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Microhabitat Selection of an Isolated Population of Green Salamanders (*Aneides aeneus*) in Southern Ohio, USA

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***Abstract*.—Microhabitat plays a critical yet often overlooked role in wildlife habitat selection, especially for amphibians, which are highly sensitive to environmental gradients and therefore more reliant on these fine-scale features. We examined the structural and environmental factors influencing microhabitat selection by Green Salamanders (*Aneides aeneus*), a habitat specialist associated with rock outcrop crevices. We focused on an at-risk, peripheral population in southern Ohio, USA, to determine whether crevice selection patterns differed from those observed in more centrally located populations. Green Salamanders were more likely to occupy deep crevices with narrow openings than shallow, wide ones. Despite inhabiting peripheral populations, salamanders in Ohio selected microhabitats similar to those used by salamanders inhabiting core populations.These crevices may offer more stable, humid microclimates and greater protection from predators. Our findings suggest that specific microhabitat features influence whether a rock outcrop can support Green Salamander populations, and we recommend incorporating microhabitat variables when developing amphibian conservation strategies.**

Key Words.—amphibian; disjunct population; habitats; Plethodontid; rock outcrop

Introduction

Microhabitat, defined as the fine-scale environmental parameters where organisms allocate their time and energy, is a crucial yet often overlooked aspect of wildlife conservation and management (Morris 1987). Understanding the microhabitat characteristics preferred by wildlife can assist wildlife managers and biologists to locate focal species, more effectively identify critical areas for preservation, and address occupancy disparities between localities unexplained by more broadly scaled habitat or landscape variables (Basile et al. 2017; Novak and Barrett 2023). Additionally, from an ecological perspective, understanding microhabitat selection can provide insight into the potential role that temperature and humidity play at a fine scale in the life histories of many species (Reagan 1974; Blouin-Demers and Weatherhead 2001; Hofmann and Fischer 2002; Lunghi et al. 2015). The scale at which organisms select microhabitat is variable and taxa dependent. For example, a shaded grove might serve as the microhabitat for cover or shelter of a White-tailed Deer (*Odocoileus virginianus*), whereas for a small Red-backed Salamander (*Plethodon cinereus*), one stone could fulfill that role.

Understanding microhabitat selection is especially important for small, terrestrial vertebrates, which are often dependent upon temperature, moisture, and shelter availability (Oatway and Morris 2007; Peterman and Semlitsch 2013). The influence of such environmental conditions on animal physiology is particularly evident in amphibians whose narrow physiological thresholds limit them to small home ranges, decrease their opportunities to locate alternative suitable microhabitats, and increase their sensitivity to local environmental changes (deMaynadier and Hunter 1995; Popescu and Hunter 2001; Vasconcelos and Calhoun 2004; Wells 2010). These physiological limitations have played contributing roles in ongoing amphibian population declines worldwide and highlight why understanding the small-scale microhabitat preferences of amphibians is increasingly imperative (Linder et al. 2003). Unfortunately, microhabitat requirements for many at-risk species of amphibian are unknown, and most amphibian conservation plans focus exclusively on environmental variables available at broad, regional scales (Basile et al. 2017).

Green Salamanders (*Aneides aeneus*) are microhabitat specialists native to the Appalachian Mountains of the Eastern U.S. and are primarily associated with the crevices of rock outcrops

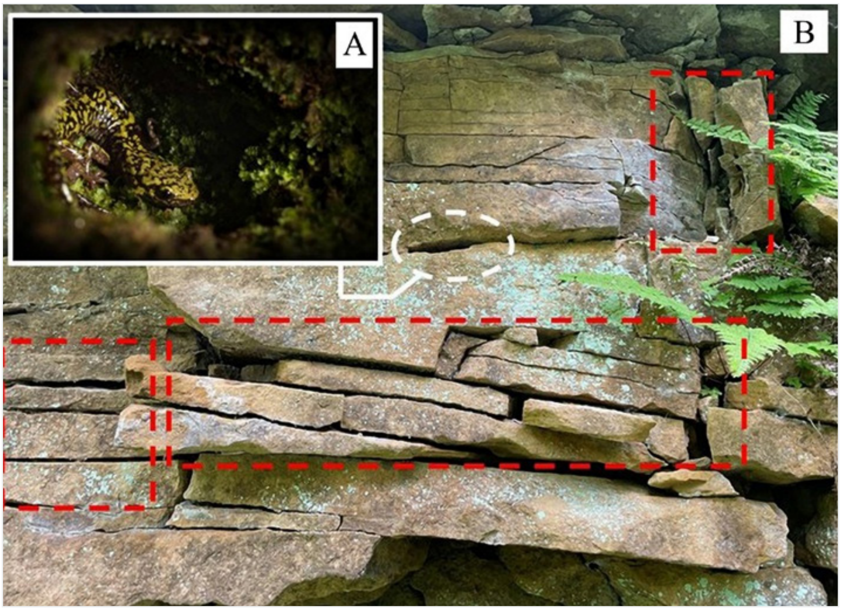

Figure 1. (A) Green Salamander (*Aneides aeneus*) within a crevice. (B) Microhabitat of Green Salamanders along a rock face in southern Ohio, USA. Dashed red boxes indicated potentially occupiable crevices. (Photographed by Aidan McCarthy).

(Gordon and Smith 1949; Gordon 1952; Fig. 1). This species is also considered semi-arboreal, reportedly inhabiting trees during warmer months (May-September; Wilson 2003; Waldron and Humphries 2005). Crevices, both within outcrops and on trees, play a vital role in nearly the entire life history of Green Salamanders, from feeding to courtship, nesting, and hibernation, and act as both a refuge from predators and as a buffer maintaining more stable temperature and humidity conditions compared to the ambient environment (Gordon 1952). Despite multiple studies showing how local microhabitat conditions play a role in whether outcrops can support Green Salamander populations, conservation plans have focused primarily on broader, landscape-level differences in outcrops, such as forest structure, aspect, and elevation (Bruce 1968; Newman et al. 2018). Therefore, improving our understanding of how environmental and structural differences influence the selection of these features is crucial for conservation and management of this species.

Green Salamanders compete to secure optimal crevices, and individuals have been observed defending crevices from other salamanders (Cupp 1980). Several studies have explored which attributes characterize optimal rock outcrop crevices used by Green Salamanders compared to other, seemingly suitable, but unoccupied crevices present nearby (Table 1). Variables most consistently found to be predictors of crevice selection include canopy cover, depth, and opening width; however, other predictors have included crevice density and distance

Table 1. Studies conducted on the crevice selection of Green Salamanders (*Aneides aeneus*) indicating location of study and variables determined to be significant: Canopy Cover = percentage of canopy vegetation covering an outcrop; Depth = deepest measurable distance into a crevice; Opening Width = vertical distance (top to bottom) of a crevice; Opening Length = horizontal distance of a crevice (left to right); Distance to Woody Vegetation = shortest distance from a crevice to woody vegetation; Height = distance of a crevice above ground; and Crevice Density = density of occupiable crevices within a defined area of rock. Samples sizes are of the number of crevices measured.

Location	Crevice Type	Significant Variables	Sample Size	Study
North Carolina	Transitory	Canopy Cover, Depth, Moisture	< 50	Gordon (1952)
South Carolina	Transitory	Opening Width	< 50	Rossell et al. (2009)
Virginia	Transitory	Canopy Cover, Depth	> 50	Smith et al. (2017)
South Carolina	Breeding	Distance to Woody Vegetation, Height, Opening Length	> 50	Rossell et al. (2019)
South Carolina	Transitory	Opening Width, Canopy Cover, Crevice Density	> 50	Novak and Barrett (2023)

to woody vegetation (Gordon 1952; Rossell et al. 2009; 2019; Smith et al. 2017; Novak and Barrett 2023). Most of this research has been conducted in the Blue Ridge Escarpment of North Carolina and South Carolina, and the Cumberland Plateau of Virginia. There has been no comprehensive analysis of crevice selection across the entire range of the species, however, and it currently remains unknown how attributes influencing crevice selection may vary across the broad distribution of Green Salamanders. Understanding the broader microhabitat preferences of this species is becoming increasingly imperative as Green Salamanders are exhibiting notable population declines across portions of their range and are protected in most of the states in which they occur (Corser 2001; Clavel et al. 2011; Soto et al. 2021).

Within Ohio, Green Salamanders are restricted to two isolated populations along the Ohio River. These two peripheral populations are separated from each other by about 97 km and are isolated from more centrally located core populations by the Ohio River. The limited distribution of Green Salamanders in Ohio is the primary reason the species is listed as Endangered in the state (Lipps 2005). Peripheral populations often experience increased extirpation risks and may exhibit different habitat selection strategies compared to core populations (Sjogren 1991; Braunisch et al. 2008; Heard et al. 2012). The microhabitat preferences of Green Salamanders in Ohio have yet to be investigated, and it is unknown how geologic and environmental differences in this region, relative to other previously studied sites, may affect crevice selection. Our objectives were to identify the structural and environmental variables that influence crevice selection in the isolated populations of Green Salamanders in southern Ohio, and to compare these variables with those influencing crevice selection in core populations across the range of the species.

Materials and Methods

***Field methods*.**—We completed surveys for Green Salamanders at 37 rock outcrops (sites) in Adams County (23 sites) and Lawrence County (14 sites), Ohio, USA. Green Salamanders had been documented previously at six of the outcrops (three in each county). No surveys had been conducted, nor had Green Salamanders been reported previously at any of the remaining 31 sites. For our study, we defined a site as a contiguous stretch of rock outcrop, or a series of outcrops < 50 m apart, where Green Salamanders have been documented. If occupied rock outcrops were > 50 m away from one another, we considered them distinct sites. Additionally, we defined population as a series of outcrops harboring Green Salamanders with the reasonable possibility of dispersal between outcrops. Green Salamanders are not believed to travel beyond 50 m often (Smith and Gordon 1949; Gordon 1952); however, Gordon (1952) documented two adults traveling 76 m and a juvenile traveling 106 m during a mark-recapture study suggesting that dispersal between outcrops occurs on occasion to allow gene flow between populations.

We conducted all surveys from 1 May 2023 to 15 June 2023, between 0800 and 1700. We used a flashlight to search rock crevices for Green Salamanders. To maximize personnel safety, we did not survey crevices located on steep sections of a hillside or those that required significant climbing to reach. Because Green Salamanders are semi-arboreal, we also surveyed trees within 10 m of each rock outcrop by peering under bark and shining flashlights within tree-holes.

When we located a Green Salamander within a crevice, we followed methods outlined by Rossell et al. (2009) to measure variables for each occupied crevice, and for three randomly selected unoccupied crevices per occupied crevice. To select associated unoccupied crevices, we used a random number generator to produce a direction (0°–360°) followed until an unoccupied crevice was located. If we could not locate a suitable crevice along the random direction, we generated a new random direction and repeated the process until one was found. Some occupied crevices had fewer than three associated unoccupied crevices measured when an outcrop had a low density of crevices. We considered unoccupied crevices as suitable if their opening was at least 3 mm wide and large enough for a juvenile Green Salamander to use.

We measured four structural variables: (1) Maximum depth was the deepest visible point within a crevice or the deepest point our probe was able to reach beyond this point; (2) Opening width was the distance from top to bottom of a crevice; (3) Opening length was the distance from left to right across a crevice; and (4) Overhang distance was the horizontal distance of cover provided by the closest overhanging ledge. Proximity to arboreal habitat is reportedly a significant factor affecting crevice selection (Smith et al. 2017; Novak and Barrett 2023); thus, we included distance to woody vegetation (distance from crevice opening to nearest woody vegetation stem) as a measured variable. We also measured humidity (%) and temperature (°C) within and outside (ambient) of crevices using a handheld GSP-6 Digital Temperature and Humidity Data Logger (Elitech Technology, Inc., San Jose, California, USA). To maximize accuracy, we placed the probe of the data logger within each crevice for at least 30 sec or until estimated values stabilized. We measured ambient humidity and temperature once for each group of an occupied crevice and associated unoccupied crevices using the same methodology. We subtracted temperature and humidity values within crevices from ambient conditions to create humidity and temperature differential variables.

Data analysis.—We fit Bayesian Binomial Generalized Linear Mixed Effect Models using the brms package in RStudio to determine which of our variables best predicted crevice selection (Bürkner 2017; R Core Team 2023). Prior to assessing models, we tested each variable for collinearity using the sjp.corr function in the package sjPlot (Ludecke 2023). We centered each variable to a mean of zero and scaled them to one standard deviation. In addition to crevice variables, we explored random effects to account for structural dependencies in our models. The random effects we assessed included site (the individual rock outcrop of each measured crevice), salamander ID (the salamander associated with each measured crevice), and day of year. We retained random effects with a credibility interval not overlapping zero in our final model regardless if the overall impact of the random effects were likely negligible. We fit and compared models with both uninformed and informed priors. The inclusion of informed priors allowed us to incorporate the findings of previous studies and expert opinion into our parameters allowing for a more biologically relevant analysis (Choy et al. 2009). Therefore, we used previous literature to incorporate priors that reflected the anticipated direction of effect (positive or negative) on each variable of interest on Green Salamander crevice selection (Gordon 1952; Rossell et al. 2009; Smith et al. 2017; Novak and Barrett 2023). We ran an initial model with all uncorrelated variables hypothesized to affect crevice selection, which was eventually simplified to only include variables with highest probability of affecting selection (probability of direction ≥ 95%). Probability of direction (Pd) refers to the probability that the effect of a parameter is positive or negative. We used the Gelman-Rubin statistic and visual inspection of chains to confirm adequate mixing and model convergence (Gelman and Rubin 1992). We assessed goodness-of-fit using posterior predictive checks. We calculated the leave-one-out cross-validation criterion (LOO) and widely applicable information criterion (WAIC) to compare models using the loo_compare function (Bürkner 2017).

Results

We measured 135 crevices occupied by Green Salamanders and 379 associated unoccupied crevices. We removed all crevices with missing data (e.g., missing humidity or temperature data due to a broken probe) for a final data set of 114 occupied and 313 unoccupied crevices. Our final model included maximum depth, opening width, opening length, and humidity difference as meaningful predictors of crevice selection (Table 2). We included salamander ID (Estimate: 0.14 ± 0.11 standard deviation) and day of year (Estimate: 0.12 ± 0.09) in our final model as random intercepts; however, the effect size of both intercepts was likely negligible. Our final model with informed priors was statistically equivalent to our uninformed model (Appendix Table) as the estimated error of both the LOO and WAIC criterion overlapped. The parameter estimates of each model did not change dramatically and all inferences were drawn from the informed model.

On average, occupied crevices exhibited increased maximum depths and decreased average opening

Table 2. Posterior distribution of top supported model examining crevice selection by Green Salamanders (*Aneides aeneus*) in Ohio, USA. Humidity difference refers to the difference between humidity levels measured in crevices compared to outside of crevices. Acronyms are Mean ES = average effect size of each variable, 95% credible interval (CI) = effect interval that contains all points within the interval that have a higher probability density than points outside the interval; Probability of direction (Pd) = proportion of the posterior distribution that is of the median's sign (positive or negative; Makowski et al. 2019), ESS = effective sample size of each parameter that measures how many samples are represented from the Markov Chain Monte Carlo chain. A higher ESS indicates a more reliable estimate, and a minimum ESS of 1,000 is necessary for stable estimates (Bürkner 2017).

Variable	Mean ES	95% CI	Pd	ESS
Maximum Depth	0.71	(0.44, 0.99)	100%	6,418
Opening Width	-2.18	(-3.16, -1.35)	100%	5,405
Opening Length	-0.65	(-1.07, -0.25)	99.98%	6,652
Humidity Difference	0.29	(0.06, 0.53)	99.25%	6,652

Table 3. Characteristics of 135 occupied crevices and associated 379 unoccupied crevices measured in an isolated population of Green Salamanders (*Aneides aeneus*) in southern Ohio, USA. Values reflect mean ± standard error. Variable are Maximum Depth = deepest measurable distance into a crevice, Opening Width = vertical distance (top to bottom) of a crevice, Opening Length = horizontal distance of a crevice (left to right), Temperature and Humidity Differences = difference between those respective values within crevices and the ambient environment, Distance to Woody Vegetation = shortest distance from a crevice to woody vegetation, and Overhang Distance = horizontal distance of cover provided by the closest overhanging ledge.

Crevice Variable	Occupied	Unoccupied
Maximum Depth (mm)	125.0 ± 73.0	91.0 ± 60.7
Opening Width (mm)	15.3 ± 32.8	24.7 ± 24.7
Opening Length (mm)	115.5 ± 119	148.9 ± 169.2
Humidity Difference (%)	10.4 ± 15.3	6 ± 12.2
Temperature Difference (°C)	-3.4 ± 8.6	-2.2 ± 6.8
Distance to Woody Vegetation (cm)	116.4 ±147.8	153.2 ± 65.4
Overhang Distance (cm)	27.8 ± 33.1	27 ± 38.1

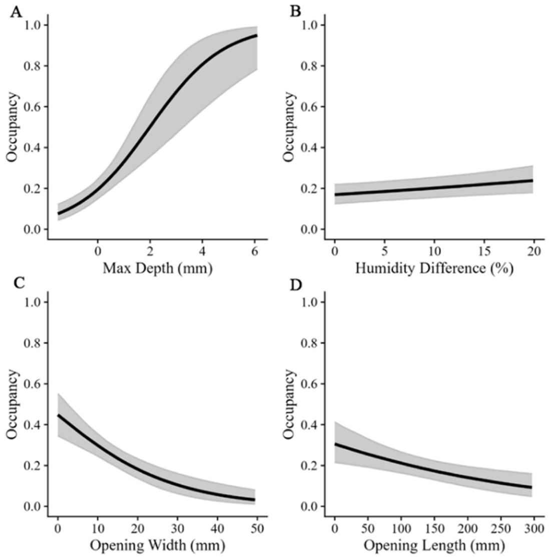

Figure 2. Conditional effects of (A) maximum depth, (B) humidity differential, (C) opening width, and (D) opening length on the probability of crevice selection by Green Salamanders (*Aneides aeneus*) in southern Ohio. Solid lines represent the mean estimate, and the shaded region represents the 95% credible interval around the mean.

widths and lengths relative to unoccupied crevices. In short, occupied crevices were deeper and exhibited smaller openings (Tables 2, 3; Appendix Figure). Additionally, occupied crevices were found to exhibit higher humidity compared to associated unoccupied crevices (Table 3) however, the overall effect of this variable is minimal, with only a 0.07 change in the probability of crevice selection across an 20° C humidity differential (Fig. 2). On average, occupied crevices were 4.4% more humid compared to associated unoccupied crevices. Distance to woody vegetation, overhang distance, and our temperature differential variable were all found to have negligible effects on crevice selection.

Discussion

Our study indicates that Green Salamanders in southern Ohio select crevices with attributes similar to crevices selected by salamanders in core populations. Green Salamanders in these peripheral populations were more likely to occupy deep crevices with narrow openings than shallow crevices with wide openings. The importance of maximum depth to the selection of crevices by Green Salamanders supports the findings of Smith et al. (2017) who reported a mean occupied crevice depth of 163 mm compared to our mean depth of 125 mm. Previous studies reported maximum depth not to be a significant variable for predicting crevice selection (Novak and Barrett 2023; Rossel et al. 2009). Novak and Barrett (2023), however, noted that this inconsistency may be due to the difficulty of locating Green Salamanders within deeper crevices. Novak and Barrett (2023) and Rossell et al. (2009) reported lower mean depths (38 mm and 61 mm, respectively), which may further contribute to these differences. The difficulty in searching deep within crevices is a limitation of our study, and we likely inaccurately identified some occupied crevices as unoccupied. Thus, our results may underrepresent the array of crevices occupied by the species.

Crevices with narrower opening widths and short opening lengths are more likely to be occupied by Green Salamanders than crevices with wider openings. Rossell et al. (2009) and Novak and Barrett (2023) found that Green Salamanders prefer narrow opening widths (18 mm and 14 mm respectively), consistent with our findings (mean of 15.3 mm). Opening length has not been previously identified as a significant crevice feature, but an opening with a narrow length likely impacts crevice selection similar to narrow opening widths (Gordon 1952; Rossell et al. 2009; Novak and Barrett 2023). Smaller crevice openings possibly offer Green Salamanders increased protection from predators, and more stable temperature and humidity conditions (Gordon 1952; Rossell et al. 2009). Crevices with these characteristics may also give the species a competitive advantage over other larger-bodied salamanders, such as the Northern Slimy Salamander

(*Plethodon glutinosus*) and the Northern Spring Salamander (*Gyrinophilus porphyriticus*), which overlap in range and have been documented using similar crevice habitats (Pauley 2004; Smith et al. 2017; Wilson et al. 2024).

Previous studies have not evaluated humidity differential as a predictor of crevice selection due to the difficulty of measuring microclimates within crevices. Our results support the hypothesis that occupied crevices maintain more stable and humid conditions (Gordon 1952; Rossell et al. 2009; Smith et al. 2017). Although temperature and humidity synergistically influence amphibian microhabitat selection (Seebacher and Alford 2002; Galindo et al. 2018), our models suggest that temperature does not influence Green Salamander crevice selection in southern Ohio. Green Salamanders have been shown to tolerate warmer, drier conditions better than many other amphibians, which may give them a competitive advantage in such environments (Gordon 1952; Bruce 1968; Barrett et al. 2014; Newman et al. 2018). Thus, the species may exploit a broader thermal range within crevices provided that high enough humidity thresholds are met (Galindo et al. 2018).

Distance to woody vegetation also has been identified as a potential factor influencing Green Salamander occupancy and crevice selection in some regions (Smith et al. 2017; Novak and Barrett 2023), but we found no such effect at our sites in Ohio. Smith et al. (2017) propose that proximity to vegetation may benefit Green Salamanders by providing additional shade or by reducing the energy and time required to access arboreal foraging habitats. The shading hypothesis seems particularly relevant, as canopy cover has been consistently linked to Green Salamander occupancy (Gordon 1952; Smith et al. 2017; Novak and Barrett 2023). Although we initially measured canopy cover, our method of selecting unoccupied crevices near occupied ones resulted in minimal variation between the two groups. This likely led to differences between both canopy cover and distance to woody vegetation to be biologically irrelevant. The extent of arboreal habitat use by Green Salamanders in Ohio remains unclear, although we observed two individuals within tree-holes during our surveys.

Our data indicates that the presence of rock outcrops alone may not be enough to sustain Green Salamanders, or other outcrop and crevice specialists, because the quality and attributes of crevices present plays a role in whether an outcrop can support a population. In the context of Green Salamanders and other outcrop specialists, land managers should consider both the habitat features surrounding an outcrop and the microhabitat features within an outcrop to develop more all-encompassing management and conservation plans. We recommend that, for decisions regarding land preservation, survey prioritization, or land acquisition for Green Salamanders in Ohio, stakeholders prioritize outcrops with a high density of crevices 100 mm deep and with openings < 15 mm wide. Focusing on outcrops with these attributes can make for more efficient surveying and can prioritize outcrops with the microhabitat conditions required to support healthy Green Salamander populations.

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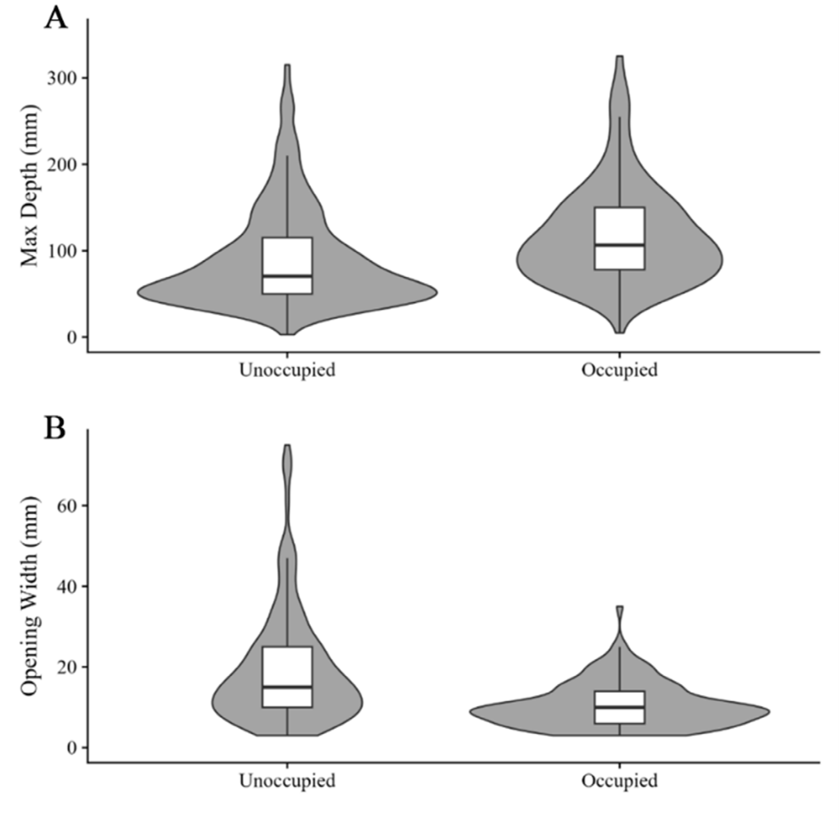
Appendices

Appendix Table. Informed priors selected for Bayesian Binomial Generalized Linear Mixed Effect Models. Variances of 0.5 were given to maximum depth and humidity difference because we had high confidence of effect based upon scientific literature (Gordon 1952; Rossell et al. 2009; Smith et al. 2017; Novak and Barrett 2023) and expert opinion. All other variables received variances of 1. Mean of effect was set to 1 from variables with positive expected effects and -1 for variables with negative expected effects.

Variables	Mean	Variance	Estimated Effect Direction
Maximum Depth (mm)	1	0.5	Positive
Opening Width (mm)	-1	1	Negative
Opening Length (mm)	-1	1	Negative
Humidity Difference (%)	1	0.5	Positive
Temperature Difference (°C)	-1	1	Negative
Distance to Woody Veg. (cm)	-1	1	Negative
Overhang Distance (cm)	1	1	Positive



Appendix Figure. Box and violin plots of the differences between (A) maximum depth and (B) opening width of crevices occupied and unoccupied by Green Salamanders (*Aneides aeneus*) in southern Ohio, USA. Max Depth is the deepest measurable distance into a crevice and Opening Width = vertical distance (top to bottom) of a crevice. Boxes indicate the middle (50%) interquartile range of observed data while vertical lines indicate upper and lower 25% of data. Wider regions of violin plot indicate values that occur more frequently.