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RESEARCH ARTICLE

Should landscape variation in population status be assessed with individual- or population-level indicators?

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Abstract

Monitoring trends in wildlife populations is essential to effective management. Evaluating only a single metric can be cost-effective; however, how a given metric responds to environmental variation may differ from other population- or individual-level metrics. Consequently, conclusions about the effect of environmental variation on a species should consider the relationship between different metrics. We investigated how population-level metrics (occupancy and relative abundance) and an individual-level metric (body condition) responded to landscape variation in 3 semi-aquatic salamander species. In the summer of 2015 and 2016, we conducted repeated count surveys at 71 streams on the Cumberland Plateau, Tennessee, USA, actively counting and measuring salamanders. We estimated occupancy and abundance of larval and post-metamorphic animals using community-occupancy and community-N mixture models, respectively. We estimated body condition of the most observed life stage for each species using a standardized mass index. All models included the same set of covariates for comparison. Occupancy and abundance responses for each life stage-by-species combination were positively correlated for 4 of 6 combinations, with salamander abundance responding to a larger suite of covariates. Body condition was not linked to covariates in the same fashion as population-level metrics, although consistency across species was detected for 1 covariate, watershed size. Our results indicate that inter-specific and inter-life stage variation in

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evaluated metrics is present within salamanders of this study system. Management for populations of salamanders in the region should consider monitoring multiple response metrics, to capture both population- and individual-level responses, as these may not always be correlated.

KEYWORDS

abundance, Bayesian, body condition, Cumberland Plateau, occupancy, population modeling, wildlife

Effective monitoring of wildlife populations is essential to enhancing our understanding of ecological processes and increasing resilience of populations in the face of predicted future disturbances. Commonly, site-occupancy and abundance are used as measures of population responses to spatio-temporal variation (Barr and Babbitt 2002, MacKenzie et al. 2003, Russell et al. 2005, Welsh et al. 2005, Grant et al. 2014). Occupancy and abundance are often positively correlated (Gaston et al. 2000, Zuckerberg et al. 2009, Passy 2012); however, relationships are dependent on the spatio-temporal scale of sampling (Miguet et al. 2016, Steenweg et al. 2018). Occupancy often provides an assessment at broad spatial and temporal scales and is linked to colonization and extinction processes (Royle and Dorazio 2009, Noon et al. 2012). Conversely, abundance patterns are expected to vary at finer spatial and temporal scales, and are closely associated with reproduction and survival (Baruah et al. 2020). Implicitly, these models assume that shifts in population occupancy and abundance are linked to the processes controlling individual fitness within populations.

In addition to occupancy and abundance, individual-based metrics can provide important insights, directly linking spatial heterogeneity and ecological processes (Welsh et al. 2008). Condition indices have been used with mixed success in ecology, relying on relationships between external morphological characteristics and body fat content (Peig and Green 2009, MacCracken and Stebbings 2012). Because body fat reserves (measured directly or indirectly through body condition indices) are positively associated with reproductive success and survival (Jakob et al. 1996, Peig and Green 2009), body condition measurements provide fitness-associated, individual-level data. Two arguments against the use of body condition as a proxy for fitness are that most species have unverified relationships between lipid content and morphological traits and that there is potential for non-linear relationships that could yield inaccurate inferences (Green 2001). Despite these critiques, condition indices provide important information about whether individuals weigh more or less than expected based on a measure of size (Green 2001). Therefore, higher condition indices suggest that individuals have greater energy reserves to overcome challenging conditions and that they are successful in acquiring resources while coping with current challenges. Body condition can be affected by wildlife threats including climate, habitat fragmentation, and urban encroachment (Maceda-Veiga et al. 2014, Liles et al. 2017). Collectively, quantifying the mean body condition index of individuals within a population directly estimates a parameter closely linked with demographic processes including reproduction and survival.

In addition to evaluating the effect of environmental conditions on a single response metric, understanding how a species responds to variation, across multiple metrics, can provide insights into the relationship between individual- and population-level processes (Welsh et al. 2008). Heterogeneity in how different metrics respond to environmental change is linked to the spatial and temporal scales over which a response metric changes (Miguet et al. 2016). For example, occupancy and abundance are not always correlated and extreme spatial heterogeneity can yield patterns that are difficult to interpret (Welsh et al. 2013, Guillera-Arroita et al. 2014). Researchers have also shown that the processes yielding occupancy patterns can be dissimilar from those yielding patterns in abundance despite occupancy studies regularly invoking positive relationships between these 2 metrics

(Peterman et al. 2013, Welsh et al. 2013, Steenweg et al. 2018). Condition indices based on individual morphology incorporate abiotic and biotic interactions occurring across much smaller spatial and temporal scales (Ousterhout et al. 2015). Consequently, condition indices can be highly variable and fluctuate considerably over short time scales, potentially providing a more sensitive response metric than occupancy or abundance. Ultimately, evaluating populations across multiple scales allows practitioners to understand the relationship between individual success and population outcomes.

Amphibians represent a useful model for evaluating the similarity in responses between condition indices and population-level metrics. Amphibians are regularly invoked as good indicators of environmental quality despite studies documenting wide variation in tolerance to environmental change (Vitt et al. 1990, Kerby et al. 2010, Cecala et al. 2018). Beyond these traits, small amphibians have established morphometric relationships with body fat content (MacCracken and Stebbings 2012) and body size has been documented to vary across environmental gradients (Welsh et al. 2008, Gade et al. 2023). Furthermore, occupancy and abundance of stream-breeding amphibians are sensitive to changes in fine- and broad-scale environmental gradients linked to habitat suitability for larval and adult life stages (Surasinghe and Baldwin 2014, Grant et al. 2016, Gould et al. 2017, Cecala et al. 2018, Gould and Peterman 2021). Consequently, evaluating population-level (e.g., occupancy, abundance) and individual-level (e.g., body condition) indexes should be considered for effective population management.

In this study, we used landscape-scale survey data to model salamander occupancy, abundance, and body condition as a function of several environmental variables predicted to be important in influencing their distribution and performance. Our objective was to determine how responses to site environmental condition varied between species and across life stages of the same species. Specifically, we hypothesized that occupancy and abundance responses would be positively correlated, as has been reported for other species (Gaston et al. 2000). Further, we did not have clear expectation for the relationship between salamander abundance and body condition, as evidence for the presence (Welsh et al. 2008, Currinder et al. 2014, Lunghi et al. 2018) and absence (Karraker and Welsh 2006, Mazerolle et al. 2021) of positive correlations has been documented.

STUDY AREA

Our study included 71 sites, located in a 9-county region of the southern Cumberland Plateau of Tennessee, USA, oriented along a north-south axis (Bledsoe, Cumberland, Franklin, Grundy, Marion, Morgan, Sequatchie, Van Buren, and White counties). Our study region extended across roughly 145 km of the plateau, south from the Cumberland Mountains and north of the Tennessee River. The southern Cumberland Plateau of Tennessee has high topographic variability with shallow-gradient, sandy headwater streams that flow over sandstone bluffs into steep cove streams dominated by colluvium and ultimately limestone bedrock. The elevation of the plateau, across our study area, ranged between 700–1,000 m. Xeric pine (*Pinus* spp.) and oak (*Quercus* spp.)-hickory (*Carya* spp.) forests at high elevations give way to mesic cove forests with cool and humid microclimates at lower elevations (Evans et al. 2001). Annual season on the Cumberland Plateau consist of autumn (Oct–Nov), winter (Nov–Mar), spring (Apr–June), and summer (Jul–Sep). Although the southern Cumberland Plateau has been recognized for its biological diversity (Jenkins et al. 2015), little area has state or federal protection, and areas recently acquired for protection tend to be in poor condition from the high-intensity and widespread conversion of hardwood forests to pine plantations (McGrath et al. 2004, Evans et al. 2017). Dominant land uses include residential, livestock and timber farming, state parks, and state wildlife management areas. The study was conducted during the summer of 2015 and 2016. The mean maximum temperatures for June and July in 2000–2016 were 31.7°C and 32.2 °F, respectively. The mean precipitation for the same time-period was 0.43 cm and 0.46 cm for June and July, respectively. Several common taxa known to predate salamanders in the region include wild turkey (*Meleagris gallopavo*), panfish (Centrarchidae), raccoon (*Procyon lotor*), and snakes (water snakes [*Nerodia* spp.], ring-necked snake [*Diadophis punctatus*], and common garter snake [*Thamnophis sirtalis*]).

METHODS

Salamander communities and study design

The southern Cumberland Plateau hosts a high diversity of stream-breeding salamander species from the lungless salamander family, Plethodontidae (Gould et al. 2017). These species are all biphasic, requiring an aquatic larval stage with a semi-aquatic adult life stage. The 3 focal species of this study exist along a continuum of larval period length and adult terrestrial habitat reliance (Petranka 1998, Lannoo 2005). The spotted dusky salamander (*Desmognathus conanti*) has a short larval period (<13 months) and the most aquatic adult life stage in this community. The southern two-lined salamander (*Eurycea cirrigera*) has a moderate length larval period (1–2 yr) and a semi-aquatic adult life stage. In the northern portion of the study area, Blue-ridge two-lined salamanders (*E. wilderae*), a similar species, may also have been present and detected as southern two-lined salamander; however, larvae and adults of these species are ecologically similar and we believed aggregating these species would not affect our results. Finally, the red salamander (*Pseudotriton ruber*) has a long larval period (1.5–3.5 yr) and an adult life stage that uses aquatic and directly adjacent terrestrial habitat.

We selected 71 stream sites, across the southern Cumberland Plateau (Drukker et al 2020) using a stratified random approach, first prioritizing sites located on state-owned property before identifying privately owned sites to fill in the geographical distribution of our study region. We surveyed 50 sites in May–July 2015 and 21 sites in May–June 2016. At each site, we designated a 150-m-long transect. Within that transect, we surveyed 15 5-m-long plots separated by 5 m. Each plot included the full width of the stream and up to 1 m on both banks. We surveyed all plots on 3 consecutive days using active surveys that included dipnetting, flipping logs and rocks, and sorting through leaf litter in the stream and on the bank. We repeated sampling on consecutive days for logistical reasons and to collect water temperature over multiple days. When we captured salamanders, we identified them to species and life stage, and measured their snout-vent length (SVL) from snout to posterior opening of the cloaca, total length (TL), and mass. We did not mark individuals before resurveying sites on consecutive days because individual recapture probability was low. We minimized the potential for double counting error by removing any replicate adults and larval red salamanders that had similar length and mass measurements (variation of <5% for both measurements) from the data for analyses of body condition.

Site characterization

We selected 6 factors to characterize sites: forest cover, elevation, aspect (northness and eastness), slope, and stream drainage area (Wilkins and Peterson 2000, Dodd and Dorazio 2004, Gould et al. 2017, Cecala et al. 2018, Gould and Peterman 2021). Although stream amphibians are sensitive to watershed forest loss (Crawford and Semlitsch 2008, Peterman et al. 2011), variation in occupancy exists even among streams with high watershed forest cover (Cecala et al. 2018, Weaver and Barrett 2018). Elevation is known to affect salamander body size and surface activity (Caruso et al. 2014, Connette et al. 2015, McEntire and Maerz 2019). Aspect often influences humidity and soil moisture gradients that can lead to drier microhabitats and shifts in vegetative communities (MacHattie and McCormack 1961). Finally, stream slope and drainage area are often linked to flow regime, with large drainages associated with flood magnitudes that may prohibit stream salamanders from maintaining their position in the watershed (Barrett et al. 2010, Knoll et al. 2015).

At each point, we extracted covariates using the coordinates of the downstream end of our transects. We obtained elevation, slope, and aspect from 10-m digital elevation models of the southern Cumberland Plateau. We calculated drainage using hydrology tools in ArcGIS (Esri 2015). We transformed aspect to northness (sine) and eastness (cosine). Finally, we overlaid watershed boundaries on 2011 land cover data (Homer et al. 2015) to calculate watershed forest cover, which included categories of hardwood forest, mixed forest, and pine forest, and extracted the values at each point. We scaled all parameters using the z-score transformation for analyses.

Statistical analyses

Body condition index

To calculate body condition, we used the scaled mass index (SMI) defined by Peig and Green (2009). This metric has been documented to be the best available indicator of the relative size of energy reserves in small endo- and ectotherms like stream salamanders. This method uses a standardized major axis regression and calculates the scaled mass index using this formula:

$$\text{SMI}= M_i\left(\frac{L_0}{L_i}\right)^{b_{SMA}},$$

where M_i and L_i are the mass and SVL of each individual, respectively; b_{SMA} is a scaling exponent extrapolated from the regression of mass on SVL; and L_0 is the mean SVL of the measured individuals (Peig and Green 2009). We calculated the scaling metric and mean SVL separately for each species and life-stage combination evaluated in this study. We measured SVL to the nearest 0.1 mm and mass to the nearest 0.1 g.

We evaluated landscape predictors (Table 1) of the scaled mass index of each of our study species with their most detected life stage. To model these relationships, we used Bayesian multi-level models using package BRMS (Bürkner 2017) in R (R Core Team 2013). We fit a generalized linear model with a gamma response family for each species, as the SMI values were continuous, positive values. We evaluated model fit via visual inspection of posterior chain convergence and estimating Bayesian *P*-values for each model.

Abundance and occupancy models

To evaluate abundance and occupancy, we modeled all species using a multi-species N-mixture and occupancy framework while accounting for imperfect detection (Kéry and Royle 2015, Ennen et al. 2021, Gould and Peterman 2021). Despite recent concerns on the reliability of N-mixture models (Barker et al. 2018, Link et al. 2018), evidence suggests that for small vertebrate species they remain a useful analytical tool for estimating relative abundance

TABLE 1 Summary of landscape variation at stream salamander study sites on the southern Cumberland Plateau of Tennessee, USA, in the summers of 2015 and 2016. Included are the variables included in the models for body condition, occupancy, and abundance.

	Mean	Min.	Max.
Elevation (m)	508	323	585
Forest cover (%)	73	0	100
Drainage area (m^2)	60,633	9	444,230
Slope (%)	8	0	54
Northness	0.11	−0.99	1
Eastness	0.03	−0.99	1

(Ficetola et al. 2018, Costa et al. 2019, Costa et al. 2020). Additionally our repeated sampling design minimized any concerns associated with population closure, as all visits were conducted within a 3–4-day window. For each species, we modeled post-metamorphic and larval responses separately. We modeled latent abundance and site occupancy as a function of the same site-specific covariates included in the SMI models (Table 1).

For latent abundance N_{ikm} for life stage m of species k at site i, we modeled

$$N_{ikm} \sim \text{Poisson}(\lambda_{ikm}),$$

$$\log(\lambda_{ikm}) = \alpha 0_{km} + \beta_{km} \times X_i,$$

where α0 is the latent abundance model intercept for life stage m of species k, and β is a matrix of species and life stage-specific parameter estimates for the effect of covariates X at site i.

We modeled the observation process as:

$$y_{ijkm} | N_{ikm} \sim \text{Binomial}(N_{ikm}, p_{ijkm}),$$

$$\log\text{it}(p_{ijkm}) = \beta 0_{km},$$

where y_{ijkm} is the observed count of salamanders and p is the individual detection probability for each species k and life stage m combination. We modeled individual detection probability as an intercept-only model, where β0 is the model intercept for life stage m of species k. We modeled all abundance parameters from the matrix β with noninformative, normally distributed priors, with a mean of 0 and precision of 1. We modeled the abundance intercept term using a normally distributed prior with hyperparameters for the mean μ_{abund} and precision τ_{abund}.

$$\alpha 0_{km} \sim \text{dnorm}(\mu_{\text{abund}}, \tau_{\text{abund}})$$

$$\mu_{abund} \sim \text{dnorm}(0, 11)$$

$$\tau_{\text{abund}} \sim \text{dgamma}(0.1, 0.1).$$

We modeled the individual detection intercept term ($\beta 0_{km}$) with hyperparameters for the mean μ_{detect} and precision τ_{detect}. The hyperprior for μ_{detect} was normally distributed with a mean of −1 and precision of 1, as we expected all species to have individual detection probabilities of <0.5. We maintained the same hyperpriors for the precision estimate.

For occupancy Z_{ikm} for life stage m of species k at site i, we modeled

$$Z_{ikm} \sim \text{Bernoulli}(\psi_{ikm})$$

$$\log\text{it}(\psi_{ikm}) = \alpha 0_{km} + \beta_{km} \times X_i + year_{ik},$$

where α0 is the occupancy model intercept for life stage m of species k, and β is a matrix of species and life stage-specific parameter estimates for the effect of covariates X at site i on occupancy. Here, X covariates include forest cover, elevation, watershed size, northness, eastness, and slope. The year term here is a random species-level intercept for the effect of year when sampling occurred.

We modeled the observation process as

$$z_{ijkm} | Z_{ikm} \sim \text{Bernoulli}(Z_{ikm}, p_{ijkm}),$$

$$\log\text{it}(p_{ijkm}) = \beta 0_{km},$$

where z_{ijkm} is the observed presence or absence of salamanders and p is the probability of capture for each species k and life stage m combination, as before in the abundance model. For all parameters in the occupancy and detection models, priors were normally distributed around community hyperparameters μ and τ, where each mean parameter was normally distributed with a mean of 0 and precision of 0.1. We calculated the hyperparameter τ by taking the inverse of the squared standard deviation for each parameter, σ^2, which we modeled with a diffuse uniform prior between 0 and 4. To help with model convergence, we modeled the standard deviation hyperprior for α0 uniformly between 0 and 8. To further help with model convergence, we modeled the standard deviation hyperprior for β0 uniformly between 0 and 2.

We fit models with JAGS in R using package jagsUI (Kellner 2019). We ran the models for 270,000 iterations, with a burn-in of 70,000 and a thinning rate of 10, across 3 parallel chains, yielding 60,000 samples. We examined Markov chain Monte Carlo chains and deemed models had reached convergence when all Gelman-Rubin (Gelman and Rubin 1992) values were sufficiently low (<1.05). Following this, we ran a Pearson's product moment correlation test between model-derived estimates of latent occupancy and relative abundance. We considered correlations strong if values exceeded 0.3. We describe all model effects as providing strong evidence for an effect if 89% highest posterior density intervals did not overlap zero. Finally, we derived density per linear meter of stream by dividing the predicted relative abundance at each site by the length of each site (150 m).

RESULTS

We captured 1,238 individuals across our target species including spotted dusky salamander (post-metamorphic = 496, larval = 16), southern two-lined salamander (post-metamorphic = 75, larval = 545), and red salamander (post-metamorphic = 29, larval = 77). Unlike occupancy and abundance metrics, we were unable to model body condition of both life stages for our 3 focal species because captures were dominated by 1 life stage. Post-metamorphic life stages were far more common in the sample of spotted dusky salamanders, whereas larval life stages were far more common for southern two-lined salamanders and red salamanders.

Body condition

For all species, SMI was negatively associated with east-facing aspect (Figure 1; Table 2). Post-metamorphic spotted dusky salamander SMI increased 2.62 times (89% highest density interval [HDI] = 1.04–4.14 times) for every 1-km^2 increase in drainage area and 1.13 times (1.05–1.20 times) for every 1-unit change in north-facing aspect. Conversely, larval southern two-lined salamander SMI declined 0.26 times (0.07–0.45 times) for every 1-km^2 increase in drainage area. No other covariates were significantly linked to SMI.

Occupancy

Overall, spotted dusky salamander, southern two-lined salamander, and red salamander were predicted to occupy 71.8%, 72.7%, and 61.9% of surveyed sites, respectively. Of the 13 sites where no salamanders were detected, only 2 had a >50% probability of no species being present. Mean species detection was highest for southern two-lined salamanders (55.6%), followed by spotted dusky salamanders (49.3%), and lowest for red salamanders (35.6%).

The community-mean effect of quadratic transformation of elevation on occupancy probability was negative (odds ratio [OR]: mean = 0.74, 89% HDI = [0.52–0.96]; Figure 2A; Table 2), indicating across all species, occupancy probability was lowest at either high or low elevation sites. At the species level, quadratic elevation was negatively associated with post-metamorphic and larval spotted dusky salamander and post-metamorphic southern two-lined salamander occupancy probability (Figure 2A).

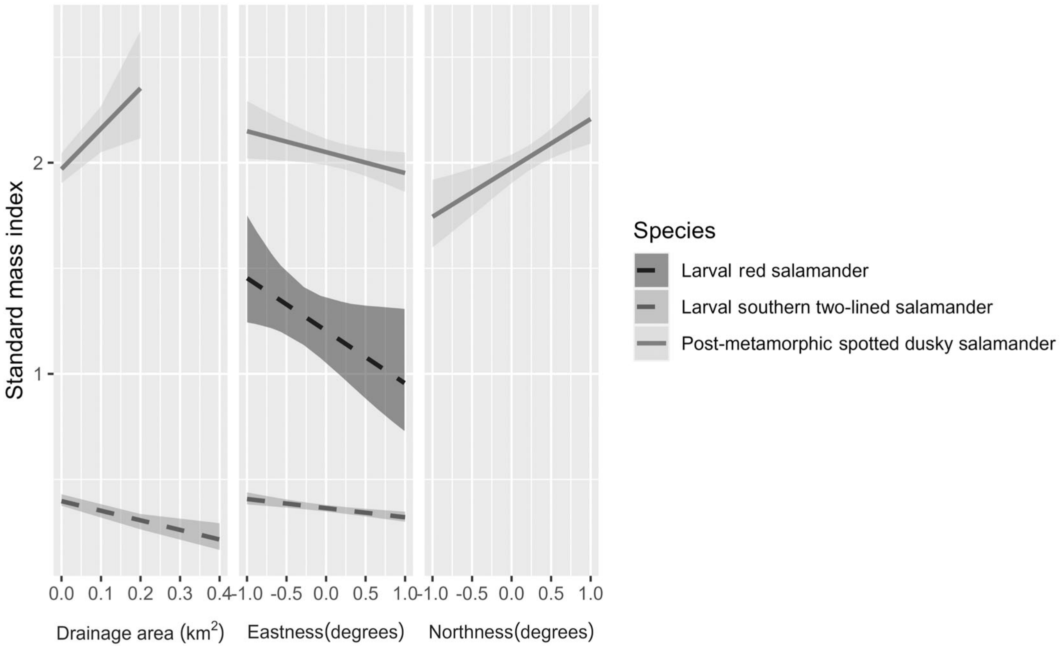

FIGURE 1 Marginal effects of spatial variables on standardized mass index (SMI) of larval southern two-lined salamanders, larval red salamanders, and post-metamorphic spotted dusky salamanders collected and measured on the Cumberland Plateau, Tennessee, USA, 2015–2016. Marginal plots represent the effect of individual variables on SMI, holding all other covariates at their mean. The bold black line represents the mean response. Grey shaded intervals represent the 89% highest density interval.

Drainage area was the second-most influential predictor of occupancy probability (Table 2; Figure 3A). The community-mean was generally lower in streams draining larger areas; however, the relationship was not significant. Larval animals responded more consistently negative (OR: 0.64 [0.21–1.04]) than post-metamorphs (OR: 1.17 [0.47–1.84]). Larval spotted dusky salamander exhibited the strongest negative response to drainage area (OR: 0.44 [0.10–0.86]).

There was no consistent response to forest cover, aspect transformations, or slope, across the salamander community. Forest cover had a significant, positive effect on post-metamorphic spotted dusky salamander occupancy; however, we did not detect relationships for forest cover and larval occupancy in this species. We did not detect strong evidence for an effect of forest cover on occupancy in any other species, in either post-metamorphic or larval life stages.

Abundance

Abundance responses had greater interspecific and life-stage variation than those reported for occupancy (Table 2). Post-metamorphic and larval spotted dusky salamander and southern two-lined salamander abundance was negatively associated with the quadratic elevation term (Figure 2B). No other relationship was detected between red salamander and elevation terms.

Eastness had a strong negative effect on the abundance of larval spotted dusky salamanders (rate ratio: 0.62, 89% HDI = 0.39–1.00) and both life-stages of southern two-lined salamanders (larval: 0.79, 0.72–0.85; post-metamorphic: 0.55, 0.41–0.73), while having a positive effect on post-metamorphic spotted dusky salamanders

TABLE 2 Direction of occupancy, abundance, and standardized mass index (SMI) responses of stream salamanders to landscape covariates on the southern Cumberland Plateau of Tennessee, USA, in the summers of 2015 and 2016. Positive and negative signs indicate 89% highest density intervals (HDI) did not overlap zero and contained only positive or negative values; NS indicates non-significant responses, where some proportion of the 89% HDI overlapped zero.

		Occupancy		Abundance		
Species	**Metric**	**Post-metamorphs**	**Larvae**	**Post-metamorphs**	**Larvae**	**SMI**
Spotted dusky salamander	Elevation^2	-	-	-	-	NS
	Watershed size	NS	-	-	-	+
	Northness	NS	NS	NS	+	+
	Eastness	NS	NS	+	-	-
	Forest cover	+	NS	+	+	NS
	Slope	NS	NS	+	-	NS
Southern two-lined salamander	Elevation^2	-	NS	-	-	NS
	Watershed size	NS	NS	+	-	-
	Northness	NS	NS	+	-	NS
	Eastness	NS	NS	-	-	-
	Forest cover	NS	NS	NS	+	NS
	Slope	NS	NS	NS	NS	NS
Red salamander	Elevation^2	NS	NS	NS	NS	NS
	Watershed size	NS	NS	NS	-	NS
	Northness	NS	NS	NS	-	NS
	Eastness	NS	NS	NS	NS	-
	Forest cover	NS	NS	NS	NS	NS
	Slope	NS	NS	NS	+	NS

(1.28, 1.15–1.43). Similarly, abundance of larval southern two-lined salamander (0.73, 0.66–0.79) and red salamander (0.77, 0.61–0.99) was negatively associated with northness, although larval spotted dusky salamander (1.79, 1.09–3.00) and post-metamorphic southern two-lined salamander (1.58, 1.20–2.12) abundance exhibited a positive response. Larval (0.54, 0.32–0.95) and post-metamorphic (1.17, 1.07–1.28) spotted dusky salamander exhibited differing, significant responses to slope, with larval abundance negatively and post-metamorphic abundance positively associated with stream slope. Larval red salamander abundance also exhibited a positive relationship with slope (1.45, 1.23–1.72).

Forest cover was positively associated with abundance in both life stages of spotted dusky salamander (larval: 1.49, 1.00–2.64, post-metamorphic: 1.32, 1.19–1.49). Larval abundance in all 3 species was negatively associated with drainage area (Figure 3B). Additionally, post-metamorphic spotted dusky salamander abundance also exhibited a negative response to drainage area size. Post-metamorphic southern two-lined salamander, however, had a significant positive response to drainage area, differing from the larval life stage of this species.

Density of salamanders per linear meter of stream was greatest for southern two-lined salamander (0.12 [0.11–0.14]; 0.01 post-metamorphs, 0.11 larvae), then spotted dusky salamander (0.07 [0.06–0.08], 0.06, 0.01), and finally red salamander (0.03 [0.02–0.05]; 0.01, 0.02). Mean individual detection rates were similar for spotted dusky salamander (34.6% [26.9–41.7]) and southern two-lined salamander (33.4% [27.4–39.2]) and lowest in red

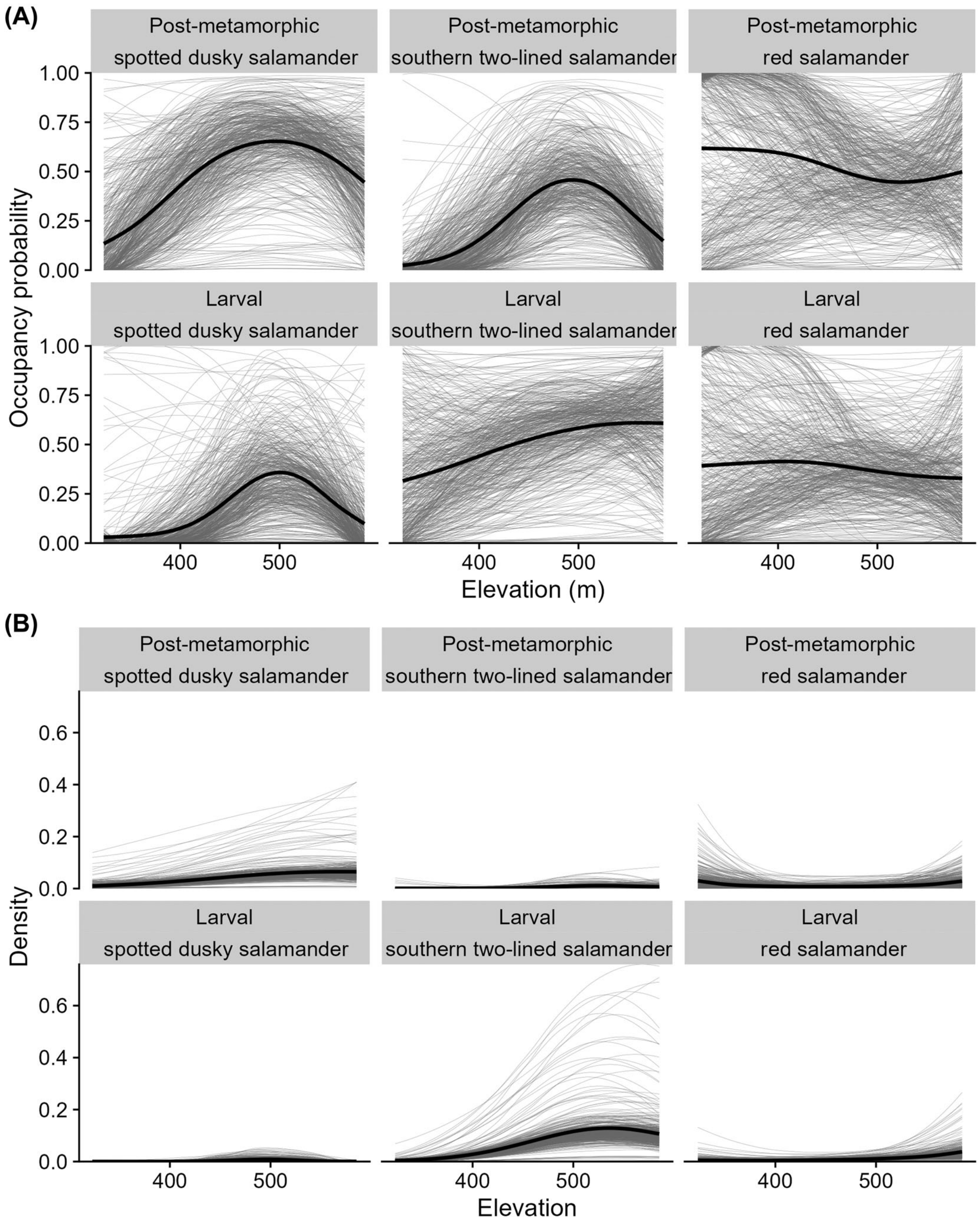

FIGURE 2 Marginal effects of elevation on the occupancy (A) and density per linear meter (B) of post-metamorphic and larval southern two-lined salamanders, red salamanders, and spotted dusky salamanders on the Cumberland Plateau, Tennessee, USA, summer 2015 and 2016. Lines indicate a randomly sample of 500 posterior estimates for the effect of elevation and the intercept for both occupancy and abundance. Bold black lines indicate the mean estimate across all samples of the posterior. Occupancy indicates the probability of site occupancy given elevation. Density indicates the number of animals per linear meter of stream.

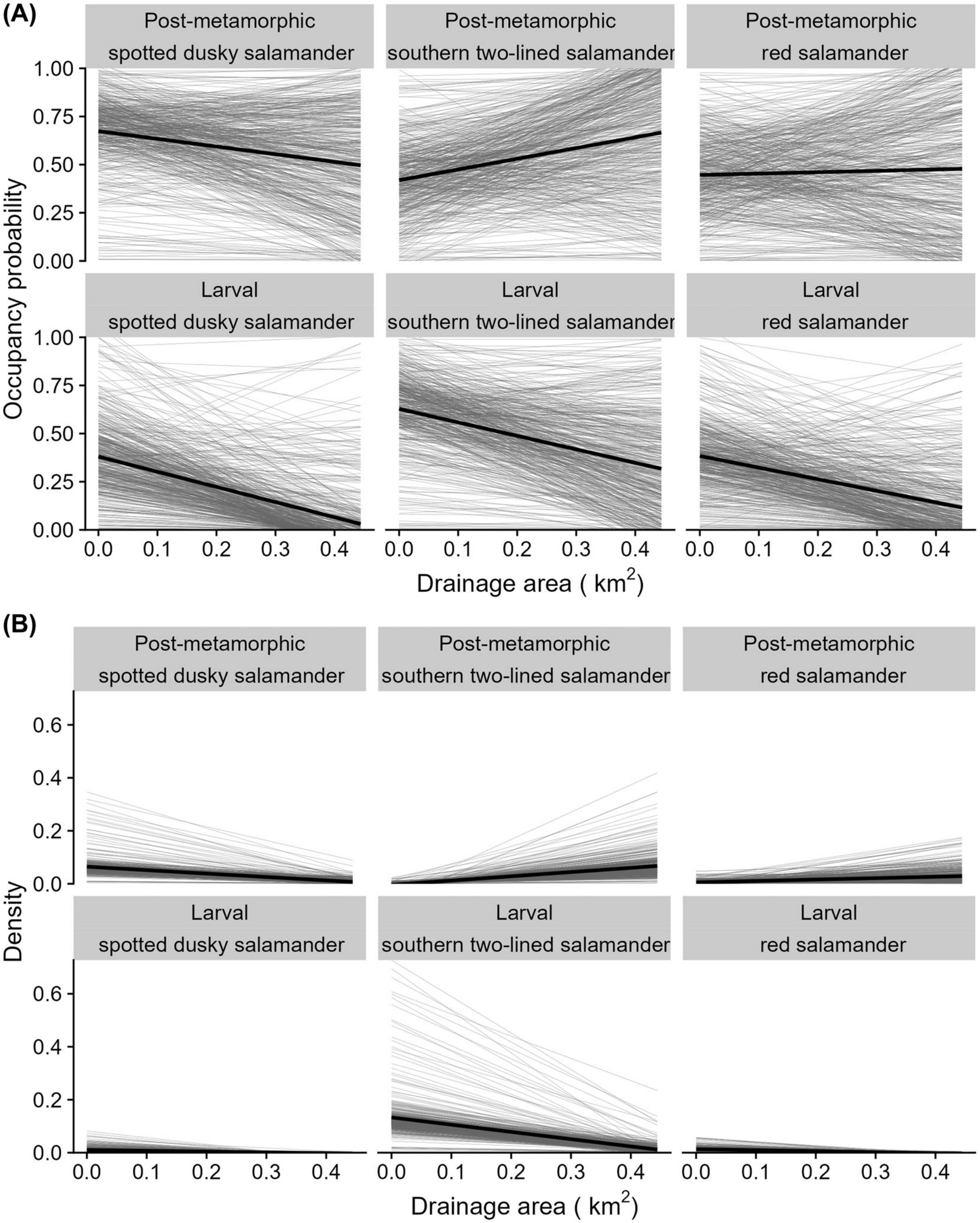

FIGURE 3 Marginal effects of drainage size on the occupancy (A) and density per linear meter (B) of post-metamorphic and larval southern two-lined salamanders, red salamanders, and spotted dusky salamanders on the Cumberland Plateau, Tennessee, USA, summer 2015 and 2016. Lines indicate a random sample of 500 posterior estimates for the effect of elevation and the intercept for both occupancy and abundance. Bold black lines indicate the mean estimate across all samples of the posterior. Occupancy indicates the probability of site occupancy given drainage area. Density indicates the number of animals per linear meter of stream.

salamander (20.6% [12.4–28.5]). Mean life-stage-level detection was higher for post-metamorphs (34.7% [29.1–40.3]) than larvae (24.4% [17.6–30.6]).

Latent occupancy was positively correlated with relative abundance for 4 of 6 species-life stage combinations. The strongest relationship was observed for post-metamorphic spotted dusky salamanders ($R = 0.54$). For both life stages of southern two-lined salamanders (larval $R = 0.43$, post-metamorphic $R = 0.45$) and larval red salamander ($R = 0.44$), relationships were similarly positive. We did not observe a significant correlation for larval spotted dusky salamander ($R = 0.27$) or post-metamorphic red salamanders ($R = 0.28$).

DISCUSSION

Our results indicate that species sensitivity to environmental gradients depends on the biological metric being evaluated, and that responses may differ across life stages. Further, latent occupancy and relative abundance were positively correlated for post-metamorphic animals in the 2 most common species. In all instances where a covariate had a significant effect on occupancy, we observed a similar effect on abundance; however, the opposite was not true, as salamander abundance was influenced by variables that had no significant influence on occupancy. Additionally, although body condition did respond to variables associated with occupancy and abundance, the direction of the effect was sometimes incongruent with occupancy and abundance. Our results suggest studies of salamander species occupancy can provide a generalized understanding of abundance patterns, supporting previous findings (Wilkins and Peterson 2000, Cecala et al 2018). Further, of the data used here, salamander abundance data provided the greatest insight into habitat quality for these communities, as it varied significantly with a greater number of environmental characteristics.

The effects of elevation and drainage area on occupancy and abundance were similar in direction (positive or negative), within each species-lifestage combination; however, the magnitudes of these effects were weaker for occupancy (Figures 2 and 3; Table 2). Occupancy patterns are influenced by processes occurring at larger spatial and longer temporal scales than abundance, and it is logical that, holding scale equal, abundance should be more sensitive to environmental factors (McGill 2010, Miguet et al. 2016). Additionally, positive relationships between salamander occupancy and abundance have been reported elsewhere (Russell et al. 2004, 2005; Welsh et al. 2008). We report corroborative evidence that occupancy and abundance responded similarly, with abundance being a more sensitive indicator (greater number of significant responses) of local habitat suitability than occupancy.

The relationship between population-level metrics and body condition remains unclear, as variation was present in responses within and between species. The absence of consistent, shared responses to environmental variation may indicate negative density dependence, where larger populations have lower individual body conditions. Under this scenario, temporal fluctuations in abundance and individual body condition could reasonably result in non-significant or opposing responses to environmental conditions between these 2 metrics. For example, mean post-metamorphic spotted dusky salamander occupancy and abundance declined with drainage area, despite body condition increasing. Although the specific mechanism is unclear, several potential hypotheses could explain this relationship and require further study. Both prey and predator size increase with drainage area, and large individuals that are able to avoid predators could have access to different prey resources in larger streams (Vannote et al. 1980). Alternatively, negative density dependence in small headwater streams could reduce overall foraging success and increase energy expenditure (Bissell and Cecala 2019). Similarly, post-metamorphic spotted dusky salamander body condition was lower in more east-facing streams, despite abundance being higher. These contradictory patterns could indicate negative density dependence or that these 2 metrics are affected by different processes (Altwegg 2003). Body condition of all species was negatively associated with eastness, which may be a metric- or region-specific response. In this area of the southern Cumberland Plateau, west-facing drainages are dissected with high drainage density, whereas east-facing drainages tend to be small and isolated with fewer stream nodes. Therefore, variation in the stream network structure could contribute to the availability and diversity of resources between east- and west-facing drainages in this region (Altermatt and Fronhofer 2018, Anderson and Hayes 2018).

Similarity between responses to covariates tended to exist within life stages of different species, more so than between life stages of the same species. Recent work on stream salamanders has observed considerable variation in abundance responses to spatial variation between species, and this has been attributed to life-history traits (Gould and Peterman 2021). Despite post-metamorphic responses being highly variable, larval responses to landscape variables in the present study were similar. For example, larval salamander abundance was negatively associated with watershed size, across all species, while post-metamorphic responses were inconsistent. The observed differences may be attributed to higher larval mortality and displacement in larger streams (Hairston 1987, Barrett et al. 2010). Post-metamorphic salamander abundance was more responsive to variables associated with both aquatic and terrestrial habitat. Although the presence of larval animals inherently means reproductive adults are also present, these results suggest that areas of higher density and habitat suitability within streams differ across life stages.

Variation in post-metamorphic responses among species is likely due to variation in their life history, namely the extent to which post-metamorphic salamanders use terrestrial habitat (Drukker et al. 2017, Gould and Peterman 2021). The density of the most terrestrial species, southern two-lined salamander, was positively associated with larger, more northwest-facing streams, which are associated with cooler terrestrial conditions than more southeast aspects (MacHattie and McCormack 1961). Conversely, the density of the most aquatic species, spotted dusky salamander, declined with drainage area, which is generally associated with increased flow rates and increases in exploitative and interference competition with other aquatic predators (Vannote et al. 1980, Hairston 1986, Creed 2006, Cecala et al. 2020). The direction and sensitivity of population responses to landscape, interspecific, and intraspecific variation across life stages seems linked to the extent to which a species relies on aquatic habitat post-metamorphosis.

It is possible that some of the observed patterns in occupancy and abundance are related to detection processes that we could not effectively account for. Our models of detection did not include visit- or site-specific covariates, which may have influenced salamander availability for detection and surveyor ability to detect animals. We maintained consistent survey methodology over time; however, we make assumptions that populations are closed within the survey period. We believe that over the 3–4-day survey at any given site, population status can be safely assumed to be closed; however, surveys timed at different points in the season may have differing numbers of larval animals because of timing of reproduction and metamorphosis. Timing and selection of sites throughout the season should not have biased any of the data, to systematically underestimate larval densities, relative to landscape covariates, so we believe this was not a significant issue. Our estimates of larval salamander density, especially southern two-lined salamander, are significantly lower than density estimates for similar species reported in the region (Peterman and Truslow 2008, Nowakowski and Maerz 2009). This likely reflects a combination of lower latent densities in the study region and our use of a less-effective diurnal sampling methodology. Once again, we do not believe this systematically biased our inference regarding predictor variables, as we observed a significant positive correlation in larval occupancy and abundance for the 2 most common larval species.

MANAGEMENT IMPLICATIONS

First, our findings indicate species-specific variation in stream salamander commonness even when watersheds are fully forested. Secondly, our results suggest that managers evaluating trends in occupancy are likely capturing broad patterns in abundance. Alone, however, occupancy may not fully capture population-level responses to environmental management, as abundance was more sensitive to environmental conditions. Furthermore, stream salamander body condition was moderately sensitive to environmental condition, and higher body condition seemingly indicated environmental conditions that had limited influence on population size. Body-condition indices remain useful tools for characterizing individual fat stores, fecundity, and survival probability, and management for individual traits will differ from managing for population size in these species. Although assumptions about occupancy correlating with abundance were validated here, researchers and managers need to be clear about the response metric that is most closely aligned with their goals. Management for populations of salamanders in the region should consider monitoring multiple response metrics, to capture both population- and individual-level responses, as these may not always be correlated.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

ETHICS STATEMENT

Research was carried out in compliance with protocols approved by the University of the South Animal Care and Use Committee (Cecala-3-2015; Cecala-2-2016) and the Tennessee Wildlife Resources Agency (3970).

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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