Herpetological Conservation and Biology 19(1):23–32.
Submitted: 7 August 2023; Accepted 15 January 2024; Published: 30 April 2024.

WOODY UNDERSTORY VEGETATION REMOVAL ALTERS THE MICROCLIMATIC PROFILES OF ROCK CREVICES USED BY GREEN SALAMANDERS (*ANEIDES AENEUS*) IN THE CUMBERLAND MOUNTAINS OF VIRGINIA, USA

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Abstract.—**Anthropogenic vegetation removal is a major source of disturbance for rock outcrops embedded within forest habitats, particularly for rock outcrop specialists of high conservation concern such as those in the Green Salamander *(Aneides aeneus)* complex. Researchers have long advocated for the preservation of forested buffers around rock outcrop habitat to safeguard crevices used by Green Salamanders against extreme temperatures and to maintain high moisture levels, although scant empirical data exists in the literature to support these recommendations. I performed a season-long survey of microclimatic characteristics within crevice refugia at a rock outcrop complex in the Cumberland Mountains of southwestern Virginia, USA, experiencing recent Green Salamander declines coincident with woody understory removal for rock climbing development. Crevices in outcrops experiencing adjacent understory vegetation removal were up to three times warmer and six times drier than crevices not impacted by the development of climbing routes. The forest canopy remained intact at both sites, which suggests the potential for negative impacts of understory vegetation removal on resident salamanders.**

Key Words.—amphibian; Appalachia; disturbance; habitat; rock climbing; tree

INTRODUCTION

Crevice-dwelling salamanders, or salamanders that inhabit cracks and crevices in vertical rock substrate, are a unique group of amphibians whose microhabitat requirements place them under high conservation concern (Gordon 1952; Cupp 1991; Petranka 1998; Niemiller et al. 2022). In the Appalachian Mountains of eastern North America, the Green Salamander (*Aneides aeneus*) complex (Patton et al. 2019) comprises the species most heavily specialized to crevice refugia. Green Salamanders occupy crevice refugia for substantial portions of their life cycles, with past studies identifying physical attributes associated with transitory crevice selection and the use of rock crevices as nest sites (Rossell et al. 2009; Smith et al. 2017; Rossell et al. 2019; Novak and Barrett 2023).

Green Salamanders are also dependent on the vegetative contexts surrounding rock outcrops, exhibiting at least periodic arboreal behavior by climbing into trees and other woody vegetation surrounding outcrops during summer months (Wilson 2003). Although the specific behaviors that Green Salamanders undertake during bouts of arboreal activity are still largely unknown, salamanders preferentially select particular species of trees located close to rock crevices when engaging in arboreal behavior (Waldron and Humphries 2005; John et al. 2019). Similarly, Green Salamanders select rock crevices located close to nearby woody vegetation (Smith et al. 2017) and occupy rock outcrops possessing higher nearby tree densities (Hinkle et al. 2018), both presumably a function of the ability for nearby woody vegetation to either facilitate movement to and from crevices and arboreal habitat or modulate the microclimate of crevice refugia through shading.

Green Salamanders have experienced historic declines associated with habitat disturbance (Snyder 1991; Corser 2001; Staudt et al. 2013), leading many researchers to recommend the preservation of intact buffers of undisturbed woody vegetation directly adjacent to rock outcrops as a best management practice (Petranka 1998; Waldron and Humphries 2005; Miloski 2010; Hinkle et al. 2018). Although the widths of recommended buffers vary, these recommendations assume that woody vegetation adjacent to rock outcrops modulates the microclimatic characteristics of rock faces through enhanced shading and decreased insolation, leading to lower temperatures and higher moisture levels in crevices used by Green Salamanders (Pauley and Watson 2005). Recent work has indirectly supported this assumption. For example, John et al. (2019) found a difference between Green Salamander body temperatures in crevice refugia and ambient temperatures, while Novak and Barrett (2023) found that within-site microhabitat features possessing the ability to alter microclimatic characteristics significantly predicted Green Salamander presence. Broader-scale modeling studies have also reinforced the mechanistic roles of temperature and moisture constraints on Green Salamander habitat suitability (Newman et al. 2022).

Despite these findings, little to no empirical data exist in the literature examining if and how woody vegetation removal alters the microclimatic characteristics of rock faces and their component crevices. These knowledge gaps preclude a detailed understanding of how such vegetation removal may contribute to Green Salamander declines and how appropriate best management practices, including effective buffer widths, can be most effectively designed for Green Salamander populations. I sought to address these knowledge gaps through a comparison of microclimatic profiles in crevices at a rock outcrop complex impacted by woody understory vegetation removal for rock climbing development in the Cumberland Mountains of southwestern Virginia, USA. Specifically, I compared temperature and relative humidity levels between crevices in rock outcrops where woody vegetation removal had occurred from rock climbing development and outcrops unimpacted by such development from the same site. I discuss the results of these comparisons and their implications for understanding the microclimatic dynamics of rock outcrops in response to anthropogenic disturbance, providing recommendations to enhance future work and the development of management recommendations for Green Salamander populations.

Materials and Methods

Study site.—I performed surveys at The Labyrinth, an approximately 1.5 ha collection of rock outcrops on the northern slope of Stone Mountain above Norton, Virginia, USA (exact geographic coordinates withheld due to conservation concerns). Rock outcrops at this site are erosional remnants derived from ridgetop Pennsylvanian sandstone, each approximately 20 × 30 m in size and 8–10 m in height. The site is located within a mature, second-growth Northern Hardwood Forest, with maples (*Acer* spp.), birches (*Betula* spp.), and Fraser Magnolia (*Magnolia fraseri*) abundant in the overstory and with Great Rhododendron (*Rhododendron maximum*) as the predominant woody understory plant species.

Figure 1. Representative visual examples of surveyed habitat of the Green Salamander (*Aneides aeneus*) complex at an area impacted by rock climbing development on Stone Mountain in Norton, Virginia, USA. (A) An impacted site with woody understory vegetation completely removed adjacent to and on top of rock outcrops, and (B) a reference site unimpacted by woody understory vegetation removal located 50 m away from the outcrops pictured in panel A. (Photographed by Walter H. Smith)

Rock climbing development has occurred at The Labyrinth intermittently since 2015, with activities mostly constrained to vegetation removal for the development of climbing routes and boulder problems on several sandstone outcrops at the site. Specifically, all understory woody vegetation, primarily *R. maximum*, has been cut away from the top surface of the outcrop and within an approximately 5 m buffer of the base of the outcrop at locations where climbing routes have been developed (Fig. 1). Approximately

70% of the site has been modified for climbing development, with remaining outcrops undisturbed. Green Salamanders have historically been abundant at the site (Smith et al. 2015), with anecdotal evidence of salamander declines (Anna Smith et al., unpubl. report) occurring coincident with the start and expansion of climbing development activities.

***Habitat comparisons*.**—Because widely varying structural characteristics of rock crevices may influence microclimatic characteristics of those crevices, I first performed a general comparison of habitat variables at crevices in rock outcrops impacted and unimpacted by woody understory removal at the study site. Specifically, I selected 30 crevices each from outcrops impacted and unimpacted by vegetation removal. I chose this sample size based on the limited availability of rock outcrops at the study site unimpacted by woody vegetation removal and the ability to select spatially independent crevices at each outcrop while maximizing sample size. I selected crevices randomly from available outcrops, with the constraint that selected crevices were located at least 5 m from the nearest selected crevice to maximize independence in habitat variables and microclimatic conditions between crevices. I also only selected crevices from portions of the rock outcrop accessible from the ground (generally up to about 2 m above the ground surface).

Prior to monitoring microclimatic characteristics at each crevice, I examined generalized habitat differences between impacted and unimpacted crevices (hereafter referred to as reference crevices). Specifically, I measured the following habitat variables at each crevice: (1) crevice dimensions (maximum height, width, and depth); (2) minimum height of the crevice opening above the ground surface; (3) percentage canopy cover at the crevice opening; (4) aspect of the crevice; (5) basal area of the forest surrounding the crevice; (6) the number of woody stems within 5 m of the crevice; and (7) the number of cut woody stems within 5 m of the crevice. I measured crevice dimensions as the maximum height and width of the crevice, as well as the maximum depth that a 5 mm diameter probe could be inserted into the crevice. I measured aspect (degrees azimuth) at the crevice opening, with percentage canopy cover estimated using a spherical forest densiometer (Forest Densiometers, Marianna, Florida, USA). I estimated basal area using a Jim-Gem rectangular cruising prism (Jim-Gem, Jackson, Mississippi, USA) and I counted all woody and cut stems using visual counts at each location.

I examined differences in habitat variables between impacted and reference crevices using a nonparametric Mann-Whitney Test in R v.4.2.1 (R Development Core Team 2018). I used a nonparametric test for this analysis due to heteroscedasticity that could not be corrected via data transformations. Because this approach resulted in the same analysis being run multiple times on the same dataset, I adjusted significance levels using the False Discovery Rate (Narum 2006) to account for an increasing chance of Type I error resulting from multiple comparisons ($\alpha = 0.018$).

***Microclimate comparisons*.**—I measured microclimate variables (temperature and relative humidity or RH) at all crevices at monthly intervals from April to October 2022. I did not record any measurements in July 2022 due to abnormally wet conditions that did not allow for a day without active precipitation or recent precipitation, which would have skewed humidity measurements due to saturated substrate. I performed all site visits on days without recent (within 24 h) precipitation and with dry substrate, with all visits performed at the typical peak of diurnal heating (seasonally 1400–1600) to minimize temporal variability in weather conditions throughout a standard 24 h period.

I used a TPI-597C1 digital hygrometer/psychrometer with a 30 cm-long probe, accurate to ± 2% RH and ± 0.1° C (Test Products International, Beaverton, Oregon, USA) to obtain temperature and RH measurements at each crevice. I specifically took two measurements at each crevice, including an ambient reading measured 1 m from and at the same height above ground as the crevice opening and a reading of the crevice interior taken at the back of the crevice at its maximum depth. I also randomized the order I visited rock outcrops during surveys to minimize the potential for measurements to be influenced by the timing of measurements during each survey period. During each survey visit, I also surveyed all accessible crevices at each outcrop for the presence of Green Salamanders using an LED headlamp.

Rock crevices are presumably ideal refugia for amphibians due to their ability to modulate temperature and moisture levels relative to the surrounding environment (John et al. 2019). Following data collection, I used Linear Mixed Effects Models to examine responses in differential temperature (ΔT) and RH (ΔRH) between ambient and crevice interior conditions across impacted and reference sites and across the study period. I specifically evaluated three candidate models for each of ΔT and ΔRH as response variables: (1) a model containing site status (impacted versus reference) alone; (2) a model containing survey month alone; and (3) a model examining an interaction between site status and month. Although crevice depth did not differ significantly between reference and impacted crevices, variable crevice depths could influence temperature and RH measurements at each location. I therefore included crevice depth as a factor in all models. Additionally, I included rock outcrop location as a random factor in all models because multiple crevices derived from the same larger rock outcrop may be exposed to the same thermal regimes from their parent substrate and therefore may not be fully independent.

I constructed and evaluated all models using the lmer function in the lme4 package in R (Bates et al. 2015). I used Akaike's Information Criterion corrected for small sample sizes (AICc) to evaluate candidate models via the anova function in the car package in R, with pairwise differences between reference and impacted sites across months evaluated using the emmeans package (Lenth et al. 2018). I considered models with ΔAICc < 2.0 as strongly competitive (Burnham and Anderson 2022), indicating that these models were equally as plausible as the model with the lowest AICc score.

RESULTS

Crevices from impacted and reference portions of the site exhibited similar physical attributes, with the exception of variables related to the vegetative contexts surrounding each crevice (Table 1). Crevice height (W = 245.5, n1 = n2 = 30, *P* = 0.220), width (W = 130, n1 = n2 = 30, *P* = 0.060), depth (W = 227.5, n1 = n2 = 30, *P* = 0.465), and distance above ground (W = 180, n1 = n2 = 30, *P* = 0.597) were not significantly different between impacted and reference sites, and both sites possessed similar crevice aspects (W = 164.5, n1 = n2 = 30, *P* = 0.344). Crevices at impacted sites did, however, possess less canopy cover than those at reference sites (W = 95, n1 = n2 = 30, *P* = 0.001), with fewer woody stems (W = 13.5, n1 = n2 = 30, *P* < 0.001) and more cut stems (W = 290, n1 = n2 = 30, *P* = 0.002) at impacted sites. Basal area, which was primarily driven by large canopy trees that were not removed during climbing development, did not differ between impacted and reference sites (W = 34.5, n1 = n2 = 30, *P* = 0.049).

TABLE 1. Attributes (mean ± 1 standard deviation) of rock crevices and parent outcrops at sites experiencing (Impacted) and lacking (Reference) woody understory vegetation removal for rock climbing development on Stone Mountain in Norton, Virginia, USA. The terms Height, Width, Depth, and Distance Above Ground refer to the maximum crevice height, width, and depth and to the minimum distance above the ground surface, respectively. The terms # Stems and # Cut Stems refer to the number of woody stems and cut stems within 5 m of each rock crevice. Asterisks (*) denote significant differences between Impacted and Reference sites (Mann-Whitney Test, $\alpha = 0.018$).

Attribute	Impacted	Reference
Aspect (azimuth)	195.7 ± 73.1	206.5 ± 109.4
Canopy Cover (%)*	97.4 ± 2.0	99.8 ± 0.5
Height (cm)	45.9 ± 53.3	30.0 ± 45.8
Width (cm)	16.2 ± 27.5	20.6 ± 17.1
Depth (cm)	19.4 ± 18.1	18.3 ± 19.5
Distance Above Ground (cm)	95.9 ± 51.5	113.9 ± 71.7
# Stems*	0.9 ± 1.3	5.4 ± 1.8
# Cut Stems*	2.1 ± 2.4	0.1 ± 0.3
Basal Area (m^2/ha)	9.3 ± 6.1	7.5 ± 4.4

A single model containing a status by month interaction was strongly competitive (ΔAICc < 2.0) for crevice temperature (Table 2). Specifically, differences between ambient and crevice temperatures were significantly less in impacted crevices across all months except for September, indicating warmer interior crevice conditions at impacted sites (Fig. 2). A fall frontal passage and associated temperature drop immediately preceded the September survey visit and likely influenced ambient conditions during that survey. Mean monthly crevice interior temperatures at impacted sites were as much as three times warmer, relative to ambient conditions, than those at reference sites throughout the study period.

A single model containing a status by month interaction was also strongly competitive for crevice RH (Table 3). Differences between ambient and crevice RH values were significantly less in impacted crevices across all months except for April and August, indicating drier crevice interior conditions at impacted sites (Fig. 3). April measurements occurred prior to local leaf-out, which may have influenced RH measurements during that monthly survey visit. Although still significant, differences between impacted and reference sites were reversed in August because outflow from an approaching thunderstorm rapidly increased ambient RH to 90–95% during the survey visit and prior to the onset of rainfall. Mean monthly crevice interior RH values at impacted sites

Table 2. Linear Mixed Effects Model results for four candidate models explaining variability in temperature differentials between crevice interiors and ambient conditions (ΔT) at a site impacted by rock climbing development on Stone Mountain in Norton, Virginia, USA. The term Location Only refers to the model including only outcrop location as a random factor, Status refers to the model including crevice type (impacted versus reference) only, Month refers to the survey month only, and Status*Month refers to an interaction between status and survey month. Abbreviations are npar = the number of parameters, AICc = Akaike's Information Criterion corrected for small sample sizes, and logLik = the log-likelihood value.

Model	npar	AICc	ΔAICc	logLik	Wald X^2	*P*-value
Status *Month	10	307.6	0	-143.77	27.32	< 0.001
Month	9	332.9	25.3	-157.44	165.83	< 0.001
Status	5	490.7	183.1	-240.35	22.81	< 0.001
Location Only	4	511.5	203.9	-251.75	--	--

were as much as six times drier, relative to ambient conditions, than those at reference sites throughout the study period (Appendix Table).

I rarely encountered Green Salamanders during crevice surveys, consistent with past anecdotal evidence of Green Salamander declines at the study site. I only encountered two Green Salamanders during the duration of the study; both individuals were adults found within crevices at rock outcrops lacking impacts from rock climbing development. Neither individual occupied a crevice randomly selected for inclusion in microclimate monitoring, although one salamander occupied an adjacent crevice about 20 cm from a selected reference crevice. I did not encounter any Green Salamanders within crevices at sites impacted by woody vegetation removal; furthermore, I did not encounter other species of salamanders at the study site.

Discussion

I found a strong signal of drier and warmer crevice conditions at rock outcrops impacted by understory removal at a rock-climbing area showing anecdotal evidence of recent Green Salamander declines. Crevice interiors at impacted sites were not only significantly warmer and drier than those at reference sites but also remained this way throughout most of the active season of the species, spanning several major climatological transitions through the spring, summer, and fall months. Collectively, these results confirm long-standing assumptions that vegetation located adjacent to rock outcrops exerts significant influences on the microclimatic profiles of available crevice refugia (Gordon and Smith 1949; Pauley and Watson 2005; Novak and Barrett 2023).

That removal of woody vegetation, adjacent to rock faces, alters the temperature and moisture regimes of rock substrate is not surprising. Vegetation shades rock faces from direct sunlight and can reduce wind velocity (a contributor to moisture loss) relative to bare, exposed surfaces via increased boundary layer friction (Pringle et al. 2003; Muller et al. 2004; Jain 2014). My study did not explicitly examine the mechanisms through which vegetation removal may cause a shift in temperature and moisture regimes; however, the reduced canopy cover observed at crevices experiencing woody understory removal indirectly supports decreased shading of rock faces and their component crevices as one potential mechanism for observed patterns in temperature and moisture levels. An interesting facet of my study is that woody understory vegetation was the only habitat feature manipulated at impacted sites. A full, mature forest canopy remained intact throughout the study site, and there was no visible evidence of mosses and lichens being scrubbed or otherwise removed from rock surfaces during site preparation. This suggests that seemingly small changes in habitat conditions, in this case variation in only one level of the overall forest structure, may be capable of exerting significant influences on the microclimatic dynamics of available microhabitat in rock outcrop complexes. Indeed, past work has demonstrated that small-scale variability in rock outcrop microclimates influences habitat suitability for other taxa, including vascular plants (Garcia et al. 2020), lichens (Kuntz and Larson 2020), and snakes (Pringle et al. 2003).

Although the results of my study show a distinct difference in temperature and moisture levels between rocks impacted and unimpacted by woody understory removal, there are several important limitations and caveats that need considering relative to applying these data to other study systems. First, all woody understory vegetation was removed from the base and upper surfaces of certain rock outcrops to facilitate their use as recreation sites for rock-climbing. The effect that less destructive activities, such as less intensive vegetation removal, has on the microclimatic characteristics of crevices is unknown. Several researchers have also implicated timber harvesting adjacent to or near rock outcrops as a contributor to Green Salamander declines (Corser 2001; Wilson 2003), although the potential impacts of these more expansive vegetation manipulations on temperature and moisture levels in and around

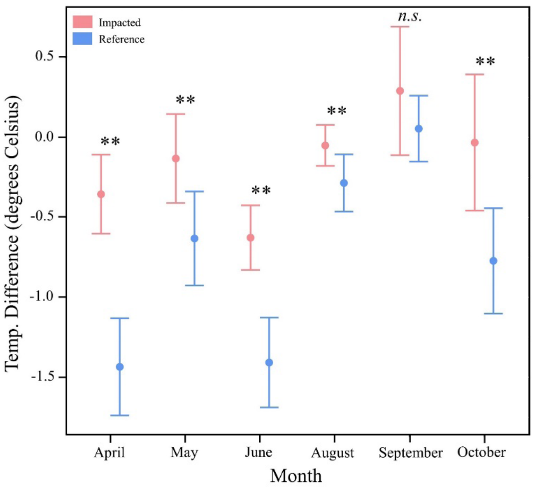

Figure 2. Comparison of temperature differences between crevice interiors and ambient conditions (mean ± 1 standard deviation) at rock crevices in impacted (red) and reference (blue) rock outcrops on Stone Mountain in Norton, Virginia, USA, in 2022. Labels denote significance levels of comparisons between impacted and reference crevices within each respective month (n.s. = no difference; ** $P < 0.01$).

rock outcrops remain unaddressed. Additionally, the effects that rock outcrop configurations, different geologic strata, and climatic variability across the range of a species have on the temperature and moisture profiles of crevices is unknown. These factors may be productive areas of focus for future work.

Table 3. Linear Mixed Effects Model results for four candidate models explaining variability in relative humidity differentials between crevice interiors and ambient conditions (ΔRH) at a site impacted by rock climbing development on Stone Mountain in Norton, Virginia, USA. Location Only refers to the model including only outcrop location as a random factor, Status refers to the model including crevice type (impacted versus reference) only, Month refers to the survey month only, and Status*Month refers to an interaction between status and survey month. Abbreviations are npar = the number of parameters, AICc = Akaike's Information Criterion corrected for small sample sizes, and logLik = the log-likelihood value.

Model	npar	AICc	ΔAICc	logLik	Wald X^2	P-value
Status *Month	10	1662.5	0	-821.24	21.61	< 0.001
Month	9	1682.1	19.6	-832.05	90.40	< 0.001
Status	5	1764.5	102.0	-877.25	19.43	< 0.001
Location Only	4	1781.9	119.4	-886.97	n.a.	n.a

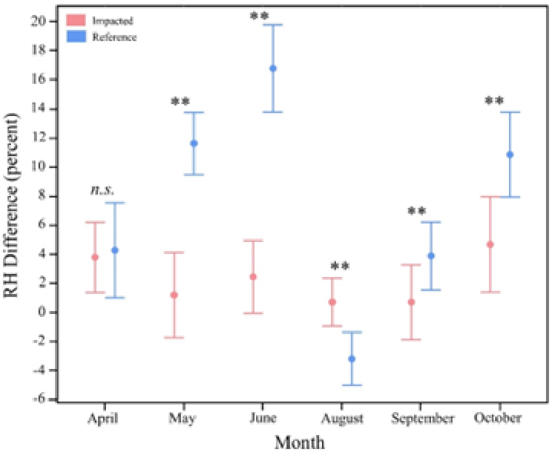

Figure 3. Comparison of relative humidity (RH) differences between crevice interiors and ambient conditions (mean ± 1 standard deviation) at rock crevices in impacted (red) and reference (blue) rock outcrops on Stone Mountain in Norton, Virginia, USA, in 2022. Labels denote significance levels of comparisons between impacted and reference crevices within each respective month (n.s. = no difference; ** $P < 0.01$).

Another limitation of this study is that it does not directly link altered microclimatic profiles in crevice refugia to Green Salamander declines. Although a significant difference in crevice temperature and moisture levels exists between impacted and reference outcrops, this study commenced after habitat manipulations had been performed at the study site, precluding the use of a full before-after control-impact (BACI) or similar design (Underwood 1992; Stewart and Bence 2001) that could have more directly examined changes in temperature, moisture, and salamander abundance over time. Plausible mechanisms exist, however, linking the findings of this study to Green Salamander declines at sites experiencing woody vegetation removal. As plethodontids, Green Salamanders and other crevice-dwelling taxa are constrained by both temperature and moisture extremes (Gordon and Smith 1949; Gordon 1952; Feder 1983), a factor that likely predisposes these species to seek refuge in crevices. Habitat modifications that significantly warm and dry the interior of these refugia may make them less suitable for salamanders. John et al. (2019), for example, found that body temperatures of Green Salamanders within crevice refugia are significantly cooler than ambient conditions, suggesting that crevices with larger temperature differentials relative to the surrounding environment are critical for the species.

Overall, the results of my study support previously stated speculative concerns about the potential for vegetation removal around rock outcrop habitat to alter the temperature and moisture regimes of refugia available to Green Salamanders. Although I did not directly examine the effectiveness of varying buffer widths, understory manipulations alone were enough to exert changes on the temperature and moisture levels of rock crevices, even when the canopy was left intact. These results underscore the need to generally protect vegetated buffers around rock outcrops serving as Green Salamander habitat. Within the context of the vegetation removal for rock-climbing activities that I examined, encouraging climbers and climbing advocacy groups to develop routes around existing vegetation rather than trimming vegetation back from outcrop surfaces is likely a key best management practice that can limit microclimatic impacts to rock outcrop substrate. As our understanding of the microclimatic dynamics of such rock outcrops and the physiological constraints of their resident fauna improves, incorporating temperature and moisture regimes into evaluations of varying buffer sizes will likely be paramount to appropriately design robust best management practices for these habitats.

Acknowledgments.—Katie Dunn, Hunter Hill, and Garrett Stiltner provided valuable assistance during field visits. Fred Ramey of the City of Norton provided access to the study site as part of an ongoing effort to survey Green Salamanders on lands under its management. Surveys for this project were performed under Virginia Department of Wildlife Resources Scientific Collecting Permit Number 2907603.

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Appendix Table. Temperature (T, °C) and relative humidity (RH, percent) values (mean ± 1 standard deviation) for crevice interiors and ambient conditions at impacted (n = 30) and reference (n = 30) crevices across monthly survey visits at a rock outcrop complex on Stone Mountain in Norton, Virginia, USA in 2022.

	Impacted				Reference			
Month	$T_{crevice}$	$T_{ambient}$	$RH_{crevice}$	$RH_{ambient}$	$T_{crevice}$	$T_{ambient}$	$RH_{crevice}$	$RH_{ambient}$
April	18.89 ± 0.34	19.24 ± 0.61	58.67 ± 6.03	54.93 ± 2.20	15.30 ± 0.77	16.73 ± 0.68	69.55 ± 3.44	65.26 ± 3.18
May	17.93 ± 0.55	18.06 ± 0.60	53.26 ± 3.18	52.04 ± 2.25	16.68 ± 0.33	17.32 ± 0.27	71.04 ± 4.48	59.4 ± 2.46
June	23.14 ± 0.48	23.77 ± 0.40	39.77 ± 2.34	37.37 ± 1.74	20.79 ± 0.61	22.20 ± 0.54	62.60 ± 8.81	45.6 ± 3.17
August	21.41 ± 0.58	21.45 ± 0.54	86.86 ± 3.55	86.28 ± 3.47	20.25 ± 0.26	20.53 ± 0.24	93.69 ± 0.96	94.88 ± 0.98
September	9.54 ± 0.63	9.28 ± 0.36	79.57 ± 3.29	78.86 ± 1.92	9.47 ± 0.18	9.41 ± 0.25	83.91 ± 2.28	80.01 ± 0.58
October	13.00 ± 0.93	13.07 ± 0.91	62.28 ± 4.15	57.66 ± 2.84	11.55 ± 0.39	12.33 ± 0.16	72.22 ± 4.38	61.22 ± 1.78