictor variables to z-scored values to have a mean of 0 and standard deviation of 1. We also included site-specific intercepts in the process model to account for any spatial autocorrelation. We modeled the detection process as a function of survey day to account for potential capture-shy behaviors and substrate previously demonstrated to be important in modeling detection probability in this region (Bailey et al. 2004; Cecala et al. 2013; Gould et al. 2017). We evaluated the joint model using Bayesian inference implemented in WinBUGS

Table 1. Description and hypotheses behind environmental variables used to model the Cumberland Dusky Salamander (*Desmognathus abditus*) occupancy and detection on the southern Cumberland Plateau, North America.

Parameter	Mean	SE	Range	Hypothesis	Citation
Aspect (° from north)	86	6	(0.5–175)	Salamanders will show a preference for Northern aspects.	Harper and Guynn 1999
Cove (Yes or No)	0.47	0.06	(0–1)	Salamanders will show a preference for cove habitats that shift in soil moisture, soil fertility, climate, gradient, and vegetation.	Ford et al. 2002, McGrath et al. 2004
Drainage area (ha)	606	105	(0.1–4,444)	Salamanders will show a preference for smaller headwater streams.	Ford et al. 2002; Petranka 1998
Elevation (masl)	508	6	(323–585)	Salamanders will be more common at higher elevations.	Ford et al. 2002
Forest cover (%)	72.6	2.9	(0–100)	Salamanders will be positively correlated with increased forest cover.	Tilghman et al. 2012; Price et al. 2006; Lowe and Bolger 2002
Latitude	35.564	0.032	(35.033–36.179)	We predicted preference for higher latitudes given their known range.	Anderson and Tilley 2003
Substrate	2.47	0.13	(1–3.5)	Salamander detection often increases with larger dominant substrates.	Gould et al. 2017

(Lunn et al. 2000) using non-informative priors using normal (0,0.37) for coefficients and half-cauchy (1) for variance. We ran 660,000 iterations and excluded the first 60,000 iterations as the burn-in period using information from the Gelman-Rubin statistic (Gelman and Rubin 1992). We thinned iterations by a rate of 15 to reduce model autocorrelation. We evaluated estimates of the 95% credible intervals for the parameter posterior distributions and assumed that parameters with at least 75% of their distribution either above or below zero were biologically important (Gould et al. 2017). To identify any spatial patterns in occupancy, we visually evaluated the spatial distribution of random intercepts from our occupancy model using R program Spatstat (Baddeley et al. 2015).

Demographic surveys.—We performed capture-mark-recapture surveys May-July 2016 at six occupied sites; three located at the northern range limit of their range and three located at the southern range limit (Fig. 2). We established 100 m survey transects with the upstream edge of the transect at approximately the point where the stream descended off the plateau and into the cove. We conducted visual encounter surveys by lifting cover objects, sifting through leaf litter, dipnetting, and using a flashlight to survey crevices in bedrock in the stream and surrounding banks. We surveyed the entire stream width and up to one meter on both stream banks. For each postmetamorphic salamander captured, we recorded location, measured SVL, TL, and mass, marked it with visible implant elastomer (Northwest Marine Technology Inc., Shaw Island, Washington, USA; Grant 2010), and then released it at the capture location. We surveyed transects for three consecutive days every two weeks for a total of five primary periods following assumptions of the robust design capture-mark-recapture model (Pollock 1982). Post-hoc evaluation of the data revealed differences between northern and southern populations; consequently, we compared populations to determine if southern populations could be exhibiting climate associated stress (e.g., smaller body sizes, more limited distributions, lower densities, different population parameters; Walls 2009; Milanovich et al. 2010; Caruso et al. 2014; Liles et al. 2017).

We used multi-model inference to identify the best-fitting models to estimate demographic parameters for *D. abditus* including survival, capture and recapture probabilities, temporary emigration, and population size. We modeled survival as either being time dependent, regional (north versus south), or constant. For our models, we assumed that capture and recapture probabilities were equal but allowed capture probabilities to vary with different time parameters (sampling day or week), site, or region. We modeled temporary emigration was as being either random (probability of moving underground the same as moving above ground) or Markovian (probabilities of moving above or below ground are different), and we modeled temporary emigration as a factor of site, region, and time (Kendall et al. 1997; Bailey et al. 2004). We modeled population size as a site-specific parameter that was constant throughout the season because we did not mark larvae.

We evaluated goodness-of-fit of the most parameterized model using Program RDSURVIV (Hines 1996). The results indicated some overdispersion of our data relative to the model, so we adjusted the c-hat to 2.3 before assessing which models best fit our data. We evaluated model likelihoods given our data using Akaike's Information Criterion (AIC) adjusted for small

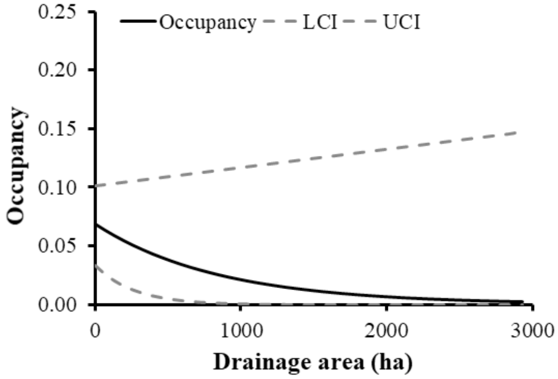

Figure 3. Relationship between patch occupancy of the Cumberland Dusky Salamander (*Desmognathus abditus*) and stream drainage area with the 95% credible interval (LCI = lower credible interval; UCI = upper credible interval).

Table 2. Estimates of environmental associations with detection probability and occupancy probability of the Cumberland Dusky Salamander (*Desmognathus abditus*). Mean, lower and upper 95% credible intervals (LCI and UCI respectively) of parameter estimates were obtained from the posterior distribution.

Parameter	Mean	LCI	UCI
Detection probability			
Day	0.38	0.01	0.93
Substrate	0.56	0.05	0.98
Occupancy probability			
Aspect	-0.34	-1.31	0.61
Cove	1.09	-0.03	2.34
Drainage area	-0.77	-2.44	0.60
Elevation	-0.25	-1.16	0.66
Forest cover	0.30	-0.77	1.50
Latitude	0.34	-0.60	1.30

sample sizes (AIC_c) in Program MARK. We used a forward stepwise model building approach maintaining consistent model structure among all parameters not being evaluated. We then used the best fitting model structure within a parameter for the next parameter until a final model with the best fitting model structure for each parameter was obtained (Table 2). After completion of model building, we evaluated AIC_c values and performed model averaging to account for parameter and model uncertainty in estimation of population parameters from the best fitting models ($\Delta AIC_c < 2$). To develop population size estimates, we corrected the estimated population size at any given capture period by the effective capture probability that incorporates capture probability and temporary emigration rates to develop a more complete estimate of population size known as the super population size (Bailey et al. 2004).

Life-history timing, size distributions, and site fidelity.—Because basic life-history data are unavailable for *D. abditus*, we documented body sizes, growth patterns, and movement patterns. Disjunct population clusters could potentially have different natural history parameters associated with stream characteristics or climate, and therefore, we evaluated if size, growth, or movement differed between population clusters. We obtained size distributions from the first capture of individuals at capture-mark-recapture sites. We obtained growth rates of *D. abditus* from size differences of recaptured individuals from their first capture to their last capture, and we corrected the differences for the number of days between captures. Body condition was calculated by using a scaled mass index (SMI) recommended for small vertebrates (Peig and Green 2009). We compared adult body size (SVL) and body condition from capture-mark-recapture surveys between northern and southern population clusters using Kolmogorov-Smirov tests, and variability was compared using a Bartlett test. We could not determine the sex of all individuals externally, and therefore, we excluded this information as a covariate of size. To determine if in-stream movements by *D. abditus* are absent or biased upstream or downstream, we evaluated the skew and kurtosis of the distribution of individual movement distances between captures (package moments; Komsta and Novomestky 2015). We evaluated morphological and movement data in R (R Core Team 2015).

Results

Distribution surveys.—We found 1,273 individuals of eight species of salamanders during our surveys, including *D. abditus* (n = 49), *D. conanti* (n = 432), D. welteri (n = 2), *Eurycea longicauda* (n = 66), *E. lucifuga* (n = 1), *E. wilderae* (n = 615), *Pseudotriton ruber* (n = 106), and *Gyrinophilus porphyriticus* (n = 2). Occupancy patterns of co-occurring species are reported elsewhere (Gould et al. 2017). Evaluation of site-specific parameters suggested that we sampled a range of conditions for each of our predictor variables, and Pearson's pairwise comparisons revealed that none of our covariates were correlated (Table 1). Daily detection probability for *D. abditus* was 0.54 ± 0.04 overall and was positively associated with bedrock (Table 2). This detection rate indicated that a three-day survey can confirm absence of *D. abditus* with a probability of 90.3%. We found that *D. abditus* were exclusively cove dwelling and preferred small watersheds (Table 2). Occupancy was predicted to increase 109% for streams located in coves relative to those on the plateau (Table 2). They were also 77% more likely to occupy watersheds that were one standard deviation smaller in watershed area than watersheds closer to the mean

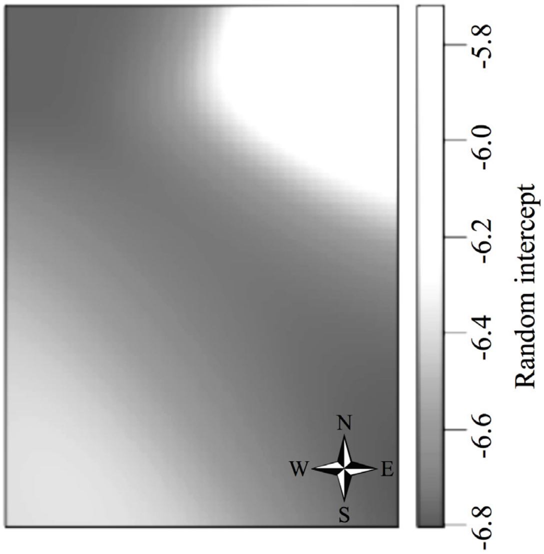

Figure 4. Interpolated random intercepts that varied by site. Lighter values indicate areas more likely to be occupied, whereas darker areas represent regions less likely to be occupied by the Cumberland Dusky Salamander (*Desmognathus abditus*). This interpolation supports field observations that suggested that *D. abditus* was unlikely to occupy sites in the middle of its distribution.

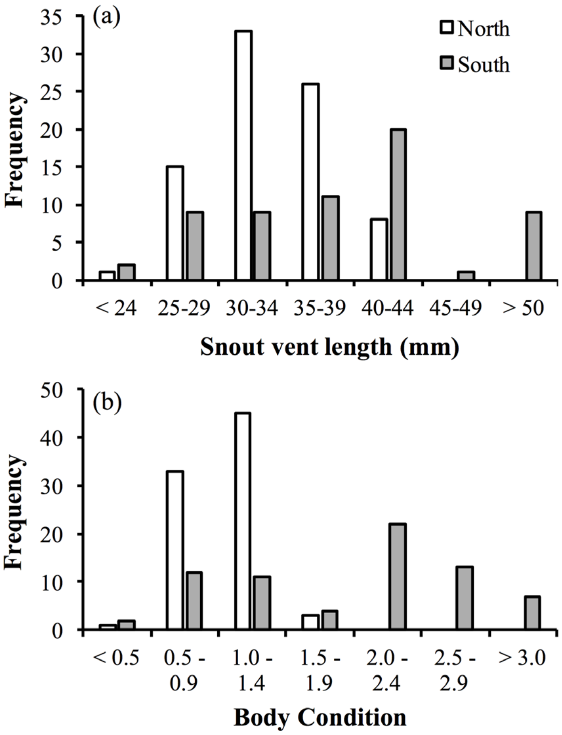

Figure 5. Body size (SVL) distribution (a) and distribution of body condition (b) quantified by the scaled mass index (SMI; Peig and Green 2009) of the Cumberland Dusky Salamander (*Desmognathus abditus*) in three populations in each of the two population clusters (north and south).

watershed area of our study sites (Fig. 3). Cove and drainage area were 3.2 and 3.0 times, respectively, more important in predicting *D. abditus* occupancy than other predictors (Table 2). Aspect, elevation, forest cover, and latitude were excluded from biological significance by having < 75% of their credible interval located in either the positive or negative scale (Table 2). Visual evaluation of the spatial distribution of random intercepts for watersheds support observations in the field that *D. abditus* were absent from the center of their range (Fig. 1). *Desmognathus abditus* were not found in any surveys of sites (n = 25) located between Gruetli-Laager, Tennessee, and Grassy Cove, Tennessee (Fig. 4).

Demographic surveys.—Overall, we captured 144 individuals at six sites represented by 231 captures. The number of capture occasions per individual varied among sites from 1.05–2.54 captures per individual. Most recaptures occurred on consecutive days within a secondary capture period. Collectively, the two best fitting models ($\Delta AIC_c < 2$; models 1 and 2; Table 3) resulted in model-averaged estimates of regionally varying survival, regionally variable random temporary emigration, and regionally variable capture probability with site-specific estimates of abundance (Table 3). The only difference between the top two ranked models was constant (model 1) versus regionally varying survival (model 2; Table 3). Bimonthly survival estimates overlapped widely between the regions and were 0.51 ± 0.10 (southern cluster) and 0.44 ± 0.22 (SE; northern cluster; Table 4). Capture probabilities were high and ranged from 0.30–0.51 and did not differ between regions (Table 4). Temporary emigration was variable by region with the northern cluster exhibiting a probability of retreating to underground refugia of 0.83 ± 0.24; whereas, southern populations retreated with a probability of 0.162 ± 0.22 (Table 4). Population estimates per site ranged from 15–209 individuals (Table 5). These represent mean densities ranging from 0.15–2.09 individuals per linear stream meter (Table 5). However, when we calculated densities from only the habitat where individuals were found, densities increased to a range of 3.0–16.1 individuals per linear stream meter (Table 5). These small habitat areas were typically characterized by vertical water features, such as waterfalls and seeps.

Life-history timing, size distributions, and site fidelity.—Postmetamorphic individual body size and body condition were significantly different between population clusters with northern populations being smaller and less variable (SVL, 33.0 ± 0.50 mm; SMI, 0.99 ± 0.03) than southern populations (SVL, 39.4 ± 1.00 mm, *D* = 0.549 *P* < 0.001, Fig. 5a; SMI, 1.90 ± 0.10, *D* = 0.620, *P* < 0.001, Fig. 5b). Growth rates, however, did not differ among regions for length (SVL,

Table 3. Model ranking from a forward stepwise progression to develop the best fitting models for the Cumberland Dusky Salamander (*Desmognathus abditus*). Stepwise procedures began with capture probability set equal to recapture probability. Parameters were modeled with site (S) or region (R) specific, and/or with daily (d) or weekly (w) variation. Temporary emigration was modeled as random (r) or Markovian (M).

	Survival			Temporary Emigration					Capture Probability						
Model	S	R	w	r	M	S	R	w	S	R	d	w	$QAIC_c$	$\Delta QAIC_c$	$QAIC_c$ *w*
1				X			X			X			187.13	0.00	0.651
2		X		X			X			X			189.01	1.89	0.254
3				X		X				X			192.11	4.98	0.054
4		X		X		X				X			194.00	6.88	0.021
5			X	X		X				X			194.56	7.44	0.016
6			X	X		X				X			198.41	11.29	< 0.001
7	X			X		X				X			198.41	11.29	< 0.001
8		X	X	X		X				X			201.62	14.50	< 0.001
9	X		X	X		X				X			212.44	25.32	< 0.001
10	X		X	X		X				X			212.44	25.32	< 0.001
11	X		X	X						X			215.71	28.58	< 0.001
12	X		X		X	X				X			217.64	30.51	< 0.001
13	X		X	X			X			X			217.71	30.58	< 0.001
14	X		X		X					X			218.32	31.20	< 0.001
15	X		X	X			X	X		X			222.12	34.99	< 0.001
16	X		X		X		X			X			223.01	35.88	< 0.001
17	X		X		X		X	X		X			226.05	38.92	< 0.001
18	X		X	X		X		X		X			227.44	40.31	< 0.001
19	X		X		X	X		X		X			228.78	41.66	< 0.001
20	X		X		X	X		X		X			228.78	41.66	< 0.001
21	X		X		X	X		X					233.64	46.51	< 0.001
22	X		X		X	X		X		X	X		237.52	50.39	< 0.001
23	X		X		X	X		X	X				237.87	50.74	< 0.001
24	X		X		X	X		X		X		X	244.52	57.39	< 0.001
25	X		X		X	X		X	X		X		245.55	58.42	< 0.001
27	X		X		X	X		X			X	X	245.90	58.77	< 0.001
28	X		X		X	X		X	X			X	246.89	59.76	< 0.001
29	X		X		X	X		X		X	X	X	247.50	60.37	< 0.001
30	X		X		X	X		X	X		X	X	248.62	61.49	< 0.001

$D = 0.476$, $P = 0.431$), mass ($D = 0.404$, $P = 0.538$), or body condition (SMI, $D = 0.429$, $P = 0.451$). For both population clusters, median growth in length was 0.032 ± 0.083 mmd^{-1} or 2.2 mm for the 70-d study period. Mass increased 0.006 ± 0.007 gd^{-1} or 0.43g for the study period. Body condition declined over the study period at a rate of 0.016 ± 0.008 d^{-1}. Both distributions of movement differed from a normal distribution (south, $W = 0.717$ $P < 0.001$; north, $W = 0.224$, $P < 0.001$). Departure from normality was largest in the northern population cluster with greater kurtosis (north, 35.4; south, 7.5) and greater skew (south, -5.53; north, -0.61) than the southern population cluster. High kurtosis indicated that most individuals captured in each population cluster remained at their capture location. In the northern cluster, three individuals moved as much as 25 m downstream and one moved 7 m upstream between captures (Fig. 6a). In contrast, 12 individuals from the southern cluster moved from their capture location, but none moved more than 3 m (Fig. 6b). We found larvae in peripheral streamside seeps on 29 January 2016 and 31 May 2016. Although we did not find egg masses, we did find females with sperm caps extruding from their cloaca on 30 May and 15 July 2016. Finally, though we did not quantify the frequency of individuals, some individuals in the southern populations had keratinized

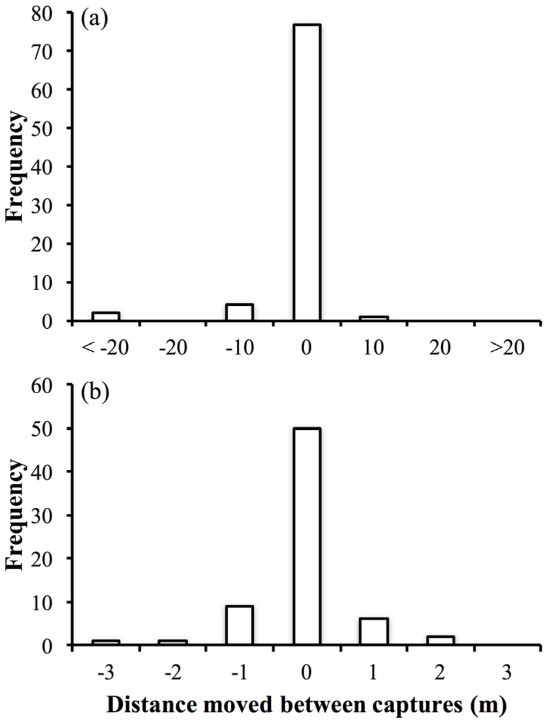

Figure 6. Distribution of distances moved between captures for three populations of the Cumberland Dusky Salamander (*Desmognathus abditus*) in the northern population cluster (a) versus three populations in the southern population cluster (b). Note that the x-axis scale is different.

toe tips, but this trait was not observed in any of the northern populations.

Discussion

Our data suggests that *Desmognathus abditus* is an uncommon salamander on the southern Cumberland Plateau in both distribution and abundance. Within this region, the species comprises two disjunct population clusters separated by approximately 85 km. Populations within each cluster are small and found only in a limited area of an occupied stream. Evaluation of occupancy patterns suggest that they are unlikely to be found outside of coves, and capture-mark-recapture surveys indicate preferences for bedrock cascades. When the substrate changes from bedrock to sand or colluvium at high or low elevations, respectively, we failed to locate *D. abditus*. These patterns are unlike those previously observed for other co-occurring stream salamander species that prefer small, flat, and sandy bottom streams located on top of the Cumberland Plateau (Gould et al. 2017). Therefore, we suggest that the ecology of *D. abditus* is unique among other species of stream-dwelling salamanders on the southern Cumberland Plateau and may require different management actions than recommended for other species.

Table 4. Model averaged parameter estimates from the top two ranked models for the Cumberland Dusky Salamander (*Desmognathus abditus*). Collectively, the estimates assume regional variation in survival, temporary emigration (random), and capture probability. LCI and UCI represent the lower and upper 95% confidence intervals, respectively.

Parameter	Region	Estimate	SE	LCI	UCI
Survival	South	0.51	0.10	0.32	0.69
Survival	North	0.44	0.22	0.12	0.82
Temporary emigration	South	0.16	0.22	0.01	0.81
Temporary emigration	North	0.83	0.24	0.14	0.99
Capture probability	South	0.38	0.07	0.30	0.46
Capture probability	North	0.40	0.05	0.37	0.51

The most parsimonious description of the distribution of *D. abditus* is to assume that it occupies the southern Cumberland Plateau from its contact zone with *D. ochrophaeus* south to northern Alabama where putative *D. ocoee* specimens have been found (Tilley and Mahoney 1996; Powell et al. 2016). We are unable to explain the gap separating the two population clusters. Other stream species occupy the region where *D. abditus* was absent (Gould et al. 2017), and sections of streams within this gap region have habitat similar to that of sites with *D. abditus*. Specimens sampled from the southern population cluster possess *D. abditus* haplotypes suggesting that this disjunct distribution was previously continuous (Anderson and Tilley 2003). However, specimens sampled from south of Sewanee, Tennessee, also possess haplotypes that appeared to be shared with an adjacent or sympatric lineage of *D. ocoee* (Tilley and Mahoney 1996; Kozak et al. 2005; Dave Beamer and Alex Pyron, pers. comm.). These specimens may represent a separate lineage or a zone of genetic contact or hybridization between these two distantly related species. Increased variance of body size and body condition of southern populations also support our inferences that southern *D. abditus* populations may have

Table 5. Estimated population sizes of the Cumberland Dusky Salamander (*Desmognathus abditus*) were corrected for temporary emigration to estimate total surface and subsurface population size (superpopulation size) with lower and upper 95% confidence intervals (LCI and UCI, respectively). Density was calculated in two ways: one was calculated as the population size corrected for the sampled stream length, whereas the corrected density estimate only considered the stream length for which *D. abditus* were found.

Site	Region	Estimate	LCI	UCI	Density	Corrected density
1	South	56	45	66	0.56	3.29
2	South	15	12	18	0.15	3.00
3	South	27	26	28	0.27	2.45
4	North	209	123	293	2.09	16.1
5	North	124	79	168	1.24	15.5
6	North	18	0	62	0.18	1.64

genetic influence from another desmognathan lineage as documented in other lineages in the Appalachian Mountains (Tilley et al. 2013). Further support for this conclusion are individuals with *D. abditus* haplotypes that possess keratinized toe tips. While keratinized toes are common to highly aquatic desmognathan lineages (e.g., *D. quadramaculatus*, *D. monticola*, *D. marmoratus*), they have not been described for other species in more terrestrial desmognathan lineages (e.g., *D. ochrophaeus*, *D. ocoee*; Petranka 1998; Caldwell and Trauth 1979).

Difficulty in locating *D. abditus* populations stem from the gap in their distribution combined with high habitat specificity. On the southern Cumberland Plateau, *D. abditus* are found only on the narrow borders of cove habitat at the edge of the plateau. In this steep transition zone, *D. abditus* are closely associated with bedrock cascade and waterfalls. In the southern population cluster, this habitat is closely associated with exposure and erosion of the Warren Point Sandstone (Knoll et al. 2015). In some streams, the exposure of Warren Point Sandstone may be limited to 8 m2. We also find *D. abditus* in surface water seeps from sandstone layers and in concrete water conveyances. This specificity to steep and often small water features make it challenging to predict precisely where *D. abditus* will occur. Although this relationship has not yet been described for closely related species (e.g., *D. ocoee*, *D. ochrophaeus*), preferences for wet, bedrock or boulder surfaces in smaller streams is similar among all three species (Niemiller and Reynolds 2011). Exposed bedrock cascades are most common in small streams, which *D. abditus* prefers, and body condition of *D. abditus* decline with increasing drainage area (Appendix A). We suggest that either large streams are less suitable or more stressful habitat, or individuals captured in large streams are dispersing among smaller stream regions and depleting their fat reserves. A recent in-situ evaluation of spatial habitat partitioning found *D. abditus* occupying more peripheral stream areas in the presence of a larger congener, indicating that competition with larger species may also drive *D. abditus* to use smaller streams (Liles et al. 2017).

Estimates of population parameters for *D. abditus* are low relative to comparative studies on closely related species. Although densities are within the lower range of densities for a closely related species (e.g., *D. ocoee*; 1.06–22m^{-1}; Huheey and Brandon 1973; Bernardo 1994), the small area of their preferred habitat results in a much lower density than described for other species in the *D. ochrophaeus* complex. Our summer estimates suggest an entire stream population of *D. abditus* is at most 293 individuals. Furthermore, the closest populations are separated by a minimum of 1.2 km (Euclidean distance), which exceeds maximum dispersal distances known for stream amphibians (Lowe 2003). Thus, this species occupies a patchy distribution with small population sizes and potentially limited gene flow (Lowe et al. 2006). One unexpected result is a regional difference in temporary emigration, which may be explained by differences in stream morphology and use by *D. abditus*. In the northern population cluster, individuals use in-stream refugia and crevices in bedrock. This ability to retreat to hyporheic zones is unavailable to individuals inhabiting bedrock based streams in the southern cluster with low temporary emigration rates. Despite variation between population clusters, bimonthly survival estimates are low in both regions. Extrapolated over the length of the summer, these rates suggest a 4–6% probability for an adult to survive the summer, which is substantially lower than annual survival rates of 63–74% estimated by Tilley (1980) for *D. ocoee*. These low survival rates may have been reduced by a prolonged drought in 2016. No individuals were found at the northern sites during our last sampling session in July when many streams experienced minimal or no streamflow. Possibly, individuals either perish during the drought or enter underground refugia to withstand the drought. We have not conducted surveys since the drought to determine if marked individuals returned to the stream channel. In other regions, drought is not known to affect adult survival, but temporary emigration estimates increase while occupancy estimates decrease (Price et al. 2012; Currinder et al. 2014).

Some similarities exist between the natural history of *D. abditus* and other species in the *D. ochrophaeus* complex likely reflecting their shared evolutionary history (Petranka 1998; Lannoo 2005; Niemiller and Reynolds 2011). Breeding phenology appears similar among the species, with breeding occurring between May and June. Larvae are present in both October and February and likely overwintering in streams. Although we did not find egg masses, females presumably brood egg masses in cracks and crevices of the waterfalls and seeps where they are found, which is similar to other species in the *D. ochrophaeus* complex (summarized in Petranka 1998). Body sizes are similar to others in the *D. ochrophaeus* complex (summarized in Petranka 1998; Lannoo 2005), but southern populations reach larger sizes. Furthermore, some of these large individuals from southern populations have an aquatic morphology (keratinized toes and keeled tail) absent from descriptions of the terrestrial morphologies (rounded tail, absence of keratinized toes) of *D. ochrophaeus* and *D. ocoee* (Fig. 1; Caldwell and Trauth 1979; Petranka 1998). Body condition declines over the summer and could be indicative of stress associated with the late summer drought. Because declines in body condition can arise from growth in length or decrease in mass, it is also possible that growth in length may have outpaced growth in mass resulting in lower body condition estimates (Liles et al. 2017). In an *ex-situ* experiment of *D. abditus* growth rates at warmer temperatures, individuals exhibited greater growth in mass than in length (Liles et al. 2017). These results predict higher body condition or heavier individuals at southern locations relative to northern locations (Liles et al. 2017), but we did not observe a difference between the population clusters. A potential explanation for the absence of these predicted difference in-situ is the relatively small difference in mean summer temperatures between the two regions (< 0.9° C; Fick and Hijmans 2017).

The ecology and natural history of *D. abditus* resembles that of closely related congeners, but the discontinuous distribution and stream morphology of the southern Cumberland Plateau places additional restrictions on the demography of *D. abditus*. Unlike closely related congeners, small population sizes and a disjunct distribution suggest that there is justification for the near threatened status of the species (Hammerson 2006). As the first study of the distribution and demography of *D. abditus*, it is unknown whether the current distribution and population sizes reflect a decline in extent or in abundance to warrant elevation of their conservation status, but the present study does reduce the area of their known range. Present day stability and maintenance of their populations could be at risk due to a lack of state and federal protection for the region (Baldwin and Leonard 2015; Jenkins et al. 2015) though select populations in each area can be found on state-managed properties. New land-use pressures for the region include home development on the plateau bluffs and quarrying (legal and illegal) for mountain stone that threaten the habitat quality of high elevation coves where *D. abditus* is found. Road development for quarrying resulted in the apparent extirpation of *D. abditus* from one known locality in the past year (pers. obs.). Long-term monitoring is necessary to observe the resilience of *D. abditus* populations to anthropogenic changes within watersheds and determine the likelihood of decline. These observations are essential to ensure the appropriate level of concern and conservation action to preserve the long-term viability of *D. abditus* populations, particularly as the climate in the region becomes drier (Ingram et al. 2013).

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LITERATURE CITED

Adams, M.J., D.A.W. Miller, E. Muths, P.S. Corn, E.H.C. Grant, L.L. Bailey, G.M. Fellers, R.N. Fisher, W.J Sadinski, H. Waddle, and S.C. Walls. 2013. Trends in amphibian occupancy in the United States. PLoS ONE, 8, 1–5. http://dx.doi.org/10.1371/journal.pone.0064347.

Alcorn, M.A., J. Deitloff, S.P. Graham, and E.K. Timpe. 2013. Sexual dimorphism in head shape, relative head width, and body size of *Eurycea aquatica* and *Eurycea cirrigera*. Journal of Herpetology 47:321–327.

Anderson, J., and S. Tilley. 2003. Systematics of the *Desmognathus ochrophaeus* complex in the Cumberland Plateau of Tennessee. Herpetological Monographs 17:75–110.

Baddeley, A., E. Rubak, and R. Turner. 2015. Spatial Point Patterns: Methodology and Applications in R. Chapman and Hall/CRC Press, London, UK.

Bailey, L.L., T.R. Simons, and K.H. Pollock. 2004. Estimating detection probability parameters for *Plethodon* salamanders using the robust capture-recapture design. Journal of Wildlife Management 68:1–13.

Baldwin, R.F., and P.B. Leonard. 2015. Interacting social and environmental predictors for the spatial distribution of conservation lands. PloS ONE, 10, 1–18. http://dx.doi.org/10.1371/journal.pone.0140540.

Beard, K.H., A.K. Eschtruth, K.A. Vogt, D.J. Vogt, and F.N. Scatena. 2003. The effects of the frog *Eleutherodactylus coqui* on invertebrates and ecosystem processes at two scales in the Luquillo Experimental Forest, Puerto Rico. Journal of Tropical Ecology 19:607–617.

Bernardo, J. 1994. Experimental analysis of allocation in two divergent, natural salamander populations. The American Naturalist 143:4–38.

Bernardo, J., and J.R. Spotila. 2006. Physiological constraints on organismal response to global warming: mechanistic insights from clinally varying populations and implications for assessing endangerment. Biology Letters 2:135–139.

Best, M.L., and H.H. Welsh Jr. 2014. The trophic role of a forest salamander: impacts on invertebrates, leaf litter retention, and the humification process. Ecosphere 5:1–19.

Bickford, D., D.J. Lohman, N.S. Sodhi, P.K. Ng, R. Meier, K. Winker, K.K. Ingram, and I. Das. 2007.

Cryptic species as a window on diversity and conservation. Trends in Ecology and Evolution 22:148–155.

Bury, R.B. 2006. Natural history, field ecology, conservation biology and wildlife management: time to connect the dots. Herpetological Conservation and Biology 1:56–61.

Caldwell, R.S., and S.E. Trauth. 1979. Use of the toe pad and tooth morphology in differentiating three species of *Desmognathus* (Amphibia, Urodela, Plethodontidae). Journal of Herpetology 13:491–497.

Camp, C.D., and J.L. Marshall. 2006. Reproductive life history of *Desmognathus folkertsi* (Dwarf Black-Bellied Salamander). Southeastern Naturalist 5:669–684.

Camp, C.D., S.G. Tilley, R.M. Austin, Jr., and J.L. Marshall. 2002. A new species of black-bellied salamander (Genus *Desmognathus*) from the Appalachian Mountains of Northern Georgia. Herpetologica 58:471–484.

Caruso, N.M., M.W. Sears, D.C. Adams, and K.R. Lips. 2014. Widespread rapid reductions in body size of adult salamanders in response to climate change. Global Change Biology 20:1751–1759.

Cecala, K.K., S.J. Price, and M.E. Dorcas. 2013. Modeling the effects of life-history traits on estimation of population parameters for a cryptic stream species. Freshwater Science 32:116–125.

Costello, M.J., S. Wilson, and B. Houlding. 2012. Predicting total global species richness using rates of species description and estimates of taxonomic effort. Systematic Biology 61:871–883.

Currinder, B., K.K. Cecala, R.M. Northington, and M.E. Dorcas. 2014. Response of stream salamanders to experimental drought in the southern Appalachian Mountains, USA. Journal of Freshwater Ecology 29:579–587.

Fick, S.E., and R.J. Hijmans, 2017. Worldclim 2: New 1-km spatial resolution climate surfaces for global land areas. International Journal of Climatology. http://dx.doi.org/10.1002/joc.5086.

Ford, W.M., M.A. Menzel, and R.H. Odom. 2002. Elevation, aspect, and cove size effects on southern Appalachian salamanders. Southeastern Naturalist 1:315–324.

Gelman, A., and D.B. Rubin. 1992. Inference from iterative simulation using multiple sequences. Statistical Science 7:457–472.

Gibbs, J.P. 1998. Distribution of woodland amphibians along a forest fragmentation gradient. Landscape Ecology 13:263–268.

Gould, P.R., K.K. Cecala, S.S. Drukker, B.A. McKenzie, and C. Van de Ven. 2017. Biogeographical factors affecting the distribution of streams salamanders on the Cumberland Plateau, USA. Science of the Total Environment 599–600:1622–1629.

Grant, E.H.C. 2010. Visual implant elastomer mark retention through metamorphosis in amphibian larvae. Journal of Wildlife Management 72:1247–1252.

Grant, E.H.C., D.A.W. Miller, B.R. Schmidt, M.J. Adams, S.M. Amburgey, T. Chambert, S.S. Cruickshank, R.N. Fisher, D.M. Green, B.R. Hossack, et al. 2016. Quantitative evidence for the effects of multiple drivers on continental-scale amphibian declines. Scientific Reports 6:25625.

Hammerson, G. 2006. *Desmognathus abditus*. The IUCN Red List of Threatened Species 2006: e.T61902A12569557. http://dx.doi.org/10.2305/IUCN.UK.2006.RLTS.T61902A12569557.en

Harper, C.A., and D.C. Guynn. 1999. Factors affecting salamander density and distribution within four forest types in the Southern Appalachian Mountains. Forest Ecology and Management 114:245–252.

Highton, R., and R.B. Peabody. 2000. Geographic protein variation and speciation in salamanders of the *Plethodon jordani* and *Plethodon glutinosus* complexes in the southern Appalachian Mountains with the description of four new species. Pp. 31–93 *In* The Biology of Plethodontid Salamanders. Bruce, R.C., R.G. Jaeger, and L. Houck (Eds.). Kluwer Academic/Plenum Publishers, New York, New York, USA.

Hines, J.E. 1996. RDSURVIV user's manual. Biological Resources Division, U.S. Geological Survey, Laurel, Maryland, USA.

Hof, C., M.B. Araújo, W. Jetz, and C. Rahbek. 2011. Additive threats from pathogens, climate and land-use change for global amphibian diversity. Nature 480:516–519.

Homer, C.G., J.A. Dewitz, L. Yang, S. Jin, P. Danielson, G. Xian, J. Coulston, N.D. Herold, J.D. Wickham, and K. Megown. 2015. Completion of the 2011 National Land Cover Database for the conterminous United States - representing a decade of land cover change information. Photogrammetric Engineering and Remote Sensing 81:5:345–354.

Huheey, J.E., and R.A. Brandon. 1973. Rock-face populations of the Mountain Salamander, *Desmognathus ochrophaeus*, in North Carolina. Ecological Monographs 43:59–77.

Ingram, K.T., K. Dow, L. Carter, and J. Anderson (Eds). 2013. Climate of the Southeast United States: Variability, Change, Impacts, and Vulnerability. Island Press. Washington, D.C., USA.

Jenkins, C.N., K.S. Van Houtan, S.L. Pimm, and J.O. Sexton. 2015. US protected lands mismatch biodiversity priorities. Proceedings of the National Academy of Sciences 112:5081–5086.

Keitzer, S.C., and R.R. Goforth. 2013. Spatial and seasonal variation in the ecological significance of nutrient recycling by larval salamanders in Appalachian headwater streams. Freshwater Science 32:1136–1147.

Kendall, W.L., J.D. Nichols, and J.E. Hines. 1997. Estimating temporary emigration using capture-recapture data with Pollock's robust design. Ecology 78:563–578.

Kirchberg, J., K.K. Cecala, S.J. Price, E.M. White, and D.G. Haskell. 2016. Evaluating the impacts of small impoundments on stream salamanders. Aquatic Conservation: Marine and Freshwater Ecosystems 26:1197–1206.

Knoll, M.A., D.B. Potter, Jr., and C. Van de Ven. 2015. Geology, hydrology, and water use atop the Cumberland Plateau in the Sewanee and Tracy City, Tennessee, area. Pp. 197–218 *In* Diverse Excursions in the Southeast: Paleozoic to Present. Holmes, A.E. (Ed.). Geological Society of America Field Guide 39, Boulder, Colorado, USA.

Komsta, L., and F. Novomestky. 2015. Moments: Moments, cumulants, skewness, kurtosis and related tests. R package version 0.14. http://CRAN.R-project.org/package=moments.

Kozak, K.H., A. Larson, R.M. Bonett, and L.J. Harmon. 2005. Phylogenetic analysis of ecomorphologcal divergence, community structure, and diversification rates in dusky salamanders (Plethodontidae: *Desmognathus*). Evolution 59:2000–2016.

Kroll, A.J., K. Risenhoover, T. McBride, E. Beach, B.J. Kernohan, J. Light, and J. Bach. 2008. Factors influencing stream occupancy and detection probability parameters of stream-associated amphibians in commercial forests of Oregon and Washington, USA. Forest Ecology and Management 255:3726–3735.

Lannoo, M. (Ed.). 2005. Amphibian Declines: The Conservation Status of United States Species. University of California Press, Berkeley, California, USA.

Liles, L.A., K.K. Cecala, J.R. Ennen, and J.M. Davenport. 2017. Elevated temperatures alter competitive outcomes and body condition in southern Appalachian salamanders. Animal Conservation 20:502–510.

Lowe, W.H. 2003. Linking dispersal to local population dynamics: a case study using a headwater salamander system. Ecology 84:2145–2154.

Lowe, W.H. 2012. Climate change is linked to long-term decline in a stream salamander. Biological Conservation 145:48–53.

Lowe, W.H., and D.T. Bolger. 2002. Local and landscape-scale predictors of salamander abundance in New Hampshire headwater streams. Conservation Biology 16:183–193.

Lowe, W., G. Likens, M. McPeek, and D. Buso. 2006. Linking direct and indirect data on dispersal: isolation by slope in a headwater stream salamander. Ecology 87:334–339.

Lunn, D.J., A. Thomas, N. Best, and D. Spiegelhalter. 2000. WinBUGS - A Bayesian modelling framework: concepts, structure, and extensibility. Statistics and Computing 10:325–337.

Martel, A., A. Spitzen-van der Sluijs, M. Blooi, W. Bert, R. Ducatelle, M.C. Fisher, A. Woeltjes, W. Bosman, K. Chiers, F. Bossuyt, and F. Pasmans. 2013. *Batrachochytrium salamandrivorans* sp. nov. causes lethal chytridiomycosis in amphibians. Proceedings of the National Academy of Sciences USA 110:15325–15329.

McGrath, D.A., J.P. Evans, C.K. Smith, D.G. Haskell, N.W. Pelkey, R.R. Gottfried, C.D. Brockett, M.D. Lane, and E.D. Williams. 2004. Mapping land-use change and monitoring the impacts of hardwood-to-pine conversion on the southern Cumberland Plateau in Tennessee. Earth Interactions 8:1–23.

Means, D.B., J.Y. Lamb, and J. Bernardo. 2017. A new species of dusky salamander (Amphibia: Plethodontidae: *Desmognathus*) from the Eastern Gulf Coastal Plain of the United States and a redescription of *D. auriculatus*. Zootaxa 4263:467–506.

Milanovich, J.R., W.E. Peterman, N.P. Nibbelink, and J.C. Maerz. 2010. Projected loss of a salamander diversity hotspot as a consequence of projected global climate change. PLoS ONE, 5, 1–10. http://dx.doi.org/10.1371/journal.pone.0012189.

Milanovich, J.R., J.C. Maerz, and A.D. Rosemond. 2015. Stoichiometry and estimates of nutrient standing stocks of larval salamanders in Appalachian headwater streams. Freshwater Biology 60:1340–1353.

Niemiller, M.L., and G. Reynolds. 2011. The Amphibians of Tennessee. The University of Tennessee Press, Knoxville, Tennessee, USA.

Peig, J., and A.J. Green. 2009. New perspectives for estimating body condition from mass/length data: the scaled mass index as an alternative method. Oikos 118:1883–1891.

Peterman, W.E., J.A. Crawford, and R.D. Semlitsch. 2008. Productivity and significance of headwater streams: population structure and biomass of the Black-bellied Salamander *Desmognathus quadramaculatus*. Freshwater Biology 53:347–357.

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

Pollock, K.H. 1982. A capture-recapture design robust to unequal probabilities of capture. Journal of Wildlife Management 46:752–757.

Powell, R., R. Conant, and J.T. Collins. 2016. Peterson Field Guide to Reptiles and Amphibians of Eastern and Central North America, 4th Edition. Houghton Mifflin Harcourt, New York, New York, USA.

Price, S.J., M.E. Dorcas, A.L. Gallant, R.W. Klaver, and J.D. Willson. 2006. Three decades of urbanization: estimating the impact of land-cover change on stream salamander populations. Biological Conservation 133:436–441.

Price, S.J., R.A. Browne, and M.E. Dorcas. 2012. Resistance and resilience of a stream salamander to supraseasonal drought. Herpetologica 68:312–323.

R Core Team. 2015. R: A language and environment for statistical computing. Vienna, Austria. http://www.r-project.org.

Smith, A.M., and D.M. Green. 2005. Dispersal and the metapopulation paradigm in amphibian ecology and conservation: are all amphibian populations metapopulations? Ecography 28:110–128.

Stuart, S.N., J. Chanson, N.A. Cox, B.E. Young, A.S.L. Rodriguez, D.L. Fischman, and R.W. Waller. 2004. Status and trends of amphibian declines and extinctions worldwide. Science 306:1783–1786.

Tilghman, J.M., S.W. Ramee, and D.M. Marsh. 2012. Meta-analysis of the effects of canopy removal on terrestrial salamander populations in North America. Biological Conservation 152:1–9.

Tilley, S.G. 1980. Life histories and comparative demography of two salamander populations. Copeia 1980:806–821.

Tilley S.G., and M.J. Mahoney. 1996. Patterns of genetic differentiation in salamanders of the *Desmognathus ochrophaeus* complex (Amphibia: Plethodontidae). Herpetological Monographs 10:1–42.

Tilley, S.G., J. Bernardo, L.A. Katz, L. López, J.D. Roll, R.L. Eriksen, J. Kratovil, N.K. Bittner, and K.A. Crandall. 2013. Failed species, innominate forms, and the vain search for species limits: cryptic diversity in dusky salamanders (*Desmognathus*) of eastern Tennessee. Ecology and Evolution 3:2547–2567.

Trice, A.E., A.D. Rosemond, and J.C. Maerz. 2015. Diet composition of two larval headwater stream salamanders and spatial distribution of prey. Freshwater Biology 60:2424–2434.

Walls, S.C. 2009. The role of climate in the dynamics of a hybrid zone in Appalachian salamanders. Global Change Biology 15:1903–1910.

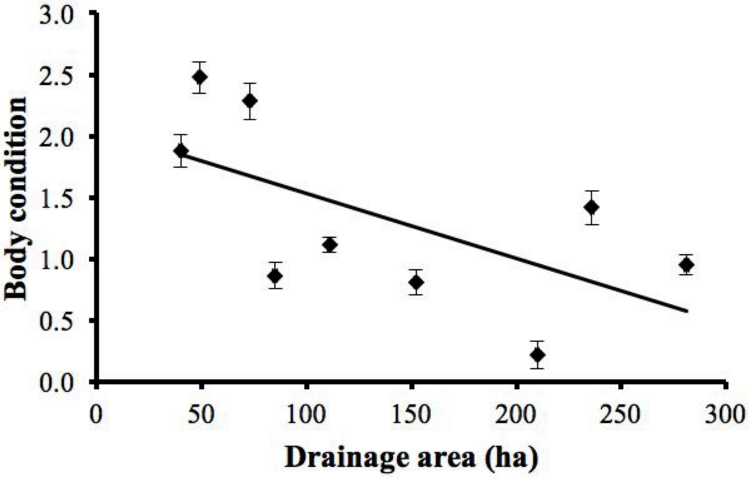
Whiles, M., K. Lips, C. Pringle, S. Kilham, R. Bixby, R. Brenes, S. Connelly, J.C. Colon-Gaud, M. Hunte-Brown, A.D. Huryn, et al. 2006. The effects of amphibian population declines on the structure and function of Neotropical stream ecosystems. Frontiers in Ecology and the Environment 4:27–34.

Whiles, M.R., R.O. Hall, W.K. Dodds, P. Verburg, A.D. Huryn, C.M. Pringle, K.R. Lips, S.S. Kilham, C. Colon-Gaud, A.T. Rugenski, et al. 2013. Disease-driven amphibian declines alter ecosystem processes in a tropical stream. Ecosystems 16:1–12.

Wolman, M.G. 1954. A method for sampling coarse river-bed material. American Geophysical Union Transactions 35:951–956.

Wray, K.P., D.B. Means, and S.J. Steppan. 2017. Revision of the *Eurycea quadridigitata* (Holbrook 1842) complex of dwarf salamanders (Caudata: Plethodontidae: Hemidactyliinae) with a description of two new species. Herpetological Monographs 31:18–46.

Appendix A. Negative correlation between drainage area and body condition (±1 SE) of the Cumberland Dusky Salamander (*Desmognathus abditus*; $t = -2.07$, $P = 0.076$, $r^2 = 0.38$; with best fit line).



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