IDENTIFYING ENVIRONMENTAL PARAMETERS TO PREDICT OCCUPANCY OF THE SOUTHERN APPALACHIAN MOUNTAIN ENDEMIC, *PLETHODON WELLERI*

A Thesis
by
ROSEMARY RONCA

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Abstract

IDENTIFYING ENVIRONMENTAL PARAMETERS TO PREDICT OCCUPANCY OF THE SOUTHERN APPALACHIAN MOUNTAIN ENDEMIC, *PLETHODON WELLERI*

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Plethodon welleri is a small-bodied salamander species that is endemic to select mountains in the Southern Appalachian Mountains and considered threatened across its entire range. Initial descriptions indicated that this species was a high-elevation, spruce-fir specialist only found above 1500m. However, historical and recent observations have documented populations outside of this range. The goal of this study was to assess environmental parameters correlated with occupancy by *P. welleri* and build a comprehensive dataset on species detection and occurrence of *P. welleri*. In 2022, sites were surveyed across the North Carolina and Tennessee portion of *P. welleri* range, and population and environmental data was collected March-November. These data have been used to model occupancy of *P. welleri* across three primary sampling seasons: spring, summer, and fall. The environmental factors that most strongly correlated with detection of this species were ambient temperature, humidity, soil moisture, and leaf litter depth, resulting in detection rates of 0.364 (spring), 0.430 (summer), and 0.518 (fall). Terrain and elevational characteristics were important in determining site occupancy for *P. welleri*, with seasonal changes in elevational habitat suitability resulting in occupancy estimates of 0.603 (spring), 0.278 (summer), and 0.466 (fall). My findings indicate that the primary drivers of occupancy and detection of *P. welleri* have to do with the evaporative risk for

this species based on environmental conditions. This study is the first to investigate the environmental covariates that influence this threatened species and will provide a framework to guide future studies and the development of effective conservation management plans.

Acknowledgments

I would like to thank my advisor, Dr. Jon Davenport for his mentorship, time, and advice throughout the completion of my project. I would also like to thank Dr. Steve Seagle and Dr. Robert Creed for their guidance and input in the completion of my project. I would also like to thank Lori Williams for her expertise in the wildlife of North Carolina and support in my work. I would like to thank my lab mate, Elyssa Winterton for her continuous support in the field and the lab as we learned the ins and outs of hierarchical occupancy models, as well as all of the members of the Davenport lab for their ongoing assistance, support, and friendships.

This project has been funded by the Appalachian State University Office of Student Research, the Tennessee Herpetological Society's Chadwick Lewis Memorial Grant, Sigma Xi Grants in Aid of Research, and the Orianne Society's Program for Reptile and Amphibian Conservation in the Southeast. I would like to express my appreciation for them helping to make this project possible.

Dedication

This thesis is dedicated to the women of Camp Juliette Low, for fostering my love for the natural world and all its creatures.

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Foreword

This thesis will be submitted to the *Journal of Wildlife Management*, a peer reviewed journal owned by The Wildlife Society. It has been formatted according to the style guide of this journal.

Introduction

Habitat degradation and fragmentation are two of the biggest threats to biodiversity worldwide, with the primary causes coming from direct (e.g., agriculture and deforestation) and indirect (e.g., climate change and pollution) human impacts (Dawson et al. 2011, González-Orozco et al. 2016, Tilman et al. 2017). While biodiversity losses extend to all taxa, amphibian species are disproportionately affected as vertebrates, with 40.7% of species worldwide being categorized as endangered by the International Union on the Conservation of Nature (IUCN), compared to 21.9% of reptile taxa, 12.9% for bird taxa, and 26.5% of mammal taxa as of 2022 (Chanson and Neam 2023, Luedtke et al. 2023). Moreover, 17% of all species assessed by the IUCN Red List as of 2020 were classified as data-deficient, meaning there is insufficient information to assess their risk factors, and many of these species are likely threatened with extinction (Borgelt et al. 2022). Amphibians historically have had one of the highest proportion of species listed as data-deficient (Böhm et al. 2013), though the recently updated 2023 Global Amphibian Assessment indicates a significant decrease since 2004 when ~23% of species were considered data-deficient. Over the past 20 years, there has been an increase in the number of assessed species, which has decreased data-deficient amphibians to 11% (Chanson and Neam 2023). This decrease coincided with an increase in the total number of amphibians species included on the IUCN Red List, which now comprises ~93% of all described amphibians and is up 40% from 2004. However, if those data deficient species are threatened in the same proportion as assessed species, that would mean ~400 more species being considered threatened with extinction. A recent study suggests that up to 85% could be threatened which would make that estimate much higher (Borgelt et al. 2022). The elevated risks for endangered and extinct species in amphibian taxa reflects their sensitivity to their surrounding environments and environmental conditions.

Amphibian species worldwide share traits that increase their sensitivity to natural and anthropogenic disturbances, including small geographic ranges, isolated populations, and specialized habitat requirements that limit dispersal (Sodhi et al. 2008, Whitton et al. 2012). The narrow geographic ranges that are characteristic of many amphibian species have been found to be dependent on the mean annual freezing conditions of the last glacial maximum (~21,000 ya), with historical precipitation variability having a significant effect on species richness of modern reptile and amphibian species (Araújo et al. 2008). Additionally, Whitton et al. (2012) found that various climatic (temperature seasonality and water availability) and environmental characteristics (habitat heterogeneity and human impacts) are largely responsible for the small range sizes seen in amphibians globally. The interactions of population traits and current environmental variables, such as small geographic ranges and seasonal changes in precipitation, likely increase the risk of extinction for amphibian species (Sodhi et al. 2008). Environmental characteristics also influence microhabitat conditions, such as soil moisture levels, temperature, and humidity, which are used by amphibian species to maintain physiological performance when surface conditions are not ideal (Farallo and Miles 2016). In turn, changes in environmental microhabitat conditions have been shown to increase variability in population trends of amphibian species (Werner et al. 2007, Gade and Peterman 2019). For example, recreational and urban development of forest roads may be responsible for changes in microhabitat conditions and lower salamander abundances (Marsh and Beckman 2004, Marsh 2007). However, it should be noted that hiking trails can be useful in estimating plethodontid salamander abundance in the Smoky Mountains and do not significantly affect microhabitat conditions (Milanovich et al.

2015). The unique habitat requirements of amphibians have led global biodiversity to be centered around the tropics (Pyron and Wiens 2013, Díaz-García et al. 2017), with expansive plethodontid biodiversity located in the deciduous forests of the Eastern United States (Kozak et al. 2009, Semlitsch et al. 2014).

While the Southern Appalachians are a global hotspot for amphibian biodiversity, specifically for plethodontid salamanders (Rissler and Smith 2010, Barrett et al. 2014), there are many potential risks for population changes in the region (Caruso et al. 2015, Grant et al. 2016). Altered environmental and climatic conditions due to climate change and deforestation are projected to significantly affect the Southern Appalachians and could lead to the decline of many amphibian species (Milanovich et al. 2010) as well as reduce activity levels of Plethodontid salamanders (Riddell and Sears 2015). Indeed, studies have projected losses of over 90% of suitable habitats and climatic niches for woodland salamander species in the Southern Appalachian Mountains by 2050 (Barrett et al. 2014, Sutton et al. 2015), though these species may be able to avoid these affects by altering surface activity patterns (Gade et al. 2020). Other risks for these animals stem from landscape-scale changes in land use due to human activities (i.e., farming and logging), which have been extensive in the Southern Appalachian Mountains (Sleeter et al. 2013). Historical clear-cutting in the Appalachian Mountains has led to long-term consequences of both animal behaviors (Burke and Nol 1998, Stone and Wallace 1998) and altered microhabitat conditions affecting amphibian communities including forest floor temperature, humidity, and soil nutrients and pH (Ash 1995, Fraterrigo et al. 2005, 2006, Semlitsch et al. 2009, Homyack et al. 2011, Kuhman et al. 2011, Smith et al. 2019). Estimated recovery rates of foraging habits and habitat availability for plethodontid species in the Southern Appalachian Mountains following clear cuts are highly variable, ranging from 20-100 years

(Pough et al. 1987, Petranka et al. 1993, 1994, Ash 1997, Ash and Pollock 1999, Harper and Guynn 1999, Petranka 1999, Ford et al. 2002, Homyack and Haas 2009, Connette and Semlitsch 2013). Salamander communities that experience slower recovery rates are at higher risk of extirpation, especially of isolated populations, meaning these communities may never return to pre-disturbance composition and abundances (Ford et al. 2002). However, other studies have shown that salamander abundance may only be moderately lower in young forests stands than mature stands meaning that the effects of timber harvests are not as dire as predicted in the past (Connette and Semlitsch 2013). These effects are likely exacerbated in rare and endemic species though, as they may share characteristics that make them particularly vulnerable to changes in landscape composition.

The southern Appalachian Mountains are home to over 50 species of endemic amphibians, with many belonging to the genus Plethodon (Milanovich et al. 2010, Barrett et al. 2014). These species, such as *P. shenandoah*, are typically restricted to mountaintop habitats as a result of reduced suitability of both climatic and microhabitat conditions since the Pleistocene (Dallalio et al. 2017), which may be responsible for genetic isolation of fragmented populations due to limited dispersal and gene flow (Mulder et al. 2019). Endemic species with geographically isolated populations are highly vulnerable to changes in landscape characteristics, as they typically have strict habitat characteristics that allow for species occurrence and survival (Sutton et al. 2015). *Plethodon hubrichti* and *P. nettingi* are two endemic species that have small, highly fragmented ranges in Virginia and West Virginia respectively (Mitchell et al. 1996, Pauley 2008), and both have been found to be highly sensitive to the effects of linear habitat fragmentation from timber harvests (Mitchell et al. 1996, Rucker et al. 2022). Additionally, competition has been found to be an important factor in the distribution of these species, as range sympatry with the common species, *P. cinereus* leads to small ranging endemics being restricted to suboptimal habitats or reductions in population sizes (Jaeger 1970, 1980, Fraser 1976, Griffis and Jaeger 1998, Kniowski and Reichenback 2009). However, some species of endemic plethodon salamanders have yet to be investigated to understand the effects of environmental and biotic parameters on their population dynamics.

Weller's Salamander, *Plethodon welleri*, is a small-bodied woodland salamander species that is considered an endemic to "sky-island ecosystems" of the Southern Appalachians in western North Carolina, northeastern Tennessee, and southwestern Virginia. Despite being recognized as an endangered species by the IUCN, listed as a federal species of concern, and a Species of Greatest Conservation Need across its range (Hammerson and Beamer 2004), fundamental studies on habitat preference, population structure, and demographic parameters have yet to be completed (Petranka 1998). Much of the available information for this species originates from observation notes rather than from species or population specific studies. This lack in directed investigations into *P. welleri* may have led to misrepresentations of the parameters of this species. For example, despite being described as a high-elevation, spruce-fir specialist, populations have been observed at elevations as low at 712m, and egg masses have been found in a variety of forest types (Hoffman 1953, Thurow 1964, Hamed and Gray 2012, Forester 2017).

The purpose of this study is to address the population ecology of *P. welleri* by generating a regional dataset to identify the key environmental parameters that influence population distribution. Developing a foundational knowledge of *P. welleri* will also allow accurate descriptions of the habitat parameters necessary for this species to occur. As previously stated, there is a discrepancy between the described and observed elevation range of this species. While this inconsistency may seem like evidence for a spatial shift in *P. welleri* populations, it may be more easily explained by two possible scenarios: 1) survey efforts being focused primarily at elevations above 1,500 m or 2) surveys occurring outside of peak activity seasons for *P. welleri*, when temperature is limiting activity to cooler climates at high elevations (Organ 1960). To address the population ecology of *P. welleri*, I surveyed seventeen sites across nine months in 2022. I hypothesized that *P. welleri* is a summer high-elevation specialist species with a seasonal association with Spruce-fir forests. I predicted that occupancy will be positively influenced by humidity and aspect, and negatively influenced by temperature.

Methods

Study Species

Originally described from specimens collected at Grandfather Mountain, NC, in 1931, *P. welleri* is a small-bodied plethodon, reaching sexual maturity at ~35mm SVL, with large adults measuring up to 92mm total length (Walker 1931). *Plethodon welleri* is distinct in coloration pattern, with a bronze or golden mottling pattern across an otherwise black body, though some populations exhibit white spotting on the ventral surface (Bishop 1943, Petranka 1998; Figure 1). This species is the naming member of the *Plethodon welleri* evolutionary group of Eastern plethodon salamanders, which also includes *P. ventralis*, *P. dorsalis*, *P. angusticlavius*, *and P. websteri* (Highton 1995). This group is closely related to the *P. wehrlei* group, and retains the ancestral size, body morphology, and coloration of the *P. cinereus* group from which it likely evolved (Highton et al. 2012).

Figure 1. Weller's Salamander, *Plethodon welleri* individual found in decaying log from Unicoi County, TN. Photo by Rosemary Ronca.

Since its original discovery in 1931, this species has been understudied in regard to its population and community ecology. Historical literature surrounding this species has primarily focused on observations in the Virginia and Tennessee portions of its range, including populations at White Top Mountain and Mount Rogers, VA (Walker 1934, Hoffman and Kleinpeter 1948, Organ 1960, Hamed and Gray 2012), and Johnson County and Unaka Mountain, TN (Hoffman 1953, Thurow 1964, Lewis 1994). Additionally, one study detailed the life history of *P. welleri* from egg mass to breeding adult of individuals found in southwestern Virginia (Organ 1960). These studies considered *P. welleri* to be a high elevation spruce-fir endemic, with populations primarily occurring above 1500m, though observations do record populations occurring as low as 701m (Hoffman 1953, Thurow 1964). Despite there being only a few main mountains identified as occupied by this species through the literature, a few records do suggest populations extend beyond these mountains to other locations in both Tennessee and North Carolina (Snyder 1946, Hoffman 1953). Indeed, Forester (2017) identified 9 populations for genetic analysis in her genomics case study, indicating that there are more populations that are not published to the literature. However, there have been very few modern studies published regarding this species, meaning we may be lacking in complete population locality data as well as critical information on demographic parameters.

Field Sites

Seventeen study sites were selected in western North Carolina and eastern Tennessee to determine detection and occupancy of *P. welleri* (Fig. 2). Sites were restricted to the known range of *P. welleri* (i.e., where museum specimens were collected or had been previously documented), with additional sites selected with no previous record of *P. welleri* to serve as false occupancy control sites. Study plots (n=55) were designated at each site for seasonal surveys, covering an elevation gradient, ranging from 670m-1634m (~2200-5400 ft, Table 1). A range of forest cover types including Spruce-fir, Oak, Pine, Hickory, and Beech dominated forests were selected for surveys. Location of survey plots were selected by randomly overlaying grids consisting of nine potential plot locations on site maps (Fig. 3). Potential plot locations were evaluated and removed if crossing or immediately adjacent to roads or trails as these may influence small-bodied plethodontid abundance (Marsh and Beckman 2004, Burger et al. 2017). Final plot locations were also haphazardly selected based on accessibility. Survey plots were 30x30m delineated squares at the selected locations set between 4 corner trees. Transects were established along each edge of the plot, resulting in four survey areas. Plots were spaced at minimum 20m apart to remain independent and maintain closed populations between plots, as small-bodied plethodontid salamanders have been found to maintain a ~5m home range throughout their lifetimes (Mathis 1991, Kramer et al. 1993, Liebgold et al. 2011, Carlson et al. 2016, Caruso and Rissler 2019).

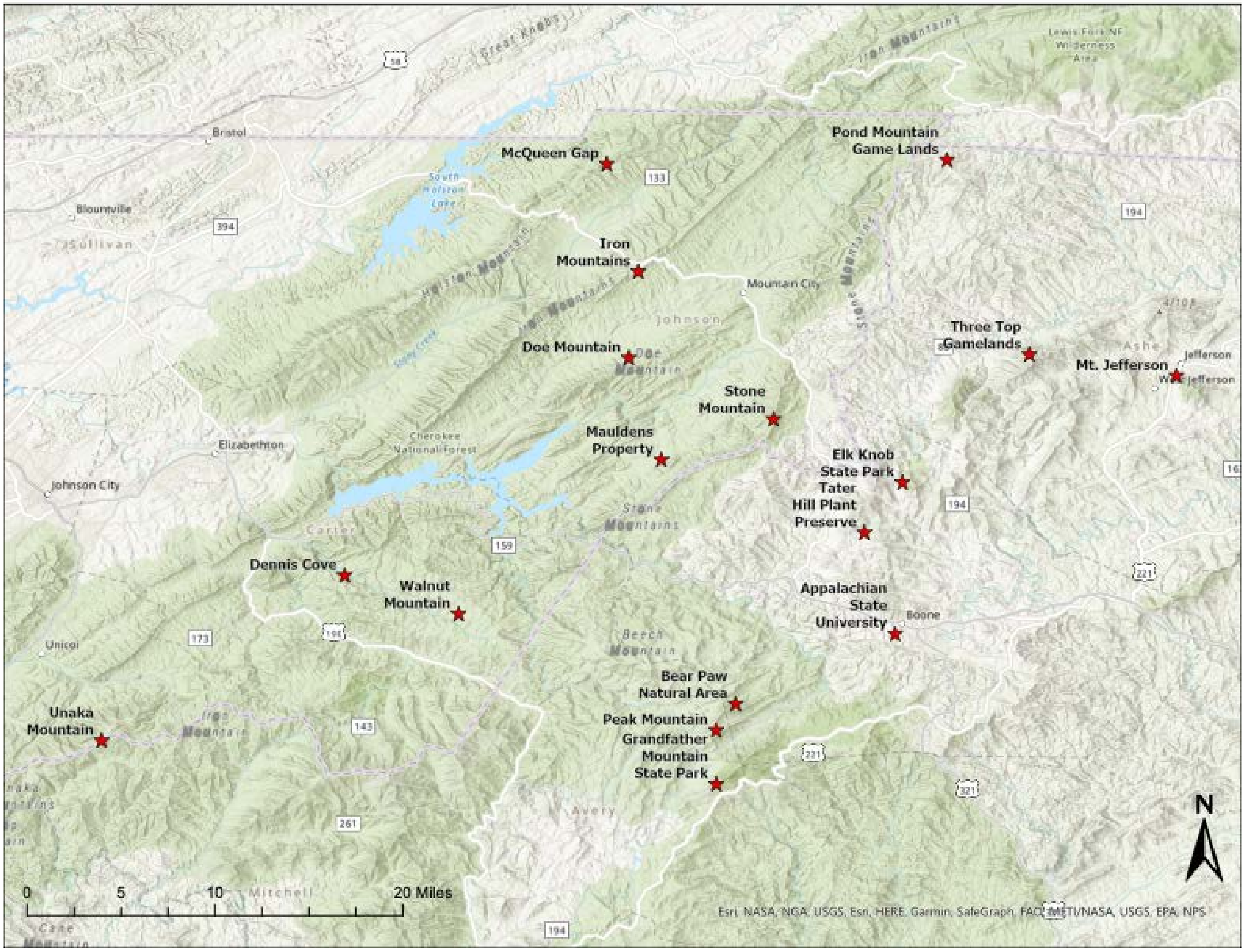

Figure 2. Site locations (n = 17) surveyed for *P. welleri* populations from March 2022-November 2022 across northwestern NC and northeastern TN. Two to six plots were set at each site, based on the variety of habitat types and range of elevation that we had access to on each mountain.

Table 1. Site identification and number of plots per sites surveyed from June 2021-November 2022. The number of plots for each site were selected based on variability in habitat type, size of site, and survey effort feasibility.

Site ID	**Number of Plots**
ASU Campus	3
Bear Paw State Natural Area	2
Dennis Cove	2
Doe Mountain	3
Elk Knob State Park	4
Grandfather Mountain	6
Iron Mountains	4
Private Property- Johnson Co., TN	3
McQueen Gap Road- Holston Mountains	2
Mt. Jefferson	3
Pond Mountain Game Land	4
Peak Mountain	3
Stone Mountain	3
Tater Hill Plant Preserve	3
Unaka Mountain	6
Walnut Mountain	2
Three Top Game Land	3

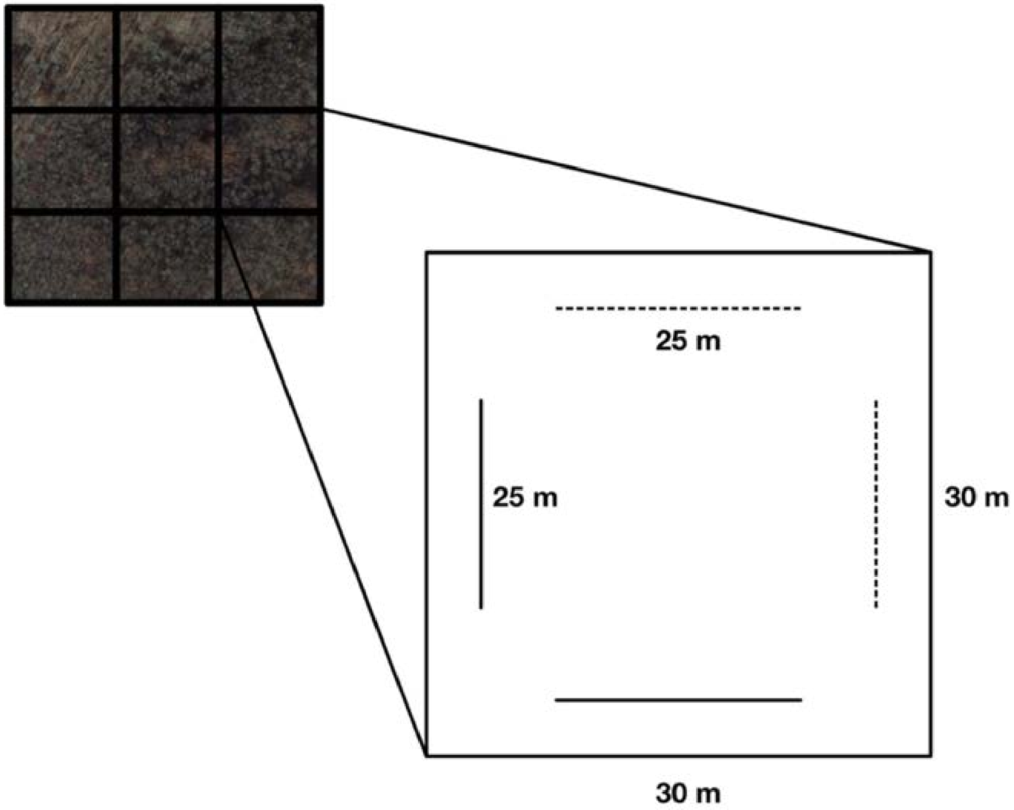

Figure 3. Plot and transect layout for survey sites located within *P. welleri range*. Grids represent nine potential plot locations, that were selected randomly. Plots were 30x30m in size, with 25x2m transects surveyed within each plot. Sampling plot design has been adopted from Otto et al. (2013).

Survey Methods

Diurnal Visual Encounter Surveys (VES) were deployed to detect species under natural cover objects (e.g., logs, rocks). Seasonal sampling periods were defined as “primary sampling periods”, and include spring (March, April, and May), summer (June, July, and August), and fall (September, October, and November). Three “secondary sampling periods” within each season identify survey visits to each plot, occurring every 3-4 weeks. Surveys were conducted along two of the four plot edges, and occurred within a 25m x 2m transect, defined by a 25m transect tape and 1m on either side of the center line. Surveyed transects were alternated between the four established survey areas, searching the same two transects every other visit to avoid creating a sampling bias or influencing localized extinctions of any salamander species (Otto et al. 2013). Surveys were not conducted during winter months (January, February, and December) due to accessibility and restricted surface activity during freezing temperatures when plethodontid salamanders retreat to climate refugia underground (Vernberg 1953).

Small-bodied plethodontid salamanders are typically found under coarse woody debris, rocks, or within moisture retaining leaf litter patches on the forest floor (Otto and Roloff 2011). In order to detect surface active salamanders, all natural cover objects within the search area were lifted and underlying microhabitat patches were searched before the cover objects were replaced to their original position. All salamanders found were collected and temporarily placed individually in plastic sandwich bags. Species, age class, cover object type, and location along transect were recorded for every individual collected. Sex and body condition data (mass (g) and snout-vent-length (SVL, mm) were also collected for all plethodon salamanders. After collecting necessary data, all individuals were returned to their approximate home site under their original cover object.

Sampling and Environmental Covariates

While conducting salamander surveys, soil moisture and pH were measured using a three-way meter (Moisture, Light, and pH Meter, HoldAll Plant Accessories, Columbus, OH, USA) every 5m along a transect. Leaf litter depth (cm) was also measured by inserting a standard ruler directly into leaf litter to the top layer of soil every 5m along the transect. Moisture, pH, and leaf litter depth data were then separately averaged across the two transects to estimate plot level conditions during each survey. Ambient environmental temperature, relative humidity, and windspeed were also measured during each survey for each plot using a Kestral 3000 Weather Meter (Kestrel Wind & Weather Meters, Boothwyn, PA) held approximately 1.5m above the ground. Calendar date of surveys and total number of cover objects lifted per plot was also recorded. Percent of closed canopy at each plot was measured using a Spherical Crown Concave Densiometer (Forest Densiometer Model C, Rapid City, MO) during each season.

Ground temperature data was collected using HOBO Pendent Temperature and Light Data Loggers placed under a cover object at each plot (Onset Brands, Bourne, MA 02532). HOBO Loggers record temperature and light data hourly, and data from the three and seven days prior to survey were averaged separately to get ground temperature by plot. Precipitation data were extracted using NASA's DAYMET Daily surface weather and climatological summaries data to determine total precipitation for the three and seven days prior to survey date, and days since last precipitation event at each plot (Ray et al. 2016, Grant et al. 2018, Thornton et al. 2020). These covariates were measured during each secondary survey period to best determine the effect of microhabitat and climatic conditions of surface activity for *P. welleri*. Hereafter, these covariates will be referred to as survey-level covariates, as they were variable between survey visits (Table 2).

Table 2. Site-level and survey-level covariates used to examine *P. welleri* habitat parameters with model code abbreviations.

Survey-level Covariates	**Code**	**Site-level Covariates**	**Code**
Soil Moisture (%)	MOIST	Elevation (m)	ELEV
Soil pH	PH	Northness (degrees)	NORTH
Leaf Litter Depth (cm)	LLD	Eastness (degrees)	EAST
Ambient Temperature (°C)	AMBTEMP	Slope (degrees)	SLOPE
Relative Humidity (%)	HUMID	Topographic Position Index	TPI
Windspeed (mph)	WIND	Terrain Ruggedness Index	TRI
Calendar Date	DATE	Heat Load Index	HLI
Canopy Cover	CAN	Productivity	PROD
Ground Temperature (°C)	GRDTEMP		
Total precipitation (mm/plot)	PRECIP		
Days since last precipitation	RAIN		
Cover Objects (per plot)	COVOBJ		

Additional site-level covariates (Table 2) were included after surveys were completed using QGIS 3.18.1 Zurich (QGIS Development Team 2020), and are covariates that remain consistent between primary sampling periods. All were included because of their previously established importance for influencing plethodontid populations (Hairston 1951, Ford et al. 2002, Bernardo and Spotila 2006, Dillard et al. 2008, Peterman and Semlitsch 2013, 2014, Grant et al. 2018, Jacobsen et al. 2020). These covariates include: elevation, slope, aspect, and topographic position, terrain ruggedness, and heat load indices for each plot. Elevation of each plot was extracted from a 30m resolution 1/3 arc sec Digital Elevation Model (DEM; The National Map, USGS v2.0) and used to derive aspect, slope, topographic position index, and terrain ruggedness index.

Due to a lack of variation in slope values obtained through raster analysis (values ranged 89.992-89.999), this covariate was removed from future analyses. Aspect was converted using the Beer's transformation method to determine Northness and Eastness (Beers et al. 1966) and has been shown to affect microhabitat conditions due to sunlight availability. This method rescales aspect to reflect plot productivity based on presumed mesic or xeric conditions based on position (McEwan and Muller 2011). Aspect was also used to calculate Heat-Load Index (HLI), which measures the potential radiation and heat a plot receives due to its slope and aspect (Jacobsen et al. 2020). The following equations are used to transform aspect(θ) into Northness, Eastness, and HLI:

$$\text{Northness} = \text{COS}(\theta)$$

$$\text{Eastness} = \text{SIN}(\theta)$$

$$\text{HLI} = \frac{1-\cos(\theta-45)}{2}$$

These adjusted covariates were selected for analyzing *P. welleri* populations as microhabitat conditions are highly influential towards salamander species with cooler, mesic habitats (northeastern facing) being more suitable than warmer, xeric habitats (southwestern facing) for many species (Harper and Guynn 1999, Mohammad 2008, Farallo and Miles 2016). These favorable conditions are a result of lower levels of solar radiation and more shade availability at northern facing slopes than southern facing slopes (Bennie et al. 2006). Topographic Position Index (TPI) represents the slope position of a focal point by comparing the average neighborhood values of the neighboring habitat in a landscape (Guisan et al. 1999). Negative TPI values indicate that the plot is in a low point (i.e., a ravine or valley), while positive values would indicate a higher area compared to the surrounding area (i.e., a ridge or peak). A TPI value close to zero would represent an area with no slope or a constant slope (Peterman and Semlitsch 2013). Terrain Ruggedness Index (TRI) is also used to evaluate the variability in elevation changes between a target location and the surrounding habitat, and can indicate the level of terrain heterogeneity of a plot compared to neighboring cells (Riley et al. 1999). TRI values can be interpreted on a scale from nearly level to extremely rugged. This index has been shown to be associated with salamander abundance and can correspond to rocky cover object availability (Romano et al. 2021).

Statistical Analysis

In order to evaluate distribution patterns of *P. welleri* across eastern Tennessee and western North Carolina, hierarchical occupancy models were constructed to estimate salamander detection rate and occupancy. Hierarchical models for occupancy can be used to approximate the distribution of cryptic species where detection rates are assumed to be less than 1 (MacKenzie et al. 2002). These models use variable survey-level covariates and continuous site-level covariates to identify environmental and habitat parameters that best explain the variability seen in presence and absence data collected from each secondary survey period. It is assumed that survey-level covariates affect surface activity levels of plethodontid salamanders, and this can influence the detectability of these animals (MacKenzie et al. 2002, Bailey et al. 2004*a*, *b*). Site-level covariates are continuous between survey visits and are thought to influence whether a species is able to occupy a location. Occupancy models assume plots are independent, and closed to emigration, colonization, and extinction within each primary sampling period. This means that occupancy status remains continuous, either occupied, represented by a 1, or unoccupied, represented by a 0, within the spring, summer, and fall primary sampling seasons (MacKenzie et al. 2002). This study satisfied these assumptions as plots were separated by at least 20m, which is more than the expected home range of *P. welleri,* and the study was conducted within a nine-month time period, with season being defined by continuous three-month periods when population occupancy would likely not change.

All hierarchical occupancy models were fitted in R (RStudio Team 2020) using the package 'unmarked' (Fiske and Chandler 2011). This package is specifically designed to estimate population parameters of species without using traditional capture-mark-recapture surveys while accounting for imperfect detection.

Static Occupancy Modelling

A stepwise model selection technique was employed to determine the top covariate predictors for each model factor. These models are based on two parameters, the occupancy probability and detection probability. The initial steps of static (single season) occupancy models include computing the detectability of the target species across a landscape during a primary survey period, denoted as the conditional capture probability (p_{it}), while holding the state parameter (occupancy, ψ_i) constant. Occupancy probability represents the likelihood of a target species being present at a particular site. The initial occupancy state for each site can be expressed using the following equation and described whether the target species was observed at site i (Royle and Kéry 2007):

$zi \sim Bernoulli(\psi i)$, with the variables representing:

z: true site occupancy of site i

ψ: the probability of the target species occupying site i

Given that a site is occupied ($z_{i,t}$), an observational model is then calculated to explain the probability of detecting the target species at the site:

$yi|zi \sim Bernoulli(pi * zi)$, with additional variables representing:

y: presence or absence data of site i

p: the probability of detecting a target species at site i

With these initial models, we can then estimate detection and occupancy probabilities using the following equations:

$logit(p_i)=\alpha 0 + \alpha 1 * surveycovariate1 + \alpha 2 * surveycovariate2 + \ldots + \alpha X * surveycovariateX$

$logit(\psi_i)=\beta 0 + \beta 1 * sitecovariate1 + \beta 1 * sitecovariate2 + \ldots + \beta X * sitecovariateX$

The detection probability calculated is also known as the conditional capture probability and is defined as the probability that an individual from the target species will be captured given that it is present at the site. Due to salamander populations residing primarily below ground with limited surface-level activity, this conditional capture probability is expected to be less than 1

(Bailey et al. 2004*a*, Semlitsch et al. 2014). In the process of calculating p_{it}, detection covariates (survey-level covariates) are incorporated into models to identify the covariate that best explains the variability of *P. welleri* detection. With the exception of precipitation data, all detection covariates were collected in the field during salamander surveys. Correlation tests were conducted to determine dependent versus independent covariates within each primary survey period, and models were constructed with each detection covariate being run separately and combined with other non-correlative covariates. Additional null models were run to account for the possibility that no detection covariates were responsible for the observed variation: (*p(.)psi(.)*), or that all covariates were equally responsible: (*p(AMBTEMP+HUMID+WIND+MOIST+PH+LLD+ DATE +PRECIP+RAIN+CAN+GRDTEMP+COVOBJ)PSI(.)*). Model selection using Akaike Information Criteria (AIC) determined top and competing models for detection probability of *P. welleri*. Competing models are models with a ΔAIC score ≤ 2.00.

Once the conditional capture probability of *P. welleri* has been determined, occupancy models can be used to calculate the probability that a target species will occupy a given site within the survey range, known as the occupancy estimate, and denoted as ψ. Site-level covariates are included at this step to determine which has the most influence on occupancy probability of the target species. Similarly, covariates were tested for correlations and models were run incorporating non-correlative covariates. Models were constructed using both a constant p_{it}, as well as the previously determined top model for detection probability, and null models (1) *p(.)psi(.),* 2) *p(.) psi(NORTH+EAST+ELEV+TPI+TRI+HLI),*

3) *p(TOP_DETECTION_COVARIATE)psi(.),* and 4) *p(TOP_DETECTION_COVARIATE) psi(NORTH+EAST+ELEV+TPI+TRI+HLI)*) were included. AIC scores were again compared to determine top and competing models, and the top model was utilized to determine ψ.

Results

Surveys

During the spring sampling period (March-May), 38 of the established 56 plots were surveyed, all 56 plots were surveyed during the summer sampling period (June-August), and 29 of the 56 plots were surveyed in the fall (September-November). Each plot being surveyed was visited on three occasions within a primary sampling season. These surveys yielded a total of 1,447 salamanders representing 10 species, from four genera all within the family Plethodontidae (Table 3). A total of 143 *Plethodon welleri* individuals were encountered across all survey periods. *Plethodon welleri* individuals were encountered at 23 of the total 56 surveyed sites throughout 2022 surveys, with detections occurring at 18 plots in the spring, and 12 plots each in the summer and fall. The 2022 surveys identified *P. welleri* populations in a variety of forest stands (identified by dominant tree species from visual inspections) including pine, maple, oak, tulip poplar, ash, birch, and spruce-fir (Table 4). Individuals were also found across an elevational gradient between 700m and 1600m, though populations at all elevations were not encountered in all three sampling seasons (Fig. 4).

Table 3. Raw counts of salamander species encountered during primary sampling periods in 2022.

Species encountered	**Spring Sampling**	**Summer Sampling**	**Fall Sampling**	**Total**
Plethodon welleri	53	28	62	143
Plethodon cinereus	68	62	62	192
Plethodon cylindraceus	24	46	23	93
Plethodon montanus	124	315	88	527
Plethodon richmondi	58	61	48	167
Plethodon yonahlossee	10	33	3	46
Desmognathus orestes	35	125	26	186
Desmognathus organi	8	11	0	19
Eurycea wilderae	15	31	27	73
Pseudotriton ruber	1	0	0	1
Total Count	**396**	**713**	**338**	**1,447**

Table 4. Seasonal *P. welleri* occupancy at study plots with identified populations across three primary sampling periods during 2022. Plots are listed in order of elevation, with dominant tree species identified and occupancy within a primary sampling period indicated by a black box. Plots that were not surveyed in a season are identified by NS.

Plot Code	Elevation (m)	Dominant Tree Species	Plot Occupied		
			spring	*summer*	*fall*
1	712.38	White Pine		■	■
2	712.61	Maple	■		NS
3	799.34	-	■		■
4	807.70	-	■		
5	861.16	Maple			■
6	910.59	Maple	■		■
7	913.42	Maple	■		■
8	958.34	Maple	■		■
9	978.08	Maple			■
10	993.40	Oak	■	■	NS
11	1046.77	-	NS	■	■
12	1062.94	Tulip Poplar	■		NS
13	1322.91	Oak	■	■	■
14	1352.71	Oak	■		■
15	1370.10	Oak	■	■	NS
16	1379.04	Oak	■	■	■
17	1458.82	Oak	■	■	■
18	1459.81	Oak	■	■	
19	1463.16	White Ash	■		
20	1486.61	Birch	■	■	NS
21	1487.22	Birch	■	■	NS
22	1494.95	Spruce	NS	■	NS
23	1634.94	Spruce-Fir		■	

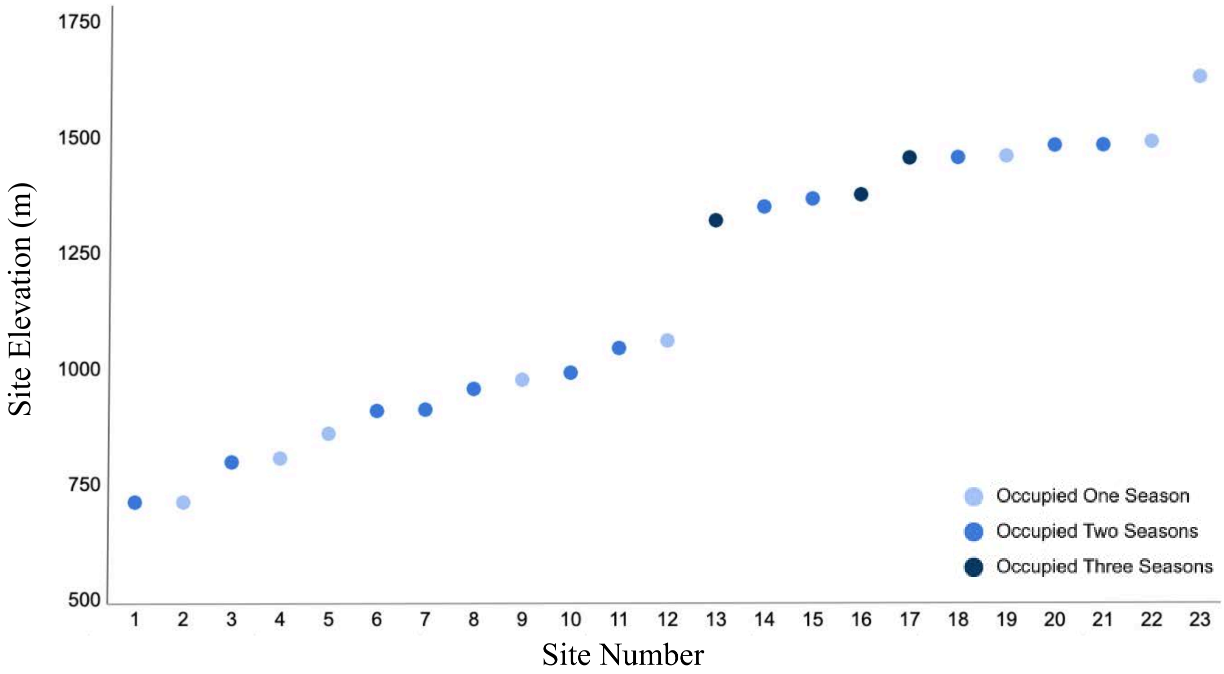

Figure 4. Seasonal occupancy of sites (n=23) with identified *P. welleri* populations across an elevational gradient in the Southern Appalachian Mountains in Tennessee and North Carolina. Light blue points represent plots occupied by *P. welleri* during one of the three seasons sampled in 2022. Medium blue points were occupied during two sampling seasons, and dark blue points were occupied during all three sampling seasons of 2022.

Detection Covariates

For the spring primary sampling period, the best supported model to explain the trends in detection of *P. welleri* was identified as ambient temperature (Table 5) with an estimated model-averaged conditional capture probability of p_{it}=0.364 (SE=0.091; Table 6). Individuals were less likely to be detected as temperatures increased in the spring, with no individuals encountered when temperatures were above 27.1°C (Fig 5). Eight additional competing models were identified, though these included the interactive effect of ambient temperature and another detection covariate. Competing models are defined as any model with a ΔAIC value $\leq$2.00.

For the summer primary sampling period, the best supported model for detection of *P. welleri* was the interaction of soil moisture and leaf litter depth (Table 5; Fig. 6). *Plethodon welleri* detections occurred when leaf litter depth was moderately shallow, under 4cm, and increased as soil moisture increased. Seven competing models were identified with a ΔAIC value $\leq$2.00. These competing models included interactions between soil moisture and days since last precipitation, leaf litter depth and days since last precipitation, cover object count, windspeed, and ground temperature (averaged over seven days prior to survey), as well as non-interactive leaf litter depth and windspeed covariates. The model-averaged conditional capture probability estimates increased from 0.364 in spring sampling to 0.430 in summer sampling (p_{it}=0.430, SE=0.107; Table 6).

For the fall primary sampling period, the best supported model for detection of *P. welleri* was relative humidity (Table 5; Fig. 7). *Plethodon welleri* individuals were encountered primarily when humidity rates were above 69.2%, though one individual was found at 33.2% humidity. The model-averaged conditional capture probability was estimated to be p_{it}=0.518 (SE=0.102; Table 6). Thirteen competing models were identified with a ΔAIC value $\leq$2.00.

Competing models included the interactions between humidity and soil pH, precipitation (total of three days prior to survey), windspeed, calendar date, cover object count, ambient temperature, days since last precipitation, canopy cover, soil moisture, ground temperature (averaged over 3 days prior to survey), and leaf litter depth, as well as the interactions between soil moisture and Julien date, and windspeed and days since last precipitation.

Table 5. Competing models selected using AIC for detection of *P. welleri* from three primary sampling seasons (spring, summer, fall). Detection covariates abbreviations can be found in Table 2. Model selection based on the number of parameters, Akaike's Information Criterion (AIC), the difference between AIC values, model weights (AICwt), and cumulative model weights (cltvWt). Additional models not shown once ΔAIC total reached 2.00. 'p' indicates detection covariate and 'psi' indicated occupancy covariate.

	nPars	AIC	ΔAIC	AICwt	cltvWt
spring					
p(AMBTEMP)psi(.)	3	110.34	0.00	0.2015	0.20
p(AMBTEMP+LLD)psi(.)	4	111.16	0.82	0.1336	0.34
p(AMBTEMP+CANOPY)psi(.)	4	111.78	1.44	0.0982	0.43
p(AMBTEMP+DATE)psi(.)	4	112.03	1.69	0.0865	0.52
p(AMBTEMP+HUMID)psi(.)	4	112.16	1.82	0.0812	0.60
p(AMBTEMP+MOIST)psi(.)	4	112.27	1.94	0.0766	0.68
p(AMBTEMP+PRECIP3)psi(.)	4	112.34	2.00	0.0742	0.75
p(AMBTEMP+PH)psi(.)	4	112.34	2.00	0.0741	0.83
p(AMBTEMP+RAIN)psi(.)	4	112.34	2.00	0.0741	0.90
summer					
p(MOIST+LLD)psi(.)	4	103.25	0.00	0.0778	0.078
p(LLD+RAIN)psi(.)	4	103.98	0.73	0.0539	0.132
p(LLD)psi(.)	3	104.13	0.88	0.0500	0.182
p(LLD+COVOBJ)psi(.)	4	104.16	0.91	0.0493	0.231
p(MOIST+RAIN)psi(.)	4	104.67	1.42	0.0382	0.269
p(WIND)psi(.)	3	104.84	1.59	0.0352	0.304
p(WIND+LLD)psi(.)	4	104.94	1.68	0.0335	0.338
p(LLD+GRDTEMP7)psi(.)	4	105.12	1.87	0.0306	0.368
fall					
p(HUMID)psi(.)	3	81.88	0.00	0.0783	0.078
p(HUMID+PH)psi(.)	4	82.18	0.29	0.0676	0.146
p(HUMID+PRECIP3)psi(.)	4	82.20	0.32	0.0669	0.213
p(HUMID+WIND)psi(.)	4	82.25	0.37	0.0652	0.278
p(HUMID+DATE)psi(.	4	82.75	0.87	0.0507	0.329
p(HUMID+COVOBJ)psi(.)	4	82.80	0.91	0.0497	0.378
p(MOIST+DATE)psi(.)	4	83.06	1.18	0.0434	0.422
p(AMBTEMP+HUMID)psi(.)	4	83.14	1.26	0.0417	0.464
p(HUMID+RAIN)psi(.)	4	83.30	1.42	0.0385	0.502
p(WIND+RAIN)psi(.)	4	83.73	1.84	0.0312	0.533
p(HUMID+CANOPY)psi(.)	4	83.77	1.88	0.0306	0.564
p(HUMID+MOIST)psi(.)	4	83.79	1.91	0.0302	0.594
p(HUMID+GRDTEMP3)psi(.)	4	83.80	1.92	0.0300	0.624
p(HUMID+LLD)psi(.)	4	83.88	1.99	0.0289	0.653

Table 6. Model averaged predictions of conditional capture probability for *P. welleri* from repeated surveys across three primary sampling periods, each with three secondary sampling periods in the Southern Appalachian Mountains of northwestern North Carolina and northeastern Tennessee.

Primary Sampling Period	Conditional Capture Probability (p_{it})	SE
Spring	0.364	0.091
Summer	0.430	0.107
Fall	0.518	0.102

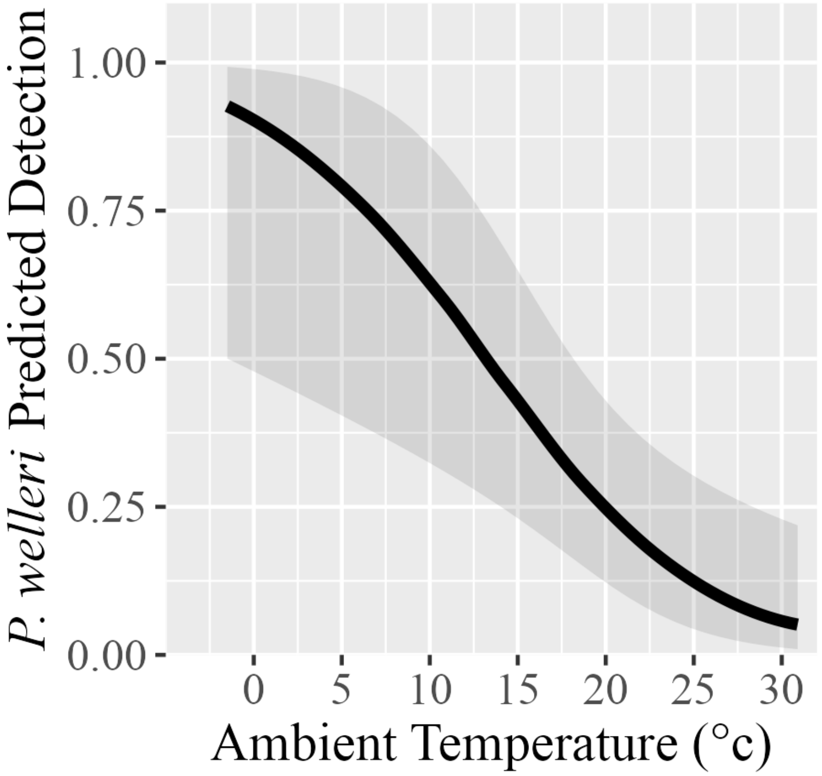

Figure 5. *Plethodon welleri* detection rate as a function of ambient temperature during spring survey period (March-May 2022). Ribbon depicts 95% confidence interval.

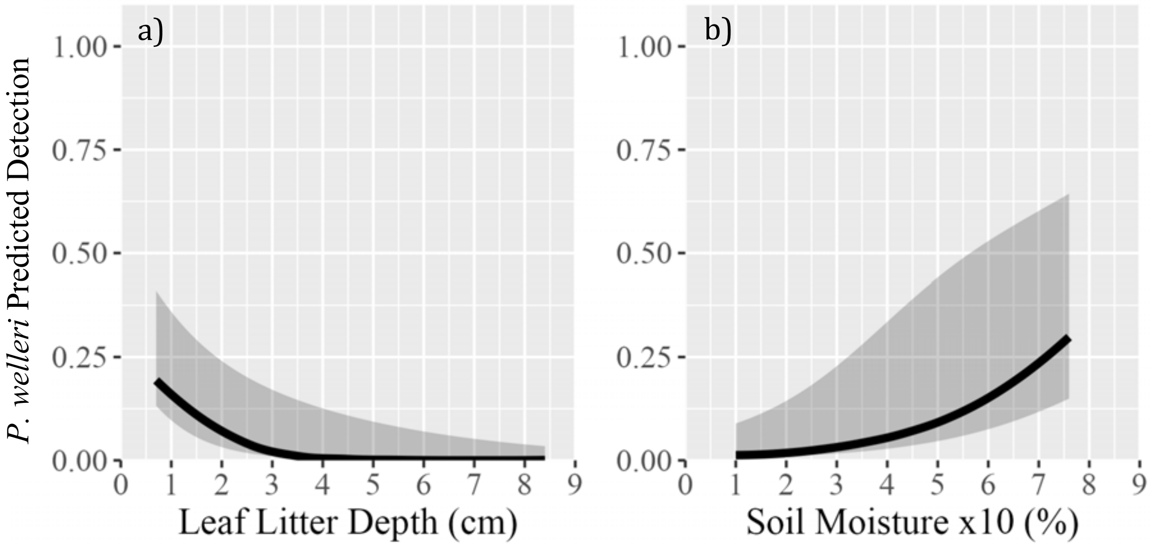

Figure 6. *Plethodon welleri* detection rate as a function of (a) leaf litter depth and (b) soil moisture during the summer sampling period (June-August 2022). Ribbon depicts 95% confidence interval.

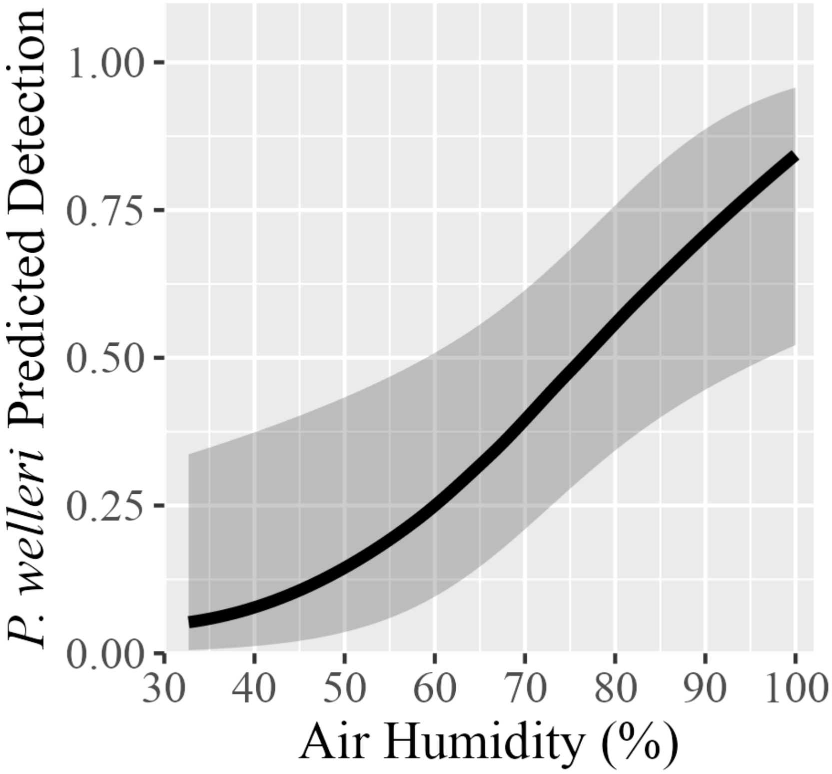

Figure 7. *Plethodon welleri* detection rate as a function of humidity during the fall sampling period (September-November 2022). Ribbon depicts 95% confidence interval.

Occupancy Probabilities

Plethodon welleri was found to have higher estimates of occupancy in both spring and fall sampling periods than in the summer sampling period. For the spring sampling period, initial model selection identified the null model as the best supported occupancy model (Table 7). Due to the proximity of AIC scores between this and competing models, I elected to use the terrain ruggedness index as the top model, with occupancy probability increasing as TRI value increased. The model averaged estimate of occupancy probability in the spring sampling period was 0.602 (SE=0.141; Table 8; Fig. 8).

For the summer sampling period, the best supported model for estimating occupancy of *P. welleri* was identified as topographical-position index, with a positive relationship of increasing occupancy as TPI increased (Table 7). Six other competing models were identified, including northness, terrain-roughness index, elevation, our null model, and heat-load index. This sampling period had the lowest model-averaged estimates of occupancy across seasons (ψ=0.278, SE=0.079; Fig. 9).

For the fall sampling period, the elevation of survey plots was identified as the best indicator of *P. welleri* occupancy (Table 7). Occupancy of *P. welleri* was negatively influenced by elevation in this season, with lower elevation sites being more likely to be occupied than higher elevation plots. The model averaged estimate for occupancy probability of *P. welleri* in the fall was lower than that of the spring sampling period, but higher than the summer sampling period (ψ=0.466, SE=0.11; Fig. 10). There were no competing models with a ΔAIC score of <2.00 for estimating occupancy in the fall sampling period.

Table 7. Competing models selected using AIC for occupancy of *P. welleri* from three primary sampling seasons (spring, summer, fall). Detection and occupancy covariates abbreviations can be found in Table 2. Model selection based on the number of parameters, Akaike's Information Criterion (AIC), the difference between AIC values, model weights (AICwt), and cumulative model weights (cltvWt). Additional models not shown once ΔAIC total reached 2.00. 'p' indicates detection covariate and 'psi' indicated occupancy covariate.

	nPars	AIC	ΔAIC	AICwt	cltvWt
spring					
p(AMBTEMP)psi(.)	3	110.34	0.00	0.26343	0.26
p(AMBTEMP)psi(TRI)	4	110.66	0.32	0.22477	0.49
p(AMBTEMP)psi(TPI)	4	112.18	1.85	0.10472	0.59
p(AMBTEMP)psi(HLI)	4	112.21	1.87	0.10333	0.70
p(AMBTEMP)psi(EAST)	4	112.25	1.91	0.10152	0.80
p(AMBTEMP)psi(NORTH)	4	112.30	1.97	0.09856	0.90
summer					
p(MOIST+LLD)psi(TPI)	5	102.03	0.00	0.1804	0.18
p(MOIST+LLD)psi(NORTH)	5	102.43	0.40	0.1478	0.33
p(MOIST+LLD)psi(TRI)	5	102.48	0.45	0.1444	0.47
p(MOIST+LLD)psi(ELEV)	5	102.50	0.47	0.1426	0.62
p(MOIST+LLD)psi(.)	4	103.25	1.22	0.0980	0.71
p(MOIST+LLD)psi(HLI)	5	103.39	1.36	0.0915	0.80
fall					
p(HUMID)psi(ELEV)	4	78.04	0.00	0.55161	0.55

Table 8. Model averaged predictions of occupancy probability for *P. welleri* from repeated surveys across three primary sampling periods, each with three secondary sampling periods in the Southern Appalachian Mountains of northwestern North Carolina and northeastern Tennessee.

Primary Sampling Period	Occupancy Probability (ψ)	SE
Spring	0.602	0.141
Summer	0.278	0.079
Fall	0.466	0.11

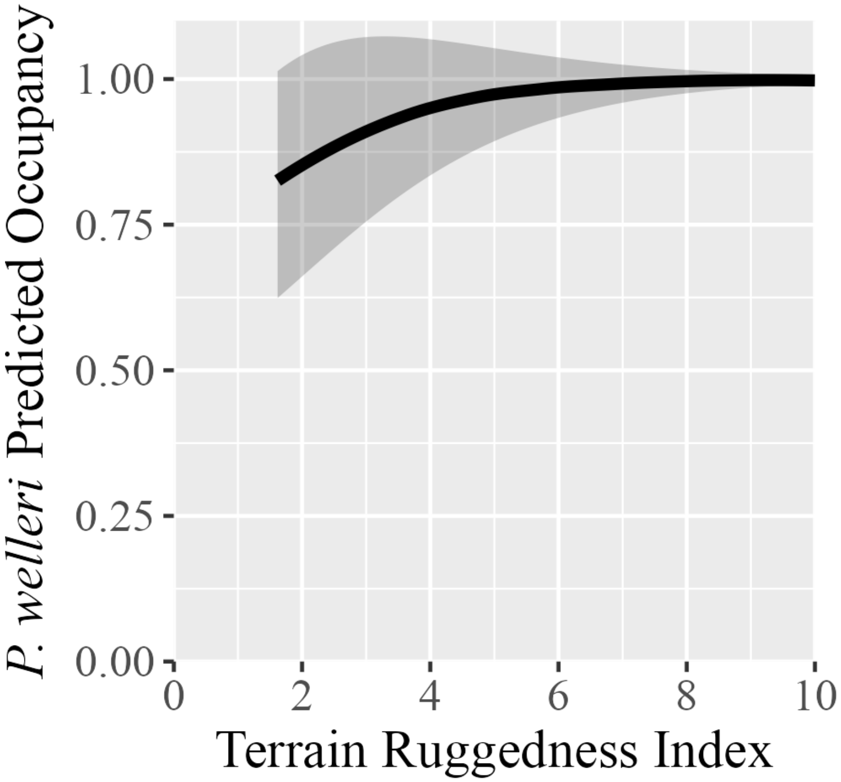

Figure 8. Occupancy probability of *P. welleri* in spring sampling period (March-May) is positively related to terrain-roughness index. Ribbon detects 95% confidence interval.

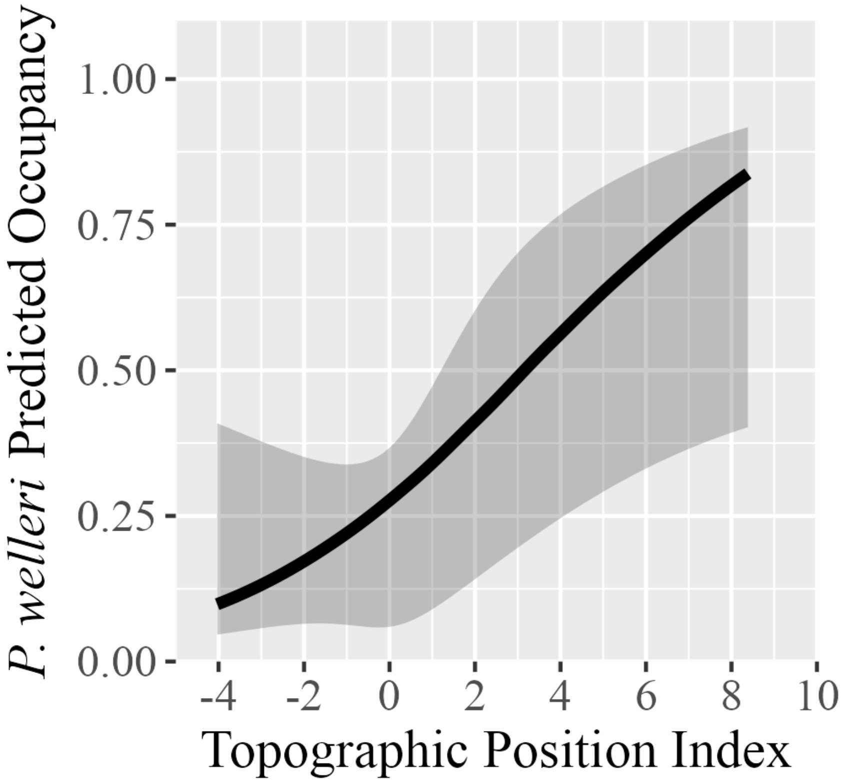

Figure 9. Occupancy probability of *P. welleri* in summer primary sampling period (June-August) is positively related to topographic position index. Ribbon depicts the 95% confidence interval.

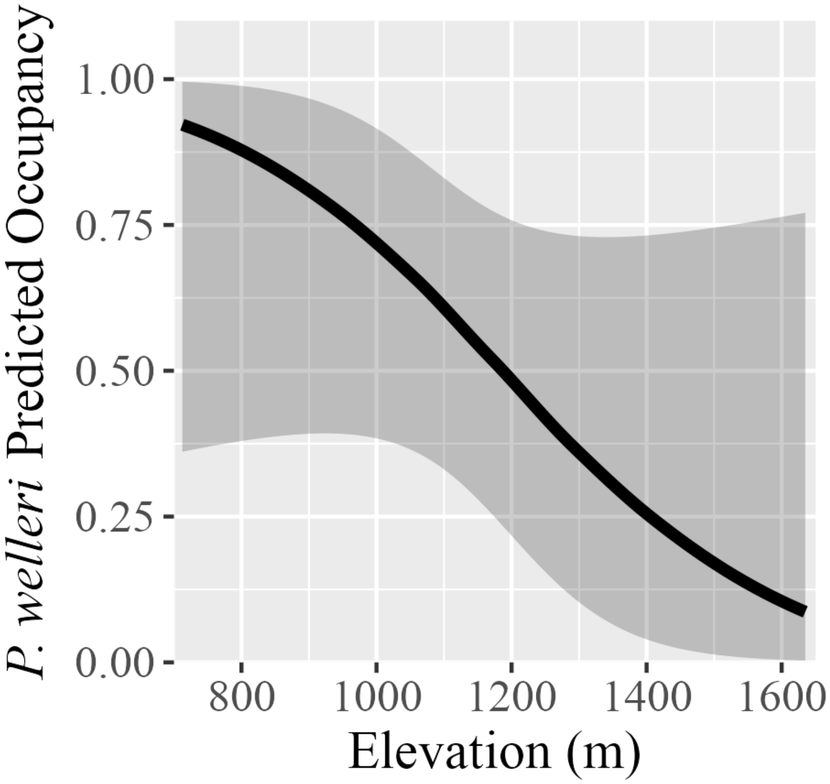

Figure 10. Occupancy probability of *P. welleri* in fall primary sampling period (September-November) is negatively related to elevation of survey plots. Ribbon depicts the 95% confidence interval.

Discussion

Using a hierarchical occupancy modelling framework, I was able to estimate seasonal occupancy, and detection probabilities of *P. welleri* throughout the North Carolina and Tennessee portion of their range. I found evidence that the occupancy of *P. welleri* ranged between 0.278 and 0.608 seasonally in 2022 and was most influenced by the geographic position of the sites surveyed. I also found that surface activity of *P. welleri* was highest in the fall season, indicating that this may be a primary activity season for this species. This corresponds to fall being the primary mating season for *P. welleri,* when males and females engage in courtship behaviors. Detection estimates revealed that temperature and microhabitat availability affect surface activity patterns of *P. welleri.* Overall, the data collected in this study supported the idea that microclimatic conditions are primary drivers for plethodon species and suggests that access to surface level refugia influences the presence of *P. welleri* populations at a location (Farallo and Miles 2016).

Understanding the distribution patterns of endemic species, especially those that are considered rare or threatened, in the Southern Appalachian Mountains is of vital importance for conserving the biodiversity of this region in the future. Many of the endemic plethodon species in the southern Appalachian Mountains, including *P. hubrichti* and *P. punctatus*, have narrow distributions and may have less adaptive potential to respond to climate change than those with wider ranging distributions (Markle and Kozak 2018). Presently, many Plethodontid salamanders endemic to this region are commonly restricted to montane habitats, with climatic conditions at lower elevations restricting occupancy and colonization ability (Kozak and Wiens 2006). In the face of changing climate, suitable habitats for many Plethodon salamanders are projected to disappear and could result in the loss of connectivity between populations (Milanovich et al.

2010, Jacobsen et al. 2020), which in turn may lead to a reduction in gene flow and genetic variation of species (Rowan et al. 2022). *Plethodon welleri* was indeed found to have limited gene flow between populations due to a lack of connectivity between populations (Forester 2017). However, distributional patterns (population presence at a variety of elevations and climatic characteristics) suggests this species may have the adaptive capacity to withstand rising temperatures (Forester 2017). Additionally, a recent study suggested that the effects of climate change may be milder in some portions of the Southern Appalachian Mountains than in other mountainous regions of the United States, with the mountains on the northern portion of the Tennessee/North Carolina border potentially seeing only a moderate decline in mean winter temperatures (Eck et al. 2018). Changes to precipitation trends have also been found to be milder in the Southern Appalachian Mountains as opposed to the broader southeastern United States, with warm seasons experiencing more frequent precipitation events with decreased dry spell lengths (Kinlaw et al. 2019). These trends will likely lead to longer active periods for plethodontid species in this region with reduced risks of desiccation in summer months and more hospitable surface conditions in the winter. These studies suggest that *P. welleri* may have a greater buffer to future disturbances and climate change than previously thought, though these factors still pose a threat to the long-term survival of this species.

Within the genus plethodon, one of the major drivers of distribution patterns is access to suitable climatic conditions that are required for reproduction, cutaneous respiration, and overall species survival (Feder 1983, Milanovich et al. 2010). Using hierarchical occupancy models to estimate detection and occupancy of *P. welleri*, I found that environmental conditions heavily influenced surface activity throughout the three primary seasons sampled. Specifically, surface activity was highest during cool, moist conditions, where the risk of evapotranspiration and desiccation was lower (Spotila 1972, Riddell and Sears 2015). Occupancy of a site was influenced by the elevational position of the site relative to the surrounding landscape (Figs. 5-7), characteristics of which relate to the levels of solar radiation and severity of seasonal climatic shifts that may alter soil characteristics, thus affecting plethodontid salamanders. Directional shifts in site occupancy by *P. welleri* across the elevational gradient surveyed supports my hypothesis of strict seasonal activity patterns of *P. welleri*, with high elevation occurrences being primarily focused to summer months.

Detection Estimates

The detection estimates for *P. welleri* determined in this study ranged between 0.364-0.518 in the 2022 field season. This means that we had an ~36-52% chance of encountering an individual at a study plot given that they occurred at the plot during the time of survey. These estimates are consistent with other natural cover object studies investigating plethodontid species in this region. Bailey et al. (2004*a*) estimated occupancy and detection of seven plethodontid species from 1999-2001. The detection estimates from their 1999 study season ranged from 0.32-0.67 and declined for six of the species in the 2000 and 2001 seasons. Similarly, a 2009 study found the detection rates of *P. cinereus* were 0.59 ± 0.07 within 6 forest stands in Michigan when conducting natural cover object surveys (Otto and Roloff 2011). Lastly, a 2018 study found the detection rates of *P. richmondi and P. kentucki* in southeastern Kentucky to be 0.36 and 0.24, respectively (Baecher and Richter 2018). Thus, my data for *P. welleri* surface activity trends are similar to those of other Plethodon species, and the majority of individuals at an occupied site were likely occupying subterranean refugia despite surface-level microhabitat availability.

Throughout the 2022 survey periods, detection of *P. welleri* was influenced strongly by environmental variables relating to temperature and moisture availability. These covariates are known to affect desiccation risk, specifically with activity occurring primarily when desiccation risks would be lower (i.e., moderate air temperatures, moisture collections within or under leaf litter cover, and higher air humidity levels). In the spring season, detections occurred between -1.5°C and 27 °C, which is typical of plethodontid salamanders as temperature extremes lower metabolic rates and reduces movement ability in cold weather (Vernberg 1953, Leclair et al. 2008, Sanchez et al. 2020) or increases evaporative risk in hot weather (Spotila 1972). In the summer, models indicated that leaf litter depth and soil moisture were the most influential detection covariates. Specifically, *P. welleri* individuals were most likely to be encountered when there was sufficient ground coverage by leaf litter and ground water collections in the soil to maintain their dermal moisture layer. Baecher and Richter (2018) similarly found that soil moisture affected the density of *P. richmondi* in old-growth Appalachian forests in Kentucky, in addition to reduced solar radiation and generally mesic conditions. Additionally, fall detection was positively correlated with humidity, meaning *P. welleri* individuals were more likely to be detected at the surface when humidity levels were higher, which supports previous findings that plethodon salamanders prefer higher levels of humidity when surface active (Spotila 1972, Hocking et al. 2021, Rucker et al. 2022).

Salamanders from the family Plethodontidae are lungless meaning that they rely entirely on cutaneous respiration for gas exchange (Feder and Burggren 1985, Petranka 1998), and those in the genus plethodon, such as *P. welleri,* have the added challenge of being fully terrestrial. Thus, the risk of evapotranspiration and desiccation are significant factors in determining surface activity levels and foraging seasons of plethodon Salamanders (Spight 1968, Spotila 1972, Riddell and Sears 2015, Farallo et al. 2018). The findings regarding *P. welleri* detection patterns from this study are in line with other studies regarding the effects of desiccation on similar plethodon species. Jaeger (1978, 1980) illustrated the importance of moisture retaining leaf litter in facilitating foraging of ground dwelling plethodon salamanders where the environmental ambient temperature affected the ability of *P. cinereus* to find and consume prey. As with previous research, my research reinforces how vital it is for these salamanders to be active when climatic conditions are suitable for maintaining a protective moisture barrier across their dermal surface.

Occupancy Estimates

My study also examined the effects of several environmental covariates on the likelihood that *P. welleri* would occupy a site. Over the course of the 2022 sampling seasons, nine of the 17 sites surveyed were occupied by *P. welleri*. My models indicated that occupancy was highest in the spring season, with ~60% probability of any site within the study range being occupied by *P. welleri* (Fig. 8). Specifically, I found that occupancy was influenced by terrain ruggedness, topographic position, and elevation. Based on the data collected, seasonal patterns in occupancy show that *P. welleri* are most likely to occur at sites with heightened levels of heterogeneity in the spring compared to its surrounding habitat (described by the terrain ruggedness index), primarily at the level of geological formations influencing small-scale changes in elevation. It should be noted that in general, TRI values in the southern Appalachian Mountains are low, as reflected in this study. This is likely due to the southern Appalachians being made up of a fine-scaled mosaic of closed forests, open fields, and wetlands, with finer-grained geographical heterogeneity due to geological formations beneath the surface. Summer occupancy is correlated to topographic position, with *P. welleri* apparently selecting against ravines and valley habitats, preferring habitats higher up on slopes. Finally, *P. welleri* occupancy in the fall was negatively correlated with plot elevation, with this species primarily occurring at sites under 1000m (3,281 ft). It is important to consider that elevation in the southern Appalachian Mountains has been found to act as a surrogate for mean temperature and precipitation, with temperatures decreasing and precipitation increasing as elevation increases (Donley and Mitchell 1939, Dickson 1959). This indicates that *P. welleri* primarily occupies areas with warmer temperatures and moderate precipitation in the fall, possibly due to higher elevation sites being more prone to cold temperatures, and freezing precipitation events.

These site characteristics have previously been investigated surrounding plethodon salamanders in the Southern Appalachians, though the results of previous studies have differed from those of my study. Terrain ruggedness was not found to commonly affect the occupancy patterns of plethodon salamanders in this region, which may indicate that *P. welleri* is more selective for topographical formations than other species found in this region and could be a reason for *P. welleri* being less common. Though topographic position has been found to affect the abundance of *P. kentucki and P. shermani* across portions of their ranges (Connette and Semlitsch 2013, Baecher and Richter 2018), it has not been found to have any apparent influence on the occupancy status of a site for other plethodon species. Elevation, however, is commonly recognized as having an influence on distribution patterns of plethodon salamanders (Buhlmann et al. 1988, Bailey et al. 2004*b*, Gade and Peterman 2019).

Given that *P. welleri* co-occurs with other plethodontid species across their range, habitat selection may be an example of interspecific niche partitioning, as areas with higher levels of topographic variation can significantly increase the species richness of plethodon salamanders in the Eastern United States (Marshall and Camp 2006). Over the course of this study, I observed *P. welleri* individuals occurring within 5m of *P. yonahlossee*, *P. cinereus, P. richmondi, P. montanus, P. cylindraceus, D. organi, D. orestes,* and *E. wilderae* individuals. This suggests that there is likely some degree of resource partitioning between species to support these overlaps. However, the competition and resource interactions between *P. welleri* and co-occurring species have yet to be studied and were not accounted for in my study. Future research investigating potential interspecific interactions could give insight into occupancy and detectability patterns, as well as potential responses to disturbances (Bailey et al. 2009, Gilman et al. 2010). This pattern of *P. welleri* being found in highly diverse communities was surprising when considering the original classification as being a habitat specialist, and points to this species potentially being more generalized in habitat requirements.

Despite the historical records and observations indicating that the distribution of *P. welleri* were likely limited to elevations higher than 1500m and largely associated with Spruce-Fir habitats, my study does not support these claims. I encountered populations across a large elevational gradient (720-1600m), and in a variety of habitat types including spruce-fir and hardwood-dominant (Oak, Birch, Maple, Beech, or Tulip Poplar) forests. Many of the lower elevation populations surveyed in this study are associated with previously documented high elevation populations, though several populations were found on mountains that do not reach elevations of 1500m. This study resulted in the discovery of three previously undocumented populations of *P. welleri* in the Tennessee portion of their range, all of which were found below 1500m, suggesting that future explorative search efforts may result in further expanding the distribution of *P. welleri*. These populations have been reported to state wildlife officials but are not being identified here due to conservation concerns.

Conclusions

The results of this study provide evidence that *P. welleri* does not have strong elevational associations as previously thought and could be considered a habitat semi-generalist instead of specialist, as their distribution, though patchy, encompasses a variety of habitat types. The expected elevational range for this species can be expanded to ~700m as the lower limit and increased to 1600m+ for their upper limit. Given the associations between the environmental conditions and activity of *P. welleri* as have been identified in this study, it is likely that the lower elevational limit of this species is determined by climate as opposed to biotic conditions such as interspecific interactions. This is opposite of the established North-South Hypothesis stating that southern/ lower elevation limits are set by biotic interactions, such as competition, while northern/ higher elevation limits are controlled by abiotic conditions (MacArthur 1984). Indeed, many amphibian studies have found a reversed effect on elevational trends, which may be further supported by the results of this study (Gifford and Kozak 2012, Cunningham et al. 2016, Lyons et al. 2016, Caruso et al. 2019, Paz and Guarnizo 2020). This association between lower elevational range limits and climatic conditions was illustrated in a study of *P. shenandoah*, a localized endemic within Shenandoah National Park in Virginia (Grant et al. 2018). It was found that the presence of cloud cover was a primary driver for the persistence of *P. shenandoah*, due to either the direct (increased humidity) or indirect (moss presence) effects this would have on microclimate conditions. Though I did not measure distance to nearest stream as a site-level covariate to determine occupancy in this study, a previous study focusing on *P. shermani* found that salamander abundance at lower elevations may be more associated with nearby streams while higher elevation populations are able to occur more easily further away from streams (Gade and Peterman 2019). Through the course of my study, I saw a pattern between our lower elevation populations often being within ~50m of the nearest intermittent or ephemeral streambeds, though this relationship was not tested statistically. Because *P. shermani* and *P. welleri* share characteristics (limited ranges and smaller population sizes), investigating the relationship between *P. welleri* abundance and stream presence may reveal additional information into the environmental parameters affecting the lower elevational range limit of *P. welleri.*

Additionally, populations of *P. welleri* were found to occur with other plethodontid salamander species with range overlap in this region (*Plethodon cinereus, P. richmondi, P. cylindraceus, P. yonahlossee, P. montanus, Desmognathus organi, D. orestes, and Eurycea wilderae*). This suggests that interspecific competition may not exclude *P. welleri* from suitable habitat across the majority of their elevational range, though it may affect the abundance of this species where ranges overlap. For example, researchers have shown that the effects of interspecific interactions between the broadly distributed *P. cinereus* and small-ranging *P. shenandoah* may be responsible for microhabitat partitioning in overlap zones (Amburgey et al. 2019, 2020). Resource partitioning, such as for food and habitat, is a potential driving force for competitive interactions between *P. welleri* and other small-bodied plethodon species, and further studies are needed to understand how these interactions may affect distribution and abundance patterns. Future models investigating these relationships will be invaluable for determining the community structures surrounding *P. welleri* and guiding conservation efforts, and population abundance estimates across *P. welleri's* range would be beneficial when assessing species and population trends.

The trends in occupancy of *P. welleri* throughout my 2022 study also provide evidence that the primary active seasons of *P. welleri* are the spring and fall months. The data show a steep decline in occupied sites from the spring to the summer, with a significant increase in the proportion of sites occupied in the fall months. This trend is likely reflecting the adaptive behavior seen in plethodon salamanders to seek refuge underground through vertical migrations when surface level conditions are not ideal (Riddell and Sears 2015, Riddell et al. 2018). While environmental patterns of high temperatures and low humidity in the summer months are seen at lower elevations, higher elevation habitats (particularly Spruce-Fir habitats) are known to harbor higher levels of humidity and remain cooler throughout the summer (Berry and Smith 2013). As such, sites that were labelled as occupied by *P. welleri* during the summer sampling season likely reflected habitat that maintained suitable conditions (primarily at high elevations) while other low elevation sites are more suitable for *P. welleri* during spring and fall months. Elevation-dependent climatic characteristics have also been shown to create an environmental gradient of suitable surface habitat surrounding riparian zones at lower elevations in the Southern Appalachian Mountains, leading to increased abundance patterns of plethodontid salamanders in these areas (Gade and Peterman 2019). This could also serve as an explanation for the discrepancy in expected elevation range and current population locations of *P. welleri* found in historical observations from summer months.

Management Implications

Though the current study does not address every facet of the population ecology of *P. welleri*, I have expanded our foundational knowledge of population and habitat parameters for future studies. Ultimately, understanding the activity patterns, distribution, and habitat parameters of *P. welleri* will provide a baseline of knowledge and allow further research into the threats to this species. Addressing data deficiencies and increasing our understanding of the population ecology and ecological requirements of understudied, endemic, or endangered species is vital for developing effective wildlife management plans. For species that are labelled as data-deficient, it is nearly impossible to accurately assess their needs and threats in order to provide protective measures aimed at conserving these species. Based on historical descriptions of *P. welleri*, an endemic salamander species, there has been concern over it's extinction risk. Currently, *P. welleri* is listed by the IUCN as endangered with decreasing population trends. *Plethodon welleri* is included in the Wildlife Action Plans for the three states it occurs in (North Carolina, Tennessee, and Virginia), and receives protections from state agencies (NCWRC 2015, TWRA 2015, Virginia DWR 2015) . Unfortunately, the lack of data or updated information on *P. welleri* means that when petitioned in 2015, the US Fish and Wildlife Service denied this species from being included on the Endangered Species Act and receiving federal protections (U.S. Fish and Wildlife Service 2015).

Though there are still many threats facing *P. welleri*, my study indicates that this species is at a lower risk of extinction than previously thought. Despite abundance estimates having not been completed, it is clear that *P. welleri* is distributed across a much larger range of elevations and habitats than previously thought. It appears that mitigating desiccation risk is likely a driving factor for both current distribution and activity patterns of this species across seasons. In this regard, managing lower elevation habitats to ensure access to cover objects and ground water sources in addition to reducing disturbances that may fragment populations or destroy habitat may be a beneficial goal for conservation management planning. Lower elevation populations were found to disappear in the summer months, likely migrating vertically in the soil in search of refuge for the hottest and driest part of the year. With the current climate predictions for the Southern Appalachian region, the changes in precipitation and temperature may result in longer periods of unsuitable surface conditions and could lead to shifts in activity to begin earlier in the spring or lasting later into the fall, localized extinctions of low-elevations *P. welleri* populations or, in extreme cases, this species truly becoming restricted to only high elevations. The knowledge uncovered in this study, though limited to only a foundation level of ecological preferences of this species, can be used to better evaluate the quality of habitats for *P. welleri* and should be considered in future management plans, whether species specific or umbrella plans aimed to protect the high levels of biodiversity in the Southern Appalachian Mountains.

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Vita

Rosemary Ronca was born in Decatur, GA on January 9, 1998. Her love of nature was fostered from a young age of exploring local woods and creeks and visiting the North Georgia Mountains. She continued to grow this love of the outdoors as she attended and later worked as a counselor at Camp Juliette Low, a non-profit summer camp focusing on growing confidence, leadership, and independence in young girls in the North Georgia Mountains. She attended Hendrix College in Conway, AR, where she earned her Bachelor of Arts in Biology in 2020 and discovered her passion for ecology and conservation. While attending Hendrix College, she had the opportunity to intern with the Galápagos Conservancy, a U.S. based conservation agency working to protect and restore the biodiversity found on and around the Galápagos Islands. She then decided to continue her studies at Appalachian State University in 2021, where she further explored her passion for herpetology, conservation, and field biology while working with Dr. Jon Davenport. She earned her Master of Science in Biology from Appalachian State University in December 2023.