Determining crevice preferences of lungless salamanders on the southern Cumberland Plateau of Tennessee

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Abstract.—Lungless salamanders in family Plethodontidae rely on cutaneous respiration that influences habitat selection. Refuge from warm, dry microclimates on the Cumberland Plateau may be found in crevices within sandstone and limestone bluffs where plethodontids are frequently found. The objective of our study was to describe patterns of crevice occupancy by plethodontid salamanders on the southern Cumberland Plateau. We surveyed 6.5 km of bluff habitat and measured geographical and micro-environmental factors at capture and random locations. We found seven species of plethodontid salamanders using crevice habitats, but only three species were abundant enough for statistical analyses. Green salamander (*Aneides aeneus*) occupancy was poorly explained by most of our measured variables, although it was positively associated with warmer temperatures. Northern slimy salamander (*Plethodon glutinosus*) occupancy was primarily associated with cooler temperatures and the presence of water. Cave salamander (*Eurycea lucifuga*) occupancy was positively associated with forest cover. Lungless salamanders of the Cumberland Plateau may use crevice habitat facultatively as one mechanism to avoid warm and dry conditions in the summer.

Key Words.—Crevice, Cumberland Plateau, Distribution, Microclimate, Occupancy, Plethodontidae, Green Salamander

Understanding factors driving distributions and habitat use of species is critical for understanding how species may respond to habitat loss and climate change (Parmesan 2006; Pounds et al. 2006; Rosenzweig et al. 2008). Both environmental changes yield large and small-scale change that can affect different demographic processes that culminate in species declines and shifts in their distributions (Aitken et al. 2008; Chen et al. 2011). Amphibians have behavioral traits and demographic rates that are correlated with local climate (Spotila 1972; Grover 1998; Peterman and Semlitsch 2013). Therefore, changes in microclimate from climate change or from forest loss could have strong effects on the future success of populations (Marsh and Beckman 2004; Pounds et al. 2006).

Plethodontid salamanders are from a diverse family that comprise most of the salamander diversity of the United States (Lanoo 2005). All the members of this family are lungless and respire cutaneously (Feder and Londos 1984). Skin permeability necessary for cutaneous respiration comes with an increased risk of desiccation (Spotila 1972; Feder and Londos 1984; Grover 1998). Therefore, environmental factors including temperature, water, and relative humidity can affect behaviors such as foraging and habitat selection (Spotila 1972; Feder 1983; Grover 1998; Rossell et al. 2009). Specifically, salamander activity is directly correlated with moisture content in the air, where salamanders exposed to higher relative humidity spend more time outside of refugia than those in lower humidity (Feder and Londos 1984). Standing water in forest floor refugia is positively associated with the colonization and presence of two terrestrial plethodontids (Grover 1998). Similarly, terrestrial movement of amphibians is governed by habitat heterogeneity and availability of refugia from high temperatures and low moisture (Ash 1997; Grover 1998; Marsh and Beckman 2004).

Spatial and temporal gradients of climate also affect salamander performance and influence factors affecting fitness and population viability including body size and density (Peterman and Semlitsch 2013; Caruso et al. 2014).

The southern Cumberland Plateau is characterized by thin, nutrient-poor soils with low moisture retention (Smalley 1982), perhaps contributing to low salamander densities in the region (McKenzie and Cecala *in review*; Kirchberg et al. 2016). Therefore, microhabitats that buffer extreme temperatures and low humidity may be particularly important for the ecology of plethodontid salamanders in this ecoregion. One habitat type that could perform this function is the steep sandstone bluffs that border the plateau. Vertical and horizontal crevices on bluffs provide refuge for a range of species during the warm seasons (Petranka 1998). For example, green salamanders (*Aneides aeneus*) are highly dependent on these crevice refugia and have been shown to use these crevices to minimize cutaneous water loss and regulate body temperature (Rossell et al. 2009). For this species, canopy cover positively affects the suitability of crevice habitat for green salamanders and could indicate habitat suitability for other lungless salamanders as well (Rossell et al. 2009; Tilghman et al. 2012). Descriptions of the diversity of plethodontids that use this habitat and predictors of habitat use are largely unavailable.

In this study, we sought to determine which species regularly use crevice habitat and evaluate what environmental factors are associated with their occupancy. Specifically, we evaluated the relationships between climatic factors, forest cover, and distance to subsurface habitats to occupancy of plethodontid salamanders. We predicted that salamander occupancy will be positively associated with cooler temperatures, higher canopy cover, and higher relative humidity.

METHODS AND MATERIALS

Study Region—. The Cumberland Plateau consists of relatively flat oak-hickory forests (e.g., White Oak, *Quercus alba;* Chestnut Oak, *Q. montana;* Northern Red Oak, *Q. rubra;* Pignut Hickory, *Carya glabra;* Shagbark Hickory, *C. ovata,* and Sand Hickory, *C. pallida*) bordered by sandstone outcrops and bluffs before falling away into coves with Sugar Maple (*Acer saccharum*), Red Maple (*A. rubrum*) and Tulip-Poplar (*Liridiodendron tulipifera*) dominated forests (Kuers 2007). Specifically, this study took place on the 13,500-acre campus of the University of the South in Franklin County, Tennessee, that encompasses over 20 km of sandstone bluff. Fractured sandstone bluffs provide crevice habitat that the authors have observed to be used by invertebrates and vertebrates (e.g. camel crickets [Rhaphidophoridae], centipedes [*Scolopendra* spp.], copperhead snake [*Agkistrodon contortrix*], chimney swifts [*Chaetura pelagica*], green salamanders [*A. aeneus*] and long-tailed salamanders [*Eurycea longicauda*]).

Field Data Collection—. We recorded the occupancy and identity of all salamanders and other taxa when we were confident in our species identification. Field surveys were conducted from 11 May – 28 July 2015. We haphazardly selected 10 transects of 100 m to account for potential spatial variation. Transects were selected by proximity to cove access points, which were typically old roads (Smith and Williamson 2008). We surveyed bluff stone faces and all crevices along transects located 0.5–1.9 m above the ground using a flashlight to illuminate deep crevices. We collected a series of variables from locations where salamanders were found as well as random points where they were absent for comparison. To locate random points, we randomly selected 10 distances from the start point for each transect, and we surveyed crevices located at those points. At each location that a salamander was observed and at all random points, we recorded GPS location, canopy cover using a spherical densiometer, temperature of the crevice using an infrared thermometer, relative humidity using a psychrometer, and presence of standing water like small puddles or pools. If individuals were found outside of crevices, we collected all the same data except the presence of standing water. At random points, we searched extensively to confirm salamander absence. For each detected salamander, we identified them to species but did not extract salamanders from the crevices. Daily mean ambient air temperature was provided by the historic weather data archive for The University of the South (www.sewanee.edu/offices/oess/the-domain/resources/historic-weather-data/) from a weather station located on the Cumberland Plateau within 5 km of our study transects.

Landscape Data Collection—. We used South Cumberland Conservation Action Plan database layers to delineate bluff lines (Hollingshead et al. 2010). National Land Cover Data from 2011 was used to assess the percent forest within a 150 m radius of each point (Homer et al. 2015). Forest was determined by combining categories of deciduous, evergreen, and mixed forest. We also quantified Euclidean distance to the nearest documented cave.

Data Analysis—. We used multi-model inference to assess the habitat variables that predict occupancy by different species of salamanders occupying sandstone bluffs. Models were developed using logistic regressions including salamander detections (1) or random points (0) as our response variable and habitat predictors (e.g., temperature, relative humidity, canopy cover, forest cover, permanent water, or distance to nearest cave). For each species, we assessed relative support for single factor models using Akaike's Information Criteria corrected for small sample size (AIC_c) to distinguish among models (Akaike 1973). Larger AIC_c weights indicate higher likelihood of a model to describe the data relative to other models (Burnham and Anderson 2002). Model rankings as well as coefficients and their associated variability were used to assess important relationships. Daily mean ambient air temperatures were compared to daily mean crevice random point temperatures in a two-sample t-test assuming unequal variance. All analyses were conducted in R (R Development Core Team, 2015).

RESULTS

We detected 7 species of salamander using crevices. We found 18 green salamanders, 20 cave salamanders (*E. lucifuga*), and 12 northern slimy salamanders (*Plethodon glutinosus*) — samples that we deemed sufficiently large to analyze further. All of these individuals were found in crevices except 2 green salamanders found on moss on the sandstone bluffs. Other amphibian and reptile species found to use crevices along the bluff include spotted dusky salamanders (*Desmognathus conanti*; n = 4), long-tailed salamanders (n = 1), red-spotted newts (*Notophthalmus viridescens*; n = 1), northern zigzag salamanders (*P. dorsalis;* n = 3), eastern box turtles (*Terrapene carolina*; n = 1), and ring-necked snakes (*Diadophis punctatus;* n = 4). We also surveyed 158 random points. Bluffs on this landscape remained primarily forested (97.2 ± 0.5%; SE), cool (20.97 ± 0.15 °C), and humid (77.7 ± 0.54%). Mean temperature for all random points was 21.4 ± 0.17 °C and was significantly lower than the mean ambient temperature for the time period we surveyed (23.15 ± 0.46 °C; $t_{df=40} = -4.8$, $P < 0.001$; Fig. 1).

We found that there was little support for one factor being more important than the others in predicting green salamander occupancy though it may be positively associated with temperature based on the estimate and associated standard error of the relationship between occupancy and temperature (Table 1; 0.24 ± 0.25). Northern slimy salamander occupancy was best predicted by temperature, and occupancy was predicted to decline by 0.77 for every one-degree increase in temperature. Temperature was 3.4 times better at predicting slimy salamander occupancy than the next highest ranked variable, forest cover, but evaluation of effect sizes suggest that occupancy is also more likely in less shaded and high humidity crevices closer to caves (Table 1). Finally, cave salamanders were positively associated with forest cover, which was 3.6 times more likely than distance to cave to influence their distribution. Cave salamanders were also more likely to occupy crevices closer to caves. Unlike the other two species, they were not associated with climatic variables (Table 1).

TABLE 1. Model ranking results for single predictor logistic models comparing capture locations to random points. Models are ranked from highest to lowest support, and estimates with standard errors (SE) are presented.

	AIC_c	**ΔAIC_c**	**AIC_c weight**	**Estimate**	**SE**
Green salamanders					
Temperature	121.64	0.00	0.20	0.24	0.25
Distance to cave	121.84	0.21	0.18	0.22	0.27
Relative humidity	121.90	0.26	0.18	0.19	0.23
Canopy cover	122.06	0.43	0.16	0.22	0.36
Native forest cover	122.37	0.73	0.14	0.11	0.29
Permanent water	122.53	0.90	0.13	0.02	0.25
Northern slimy salamanders					
Temperature	87.05	0.00	0.49	-0.77	0.32
Canopy cover	89.51	2.45	0.14	-0.37	0.20
Relative humidity	89.71	2.65	0.13	0.50	0.26
Distance to cave	89.79	2.74	0.12	-0.66	0.41
Native forest cover	91.15	4.10	0.06	0.81	0.84
Permanent water	91.31	4.26	0.06	0.41	0.30
Cave salamanders					
Native forest cover	123.35	0.00	0.67	3.31	2.96
Distance to cave	125.89	2.54	0.19	-0.65	0.31
Permanent water	128.22	4.87	0.06	-0.44	0.26
Temperature	128.31	4.96	0.06	-0.41	0.24
Canopy cover	131.11	7.76	0.01	-0.08	0.20
Relative humidity	131.26	7.91	0.01	0.01	0.24

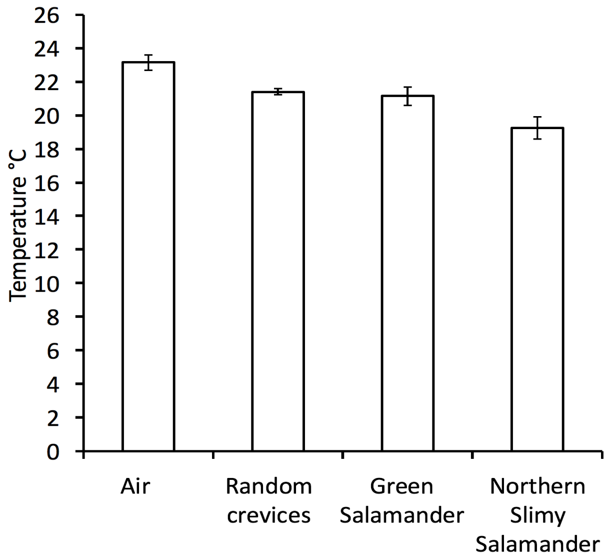

FIG. 1. Mean temperatures (± standard error) for local air temperature were higher than random points. Temperatures are also plotted for green salamanders and northern slimy salamanders which demonstrated associations with temperature.

DISCUSSION

Many species are found to use crevice habitat on the southern Cumberland Plateau. Acting as a buffer, these crevices provide refuge from extremes in temperature and humidity. In our study, we found that random crevice sites were 1.7 °C cooler than ambient air temperatures, and that salamanders selected temperatures equivalent or cooler than random crevices (Fig. 1). Avoiding thermal extremes is important for lungless amphibians to avoid desiccation and can result in decreased surface activity necessary to complete their life histories (Spotila 1972; Feder and Londos 1984). Though recent evidence suggests that green salamanders use crevice habitat extensively but not exclusively (Waldron and Humphreys 2005; Rossell et al. 2009), facultative use of crevices in warm seasons (April-October) may facilitate increased activity of lungless salamanders. Additional research is needed to determine the spatial and temporal extent of habitat use of species that use bluffs facultatively. Similarly, research determining how far individuals move to exploit this habitat and what types of behaviors salamanders use crevices for would further our understanding of the importance of crevice habitat to lungless salamanders on the southern Cumberland Plateau.

Unlike associations of other species, we observed that green salamanders were positively associated with crevice temperatures. Despite this association, they were rarely found on rock faces where ambient air temperatures would be warmer (Fig. 1). This habitat preference could also result from selection of drier habitats that would be positively associated with warmer temperatures. Recent work suggests that green salamanders prefer deeper crevices, but the relationship between crevice morphology and microclimate is unknown (Smith et al. 2017). Smith et al. (2017) also found a positive association with forest cover that was not observed in the present study. One potential explanation may be the well-forested nature of our study area. Secondly, this association could be a result of competitive interactions. Others have found vertical stratification of rock crevice use when they co-occur with slimy salamanders (Cliburn and Porter 1986, 1987). Though we did not measure crevice height, slimy salamanders were rarely found more than 0.5 m off the ground whereas green salamanders were found up to at least 1.2 m. If slimy salamanders prefer cooler temperatures, it could also be that slimy salamanders exclude green salamanders to higher, warmer crevices. Consistent with this hypothesis, our surveys and others (Rossell et al. 2009) did not find other species co-occupying crevices, and studies have reported territorial behaviors of green salamanders towards conspecifics (Cupp 1980). Similar to recent research, we also suggest that green salamanders may use far more terrestrial and arboreal habitat in addition to rock crevices (Waldron and Humphreys 2005). Notably, we found 5 green salamanders (4 adults; 1 juvenile, 23 mm SVL) during this study period considerable distances from rock crevices (0.47 – 0.61 km), either on trees, under cover on the forest floor, or crossing the road.

Climbing behaviors have previously been documented in closely related slimy salamander species, but climbing was most common during wet conditions and typically observed when in competition with other large species (Cliburn and Porter 1987; McEntire 2016). In the absence of another large plethodontid species, it is unclear how northern slimy salamanders use crevices, but their associations with climatic variables suggest a potential mechanism for crevice use. Relative humidity and temperature have previously been linked to dehydration rates in plethodontid salamanders and cessation of terrestrial activity (Spotila 1972; Feder 1983; Feder and Londos 1984). Opportunistic use of crevices may provide northern slimy salamanders additional opportunities for foraging or reproduction by allowing them to remain surface-active for longer periods of time. This hypothesis is supported by finding northern slimy salamanders in lower crevices where crevices were more likely to have small pools of standing water. Furthermore, there was a weak negative relationship between northern slimy salamander occupancy and canopy cover (Table 1). More variable climate experienced in areas with less canopy cover (Chen et al. 1999; Carlson and Arthur 2000) could encourage crevice use as a mechanism for avoiding dry forest floor conditions similar to forest floor seeps that also attract terrestrial salamanders (Grover 1998). Alternatively, crevices could be used by adult females for brooding as we found both large individuals and juveniles using crevice habitat (Trauth et al. 2006). Regardless of the mechanism resulting in crevice use, more information is necessary to evaluate whether individuals move to exploit crevice habitats or if proximity to rock crevices increases salamander body condition and density.

As their name implies, cave salamanders are most often associated with caves or limestone areas with access to subsurface habitat (Hutchison 1958; Petranka 1998; Camp and Jensen 2007). Our models corroborate these patterns with the highest occupancy estimates closest to known caves. We also note a positive association with forest cover and proximity to streams. As a stream-breeding species, these results may indicate that cave salamanders require intact forests for annual breeding migrations to streams (Petranka 1998; Semlitsch et al. 2009). Crevice habitat close to streams at high elevations on the Cumberland Plateau may increase the elevational range of the species from limestone layers up to the sandstone layers that overlie them.

Little is known about the strength of interspecific interactions in driving patterns of crevice use. Many other salamander and non-salamander species were observed in these crevices. Alongside plethodontid salamanders, wood mice (*Apodemus sylvaticus*), an eastern box turtle, and ring-necked snakes were found. As predators of salamanders, ring-necked snakes may opportunistically use crevices during foraging and could affect how salamanders distribute themselves. Furthermore, other species including dusky salamanders or long-tailed salamanders may have spatially or temporally restricted impacts on crevice-using salamanders when either close to a stream or during cooler seasons respectively. Another limitation of our study is the inability to assess how detection of species may have changed our inferences about their distributions due to the lack of repeated observations. Despite these changes, visual evaluation of residuals demonstrated no consistent spatial pattern suggesting that spatial bias is unlikely though there may have been temporal changes in detection rates (Bailey et al. 2004).

Terrestrial and stream-breeding salamanders regularly use sandstone bluff habitat at the edge of the Cumberland Plateau during the warm season. Microclimate conditions provide the clearest link to salamander occupancy patterns and suggest a potential mechanism for crevice use — to avoid high temperatures and low humidity. Facultative use of these refuges could promote additional foraging activities improving individual fitness and potentially providing a region of elevated densities relative to forest floors where salamander communities appear to be at low densities relative to other eastern North American forests (McKenzie and Cecala *in review*). More research is necessary to evaluate the significance of crevice habitat to the ecology of terrestrial salamanders on the Cumberland Plateau.

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