Variation in Seasonal Detection Probability and Site Abundance of Populations of *Aneides aeneus* and *A. caryaensis* in North Carolina, USA

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Abstract.—**Population estimates help detect trends over time and evaluate management responses; however, rare or cryptic animals can be difficult to detect, causing estimates to be lower than their true state. Animals can also change behavior and habitat use seasonally or due to local climatic factors, affecting survey results. Repeated surveys help account for imperfect detection and obtain more accurate population estimates by reducing the chance of failing to detect animals. In North Carolina, USA, during 2016 and 2017, we used N-mixture modeling, a repeated survey technique, to model abundance and detection of Green Salamanders (*Aneides aeneus*) and Hickory Nut Gorge Green Salamanders (*A. caryaensis*). We surveyed 57 rock outcrop sites with a history of species occurrence, three times per season (spring, summer, and fall; total n = 854). We examined effects of season and microclimate conditions on detection probability and effects of site characteristics on abundance. Modeling each year separately, season was the most influential variable to explain detection probability with highest detection in the fall (2016: 0.29, 2017:0.40), followed by spring (2016: 0.23, 2017: 0.26) and then summer (2016: 0.06, 2017: 0.19). Reproductive history, rock area, and aspect were the most important factors explaining variation in abundance. Sites with a history of reproduction, particularly those larger in size and more west facing, had a higher mean number of salamanders (2016: 8.43, 2017: 8.00) than non-nest sites (2016: 1.48, 2017: 1.41). For population trend monitoring of these species, we suggest managers use N-mixture models and surveying 31–60 sites three times each in the fall.**

Key Words.—amphibians; conservation; hierarchical model; Green Salamander; N-mixture; rock outcrop

Introduction

A fundamental goal of wildlife managers is to accurately assess population trends to implement and evaluate the effects of management actions, but many factors make these seemingly simple tasks very complex. One factor is that animals may be difficult to detect, leading to false absences during surveys and underestimations of their abundances at various locations (Kéry and Royle 2015). Many species exhibit seasonal variation in their behaviors (Begon et al. 2006), which may make individuals of these species easier, or more difficult, to detect in different seasons (Hyde and Simons 2001; Kéry and Royle 2015). Small vertebrates, such as terrestrial salamanders, typically exhibit seasonal variation in their behaviors and use different habitats during different stages of their life (e.g., hatchling, juvenile, and adult stages) and annual cycles (e.g., breeding and overwintering; Dodd 2010; Lunghi et al. 2015; Ficetola et al. 2018a). Therefore, accounting for variation in seasonal detectability is especially important when monitoring trends in populations of salamanders (O'Donnell and Semlitsch 2015). Hierarchical models enable researchers to address imperfect detection and make management decisions based on more accurate population data (Kéry and Royle 2015).

Two commonly used hierarchical models, occupancy models (MacKenzie et al. 2003, 2017) and N-mixture models (Royle 2004), are well suited to the challenges inherent in surveying nocturnal, cryptic, and, therefore, hard-to-detect salamanders that use a variety of habitats (Bailey et al. 2004; Bendik et al. 2016; Lamb et al. 2017; Baecher and Richter 2018; Ficetola et al. 2018a). Occupancy models use presence/absence data to model occurrence, whereas N-mixture models use census data to model abundance. Both models, however, account for detection probability, which refers to the joint probability of an individual being available for sampling and also detectable by the observer (Kéry and Royle 2015). Abundance estimates allow managers to assess population trends and detect declines before local extinctions occur, allowing for quicker responses to potential threats and providing a more detailed view on the effects of management actions (Kéry and Royle 2015). N-mixture models are comparable to mark-recapture models but lack marking techniques that can be invasive (Ficetola et al. 2018a; but also see Barker et al. 2018; Knape et al. 2018; Kéry 2018).

Figure 1. Adult Green Salamander (*Aneides aeneus*) *in situ* in rock outcrop habitat from the Blue Ridge Escarpment population in North Carolina, USA. (Photographed by Alan D. Cameron).

The Green Salamander (*Aneides aeneus*; Fig. 1) and the recently described, North Carolina endemic, Hickory Nut Gorge Green Salamander (*A. caryaensis*; Patton et al. 2019) are rare, state-listed species in need of accurate abundance estimates, but each species has inherently low detection probability. For convenience, we use Green Salamanders to refer to both species, except where noted. Green Salamanders are habitat specialists that primarily dwell in shaded rock outcrops or cliff faces, and they are found typically in mixed mesophytic forests, where suitable rock crevices are humid to moist (but not inundated with water), and free of plants, soil, or other debris (Gordon and Smith 1949; Gordon 1952; Pauley and Watson 2005). The range of these plethodontid salamanders includes the southern Appalachians mountains (Alabama, Mississippi, South Carolina, Georgia, North Carolina, Tennessee) through the central and northern Appalachians (Virginia, Kentucky, West Virginia, Maryland, Pennsylvania) of the U.S. Disjunct or isolated populations occur in the upper Midwest (Ohio, Indiana) and in several states throughout the range (Petranka 1998; Green et al. 2014). In North Carolina, Green Salamanders are distributed in two disjunct areas, the Hickory Nut Gorge of Buncombe, Henderson, Polk, and Rutherford counties, and the Blue Ridge Escarpment of Henderson, Transylvania, Jackson, and Macon counties (Bruce 1968; Wilson 2001; Beane et al. 2010).

Green Salamanders are difficult to detect in field surveys because they often occupy deep or hidden rock crevices that are inaccessible to people. Equipped with a flattened, slender body and square toe tips, Green Salamanders are excellent climbers, and in addition to their primary habitats of cool, shaded, humid rock crevices, they often inhabit woody shrubs or trees (Waldron and Humphries 2005; Miloski 2010; Thigpen et al. 2010) and other natural or artificial structures in their environment (Wilson 2003; Smith et al. 2018) for shelter, foraging, and dispersal. These habitats can provide additional challenges to surveyors as they often

are difficult to access and search thoroughly. A yellow-to-green lichen pattern on the dark body of each species of Green Salamander provides excellent camouflage and further increases the difficulty of observation (Petranka 1998). Green Salamanders are relatively slow growing, long-lived species (> 10 y) (Pauley and Watson 2005; Waldron and Pauley 2007) that seek suitable rock crevices and surrounding woody stems while nesting, overwintering, and dispersing across a forested landscape (Gordon 1952; Cupp 1991; Rossell et al. 2009; Smith et al. 2017; Rossell et al. 2019).

Reported population declines (from low relative abundance and fewer occupied sites) in the 1970s–1990s in North Carolina and regionally, caused heightened awareness of conservation needs and threats to Green Salamanders and their habitats (Corser 2001). Given the conservation concerns, documented population declines, and pending range-wide status assessment for Green Salamanders, it is vital to have comparable, long-term monitoring data among states and within regions, which hierarchical modeling can provide. Our study is the first for North Carolina and any state to assess Green Salamander populations stratified across an entire state distribution in multiple seasons. The goal of our project was to model and report seasonal variation in Green Salamander detection probabilities, estimate mean site abundance, and examine survey and site covariates at historically occupied rock outcrop sites across the range of both *A. aeneus* and *A. caryaensis* in North Carolina. In doing so, we have provided the framework to establish a long-term population monitoring methodology for the state that could also be applied regionally to aid in Green Salamander conservation and status assessments.

Materials and Methods

Field methods.—In 2016 and 2017 we monitored individually delineated, known rock outcrop sites (n = 57) with a history of occurrence for Green Salamanders; site locations are withheld due to conservation concerns and are on file with the North Carolina Wildlife Resources Commission. To maximize our sample size, we chose sites that were occupied at any time in the past and feasible to access repeatedly within time and resource constraints. Study sites were stratified across three spatial areas in western North Carolina, USA: the disjunct Hickory Nut Gorge (HNG) encompassing the range of the newly described *A. caryaensis* (Patton et al. 2019), the DuPont State Recreational Forest (DSRF), and the Blue Ridge Escarpment (BRE) outside and primarily west of the DSRF (Fig. 2). Although > 7,700 ha in size, the DSRF is a small part of the BRE but is the area with the highest density of documented *A. aeneus* sites, warranting separate consideration from the rest of the BRE (Rossell et al. 2019). All sites combined,
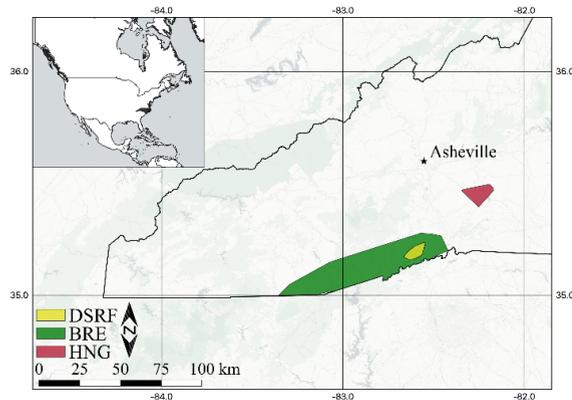
Figure 2. Geographic areas and metapopulations of Green Salamanders (*Aneides aeneus*) and Hickory Nut Gorge Green Salamanders (*A. caryaensis*) in western North Carolina, USA, used to examine seasonal detection probability and estimate abundance, 2016–2017. Area abbreviations are DuPont State Recreational Forest (DSRF), Hickory Nut Gorge (HNG), and Blue Ridge Escarpment (BRE).

across the three spatial areas, represented all aspects, were predominantly in mixed mesophytic oak (*Quercus* spp.), hardwood, and pine (*Pinus* spp.) forests, often with an ericaceous understory of Rosebay Rhododendron (*Rhododendron maximum*) and Mountain Laurel (*Kalmia latifolia*), and were within an elevational range of 416–1,019 m.

To account for site independence, we used R version 3.5.1 (R Development Core Team 2018) spatstat package version 1.61-0 (Baddeley et al. 2015) and function nndist to calculate straight-line distances between study sites (i.e., rock outcrops) that were closest to each other; mean (± one standard deviation [SD]) and ranges of distances between sites per spatial area were the following: 820.9 m (± 1,537.4; 12.4–3,911.5) for the HNG, 234.7 m (± 205.5; 77.6–771.3) for the DSRF, and 2,251.0 m (± 1,907.9; 11.3–5,022.4) for the BRE. Reported daily movements vary for Green Salamanders, with a mean distance (± one standard error [SE]) of 4.98 m (± 0.56; John 2017) and a mean distance (± SD) of 2.51 m (± 0.46; Moloski 2010), with occasional longer movements reported (Gordon 1952; Smith et al. 2018). We chose a minimum of 10 m between sites to establish independence with most sites (n = 38) separated by ≥ 100 m.

We surveyed sites in the daytime across three distinct time frames to represent seasons in an annual life cycle of Green Salamanders: spring (early-April to early-June) to represent post-hibernation emergence, dispersal, and congregation for mating; summer (late-July to early-September) to represent nesting and egg brooding, and fall (early-October to late-November) to represent a time when hatchlings are present and salamanders are congregating to prepare for overwintering (Gordon 1952; Snyder 1971; Cupp 1991). Although Green

Salamanders may be active, and thus visible, at night (Juterbock 2013), we were not able to conduct nighttime surveys because of time and resource limitations, and logistical challenges or safety concerns at some sites. Finally, we classified sites as nesting or non-nesting based on historical data and surveys in recent years. We classified a rock outcrop as a nesting site if any evidence of Green Salamander nesting was available, including documentation of any of the following: gravid females ovipositing an egg clutch, a brooding female, remnant egg material, or hatchlings in or near brood chambers.

To conduct salamander surveys, one person with extensive experience in searching for Green Salamanders (five to more than 15 y) typically made three visits (in rare instances, only two because of time constraints) to each site in each season to document species presence and record microclimate data known to be important for Green Salamander microhabitat, including air temperature and relative humidity (Gordon 1952; Snyder 1971, 1991; Hafer 1992; John 2017). After noting the date (Julian date) and start time, surveyors used a compact LED flashlight to illuminate and survey accessible rock crevices, rock outcrop surfaces, and woody shrubs and trees growing on or adjacent to rock outcrops (Waldron and Humphries 2005; Rossell et al. 2009; Smith et al. 2017). Arboreal searches consisted of visually scanning with the naked eye shrubs and tree trunks growing on rock outcrops and adjacent to rock outcrops within an approximate distance of 2–3 m. We searched tree trunks as high as we could see without an obscured view (approximately 2–3 m high) and used flashlights to peer into knotholes or other stem cavities, under contact points against rock surfaces, and under loose bark.

We counted all Green Salamanders observed, noting age class if clearly obvious based on surveyor experience. We classified salamanders into the following age classes: hatchlings, yearlings, and all other ages > 1 y old (older juveniles and adults). We identified hatchlings in fall based on their size (20–25 mm total length) and behavior of clustering in brood chambers or exploring the rock surface and moss layers during the day. Yearlings included those young emerging in the spring as hatchlings of the previous fall and were easily identified because their size did not change dramatically over their first winter. We combined and classified yearlings found in spring, summer, or the subsequent fall (approximate age of 6 mo–1 y) as such, and they simply presented as slightly larger hatchlings in their first full year. Therefore, we reserved use of the term hatchling to refer only to those newly hatched young of the year in the fall season (approximate age of 1–3 mo).

For microclimate variables, we used an Extech HD500® psychrometer with infrared thermometer

(FLIR Commercial Systems, Inc., Nashua, New Hampshire, USA) to record a single relative humidity (%) and ambient air temperature (ºC) at each rock outcrop site, during each survey (Rossell et al. 2019). We held the temperature and humidity probe approximately chest-high and within approximately 30 cm of the rock surface to measure microclimate conditions. We also recorded data associated with weather events. For HNG and BRE sites, we derived the number of days since measurable rain occurred by using data from the weather station closest to study areas that had National Weather Service archived data (e.g., cities of Asheville and Franklin, North Carolina). Although located in low-elevation river valleys compared to surrounding uplands where most Green Salamander sites occur, these weather stations provided the best available data. A permanent weather station on-site at DSRF provided archived data for that area.

We revisited all sites in this study during 2019 to collect additional site covariates that would not have changed, or changed minimally, in the 18 mo since we ended salamander surveys. On the downslope side and in the center of each rock outcrop, we measured a linear distance outward of 5 m. We flagged that point as the center of a circular plot, then measured and flagged a 5-m radius around it, with the nearest arc of the circle intersecting with the rock in multiple points of contact, depending on the shape and size of the rock. To characterize the maturity and density of surrounding forest at each site, within the plot we counted all woody stems with a diameter at breast height (DBH) ≥ 8 cm. Using a DBH tape, we measured diameter of each counted stem to obtain an average DBH for the plot. To estimate approximate area of rock faces (m^2), we used a 1-m measuring stick for reference, positioned it vertically on the downslope side in the center of the rock, and took a high-resolution, digital photograph of the site and the meter stick. We analyzed the photographs with ImageJ software (Version 1.51) to obtain an approximate length and height of rock faces to calculate rock area (Rasband, W.S. 2018. ImageJ. U.S. National Institutes of Health, Bethesda, Maryland, USA. Available from https://imagej.nih.gov/ij/. [Accessed 15 July 2019]). Finally, as an indication of site complexity and available microhabitat, we categorized suitable, available crevices for each rock outcrop (Rossell et al. 2009; 2019) into abundance classes as follows: 1, 2–4, 5–7, 8–10, and >10.

Additional site covariates were derived from a GIS using QGIS version 3.8.1 (QGIS Development Team. 2019. QGIS geographic information system. Open Source Geospatial Foundation, Beaverton, Oregon, USA. Available from http://qgis.org. [Accessed 15 July 2019]), such as elevation (m) and aspect from a digital elevation model (DEM). For aspect, we converted DEM data into a measure of eastness and northness by first converting the degrees into radians (rad = π * degrees / 180) and then using sin(aspect) for eastness and cos(aspect) for northness. For each site and a 30-m buffer around it, we used a Cartographic Tree Canopy Cover (TCC) layer (https://data.fs.usda.gov/geodata/rastergateway/treecanopycover/#table1, 2016 Edition) to derive mean percent canopy cover and the LANDFIRE Existing Vegetation Height dataset with Canopy Height layer (http://landfire.gov/evh.php, 2016 Edition) to obtain mean canopy height; both datasets have a 30-m resolution.

Statistical methods.—To better understand potential interannual differences in detection, we tested for differences in air temperature between years, and we used Welch two sample *t*-tests. We checked normality assumptions for all observation, or survey, covariates. In two observation covariates the normality assumption was violated: relative humidity (Air RH) and the number of days since the last rain event (Days Dry). For those non-normal observation covariates, we used non-parametric Wilcoxon rank-sum tests. To test for multicollinearity, we used variance inflation factor (VIF) with a cutoff value of three and made a generalized linear model with a Poisson distribution relating all the detection covariates to our counts. We considered variables to be multicollinear if the global VIF was > 3 (Zurr et al. 2010), and we implemented the test in the car package, version 3.0-5, in R (R Development Core Team 2018). We calculated data summary statistics in R (R Development Core Team 2018).

To account for heterogeneity in detection of Green Salamanders, we used N-mixture models (Royle 2004). N-mixture models use spatially replicated counts to model abundance in populations where detection probability is less than one (O'Donnell and Semlitsch 2015). To ensure accurate abundance estimates, we tested for goodness-of-fit and overdispersion (Knape et al. 2018). We used a global model to test for potential overdispersion (Kéry and Royle 2015). Both years showed minor overdispersion (chat = 1.63, 2016; chat = 1.39, 2017); consequently, we ranked abundance models by quasi-Akaike information criterion with a correction for small sample sizes (QAICc; Burnham and Anderson 2004; Kéry and Royle 2015). We tested Poisson, zero inflated Poisson, and negative binomial distributions. The negative binomial model was the best performing model using QAIC; however, the estimates were unstable when we adjusted the tuning parameter *K,* and abundance estimates were inflated (Kéry and Royle 2015; Kéry 2018). The Poisson distribution was the second-best fitting distribution; consequently, we used it rather than a negative binomial distribution. Because Royle N-mixture models have a closed population

assumption, we excluded fall hatchlings from analyses.

We included temporal, spatial, microclimate, habitat, forest-stand level, and landscape-level covariates for their potential effect on detection probability or site abundance (Appendix). We modeled each year separately and chose 18 *a priori* models (Supplemental Information Tables S1 and S2) to test effects of the above factors on detection probability in Green Salamanders. For abundance modeling, we took the best performing detection probability model and tested site covariates that could affect abundance in 24 candidate models (Supplemental Information Tables S3 and S4). We then reported the best performing model based on QAICc score.

For both detection probability and abundance models, if there was not strong support for a single top model (QAICc weight < 0.80), we averaged models until we reached a cumulative model weight of 0.80 QAICc. We implemented N-mixture models in R (R Development Core Team 2018) using package unmarked, version 0.13-0 (Fiske et al. 2017), and function pcount. We used package ggplot2, version 3.2.1 (Wickham 2016), to create all plots and tested goodness-of-fit metrics and overdispersion, and we performed model averaging using packages nmixgof, version 0.1.0 (Knape et al. 2018), AHMbook, version 0.1.4 (Kéry and Royle 2015), and AICcmodavg, version 2.2-2 (Mazerolle 2019). We used an alpha level of 0.05 for all statistical tests.

RESULTS

We surveyed 57 unique, historical rock outcrop sites nine times per year during 2016 and 2017, across three seasons (three times per season), for a total of 854 visits (405 at 45 sites in 2016 and 449 at 56 sites in 2017; we were not able to complete 55 surveys in 2017 due to logistical constraints). Surveyors conducted only daytime sampling with start times (i.e., time of day) ranging from 0726–1707. We observed at least one Green Salamander at 44 of the 57 sites (77.2%), but we found none on trees or surrounding woody stems. The maximum number of individuals we found in any single survey was 17, including fall hatchlings, or 13, excluding hatchlings. In those 854 surveys, 287 (33.6%) were successful with at least one Green Salamander observed (137 in 2016 and 150 in 2017). We found 10 or more non-hatchling Green Salamanders in six surveys at two sites. We recorded 694 observations of Green Salamanders (350 in 2016 and 344 in 2017), some of which (e.g., brooding females) were likely observed on repeat visits. Most sites, surveys, and Green Salamanders observed were in DSRF (Table 1). Excluding hatchlings, the number of salamanders observed per visit was highest in the fall of both years; 2016: (mean ± SE): spring (0.86 ± 0.13), summer (0.29 ± 0.05), fall (1.06 ± 0.19); and
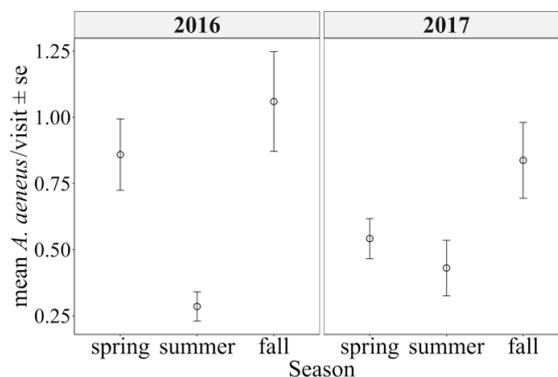

FIGURE 3. Mean number of observations of Green Salamanders (*Aneides aeneus*) and Hickory Nut Gorge Green Salamanders (*A. caryaensis*) per visit, per season, 2016–2017, in North Carolina, USA. Vertical bars represent the standard error.

2017: spring (0.54 ± 0.08), summer (0.43 ± 0.10), fall (0.84 ± 0.14; Fig. 3). Spring emergence, thus overwinter survivorship, of yearlings was highest in DSRF (Table 1). At 16 historical nest sites in 2016, we documented 14 Green Salamander nests, five of which failed, for a hatch success rate of 63%. We deemed a nest successful if we observed the presence of at least one hatchling, directly observed hatching in progress, or found fresh remnants of hatched eggs in late summer (Snyder 1971; Rossell et al. 2019). Hatch success increased in 2017 to 13 of 17 nests (76%) at 17 historical nest sites.

Summarizing the categorical site covariate for the number of suitable rock crevices, we found the following percent frequencies, all sites pooled: 1 crevice (10.53%), 2–4 crevices (21.05%), 5–7 crevices (19.30%), 8–10 crevices (17.54%), and > 10 crevices (31.58%). Aspect and other continuous site covariates are summarized in Supplemental Information Table S5. Western North Carolina experienced a moderate drought in late spring 2016 and an extreme to exceptional drought in fall of 2016 (North Carolina Drought Management Advisory Council. 2019. Drought monitor archive. Available from

TABLE 1. Count of number of Green Salamanders (*Aneides aeneus*) and Hickory Nut Gorge Green Salamanders (*Aneides caryaensis*) observed seasonally in North Carolina, USA, by spatial area and estimated age class of animals *in situ* and/or in hand, 2016–2017. Abbreviations are NA = not applicable (hatchlings were only possible in fall seasons), HNG = Hickory Nut Gorge, DSRF = DuPont State Recreational Forest, BRE = Blue Ridge Escarpment outside of DSRF, Sp = spring, and Su = summer. Hatchlings are young of the year from fall, Yearlings are 6 mo to 1 y, and Adults (and older juveniles) are > 1 y old.

| | Hatchlings | | | Yearlings | | | Adults | | |
Area	Sp	Su	Fall	Sp	Su	Fall	Sp	Su	Fall
HNG	—	—	12	0	0	0	12	0	0
DSRF	—	—	74	20	3	1	115	63	157
BRE	—	—	23	5	1	4	49	31	114

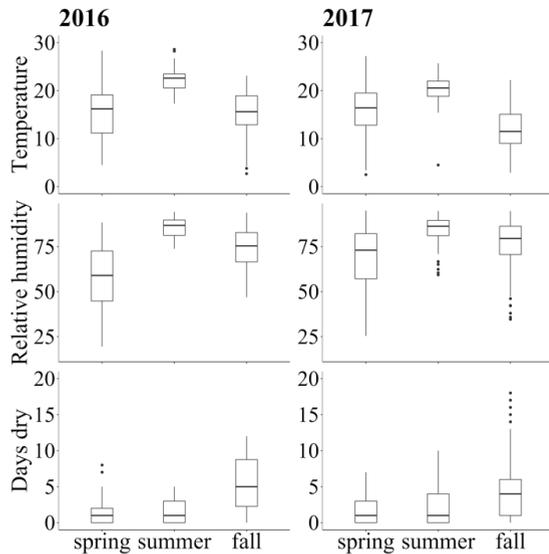**FIGURE 4.** Box plots of relative humidity (%), temperature (°C), and number of days since rain (Days dry) used as survey covariates included in detection probability models of Green Salamanders (*Aneides aeneus*) and Hickory Nut Gorge Green Salamanders (*A. caryaensis*), 2016–2017, in North Carolina, USA.

FIGURE 5. Detection probabilities (*p*) in relation to air temperature (°C), relative humidity (%), and season, 2016–2017, for Green Salamanders (*Aneides aeneus*) and Hickory Nut Gorge Green Salamanders (*A. caryaensis*) in North Carolina, USA. Gray shading represents the 95% confidence interval.

http://www.ncdrought.org/map-archives [Accessed 23 January 2019]). Air temperature (mean ± SD) in 2016 at rock outcrops (17.54° C ± 5.32) was significantly warmer than in 2017 (15.87° C ± 5.46; *t* = 4.49, df = 826.6, *P* < 0.001). Similarly, relative humidity (mean ± SD) in 2016 at rock outcrops (72.30% ± 16.38) was significantly less than in 2017 (76.72% ± 14.60; *W* = 72,269, *P* < 0.001); however, we found the number of actual days (mean ± SD) since rainfall in 2016 (2.88 d ± 3.30) did not differ significantly from 2017 (3.13 d ± 4.18; *W* = 87,010, *P* = 0.927).

We found no evidence of multicollinearity in detection covariates; all covariates had a global VIF < 3. Relative patterns among seasons were consistent between years in the observation covariates. As expected, air temperature and relative humidity were highest in the summer and similar in spring and fall, while the longest periods without rain were in the fall both years (Fig. 4). There was no significant difference between conditions at occupied verses unoccupied rocks in mean air temperature (χ^2 = 0.502, df = 1, *P* = 0.478), mean relative humidity (χ^2 = 0.889, df = 1, *P* = 0.346), or mean number of days without rain (χ^2 = 2.33, df = 1, *P* = 0.127).

For both years, detection probability models containing 0.80 or greater of the model weights contained season, air temperature, and relative humidity (Table 2). The best performing detection probability model in 2016 was Season + Air Temp (Supplemental Information Table S1) and accounted for 0.41 of the cumulative model weights (Table 2). In 2016, the top three models accounted for 0.82 of the cumulative model weights
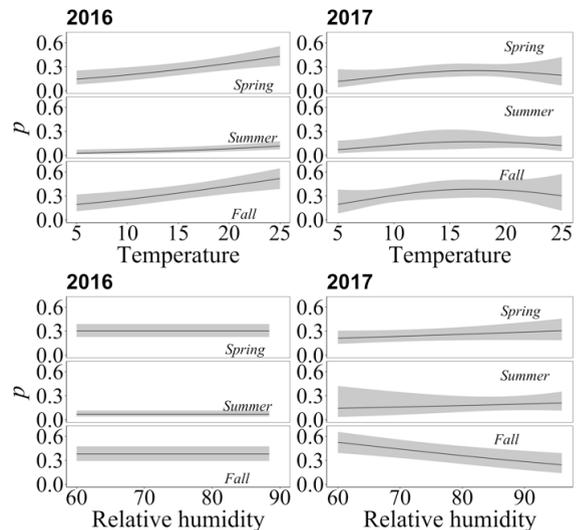
(Table 2). From model averaging, in 2016 increased air temperature overall had a positive relationship with detection probability, and relative humidity had a weak positive relationship with detection probability (Fig. 5). In 2016, holding temperature and relative humidity at their mean values, detection probability was similar in fall 0.29 (95% confidence interval [CI] = 0.22–0.38) and spring 0.23 (95% CI = 0.17–0.31) and lower in summer 0.06 (95% CI = 0.04–0.08; Fig.
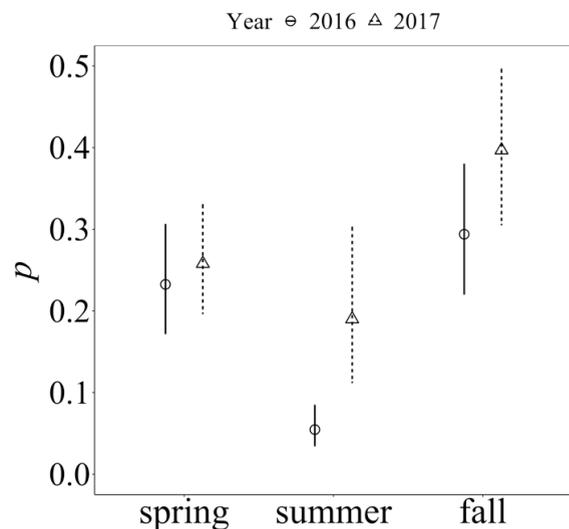

FIGURE 6. Detection probability (*p*) of Green Salamanders (*Aneides aeneus*) and Hickory Nut Gorge Green Salamanders (*A. caryaensis*) in relation to season while holding temperature and relative humidity at their mean values, 2016–2017, in North Carolina, USA. Vertical bars represent the 95% confidence interval.

TABLE 2. Best performing Green Salamander (*Aneides aeneus*) and Hickory Nut Gorge Green Salamander (*Aneides caryaensis*) detection probability models (*p*), 2016–2017, in North Carolina, USA, ranked by quasi-likelihood Akaike information criterion corrected for sample size (QAICc) and used in the model averaged predictions. Symbol W_i represents the model weight, and W_c represents the cumulative weight. The season variable has spring as the reference with comparisons to summer$_{(sm)}$ and fall$_{(F)}$.

Model	Coefficient ± SE	QAICc	W_i	W_c
2016				
p(Season + Air Temp)	-1.76 ± 0.23$_{sm}$ 0.35 ± 0.16$_F$, 0.075 ± 0.018	0	0.41	0.41
p(Season + Air RH + Air Temp)	-2.09 ± 0.32$_{sm}$ 0.19 ± 0.18$_F$, 0.010 ± 0.006, 0.082 ± 0.019	1.31	0.21	0.63
p(Season + Air RH +Air Temp + Season x Air RH)	-0.70 ± 2.17$_{sm}$ 2.63 ± 0.82$_F$, 0.020 ± 0.007, 0.078 ± 0.019, -0.019 0.032$_{sm:RH}$ -0.036 ± 0.012$_{F:RH}$	1.58	0.19	0.82
2017				
p(Season + Air RH + Air Temp + Air Temp² + Season x Air RH)	-0.24 ± 1.95$_{sm}$ 4.16 ± 0.94$_F$, 0.011 ± 0.009, 0.33 ± 0.11, -0.010 ± 0.004, -0.002 ± 0.023$_{sm:RH}$ -0.046 ± 0.013$_{F:RH}$	0	0.41	0.41
p(Season + Air RH + Season x Air RH)	-0.74 ± 1.90$_{sm}$, 4.75 ± 0.93$_F$, 0.017 ± 0.009, 0.003 ± 0.023$_{sm:RH}$ -0.0554 0.01248$_{F:RH}$	0.52	0.32	0.73
p(Season + Air RH + Air Temp + Season x Air RH)	-1.00 ± 1.90$_{sm}$ 4.58 ± 0.94$_F$, 0.018 ± 0.009, 0.03 ± 0.02, 0.004 ± 0.023$_{sm:RH}$ -0.052 ± 0.013$_{F:RH}$	1.37	0.21	0.94

6). In 2017, the best performing detection probability model was Season + Air RH + Air Temp + Air Temp² + Season x Air RH (Supplemental Information Table S2) with a cumulative model weight of 0.41 (Table 2). The top three models represented 0.94 of the cumulative model weights; therefore, we used those three models for model averaging (Table 2). Air temperature was positively related to detection probability overall (Fig. 5). Relative humidity had a positive relationship with detection probability in spring and summer; however, detection probability in the fall was negatively related to humidity (Fig. 5). The relationship between air temperature and detection probability had a quadratic term describing an optimum temperature of 15–20° C for detection in 2017 (Fig. 5). Holding temperature and humidity at their mean values, detection probability was highest in fall 0.40 (95% CI = 0.31–0.50), followed by spring 0.26 (95% CI = 0.20–0.33), and, lastly, summer 0.19 (95% CI = 0.11–0.30; Fig. 6).

For both years, abundance models containing 0.80 or greater of the model weights contained the covariates of nest rock, eastness, and rock area. All abundance variables had VIF < 3, except number of crevices, which was correlated with rock area. Therefore, we did not model number of crevices and rock area in the same abundance model. The best performing abundance model for 2016 (Nest Rock) and 2017 (Eastness + Nest Rock + Eastness × Nest Rock) included a term designating whether the site had a history of reproduction (Supplemental Information Tables S3 and S4). Not surprisingly, sites with a history of reproduction had higher mean abundances than sites without known reproduction. The top model in 2017 also included an interactive term describing eastern

aspect (eastness) along with the term designating whether the site had a history of reproduction. The interaction term between Eastness and Nest Rock indicated that there was a stronger relationship between abundance and Eastness at nest sites than sites without a documented history of reproduction. For model averaging, over 0.80 of the cumulative QAICc weight was in the top four models for both years (Table 3). In both years the top four models included terms for rock area and eastness (Table 3). Mean abundance both years was higher at sites with more western aspects and at larger rocks; however, the relationship with abundance and rock area was weak (Fig. 7). In 2016, estimated mean Green Salamander abundance per site was 8.43
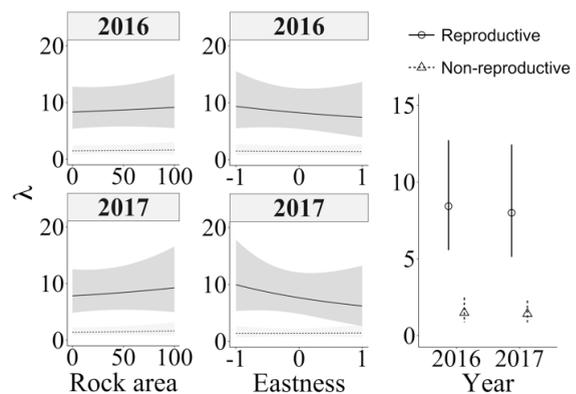

FIGURE 7. Modeled average mean abundance (λ) in relation to rock area, eastness, and reproductive history for Green Salamanders (*Aneides* aeneus) and Hickory Nut Gorge Green Salamanders (*A. carayaensis*), 2016–2017, in North Carolina, USA. For the eastness variable, 1 = an aspect of due east, and -1 = due west. Gray shading and vertical bars represent the 95% confidence interval around the line of best fit.

TABLE 3. Best performing Green Salamander (*Aneides aeneus*) and Hickory Nut Gorge Green Salamander (*Aneides caryaensis*) abundance models (λ), 2016–2017, in North Carolina, USA, ranked by quasi-likelihood Akaike information criterion corrected for sample size (QAICc) and used in the model averaged predictions. Symbol W_i represents the model weight, and W_c represents the cumulative weight.

Model	Coefficient ± SE	QAICc	W_i	W_c
2016				
λ(Nest Rock)	-1.76 ± 0.21	0	0.33	0.33
λ(Eastness + Nest Rock)	-0.24 ± 0.14, -1.74 ± 0.21	1.12	0.19	0.52
λ(Rock Area + Nest Rock)	-1.70 ± 0.21, 0.0044 ± 0.0027	1.44	0.16	0.69
λ(Eastness + Nest Rock + Eastness x Nest Rock)	-0.42 ± 0.17, -1.61 ± 0.22, 0.56 ± 0.30	2.07	0.12	0.80
2017				
λ(Eastness + Nest rock + Eastness x Nest Rock)	-0.52 ± 0.17, -1.60 ± 0.22, 0.73 ± 0.29	0	0.31	0.31
λ(Rock Area + Nest Rock)	0.0063 ± 0.0029, -1.69 ± 0.21	0.84	0.2	0.51
λ(Nest Rock)	-1.78 ± 0.20	1.12	0.18	0.69
λ(Eastness + Nest Rock)	-0.29 ± 0.14, -1.76 ± 0.20	1.28	0.16	0.85

(95% CI = 5.58–12.71) at nest rocks and 1.48 (95% CI = 0.89–2.46) at non-nest rocks (Fig. 7). Estimated mean abundance per site in 2017 was 8.00 (95% CI = 5.14–12.43) Green Salamanders at nest rocks and 1.41 (95% CI = 0.88–2.27) at non-nest rocks (Fig. 7). Over the two years, although there was a very slight decrease in the estimated mean abundance per site, the 95% CI overlapped (Fig. 7). Therefore, we did not detect any significant changes in the estimated mean abundance of Green Salamanders in the areas monitored over the course of this study.

DISCUSSION

Several recent studies have examined the ecology of Green Salamanders using occupancy and detection probability modeling in Alabama (John 2017), South Carolina (Newman et al. 2018), and Virginia (Smith et al. 2017). In 2015–2016, John (2017) used a single-season methodology to examine one population in Alabama and used observer, microclimate, and site factors such as aspect, canopy cover, percent cover of rock outcrop habitat in a defined area, and height of rock outcrops to assess detection probability and occupancy. Detection was heavily influenced by observer, while the main driver of site occupancy was rock height and rock percent cover (John 2017). In 2016, Newman et al. (2018) used survey parameters such as observer, date and time, ambient conditions, climatic data, rock size, landscape-level variables such as slope, aspect, elevation, and forest stand-level variables such as forest type, distance to water, basal area, percent canopy, and presence of site disturbance to estimate abundance and detection probability with N-mixture modeling methods. They found site and landscape features, such as the size of the rock outcrop, elevation, and aspect, as

the most important covariates for explaining variation in estimated abundance, while time of day was the most influential factor for estimating detection probability. Both the South Carolina and the Alabama studies conducted surveys only in the summer seasons (John 2017; Newman et al. 2018). In 2013 in Virginia, Smith et al. (2017) used single-season occupancy modeling to examine occupancy and detection at the microhabitat level of individual rock crevices used by Green Salamanders at one site complex from spring through fall. They found detection was strongly, but inversely, related to the amount of rain in the previous 24 h, while rock crevice features and forest context surrounding the site was important for explaining variation in crevice occupancy (Smith et al. 2017).

Although our two-year study is similar to those from South Carolina, Alabama, and Virginia, our project is the first to use detection probability and abundance estimates to monitor Green Salamanders across multiple seasons and across the known distribution of a state. Season is the main factor influencing detection probability of this species (e.g., the top nine candidate detection models for 2016 and 2017 include season). Our results support the probability of detecting Green Salamanders is higher in fall and spring compared to summer, which may explain why our overall detection probability is greater than that of similar studies recently conducted in South Carolina (Newman et al. 2018) and Alabama (John 2017). Our detection probabilities during summer (0.06 in 2016 and 0.19 in 2017) are lower than in Alabama (0.15–0.33, John 2017) but similar to South Carolina (0.03–0.12, Newman et al. 2018), which includes the same BRE metapopulation. Decreased probability for detecting Green Salamanders during summer is not surprising; during the summer months is when many Green Salamanders (with the exception of

brooding females) are using arboreal habitat (Waldron and Humphries 2005; Miloski 2010; Thigpen et al. 2010; Smith et al. 2017), dispersing across the landscape (Gordon 1952; Cupp 1991; Wilson 2003; Smith et al. 2018), or aestivating deep in rock crevices out of sight in times of hot, dry conditions (Pauley and Watson 2005). Those summer season behaviors may help explain lower detection probability at rock outcrops compared to fall and spring seasons (Snyder 1971; Gordon 1952; Cupp 1991).

There has been some disagreement in the relative importance of air temperature and relative humidity in hierarchical modeling studies of Green Salamanders. Newman et al. (2018) suggest that air temperature does not affect detection of Green Salamanders, and John (2017) found that relative humidity did clearly affect detection probability. The relative importance (via QAIC ranking) and strength of relationship of these variables in our analyses also differ between years. In 2016, with an abnormally dry spring and fall, relative humidity was not in the top model and had a non-significant slope from the model averaged predictions, suggesting that the relative importance of detection covariates may vary by longer-term or regional weather patterns, such as prolonged drought, and may explain the differences among studies in the relative importance of these covariates.

Furthermore, the influence of relative humidity might change seasonally. Our data indicate a negative relationship with detection during fall, but a positive relationship during spring and summer. Typically, Green Salamanders emerge from shelter and increase their surface activity in times of humid conditions or rainfall (Gordon 1952; Cupp 1991; Pauley and Watson 2005). Smith et al. (2017) also report finding fewer Green Salamanders during surveys within 24 h of significant rainfall and suggest that Green Salamanders leave their crevice haunts to take advantage of favorable foraging opportunities in arboreal habitats to build lipid stores ahead of the winter season and torpor (Wells 2007).

Survey start time, although a significant positive relationship for Newman et al. (2018), was not helpful for our detection models either year. We found a positive relationship with temperature, however, and because later start times are likely warmer, Newman et al. (2018) might have observed a weak correlation between air temperature and start time that did not violate any assumptions. Our data did show a weak correlation between air temperature and start time ($r = 0.32$); however, as the VIF < 3, we chose to include them in models but not both in a single model.

The number of dry days since measurable rainfall also was not significant in our models and may have been too coarse of a variable because we had to rely on archived weather station data, often from locations considerable distances away from local rock outcrop sites. Further, any potential value the variable could have had as an indicator of dryness at sites was likely better captured by relative humidity. In the future, quantifying the number of days with greater rainfall amounts (> 0.6 cm) might be a helpful survey covariate to examine.

Whether a site was a current or historical nest rock was highly significant for our abundance estimates both years, as might be expected when considering which sites are contributing new animals to the population. Nest rocks with a history of successful nest outcomes are more likely to produce successful nests in the future (Rossell et al. 2019), and thus are more likely to serve as a source for the local population. Nest rocks in particular, and occupied rock outcrops in general, are well-shaded, humid to moist but not wet, located in more mature forest, and offer a number of crevices that are relatively clear of soil, debris, or plants, wide enough to fit a salamander, and deep enough for a salamander to retreat from unfavorable ambient conditions such as times of extreme heat, cold, or dryness (Snyder 1971; Cupp 1991; Rossell et al. 2019). Nest rocks typically demonstrate all of these characteristics, provide specialized brood chambers that are higher above the ground and shorter in length (presumably facilitating an easier defense for a nesting female), and provide microclimate stability (Rossell et al. 2019). Further, our data highlight how critically important it is for managers to identify and protect nest rocks across the landscape because they are directly related to population health, and breeding adults show high site fidelity for these sites year after year (Gordon 1952; Cupp 1991; Rossell et al. 2019).

Of the additional site covariates, only rock area and eastness were useful in the top models. Our results contrast with similar studies that found certain landscape or forest stand-level characteristics, such as elevation or canopy cover, influential at the site or microhabitat level (John 2017; Smith et al. 2017; Newman et al. 2018). The GIS derived tree cover variables we used had a coarse spatial resolution (30 m). We did not have the time or resources to ground truth those data layers prior to our using them but recommend future studies examine the relationship between canopy cover and canopy height measured on the ground.

A multi-season study design, compared to single season monitoring, provides opportunities to assess all Green Salamander life stages, seasonal behavior, and habitat use, which provides managers a broad perspective of population ecology. For example, sampling during spring allowed us to monitor emergence from overwintering haunts and to observe recruitment of hatchlings from fall reproduction. Young of the year are easily distinguished from older, larger animals, even other juveniles, *in situ* without

needing to extract individuals from rock crevices. Data on relative abundance of this young age class is critical for population viability analyses and estimates of survivorship. Furthermore, the late spring season gave us a chance to see adult males occupying brood chambers, the possible pairing of breeding adults, and females preparing to oviposit, increasing our awareness of likely nest crevices.

Summer sampling provided an opportunity to find and monitor egg clutches and brooding females, and to document arboreal habitat use or dispersal (Wilson 2003; Waldron and Humphries 2005; Smith et al. 2017). Because summer detection probability at rock outcrops is inherently low as our and other recent studies demonstrate, we recommend modification of late spring and summer survey protocol at rock outcrops to include more of the surrounding forest in a standardized search effort to increase detection probability and examine non-rock outcrop habitat use, potential dispersal corridors, and dispersal distances. Arboreal use and dispersal may peak in early summer (June, Waldron and Humphries 2005), but could still be studied throughout summer and into the fall season. To overlap the timing of that activity, we suggest implementing a forest-type sampling scheme as early as May as part of spring season sampling. For example, after checking the rock outcrop for the presence of salamanders in crevices (and the presence of nests and brooding females), surveyors could then search more thoroughly, with flashlights, binoculars, and extendable cameras or borescopes, all woody stems (trees and shrubs), all downed woody debris, and all loose bark on logs or trees within a set radius (e.g., 25 m) from the rock outcrop (Waldron and Humphries 2005; Miloski 2010; Smith et al. 2017), rather than searching only those features directly on or adjacent to rocks as we did in our study. Dispersal corridors between rock outcrops could also be searched if feasible and if two or more sites are clustered (i.e., within a 25-m radius). Previous studies in the Southern and Central Appalachians on Green Salamander movements and arboreal use have included study areas of 10 m out from rocks (Thigpen 2010; Smith et al. 2017). Others suggest individuals move as little as < 5–15 m (Waldron 2000; Miloski 2010), 9 m (Gordon 1961), > 15 m (Williams and Gordon 1961), up to 17 m (John et al. 2019), > 30 m (Woods 1968), > 40 m (Canterbury 1991; Waldron and Humphries 2005), and even > 100 m (Gordon 1952) to or from rock outcrops across various temporal scales. In West Virginia, an observation of a Green Salamander under a board in a grazed pasture was 55 m away from the nearest rock outcrop (Riedel et al. 2006). In Tennessee and Virginia, Smith et al. (2018) reported Green Salamanders using artificial structures > 1 km away from the closest rock outcrop or cliff site. Also, in Tennessee a Green Salamander was found crossing a wet

road at night below road cut rock outcrops (Miller and Reynolds 2011). Similarly, in North Carolina in recent years we have received dozens of reports of incidental observations from homeowners, summer camp staff and attendees, and recreationists of Green Salamanders found on natural and artificial structures. These reports indicate Green Salamanders can disperse distances far greater than 100 m away from rock outcrops across a forested landscape, which is currently the recommended buffer size to conserve Green Salamander sites (Petranka 1998). Examining Green Salamander habitat use and dispersal away from rock outcrops could be valuable for helping inform land use decisions, such as timber management and recommended buffer sizes and configurations around Green Salamander rock outcrops, especially for known nest rocks.

Sampling in the fall season allowed us to determine nest success with the presence of hatchlings and maximize detection probability. In fall, salamanders retreat from arboreal habitat to rock outcrops where they congregate in preparation for overwintering. Many nest rocks may also serve as winter hibernacula, and we have seen evidence of this dual role of some sites (e.g., documenting hatchlings in the fall and then observing those individuals emerge at those same sites in the spring as yearlings, along with others that may have been observed the previous fall). Rock outcrops that offer both nesting and overwintering habitat likely increase Green Salamander relative abundance. Given a higher detection probability during fall, it is the best single season for long-term monitoring if the main goal is to assess population trends across a large number of sites, or if resources are limited to prevent surveys across multiple seasons.

Further, because of their relatively long lifespan (> 10 y, Pauley and Watson 2005; Waldron and Pauley 2007) and declines in population health or habitat quality may take longer than 2 y to identify for this cryptic species, we recommend a long-term sampling scheme of > 2 y for Green Salamanders. With additional years of sampling, we suggest managers employ dynamic N-mixture modeling to estimate survival and recruitment rates in addition to abundance estimates (Dail and Madsen 2011; Kéry and Royle 2015). This information will allow managers to detect declines quicker and better diagnose their causes, without a potentially invasive marking technique needed for mark-recapture modeling (Kéry and Royle 2015; Ficetola et al. 2018a). Even with more non-invasive marking methods, such as dorsal macrophotography, photographic catalogs, and pattern recognition software (Sannolo et al. 2016), a researcher must typically still have the animal in hand, which can be challenging when Green Salamanders are lodged deep into rock crevices.

Although sampling across multiple seasons allows managers to examine distinct life-cycle stages and seasonal habitat ecology according to specific objectives, we realize that not all states have agency staff, resources, or dedicated volunteers to commit to a multi-season sampling methodology at the landscape level. If managers are limited in resources and need to monitor Green Salamander population trends long-term, we recommend the fall season as the best option for repeated surveys because of the increased chance of detecting individuals and the added benefit of assessing nest success. Our data paired with a recent simulation study (Ficetola et al. 2018b) can assist managers seeking to monitor Green Salamander trends but lacking needed information for study design. We suggest managers use N-mixture models with three surveys in the fall season at 31–60 sites to detect population declines of at least 30%.

Green Salamanders are an excellent example of how variation in seasonal behaviors can affect detection and, thus, population estimates. Our results and recommendations for study design provide information that can help managers survey efficiently for this species, particularly in states or regions where detection probabilities or abundance estimates are unknown. The resulting population trends that managers can obtain will help further species conservation goals and provide a valuable monitoring tool for evaluating effects of threats, land use, and other human actions on this rare and unique salamander.

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APPENDIX. Survey and site covariates considered as potential influential factors in modeling Green Salamander (*Aneides aeneus*) and Hickory Nut Gorge Green Salamander (*Aneides caryaensis*) detection probability (p) and abundance (λ), 2016–2017, in North Carolina and their potential associated relationships (positive, negative, neutral, quadratic).

Covariate	Model Type	Description	Relationship	Sources
Air Temp	p	Air temperature (°C)	x^2	Gordon 1952; Snyder 1971; Corser 1991; Hafer 1992; John 2017
Air RH	p	Relative humidity (%)	$\pm$	Gordon 1952; Snyder 1971; Corser 1991; John 2017
Season	p	Spring, summer, fall	x^2	Gordon 1952; Snyder 1971; Cupp 1991; Corser 1991; Waldron and Humphries 2005
Days Dry	p	Number of days since rain	$\pm$	Gordon 1952; Hafer 1992; Juterbock 2013; Smith et al. 2017
Start Time	p	Survey start time	$0/+$	Hafer 1992; Juterbock 2013; Newman et al. 2018
JDate	p	Julian date	$\pm$	Gordon 1952; Cupp 1991
JDate^2	p	Julian date^2	x^2	Gordon 1952; Cupp 1991
Nest Rock	λ	Reproductive history (0,1)	$+$	Gordon 1952; Snyder 1971; Cupp 1991; Rossell et al. 2019
Spatial Area	λ	Population (DSRF, HNG, BRE)	$+$	Rossell et al. 2019
Eastness	λ	sin(Aspect)	$\pm$	Corser 1991; Newman et al. 2018
Northness	λ	cos(Aspect)	$\pm$	Gordon 1952; Bruce 1968; Corser 1991; Newman et al. 2018
Elevation	λ	Site elevation (m)	$-$	Bruce 1968; Petranka 1998; Newman et al. 2018
Elevation^2	λ	Site elevation (m)^2	x^2	Bruce 1968; Petranka 1998; Newman et al. 2018
Canopy Cover	λ	Mean canopy cover (%) within 30 m	$+$	Gordon 1952; Corser 1991; Snyder 1991; Smith et al. 2017; John 2017
Canopy Height	λ	Mean canopy height (m) within 30 m	$+$	Petranka 1998; Waldron and Humphries 2005
Number Crevices	λ	Number of suitable crevices (1, 2–4, 5–7, 8–10, >10)	$0/+$	Corser 1991; Hafer 1992; Rossell et al. 2009; Smith et al. 2017
Mean DBH	λ	Mean DBH (cm) within 5 m	$+$	Petranka 1998; Waldron and Humphries 2005
Stem Count	λ	Woody stems $\geq$ 8 cm DBH within 5 m	$+$	Petranka 1998; Wilson 2003; Waldron and Humphries 2005; Smith et al. 2017
Rock Area	λ	Area of rock face (m^2)	$+$	John 2017; Newman et al. 2018

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