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# WITHIN-SITE MICROCLIMATE AND CONNECTIVITY CAN HELP PREDICT THE PRESENCE OF DISCRETE PATCH INHABITANTS, *ANEIDES AENEUS*

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*Abstract*.—**Many animal species inhabit environments where resources are patchily distributed. In circumstances where species' populations are restricted to exist in a patchy network within an otherwise inhospitable environment, assessments of within-habitat features can help determine habitat suitability for sites with unknown occupancy status. The Green Salamander (*Aneides aeneus*) is an example of a species with a patchy distribution that inhabits rock outcrops embedded within mountainous forest landscapes. Most studies on habitat suitability for Green Salamanders have been conducted on the macrohabitat (rock outcrops), neglecting the interaction between individuals and their immediate microhabitat (rock crevices). The small size and lungless nature of Green Salamanders limit movements, affecting behaviors such as foraging, predation evasion, and searching for mates. As a result of these constraints, we predicted crevices with features related to within-habitat connectivity (i.e., structural connectivity between microhabitats) are likely to be associated with Green Salamander presence. We evaluated features that contribute to microclimate and within-habitat connectivity, including crevice width (cm), length (cm), depth (cm), temperature (°C), crevice density (1/m$^2$), nearest crevice (cm), and nearest tree (m). We surveyed 424 crevices across five sites; we found salamanders occupying 116 of the crevices, but we did not find salamanders in 310 crevices, which we classified as available but unused microhabitats. A Global Logistic Regression Model identified crevice width, canopy cover, and crevice density as significant predictors of salamander presence. Understanding critical within-site features is as equally important for conservation management as the larger site-level criteria, especially for small animals with a patchy distribution.**

*Key Words.*—Generalized Linear Mixed Model; Green Salamander; metapopulation; microhabitat; South Carolina

## INTRODUCTION

For species that inhabit discrete patches of habitat on the landscape (e.g., wetlands, reefs, rock outcrops), the suitability of the habitat is typically assessed across the entire patch to provide conservation managers with spatially explicit suitability maps to guide protection or prioritization of habitats. For example, landscape-level indices for modeling habitat selection of organisms with patchy distributions have included minimum/maximum patch area (Chapin et al. 1998; Garabedian et al. 2017), patch connectivity (Nikolakaki 2004; Kindlmann and Burel 2008), landscape topography and vegetation coverage (Goldberg et al. 2004; Dustan et al. 2013; Newman et al. 2018), and prey availability (Lewis and Garrison 1984; Benoit-Bird et al. 2013). It is equally important, however, to assess the selection of microhabitats within discrete patches (i.e., third-order habitat *sensu* Johnson, 1980) because some threshold of suitable microhabitats must exist for the overall patch to be suitable. An understanding of the third-order selection of microhabitats provides insight into how ectothermic individuals address ecological needs, such as those related to temperature (Blouin-Demers and Weatherhead 2001; Hofmann and Fischer 2002) and humidity (Reagan 1974; Lunghi et al. 2015).

Species management decisions backed by an understanding of second-order (macrohabitat) selection and third-order (microhabitat) selection are likely the most effective. A habitat conservation approach across these spatial scales would not only account for population structure (e.g., locales of presence/absence) but also within-site patterns and dynamics (e.g., distribution and movement). Some terrestrial salamanders, for example, exhibit different ecological patterns across macro- and microhabitats because they exist in homogeneous, discrete patches throughout an otherwise heterogeneous landscape. The differences between these two scales of habitat are essential in allowing regional population persistence (i.e., by maintaining heterogeneity in the macrohabitat), and individual fitness (i.e., fitness met by acquiring resources in the microhabitat).

Compared to other species of salamanders in the Southeastern U.S., Green Salamanders (*Aneides aeneus*) inhabit a highly specialized niche of moist crevices in rocky outcrops found within mixed oak forests (Wake 1963; Corser 2001) and are one of the few arboreal salamanders in the region (Gordon 1952; Waldron and

Humphries 2005). Unsurprisingly for a species with a distinctly narrow habitat niche, Green Salamanders have a decreasing population trend and are globally ranked as Near Threatened (Hammerson 2004). To ensure clarity of our definitions of scale for this paper, we will hereby refer to second-order habitat as discrete rock outcrops and third-order habitat as the crevices within the rock. Previous habitat suitability studies for Green Salamanders have focused on identifying landscape features of rock outcrop locations that are presumed to influence the physiology of a species (Bruce 1968; Hafer and Sweeny 1993; Newman et al. 2018). Past studies have identified landscape characteristics associated with maintaining stable temperature and moisture as important for the species. For example, south-facing aspect and low elevation were found to be influential factors in both presence and abundance of Green Salamanders (Bruce 1968; Newman 2018). On a third-order microhabitat scale (i.e., rock crevices), resource preferences for Green Salamanders are thought to include features maintaining stable climates; thus, deep and narrow crevices with high humidity are commonly reported predictors of abundance for Green Salamanders (Gordon and Smith 1949; Rosell et al. 2009; Smith et al. 2017).

The current literature on habitat preferences of Green Salamanders has neglected the importance of connectivity within a habitat (specifically, within a rock outcrop). As a lungless salamander relying on cutaneous respiration, the metabolic capacity and oxygen consumption of Green Salamanders are limited to 20–40% of what a lunged salamander can sustain (Full 1986; Full et al. 1988). Additionally, the surface activity of plethodontid salamanders, including Green Salamanders, is largely limited to nights with either high humidity or rainy conditions (Feder 1983; Keen 1984). These limitations on movement directly affect salamander behaviors, including hunting capabilities, evading predators, and searching for mates. Because of this, we predict within-habitat connectivity for lungless salamanders to be central for survival. We hypothesized that increased within-habitat connectivity would increase the probability of Green Salamander presence, and features related to connectivity would rank among the most influential for Green Salamander occupancy. Specifically, we predicted the likelihood of finding a Green Salamander would increase with crevice density and decrease as the distance to the nearest crevice and nearest tree increased. We also predicted Green Salamander presence would decrease as crevice width and depth increases, and increase with higher canopy cover because these features may contribute to stabilizing the microclimate of the rock crevices (Table 1).

**Table 1**. Predicted (Pred) and modeled (Estimate) relationships between crevice use and features of the crevice for populations of Green Salamanders (*Aneides aeneus*) across five sites in Greenville, Oconee, and Pickens counties, South Carolina, USA. We expected the features crevice density, nearest crevice, and nearest tree to be the best predictive rock characteristics for salamander presence. Predictions (Pred) are listed as being either positively (+) or negatively (–) correlated with salamander presence. We had no *a priori* prediction for the effect of crevice length. Columns 3–5 are the results of the Global Logistic Regression Model where site was included as a random effect; crevice width, density, and canopy cover were the three features significantly (*) associated with salamander presence. The abbreviation SE = standard error.

| Features | Pred | Estimate | SE | *P*-value |
|---|---|---|---|---|
| Crevice width (cm) | – | -1.75 | 0.72 | 0.016* |
| Crevice length (cm) | X | -0.27 | 0.32 | 0.394 |
| Crevice depth (cm) | – | -0.90 | 0.56 | 0.111 |
| Canopy cover (%) | + | 1.62 | 0.67 | 0.016* |
| Crevice density (1/m$^2$) | + | 1.02 | 0.24 | < 0.001* |
| Distance to nearest crevice (cm) | – | 0.12 | 0.19 | 0.520 |
| Distance to nearest tree (m) | – | - 0.61 | 0.53 | 0.252 |

## Materials and Methods

***Study site***.—We surveyed microhabitat (rock crevice) feature composition across five sites from July 2018 through July 2019. We completed a minimum of six surveys for each site throughout the year, with no surveys conducted in the winter season. Each site was known to be occupied by Green Salamanders in the past, as they were identified from historical records. Surveys occurred across Oconee, Pickens, and Greenville counties, South Carolina, USA, between 0900–2000. Sites varied in size from 136–1,792 m$^2$ (mean ± standard deviation = 828 ± 759 m$^2$) and were in state parks, protected land owned by the South Carolina Department of Natural Resources, and private land. One site was directly parallel to a major roadway, and one site was adjacent to powerlines. All sites were within hardwood and pine forests, with species of Great Laurel (*Rhododendron maximum*) and Mountain Laurel (*Kalmia latifolia*) common in the understory.

***Field methods***.—At every site, we laid a field tape across the long axis of the outcrop. Along every 5 m of this axis, we generated a random number to determine where a perpendicular transect would be placed (Fig. 1). We assessed every crevice that the perpendicular transect crossed for crevice depth (cm), width (cm), length (cm), canopy cover (%), distance from the nearest tree (m), distance from the nearest crevice (cm), and crevice density within a 1 m$^2$ area (Fig. 2). We measured percentage canopy cover using a spherical crown densiometer (Forestry Suppliers Inc., Jackson, Mississippi, USA). We defined crevice length as the distance from one end of the crevice opening to the other and we measured the width at the widest part of the

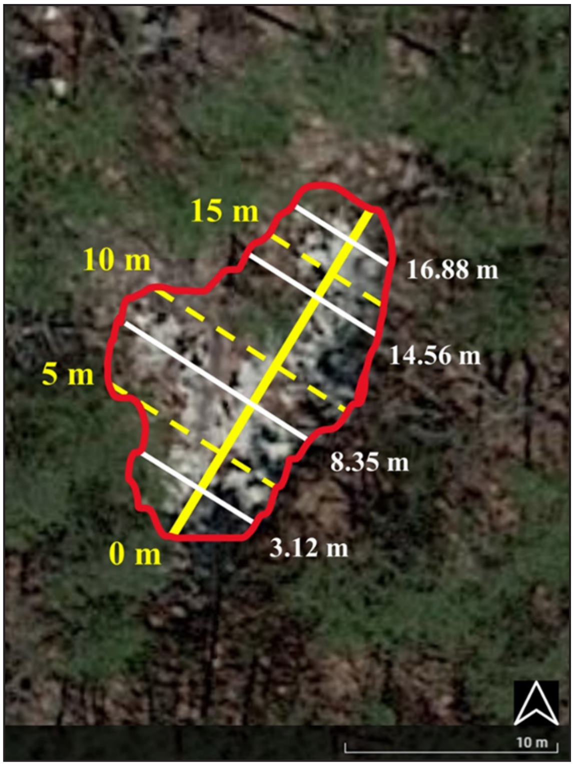

**Figure 1**. Each survey of Green Salamanders (*Aneides aeneus*) of rock outcrops in Greenville, Oconee, and Pickens counties, South Carolina, USA, began by first laying a field tape across the length of the outcrop (solid yellow line). This long axis was divided every 5 m (dashed yellow lines), and a random number generator was used to determine where a perpendicular transect (white lines) was laid within these 5 m segments. Every crevice crossed by these perpendicular transects was surveyed for salamander presence and assessed for crevice depth, width, length, humidity, distance from the nearest tree, distance from the nearest crevice, and crevice density.

crevice. We were unable to measure depth past 40 cm because most crevices are angled sharply beyond this distance. While assessing the microhabitat features, we actively searched for Green Salamanders in each crevice along each transect. When we found a salamander, we recorded the microhabitat feature data where we located the individual. We categorized crevices as used if a salamander was present or unused if no salamander was present. Instances of false unused categorizations may have occurred in deep (> 40 cm, n = 12 crevices) or jagged crevices where the entirety of the crevice was unable to be observed.

***Statistical analyses***.—We fit a binomial Generalized Linear Mixed Model using the glmer function in the lme4 package in R (R Core Team 2018) to conduct an exploratory analysis. This analysis allowed us to identify the significant microhabitat features associated with salamander presence. We tested crevice depth, width, length, canopy cover, distance from the nearest tree, distance from the nearest crevice, and crevice density for multicollinearity (correlation assigned at $|r| > 0.70$) before being added into the global model. We also performed a Multivariate Analysis of Variance (MANOVA) to determine if any of the crevice features varied by site. We centered all predictor variables to a mean of 0 and scaled them to 1 standard deviation prior to analysis. We used coefficient estimates to calculate odds ratios (95% Confidence Intervals) for the significant variables included in the global model.

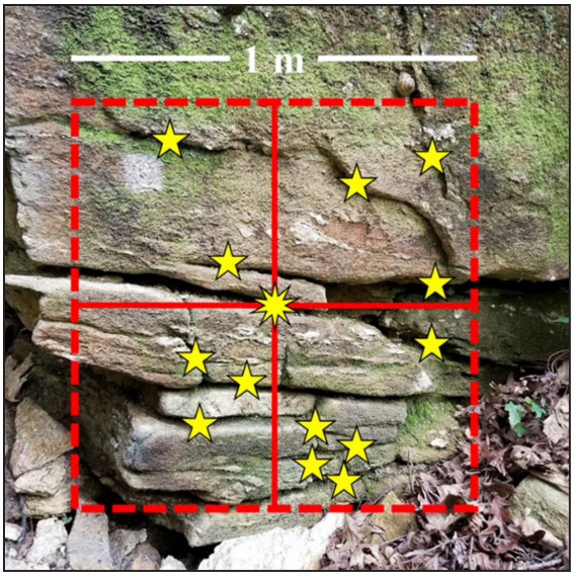

**Figure 2**. Crevice density surrounding the crevice of interest (ten-point center star) of Green Salamanders (*Aneides aeneus*) was calculated by identifying the point within the crevice of interest that is surrounded by the most crevices. A 1-m$^2$ area was measured around this point and every crevice that fell within this designated space was counted (shown as individual stars), including the crevice of interest.

## Results

We surveyed 426 crevices across five sites. We found salamanders occupying 116 of these crevices, and the remaining 310 were classified as available but unoccupied habitat (Table 2). No combination of any two variables was strongly correlated (all $r$ among all pairwise tests < 0.60), and crevice morphologies varied by site ($F_{45,1480} = 11.65$, $P < 0.001$; Table 3), so we included site as a random effect in the Generalized Linear Mixed Model to account for the shared variance between crevice features within the same rock outcrop.

Crevice width, canopy cover, and crevice density were significant features in predicting salamander presence (Table 1; Figs. 3 and 4). Crevice width was negatively associated with the probability of salamander presence. The average crevice width of the occupied crevices was 1.4 cm (± 1.6 standard error). The probability of presence increased with canopy cover and crevice density. The average canopy coverage for occupied

**Table 2**. Mean ± standard deviation of crevice features that were both occupied and unoccupied by Green Salamanders (*Aneides aeneus*) across five sites (rock outcrops) in Greenville, Oconee, and Pickens counties, South Carolina, USA.

| Crevice Feature | Occupied | Unoccupied |
|---|---|---|
| Crevice width (cm) | 1.4 ± 1.6 | 3.9 ± 5.5 |
| Crevice length (cm) | 24.0 ± 21.9 | 53.2 ± 63.9 |
| Crevice depth (cm) | 3.8 ± 4.4 | 11.8 ± 16.2 |
| Canopy cover (%) | 99.0 ± 4.4 | 95.5 ± 9.5 |
| Crevice density (1/m$^2$) | 8.0 ± 4.9 | 5.2 ± 3.2 |
| Distance to nearest crevice (cm) | 12.0 ± 22.1 | 18.3 ± 27.9 |
| Distance to nearest tree (m) | 3.7 ± 3.9 | 3.6 ± 3.9 |

crevices was 99% (± 4.4). The average crevice density surrounding occupied crevices was 8.0 crevices per m$^2$ (± 4.9). There was an overall increase in the predicted probability of salamander presence as crevice density increased, and at a density of more than seven crevices per m$^2$, the rate of change in the probability of a Green Salamander being present increased by approximately 7% with every additional 2.56 crevices.

## Discussion

As we predicted, the probability of finding a Green Salamander in a crevice decreased with an increase in crevice width, and the probability increased in crevices with increasing canopy cover, and with an increase in crevice density. Narrow-width crevices and a high canopy cover are often considered necessary components of habitat for Green Salamanders (Bruce 1968; Smith et al. 2017), presumably because these features minimize water loss. Canopy cover shades crevices and thereby prevents large temperature fluctuations from change in sunlight intensity. Furthermore, narrow crevices likely maintain a moist environment that aids in cutaneous respiration. Although high canopy cover promotes site-level occupancy (Smith et al. 2017), our results show the importance of canopy cover at individual crevices. The average percentage of canopy cover above unoccupied crevices was 95%, and the average coverage over occupied crevices was 99%. This distinction illustrates that near-complete shade is an important microhabitat feature for crevice use by Green Salamanders.

Crevice depth as a predictor for the presence of Green Salamanders has had mixed results in the past, being highly ranked as a predictor of salamander occupancy by Smith et al. (2017), but not significant by Rossell et al. (2009). Our results complement the latter, but the possibility of false absences of salamanders in deep crevices increases because of the difficulty of seeing past 40 cm and around angles within a crevice.

**Table 3**. Multivariate Analysis of Variance (MANOVA) results indicating how crevice features differ across the five sites we visited of Green Salamanders (*Aneides aeneus*) in Greenville, Oconee, and Pickens counties, South Carolina, USA. We expected the features crevice density, nearest crevice, and nearest tree to be the best predictive rock characteristics for salamander presence. Canopy cover, crevice density, distance to nearest crevice, and distance to nearest tree differed significantly between sites. The abbreviation df = degrees of freedom.

| | MANOVA | | |
|---|---|---|---|
| Features | df | *F*-value | *P*-value |
| Crevice width (cm) | 5 | 1.631 | 0.148 |
| Crevice length (cm) | 5 | 0.382 | 0.861 |
| Crevice depth (cm) | 5 | 0.555 | 0.749 |
| Canopy cover (%) | 5 | 3.056 | 0.010* |
| Crevice density (1/m$^2$) | 5 | 10.38 | < 0.001* |
| Distance to nearest crevice (cm) | 5 | 2.353 | 0.042* |
| Distance to nearest tree (m) | 5 | 299.9 | < 0.001* |

Crevice density has a positive correlation with the probability of presence of Green Salamanders and is one of the three features (crevice density, distance to nearest crevice, and distance to nearest tree) we tested related to within-site connectivity. Of these connectivity-related features, high crevice density indicates multidirectional connectivity and a potential increase in nearby suitable microhabitats. In contrast, distance to nearest crevice and distance to nearest tree measures a linear connection between only two potential microhabitats. A high density of crevices within a square meter provides a network of potentially suitable microhabitats and reduces the cost of movement between crevices. Our data show a positive relationship between use and crevice density, and there is an increase in slope beyond approximately seven crevices per m$^2$. This threshold could offer a tool for managers evaluating site-level suitability. Having high crevice density within a habitat is important because Green Salamanders are lungless and are, therefore, unable to sustain long continuous movements (Full et al. 1988). Higher densities of suitable habitat also allow for more efficient foraging, predation evasion, and mate searching (Abrahams and Dill 1989; Pitt 1999; Stephens 2008).

Our results also indicate that aspects of within-site features are essential in determining site-level suitability for Green Salamanders. Canopy cover and all within-site connectivity features (crevice density, distance to nearest crevice, and distance to nearest tree) vary significantly between sites. Understanding within-site features that are important for habitat selection is equally pragmatic for conservation management as identifying site-level features. Habitat suitability has often been described as a function of aggregate features

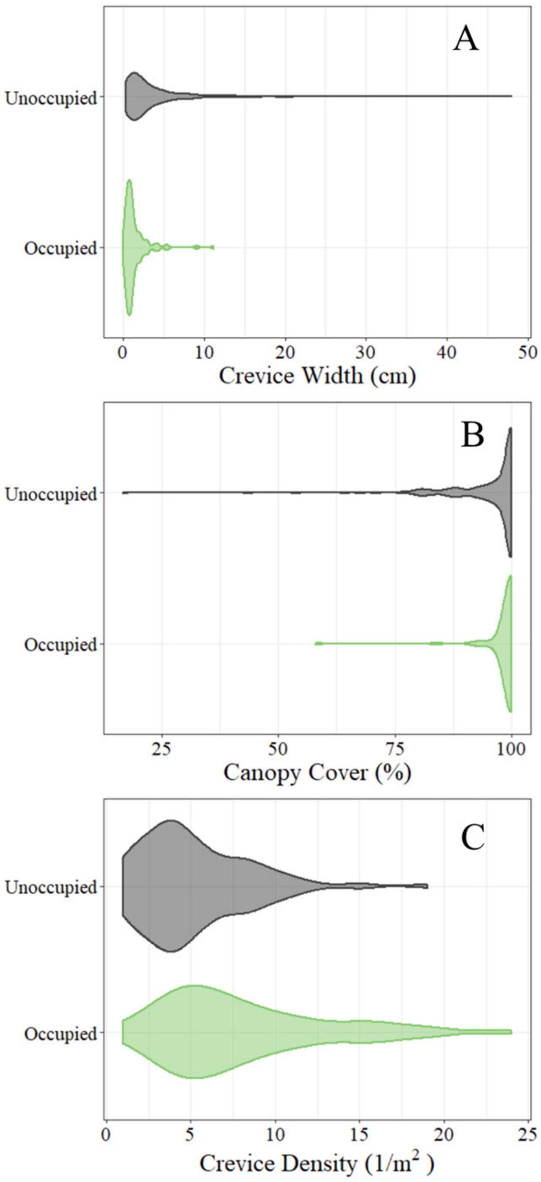

**Figure 3**. Violin plots of (A) crevice width, (B) canopy cover, and (C) crevice density for the significant ($\alpha = 0.05$) features in crevices unoccupied (grey) and occupied (green) by Green Salamanders (*Aneides aeneus*) in Greenville, Oconee, and Pickens counties, South Carolina, USA.

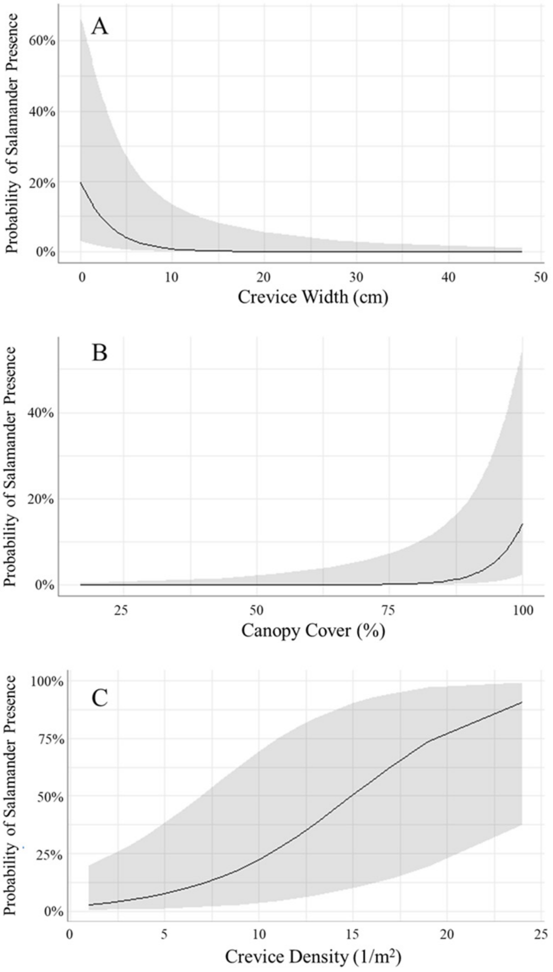

**Figure 4**. Odds ratio curves for probability of presence of Green Salamanders (*Aneides aeneus*) in relationship to (A) crevice width, (B) canopy cover, and (C) crevice density with the respective confidence intervals (gray shading).

(i.e., temperature, humidity, nutrient levels, hydroperiod, etc.; e.g., Newman et al. 2018); however, for smaller organisms, considering small-scale, patchy resources may be equally helpful when determining the suitability of potential habitat (Gade and Peterman 2019). For example, Bog Turtles (*Glyptemys muhlenbergii*) require not only a hydrologically suitable wetland, but hummocks for nesting within the site (Zappalorti et al. 2015), and Hairy Woodpeckers (*Picoides villosus*) are cavity-nesters that select habitat based on snag density (Zarnowitz and Manuwal 1985). For Green Salamanders, conservation management practices should not only focus on macrohabitat features (e.g., rock outcrop size, aspect, and elevation), but also the microhabitat features associated with refugia, nesting, and foraging. Based on our results, we propose management priorities should be given to Green Salamander habitats with thinner crevice widths (< 3 cm), very high canopy cover at sites (> 95%), and sites with high crevice density (at least seven crevices per m$^2$). If rock outcrops that meet the landscape level features preferred by Green Salamanders do not also contain these within-site features, it is possible the outcrop as a whole may not be suitable for the species.

We encourage future research on species inhabiting discrete patches to evaluate microhabitat features that could shed light on species behavior and site-level selection. Variations in microhabitat composition between sites could indicate discrepancies in site-level habitat suitability and the resulting population abundances across sites. Explicitly evaluating how the selection of microhabitat components (third-order habitat selection) influences population persistence and population growth within selected sites (second-order habitat selection) will likely benefit the conservation of patchily distributed species and identifying the threshold of microhabitat features required for an overall site to be suitable could guide how sites are prioritized within broader wildlife management efforts.

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**Kyle Barrett** is an Associate Professor of Wildlife Conservation and Ecology in the Department of Forestry and Environmental Conservation at Clemson University, South Carolina, USA. He received his Bachelor of Science in Biology from Middle Tennessee State University in Murfreesboro, Tennessee, USA, and his Master of Science in Biology from Missouri State University in Springfield, Missouri, USA. He received his Ph.D. in Biology from Auburn University, Auburn, Alabama, USA. Kyle worked as a Postdoctoral Research Fellow at the University of Georgia, Athens, USA, for 3 y and began work at Clemson University in 2012. Kyle studies how large-scale stressors such as land use and climate change influence the distribution and abundance of species. (Photographed by David Hutto, Jr.).