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**Setting the Baseline: Estimates of Current Elevational Distributions for Understanding Future Climate Effects**

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**Abstract**

Climate change is expected to systematically alter the distribution and population dynamics of species around the world. The effects are expected to be particularly strong at high latitudes and elevations and for ectothermic species with small ranges and limited movement potential, such as salamanders in the southern Appalachian Mountains. There is currently a lack of historic data collected in a way that allows for unbiased estimation of abundance for these salamanders. In this study, we sought to establish baseline abundance estimates for plethodontid salamanders (family: Plethodontidae) over an elevational gradient in Great Smoky Mountains National Park. In addition to generating this baseline data for multiple species, we describe methods for surveying salamanders that allow for meaningful comparisons over time by separating observation and ecological processes generating the data and we emphasize the value gained through abundance estimation compared with coarser occupancy estimation. We found that Jordan’s Salamander and Pygmy Salamander increase in abundance with elevation, whereas the Blue Ridge Two-lined Salamander has a mid-elevation peak (1270 m) in abundance but occurred with high probability all the way to the highest elevations in the national park (2025 m). In addition to elevation, slope, ground cover, litter depth, and distance to the nearest stream were important predictors of abundance depending on the species, whereas daily temperature, precipitation, and humidity influenced detection rates. Understanding these patterns along with detailed baseline distributions will be critical for comparison with future surveys to understand the population and community-level effects of climate change on montane salamanders. The southern Appalachian Mountains have experienced little change in temperature or precipitation over the past century but are expected to change rapidly in the future. Our data provides some of the first minimally biased information for future studies to assess changes in the abundance and distribution of salamanders in this region vulnerable to climate change stressors.

**Keywords**

**Introduction**

Climate change is a major force of biotic change worldwide. Rising temperatures and changing patterns of precipitation are known to affect phenology ([Blaustein et al. 2001](#_ENREF_4), [Beebee 2002](#_ENREF_3)), species interactions ([McKone et al. 1998](#_ENREF_41), [Winder and Schindler 2004](#_ENREF_79)), physiology ([Wang and Polglase 1995](#_ENREF_77), [McCain and Sanders 2010](#_ENREF_40), [Somero 2010](#_ENREF_69)), diversity ([McCain 2004](#_ENREF_36), [2009](#_ENREF_37), [McCain and Grytnes 2010](#_ENREF_39)), and the distribution of species ([Rowe 2005](#_ENREF_59), [Tingley et al. 2009](#_ENREF_76), [Laurance et al. 2011a](#_ENREF_29)). Many species exhibit niche tracking, the process of following limiting environmental conditions across time and space ([Moritz et al. 2008](#_ENREF_44), [Tingley et al. 2009](#_ENREF_76)). With warming temperatures, species are expected to move latitudinally towards the poles and higher in elevation in montane regions. However, not all species move in directions predicted by changing temperature due to other factors such as precipitation, land cover change, competition with resident species, and inability for rapid migration ([Rowe 2009](#_ENREF_61), [Rowe et al. 2010](#_ENREF_62), [Laurance et al. 2011a](#_ENREF_29)). Understanding the capacity of organisms to adapt and shift geographic ranges in response to rapid climate change is a major challenge facing ecologists and conservation practitioners who want to take action to protect or manage species ([Loarie et al. 2009](#_ENREF_31)).

Montane regions offer advantages for studying changes in animal distributions associated with climate change. Climate change effects are expected to be observed earlier and more consistently over elevational gradients than over larger latitudinal gradients ([Shoo et al. 2006](#_ENREF_67), [Sekercioglu et al. 2008](#_ENREF_65), [Sodhi et al. 2008](#_ENREF_68)). Species may have greater ability to move over an elevational gradient than a latitudinal gradient in response to climatic change because there are often fewer human-created barriers, and the physical distance to track a favorable climate niche is more likely within the dispersal distance for many organisms. Additionally, the steepness of the gradient allows researchers to conduct more thorough surveys compared with having to cover much larger areas across a species’ latitudinal gradient. Finally, montane regions have the potential to compress species at the tops of the mountains and create “sky islands” for species unable to move between suitable mountaintop habitats ([Milanovich et al. 2010](#_ENREF_43), [Gifford and Kozak 2011](#_ENREF_17), [Laurance et al. 2011a](#_ENREF_29)).

There has been little consensus on which traits impact a species’ ability to shift their range in response to changing climates’ ([Angert et al. 2011](#_ENREF_2)). The ability to track an existing climatic niche may be influenced by dispersal capabilities, life history, behavioral traits, diet breadth, specific habitat needs, and landscape characteristics. Laurance et al. ([2011a](#_ENREF_29)) suggested high elevation specialists are at greater risk of extinction due in part to the higher frequency of specialization among ectotherms compared with endotherms. As such, groups like montane salamanders may be especially vulnerable to climate-induced extinction. The southern Appalachian Mountains are home to the greatest diversity of salamanders in the world. In addition to having high elevation specialists in close proximity to congeneric low elevation species, this region supports species with a variety of life history traits (e.g. fully aquatic to fully terrestrial) and body sizes (e.g., 0.1 – 2,200 g). The diversity, high endemism, low vagility, and range of life history traits make salamanders in the southern Appalachian Mountains ideal for understanding elevational distributions and responses to climate change. Furthermore, recent studies suggested that southern Appalachian salamanders are declining in abundance and range ([Highton 2005](#_ENREF_21), [Caruso and Lips 2012](#_ENREF_6), [Adams et al. 2013](#_ENREF_1)) and possibly shrinking in body size ([Caruso et al. 2014 but see Peterman et al. In press](#_ENREF_7), [Peterman et al. In press](#_ENREF_48)). However, the baseline for comparison and the accuracy of these estimates have been questioned ([Connette et al. 2015](#_ENREF_9), [Grant 2015](#_ENREF_20)).

Understanding climate effects on species over elevational gradients is hindered by limitations of existing data. There is a wealth of recent and historic presence-only data from museum records and opportunistic reports, but the lack of systematic surveys limits the utility of these data ([Kery et al. 2006](#_ENREF_27), [Grant 2015](#_ENREF_20)). Opportunistic presence-only data can only be used to determine the minimum extent of a species range and resurveying of these areas only provides information about extinctions. It does not provide information on colonization, range expansions, or range shifts because there is no information about where the species did not occur ([Tingley and Beissinger 2009a](#_ENREF_73)). Additionally, systematic surveys without temporal replication have biased range estimation because false absences under-predict historic range and extinction while over-predicting colonization ([Tingley and Beissinger 2009a](#_ENREF_73)). Recent statistical developments using a combination of spatial and temporal replication allow for reduced bias of colonization and extinction estimates ([Mackenzie et al. 2002](#_ENREF_32), [MacKenzie et al. 2006](#_ENREF_33), [MacKenzie et al. 2009](#_ENREF_34)) and unbiased estimates of abundance across gradients, even in fluctuating populations ([Royle 2004](#_ENREF_63), [Royle and Dorazio 2008](#_ENREF_64), [Dail and Madsen 2011](#_ENREF_13)).

Accurate spatial distributions along elevational gradients are critical to understanding the impact of climate change on species ranges and extinction risks, but a lack of adequate abundance data has inhibited the understanding of climate change effects on range shifts and species declines in montane regions ([Shoo et al. 2005](#_ENREF_66)). Hierarchical models of abundance have great potential for estimating climate-driven range shifts and predicting the probability of extinction under various climate scenarios. These models offer the possibility of addressing concerns raised by Shoo et al. ([2005](#_ENREF_66)) and more accurately delineating ranges shifts.

Our objectives in this study were to:

1. Estimate salamander abundance along an elevational gradient in Great Smoky Mountains National Park (GSMNP) while accounting for imperfect detection using repeated spatial and temporal surveys.
2. Evaluate habitat effects on abundance and detection for species with different life history traits.
3. Highlight the importance of abundance, rather than occupancy, for monitoring population changes in space and time.

**Methods**

*Study Site*

We identified 70 potential survey sites along an elevational gradient (412 to 2,025 m a.s.l.) in GSMNP. We selected sites along route 441 from Tennessee to North Carolina and along Spur Road to the top of Clingman’s Dome (highest point in GSMNP, 3rd highest peak in eastern USA) that were within 2 km (overland walking distance) of vehicle pull-offs and a minimum of 800 m from each other to facilitate safety during nighttime surveys. We then randomly selected 45 sites (of the 70 available) for sampling: 15 at high elevation (1,501 – 2,025 m a.s.l.), 15 at mid elevation (1,001 – 1,500 m), and 15 low elevation (412 – 1,000 m). Before the first survey, we added 3 additional sites from our initial 70 to get a more even distribution over the elevation gradient on both sites of the continental divide. This resulted in 48 sites over XX km ranging in elevation from 412 m to 2,025 m (Figure 1). At each site, we established 2 – 6 transects (mean = 4.1) based on accessibility (total transects = 195). Each 25 x 4 m transect was located ≥ 50 m from the road. Transects at a site were separated by a minimum of 10 m. The geographic position (latitude and longitude) of the start and end of each transect was recorded using a handheld GPS (precision ~ 3m; Garmin 62sc).

At three of the 15 mid-elevation sites, it was impossible to effectively survey for salamanders due to the density of shrubs (*Rhododendron* spp*.* and *Leucothoe* spp*.*). Therefore, we conducted surveys at three mid-elevation sites on small recreational trails (1–3 m wide). To account for potential differences in detection on trails compared with undisturbed forest habitat, we also conducted adjacent forest and trail transects at some high and low elevation sites (e.g., 4 forest transects and 2 trail transects), resulting in 70 of 195 (36%) transects conducted on trails. The potential effect of trail was included in all statistical models (see below), but prior analyses found no significant differences between transects on trails and transects in undisturbed forest habitat ([Milanovich et al. 2015](#_ENREF_42)).

*Salamander Sampling*

We conducted nighttime visual encounter surveys (VES) along transects to locate surface-active salamanders — a more effective way to sample lungless salamanders compared to day-time VES ([Crawford and Semlitsch 2007a](#_ENREF_10)). For each survey, one of four observers (the authors) walked a transect and recorded the number of each salamander species observed within 2 m of either side of the center transect line, resulting in a 100 m2 transect survey area (25 x 4 m). Salamanders were not disturbed except to aid in further identification as needed. For each VES, observers spent a range from 10–20 minutes to conduct a VES on a transect depending on the terrain, density of vegetation, and number of animals that had to be handled for identification.

Visual encounter surveys were conducted on 1–6 occasions (occasion = night; mean = 4.31) on 21 nights between 13 June – 20 July 2012. At least 2 transects were visited at every site on at least 5 occasions. Observers were randomly assigned to a transect on the first occasion and then rotated through the transects at each site on future occasions to avoid potential observer bias. A transect was skipped if the surveyor was unavailable to conduct the survey on a given occasion, but our analysis framework accommodates such missing data. We randomly selected 3–5 sites from each of three elevations (stratified random transect selection within elevations; transects were never surveyed more than once on a given sampling occasion). On each occasion, we randomized the starting site then proceeded in the most convenient route to the other sites. This prevented sampling sites or specific elevations at the same time of night on each occasion. We conducted all surveys between 21:00 and 03:00 hours EDT.

*Habitat and Environmental Measurements*

We measured local habitat variables and calculated landscape metrics hypothesized to influence detection and abundance of salamanders. Along each transect at 5 m intervals, we measured percent canopy cover using a spherical densiometer, the proportion of a 1 m2 quadrat covered by vegetation, and leaf litter depth in each corner of each quadrat. We used the mean of these repeated observations to make inference on abundance and detection at the transect-level within each site. We derived landscape measures that included calculated slope, distance to the nearest stream, topographic position index (TPI), and topographic wetness index (TWI) from 10-m resolution digital elevation model (DEM) in ArcGIS (v9.3, ESRI). Topographic position represents a transect’s slope position relative to the surrounding landscape, and was calculated from a 10-m digital elevation model using a 100-m moving window ([Dilts 2010](#_ENREF_14)). Topographic wetness was calculated accounting for solar insolation ([azimuth= 180.0, altitude = 75.8; Theobold 2007](#_ENREF_72)). At the start of each survey, we recorded air temperature and relative humidity at each site using a handheld weather meter (Kestrel 4000). We derived spatial rainfall maps describing the 24 hr cumulative precipitation across GSMNP using spatial Kriging of rainfall estimates, based on temporal rainfall measures obtained from 24 weather stations located through GSMNP and immediately surrounding.

*Analyses*

We used *N*-mixture models to estimate abundance of species within each of our 100 m2 transects while accounting for imperfect detection ([Royle 2004](#_ENREF_63)). This model assumes population closure over the duration of the sampling period (5 weeks), but allows abundance to vary in response to transect-specific covariates and detection probability can vary in time (survey occasion) and space (transect and site). This model assumes that abundance is distributed following a Poisson distribution and that the probability of detecting an individual is conditional on abundance and distributed following a binomial distribution.

To incorporate the effects of covariates on abundance and detection, we used log and logit link functions, respectively. The most complicated model attempted for each species was

where mean abundance at transect *i* (*λi*) is a function of elevation, TWI, proportion herbaceous ground cover, leaf litter depth, distance to the nearest stream. We also included a random site effect (*εsite*) to account for spatial correlation in abundance among transects at a given site. For computational performance in JAGS, we used hierarchical centering for the random effect where is multiplied by the standard deviation (ref: Cole and Thorson). Detection probability was modeled as a logit-link function of air temperature, temperature squared, precipitation in the previous 24 hours, relative humidity, proportion herbaceous ground cover, and ground cover squared. We also found that detection was over dispersed with respect to the expectations of a binomial distribution so we included a random overdispersion term (*δij*) with a standard deviation of ([Kery and Schaub 2012](#_ENREF_26)).

We employed Bayesian methods to estimate the parameters of this model using Gibbs sampling in program JAGS (ref) implemented using the rjags package ([Plummer 2012](#_ENREF_52)) in program R ([R Core Development Team 2012](#_ENREF_71)). We used vague normal priors for all coefficients with a mean of zero and standard deviation of 10, parameterized with the precision term of one divided by the standard deviation squared. For the standard deviation of the random effects, we used half-Cauchy priors with a scale of 25 (refs: cole and thorson, Stan manual, other?). We ran 5 chains, each with 100,000 adaptation iterations then ran the next 600,000 iterations and saved every 60th iteration for inference (50,000 total iterations saved). We used the potential scale reduction factor ([Brooks and Gelman 1998](#_ENREF_5)) to test for model convergence as well as visual inspection of the chains. To evaluate model fit, we calculated a Bayesian *P*-value from chi-square statistics calculated for the observed compared with idealized (i.e. model-generated data) data ([Kery 2010](#_ENREF_25), [Kery and Schaub 2012](#_ENREF_26)). We assumed adequate fit when p-values > 0.25 and < 0.75.

**Results**

We captured a total of 9,522 salamanders of 14 species (Table 1). Many species had large elevational ranges in excess of 1,000 m. Blue Ridge Two-lined Salamander (*Eurycea wilderae*) was the most widely distributed ranging from our lowest survey location (447 m) to the highest peak in GSMNP (2,025 m). It is likely the species occurs at even lower elevations outside the park, beyond our survey transect. Jordan’s Salamander (*Plethodon jordani*)*,* Pygmy Salamander *(Desmognathus wright),* and Spring Salamander (*Gyrinophilus porphyriticus*) were also observed at the top of Clingman’s Dome and had observed ranges in excess of 900 m. There was uncertainty in the field identification and differentiation of Ocoee Salamanders (*Desmognathus ocoee*)and Imitator Salamanders (*D. imitator*)at the beginning of the study. Additionally, there is likely more than one species currently grouped as *D. ocoee* within GSMNP and they may have different elevational ranges (Tilley *personal communication*). Finally, Ocoee and Imitator Salamanders have different reported elevational distributions in GSMNP (Dodd 2004); therefore, we grouped *D. ocoee* and *D. imitator* in our summary tables but did not conduct formal analyses on their independent or combined distributions. Our surveys expanded the known range of *D. wrighti* and *P. jordani* downslope by 88 and 101 m, respectively, and extended the known range of Santeetlah Dusky Salamander (*Desmognathus santeetlah*; occurs at 1790 m) and *E. wilderae* upslope by 99 and 242 m, respectively, within GSMNP (Table 1).

Of the 14 species captured, *P. jordani*, *D. wrighti*, and *E. wilderae* were caught at a sufficient number of transects to model abundance across the sites accounting for imperfect detection. Based on comparisons of the chi-squared statistics for the observed data and idealized data, the models for all three species adequately fit the data (Table 2). The abundance of *P. jordani* and *D. wrighti* increased with elevation whereas *E. wilderae* abundance peaked at 1,270 m (95% credible interval [CRI] 1,047 – 2,025 m; Figure 2), owing to a significant quadratic effect in the model (Table 2). Ground cover and litter depth positively influenced *P. jordani* abundance, *D. wrighti* tended to be more abundant on steep slopes, and *E. wilderae* abundance decreased exponentially with distance from the nearest stream (Table 2).

We also jointly estimated the effects of environmental conditions on the probability of detecting an individual. Relative humidity was the only variable that significantly affected (positively) the detection of individuals of all three species (Table 2). *Plethodon jordani* detection was significantly affected by temperature and ground cover with optimal levels of each (significant quadratic terms). *Eurycea wilderae* also had an optimal temperature for surface activity and detection. Both *D. wrighti* and *E. wilderae* detection increased with increasing amount of precipitation in the previous 24 hours (Table 2).

Finally, our comparison of modeled abundance across our elevational gradient with modeled probability of occurrence across the same elevational gradient clearly show that much more information is present in the abundance model (Fig. X). Both *P. jordani* and *D. wrighti* show strong threshold responses at 1,000 m and 1,300 m, respectively, while *E. wilderae* showed a broad quadratic relationship with occurrence probability being highest 900–1,600 m.

Pjor

The Bayesian *P*-values for *P. jordani* was 0.339

Multivariate Rhat = 1.02

Mean ESS = 12,744 (11,801 with rstan ess)

Median ESS = 2,694 (2,120 with rstan ess)

Minimum ESS = 475 (362)

Ess for abundance estimates (mean and range)

Ess for parameters and standard deviations of the random effects

Mean rejection rate = 0.24

Median rejection rate = 0.05

The Bayesian *P*-values for *D. wrighti* was 0.467

Multivariate Rhat = 1.02

Mean ESS = 27385

Median ESS = 27639

Minimum ESS = 1361

Ess for abundance estimates (mean and range)

Ess for parameters and standard deviations of the random effects

Mean rejection rate = 0.42

Median rejection rate = 0.25

The Bayesian *P*-values for *E. wilderae* was 0.495

Multivariate Rhat = 1.00

Mean ESS = 32105

Median ESS = 33764

Minimum ESS = 7097

Ess for abundance estimates (mean and range)

Ess for parameters and standard deviations of the random effects

Mean rejection rate = 0.24

Median rejection rate = 0.17

**Discussion**

We used repeated spatial and temporal surveys to account for imperfect detection and obtain estimates of abundance of salamanders over an elevational gradient in Great Smoky Mountains National Park. Elevation was the primary predictor of abundance for all three species with sufficient data for analysis. *Plethodon jordani* and *D. wrighti* occupancy and abundance increased exponentially with increasing elevation, whereas *E. wilderae* exhibited a mid-elevation peak (Figure 2). Kozak and Wiens ([2010](#_ENREF_28)) suggest that climate niche conservatism over evolutionary time has driven the mid-elevation peak in amphibian species richness and makes amphibians particularly vulnerable to rapid climate change. In GSMNP, Gifford and Kozak ([2011](#_ENREF_17)) found that physiological constraints limit the lower elevation limit of *P. jordani* and it is possible that a similar mechanism operates with *D. wrighti.* It is unclear what processes underlie the mid-elevation peak for *E. wilderae*. This pattern could be driven by physiological constraints related to temperature and precipitation ([McCain 2010](#_ENREF_38)), but there has been little evidence for the metabolic theory of ecology shaping herpetofauna distributions along elevational gradients ([McCain and Sanders 2010](#_ENREF_40)). It is also possible that limited area at higher elevations makes it less likely for species to occur at high elevations due to limited habitat space and isolation shifting colonization-extinction dynamics and genetic diversity ([McCain 2003](#_ENREF_35), [Rowe 2009](#_ENREF_61), [McCain 2010](#_ENREF_38), [McCain and Grytnes 2010](#_ENREF_39)). This space limitation could also increase the intensity of interspecific interactions ([McCain and Grytnes 2010](#_ENREF_39)). For the Southern Appalachian Salamander (*Plethodon teyahalee*), competition with *P. jordani* has been indicated as the upper elevation limitation ([Gifford and Kozak 2011](#_ENREF_17)), and it is possible that competitive interactions limit the upslope distribution of *E. wilderae*. Habitat limitations present a final hypothesis as to the processes leading to this mid-elevation peak ([Rowe 2007](#_ENREF_60), [McCain and Grytnes 2010](#_ENREF_39)). For a species with a complex life cycle ([Wilbur 1980](#_ENREF_78)), it is also possible that the tops of mountains lack suitable stream breeding habitat, so they are less likely to migrate greater than 300 m from streams ([Crawford and Semlitsch 2007b](#_ENREF_11)). The other two species modeled are fully terrestrial and therefore are not limited by distances between complementary habitats ([Dunning et al. 1992](#_ENREF_16), [Pope et al. 2000](#_ENREF_53), [Hocking and Semlitsch 2007](#_ENREF_22)). Overall, it is unlikely that a single driver controls the elevational distribution of any of these species, even for a taxa so physiologically linked to temperature and moisture, but rather some combination of processes leads to the observed distributions ([Rowe 2009](#_ENREF_61), [McCain and Grytnes 2010](#_ENREF_39), [Tingley et al. 2012](#_ENREF_75)).

A variety of species have already altered their elevational ranges in response to climate change and other environmental factors. Birds have been found to track their climatic niche over the past century ([Tingley et al. 2009](#_ENREF_76)). Small mammals have experienced climate-related elevational range changes. Low-elevation small mammals have expanded their range while high-elevation species have contracted their ranges in Yosemite National Park over the past century ([Moritz et al. 2008](#_ENREF_44)). However, other small mammal distributions have been affected as much by changes in land-use as by climatic changes in the 20th century ([Rowe 2007](#_ENREF_60), [Rowe et al. 2010](#_ENREF_62)). Among amphibians, there have been major climate-induced declines, particularly among high elevation species ([Pounds and Crump 1994](#_ENREF_54), [Rovito et al. 2009](#_ENREF_58)). In the southern Appalachian Mountains, increases in temperature from 1974-1990 caused an upslope shift in the hybrid zone between Red-legged Salamander (*Plethodon shermani*)and *P. teyahalee*, resulting in fewer pure individuals of the high elevation specialist, *P. shermani* (Walls 2009). In general, many montane species have shifted their lower elevational limits downward over the past 80 years, likely due to maturation of forests and local climate cooling during this period ([Moskwik 2014](#_ENREF_45)). Additionally, temperature is not the only climate driver that influences elevational ranges; precipitation can have large effects on distributions ([Reich et al. 2014](#_ENREF_55), [Gillings et al. 2015](#_ENREF_19), [Rockwell et al. 2017](#_ENREF_57)). This is particularly true for amphibians, which require environmental moisture for respiration and to prevent desiccation. Many species also have complex life cycles that require ponds or streams for reproduction and the flow and hydroperiod necessary is influenced by both temperature and precipitation. Cloud cover base can also affect species distributions and interactions between species (ref: grant). Future changes in elevational ranges and abundances will likely be a result of interactions between temperature, precipitation, and land-cover (particularly forests through shading and evapotranspiration), as they will influence the environmental temperature and moisture experienced by amphibians in addition to affecting stream flow and pond hydroperiod.

Since habitat conditions beyond elevation and associated temperature and precipitation affect amphibian distributions and abundances, we explored the effect of other habitat variables. In addition to elevation, *P. jordani* were also found in greater abundance on sites with more ground cover and deeper leaf litter. This is similar to previous research, which found Seal Salamander (*Desmognathus monticola*), *D. ocoee*, and *E. wilderae* were positively associated with leaf litter ([Crawford and Semlitsch 2008](#_ENREF_12)). Deeper leaf litter likely provides a variety of benefits for *Plethodon* and *Desmognathus* spp. including increased invertebrate abundance as a food source ([Petranka 1998](#_ENREF_51), [Coleman et al. 2004](#_ENREF_8)) and cool, moist microhabitats that prevent desiccation ([Crawford and Semlitsch 2008](#_ENREF_12), [Rittenhouse et al. 2008](#_ENREF_56), [Peterman et al. 2013](#_ENREF_49), [Peterman and Semlitsch 2014](#_ENREF_50)). *Desmognathus wrighti* were found on sites with steeper slopes. *Eurycea wilderae* occurred in higher abundance at sites close to streams, which was expected based on breeding habitat requirements and previous research showing that the majority of the population is typically within 43 m of a stream ([Crawford and Semlitsch 2007b](#_ENREF_11)).

By incorporating site-specific variables related to abundance, our abundance estimates for species across the elevational gradient resulted in smoother, continuous abundance-elevation relationships. In contrast, when we condense our survey data to binary occurrence data, we see strong threshold effects predicting presence-absence of *P. jordani* and *D. wrighti*. Such information is minimally informative for monitoring population change, as it will only accommodate inferences about colonization or extinction, and not reveal gradual increases or decreases in abundance through time. This finding, while perhaps intuitive, emphasizes the need for monitoring data to be collected in a manner suitable generating unbiased estimates of abundance. Improving abundance estimates and reducing bias by accounting for imperfect detection is critical in evaluating population declines and range shifts. Without accounting for the imperfect detection, the observation process and the ecological processes are confounded, thereby obfuscating changes in population state. This confounding of uncertainties ([Nichols et al. 2011](#_ENREF_46)) can reduce the ability to detect population trends or changes in range edges or centroids ([Tingley and Beissinger 2009b](#_ENREF_74)). This is especially important in monitoring programs and assessments of at risk species, such as high elevation species, which have been suggested as especially vulnerable to climate change ([Sekercioglu et al. 2008](#_ENREF_65), [Sodhi et al. 2008](#_ENREF_68), [Gifford and Kozak 2011](#_ENREF_17), [Laurance et al. 2011b](#_ENREF_30)) and ectothermic vertebrates, such as amphibians, have a disproportionally high number of high elevation specialists compared to other taxa ([Laurance et al. 2011b](#_ENREF_30)). Amphibians are also difficult to observe, owing to their generally small size, cryptic coloration, and the fossorial nature of many species. Their activity is also a function of environmental conditions ([Keen 1984](#_ENREF_24), [O’Donnell et al. 2015](#_ENREF_47)). Therefore, accounting for variability in the activity and observation process is critical in understanding the true abundance and distributions of amphibian species. For these reasons, there has been considerable concern recently regarding the utility of analyses not accounting for imperfect detection when making inference about species abundances and distributions ([Royle and Dorazio 2008](#_ENREF_64), [Grant 2015](#_ENREF_20), [O’Donnell et al. 2015](#_ENREF_47)). The use of historical presence-only or single-visit presence-absence data limits the ability to make inference about range changes over time ([Tingley and Beissinger 2009b](#_ENREF_74), [Grant 2015](#_ENREF_20)). We lacked systematic historical data to evaluate range changes over time, but we have now established a rigorous method of sampling and analysis to detect future changes in abundance and distribution, and have highlighted the importance of collecting abundance data over occurrence data.

In addition to improving the precision of abundance estimates and reducing bias, important information can be gained from modeling the detection process. This is particularly true when the detection is more a function of animal activity and less influenced by observer traits or at least when these components of detection can be separated. In our study, temperature, precipitation, relative humidity, and herbaceous ground cover all influenced the probability of detection (Table 2). All of these variables with the exception of ground cover are likely more related to salamander surface activity and less influence on the observer’s ability to locate individuals. Therefore, we can infer that *P. jordani* and *E. wilderae* exhibited an optimal temperature for surface activity, as indicated by the significant negative squared term in the detection sub-model. This has similarly been identified for *Plethodon cinereus* in the northeastern U.S. ([Hocking et al. 2013](#_ENREF_23)). We did not find a significant effect of temperature on the detection of *D. wrighti* over the range of observed temperatures. It is possible that over a different range of temperatures or with more data we would identify an optimal temperature for activity. This seems likely as the mean estimated coefficients followed similar patterns to those of the other species but were not statistically significant (Table 2). Additionally, there are likely interactions with precipitation and temperature ([Spotila 1972](#_ENREF_70)), which we could not test for with our current data. We did find large, significant effects of both precipitation and relative humidity on detection of *D. wrighti*, as well as on *E. wilderae*. Relative humidity was also an important predictor of *P. jordani* detection but the effect size was not as large as with the other two species (Table 2). Additionally, the significant quadratic effect of ground cover on *P. jordani* detection was likely a function of their size, coloration, and behavior. When there was little herbaceous cover our detection was low because their dark coloration tended to provide camouflage in the wet leaf litter. It was also low in very dense herbaceous sites because those individuals active on the surface of the leaf litter were obscured by the dense foliage and therefore only those climbing vegetation could be seen. However, at sites with moderate herbaceous cover they were easier to observe because they were often climbing the vegetation and stood out on the green foliage but those on the ground could also still be observed through the vegetation.

Our data also supports the use of nighttime VES for estimating lungless salamander population sizes and to examine long-term trends in populations. For example, our total capture numbers within a five week period nearly matched numbers from a much greater effort across five years conducted using daytime surveys ([Dodd Jr 2004](#_ENREF_15)). Furthermore, our captures were measurably higher compared to other short-term studies less than two years using cover object searches rather than VES in the southern Appalachians ([Caruso and Lips 2012](#_ENREF_6), [Gifford and Kozak 2012](#_ENREF_18)). When considering long-term plans for analysis of the impacts of global change on species, it is important to match the sampling methods to the natural history of the species of interest. If the detection probability is too low, even hierarchical abundance models accounting for detection cannot calculate accurate abundances ([Dail and Madsen 2011](#_ENREF_13)). In the case of southern Appalachian Plethodontid salamanders, conducting VES on humid nights for these nocturnal species maximizes detection probability leading to more precise abundance estimates over time. Without accounting for variations in detection, any changes in observed counts through time are interpreted as changes in the population abundance and lead to incorrect inference regarding elevational shifts and conservation options.

The diversity of lungless salamanders in the Appalachian Highlands is vast, and distributions and surface activity vary across species as a function of habitat, season, temperature and precipitation. To understand the realized or potential consequences of global climate change, a rigorous and defensible baseline must be established. Our study of GSMNP plethodontid salamander sets such a baseline. While continued monitoring is necessary to track changes in abundance, more in-depth research, such as capture-mark-recapture, is also required to understand the potential mechanisms underlying observed changes. Global climate change is progressing rapidly, and montane plethodontid salamander populations may already be changing. Only rigorous population monitoring can bring such findings to light.

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**Tables**

**Table 1.** Number of captures and minimum and maximum elevations (meters above sea level) from this study in GSMNP during June – July 2012, along with minimum and maximum elevations reported by Dodd (2005) sampled between 1998 – 2001 and records in the Global Biodiversity Information Facility (GBIF) and VertNet databases. All records are restricted to GSMNP and species may have different ranges outside the park.

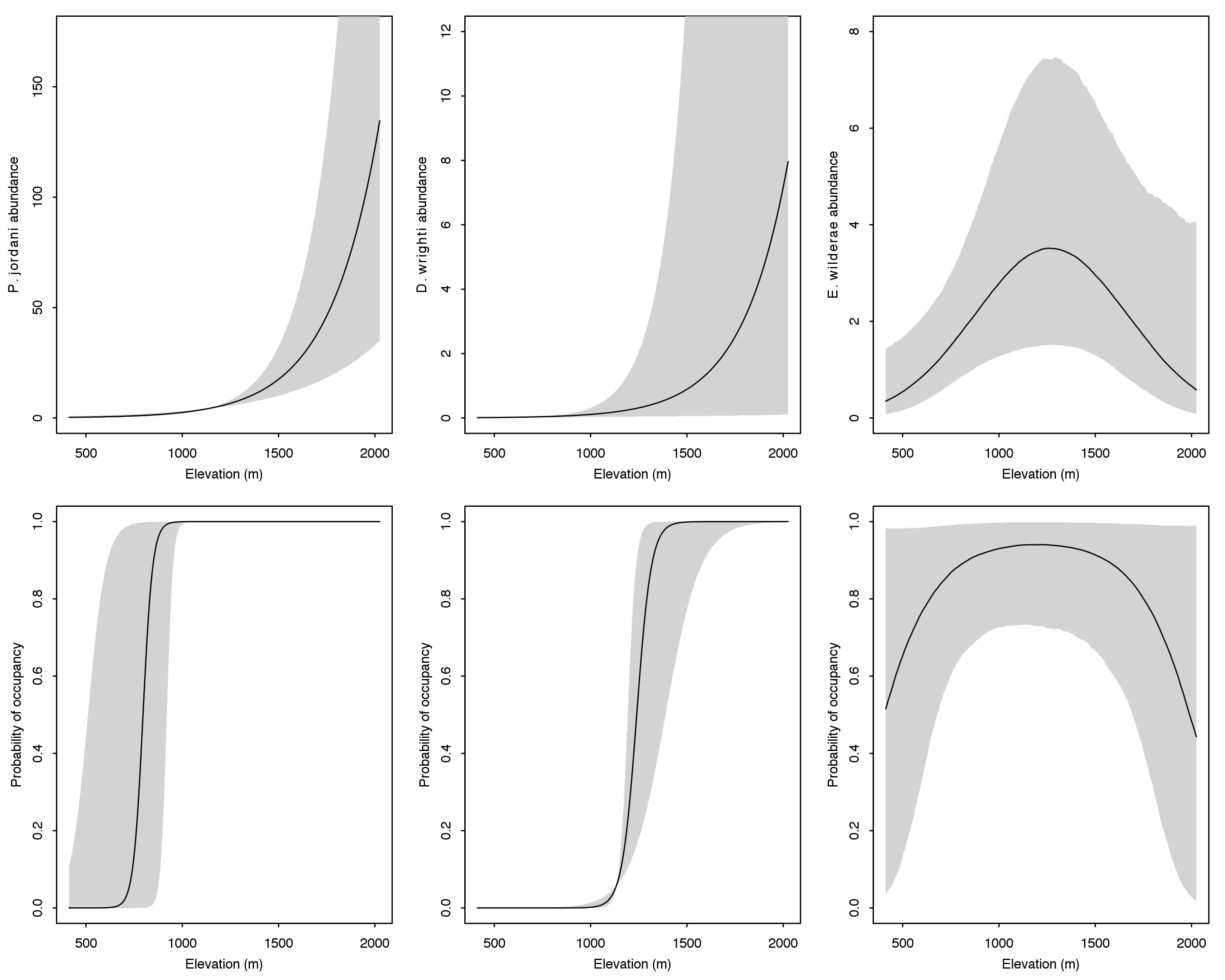
|  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- |
|  |  | Observed | | Dodd | | GBIF & VertNet | |
| Species | No. captured | Min | Max | Min | Max | Min | Max |
| *Desmognathus conanti* | 2 | 678 | 678 | ~340 | 960 | 503*c* | 2003*c* |
| *D. imitator/ocoee* | 1059 | 678 | 2022 | 756/866 | 1800/1830 | 521/534 | 2003/1819 |
| *D. monticola* | 23 | 678 | 1566 | 381 | 1646 | 391 | 1171 |
| *D. quadramaculatus* | 3 | 1499 | 1717 | 341 | 1714 (1829)b | 481 | 1582 |
| *D. santeetlah* | 13 | 678 | 1893 | 402 | 1790 | 521 | 1788 |
| *D. wrighti* | 858 | 671 | 2022 | 762 | 2025 | 843 | 2025 |
| *Eurycea wilderae* | 1021 | 447 | 2020 | 335 | 1783 | 344 | 1840 |
| *Gyrinophilus porphyriticus* | 12 | 1057 | 2021 | ~300 | 2025 | 396 | 1819 |
| *Notophthalmus viridescens* | 1 | 666 | 666 | ~300 | 663 (975)b | NA*d* | NA*d* |
| *Plethodon glutinosusa* | 4 | 670 | 1168 | 585 | 1280 | 397 | 1375 |
| *P. jordani* | 6399 | 678 | 2022 | 775 | 2025 | 810 | 2025 |
| *P. serratus* | 2 | 654 | 843 | 360 | 1527 | 447 | 1646 |
| *P. teyahaleea* | 125 | 671 | 1382 | 649 | 1516 | 515 | 1713 |
| *aPlethodon glutinosus* and *P. teyahalee* may only be confidently distinguished by molecular means in some areas with GSMNP  *b*Higher elevations reported in Dodd (2005) not found during surveys based on literature noted parenthetically  *c*Included all records of *Desmognatus fuscus* from the GBIF and HerpNet databases because *D. conanti* was not recognized as a distinct species at the time most records were collected  *d*Excluded because fewer than 10 records within GSMNP with sufficient information on location or elevation | | | | | | | |

**Table 2.** Coefficient estimates from *N*-mixture model of abundance accounting for imperfect detection for the three species we observed most frequently. Statistical significance, denoted by an asterisk, is based on the 95% credible intervals not overlapping zero. All parameter data were standardized by subtracting the mean and dividing by the standard deviation.

|  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
|  |  | *P. jordani* | | |  | *D. wrighti* | | |  | *E. wilderae* | | |  |
|  | Variable | Mean | 2.5% | 97.5% |  | Mean | 2.5% | 97.5% |  | Mean | 2.5% | 97.5% |  |
| Abundance | |  |  |  |  |  |  |  |  |  |  |  |  |
|  | N-intercept | 1.725 | 0.850 | 2.526 | \* | -1.647 | -3.372 | -0.164 | \* | 0.490 | -0.147 | 1.095 |  |
|  | Elevation | 1.985 | 1.235 | 2.948 | \* | 1.978 | 0.605 | 3.569 | \* | 3.495 | 0.491 | 6.476 | \* |
|  | Elevation2 |  |  |  |  |  |  |  |  | -3.371 | -6.447 | -0.294 | \* |
|  | Slope | 0.003 | -0.475 | 0.499 |  | 1.653 | 0.094 | 3.285 | \* | -0.318 | -0.674 | 0.041 |  |
|  | Slope2 | -0.299 | -0.848 | 0.218 |  | -1.158 | -2.782 | 0.395 |  |  |  |  |  |
|  | Northing | 0.057 | -0.056 | 0.170 |  | 0.284 | -0.042 | 0.621 |  |  |  |  |  |
|  | Easting | -0.029 | -0.130 | 0.072 |  | -0.218 | -0.486 | 0.041 |  |  |  |  |  |
|  | TPI | 0.137 | -0.005 | 0.279 |  | -0.032 | -0.439 | 0.359 |  | -0.179 | -0.509 | 0.143 |  |
|  | Trail | 0.059 | -0.613 | 0.815 |  | -0.105 | -1.328 | 1.182 |  | 0.798 | -0.092 | 1.810 |  |
|  | Log(TWI) | 0.059 | -0.053 | 0.174 |  | 0.219 | -0.032 | 0.468 |  | -0.128 | -0.372 | 0.115 |  |
|  | Canopy | -0.024 | -0.192 | 0.143 |  | -0.130 | -0.526 | 0.268 |  | 0.059 | -0.388 | 0.546 |  |
|  | Ground Cover | 0.366 | 0.100 | 0.744 | \* | 0.115 | -0.459 | 0.611 |  | -0.059 | -0.396 | 0.303 |  |
|  | Litter Depth | 0.339 | 0.185 | 0.491 | \* | 0.362 | -0.025 | 0.755 |  | 0.045 | -0.292 | 0.379 |  |
|  | Log(Stream Dist) | -0.127 | -0.330 | 0.082 |  | 0.177 | -1.006 | 1.477 |  | -0.443 | -0.801 | -0.101 | \* |
|  | Site Std. Dev. | 2.291 | 1.694 | 3.133 |  | 3.199 | 2.115 | 4.720 |  | 1.289 | 0.933 | 1.754 |  |
| Detection probability | |  |  |  |  |  |  |  |  |  |  |  |  |
|  | p-intercept | -1.062 | -1.971 | -0.317 | \* | -2.218 | -3.083 | -1.522 | \* | -1.825 | -2.471 | -1.245 | \* |
|  | Temperature | 0.233 | 0.060 | 0.407 | \* | 0.037 | -0.751 | 0.784 |  | 0.221 | -0.220 | 0.653 |  |
|  | Temperature^2 | -0.152 | -0.276 | -0.041 | \* | -0.259 | -0.679 | 0.136 |  | -0.444 | -0.769 | -0.134 | \* |
|  | 24-hr Precip | 0.043 | -0.036 | 0.127 |  | 0.389 | 0.121 | 0.680 | \* | 0.463 | 0.222 | 0.717 | \* |
|  | Ground Cover | -0.498 | -0.892 | -0.193 | \* | 0.639 | -0.028 | 1.345 |  | 0.474 | -0.040 | 0.959 |  |
|  | Ground Cover2 | 0.134 | 0.017 | 0.251 | \* | -0.308 | -0.660 | 0.036 |  | -0.241 | -0.537 | 0.048 |  |
|  | Trail | -0.158 | -0.877 | 0.479 |  | 0.291 | -1.067 | 1.391 |  | -0.090 | -1.135 | 0.770 |  |
|  | Rel. Humidity | 0.133 | 0.025 | 0.244 | \* | 0.903 | 0.475 | 1.382 | \* | 0.723 | 0.374 | 1.101 | \* |
|  | Random Obs. Std .Dev. | 0.734 | 0.571 | 0.959 |  | 1.664 | 1.222 | 2.199 |  | 1.869 | 1.453 | 2.333 |  |
| Fit | |  |  |  |  |  |  |  |  |  |  |  |  |
|  | Fit-Data | 554.0 | 434.7 | 679.0 |  | 201.9 | 151.9 | 264.1 |  | 261.7 | 207.3 | 330.1 |  |
|  | Fit-Ideal | 534.0 | 425.5 | 650.1 |  | 198.7 | 148.7 | 258.4 |  | 260.3 | 208.0 | 324.9 |  |

**Figures**

**Macintosh HD:Users:Dan:Documents:Research:SmokysElevation:Analysis:Nmix vs GLMM vs GLM Prediction Plots.pdf**

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Data Accessibility

**• Competing Interests Statement**

**• Author Contributions section**