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Predicted alteration of surface activity as a consequence of climate change

MEAGHAN R. GADE,[1,7] GRANT M. CONNETTE,[2] JOHN A. CRAWFORD,[3] DANIEL J. HOCKING,[4] JOHN C. MAERZ,[5]
JOSEPH R. MILANOVICH,[6] AND WILLIAM E. PETERMAN[1]

[1]*School of Environment and Natural Resources, The Ohio State University, 2021 Coffey Road, Columbus, Ohio 43201 USA*
[2]*Conservation Ecology Center, Smithsonian Conservation Biology Institute, Front Royal, Virginia, USA*
[3]*National Great Rivers Research and Education Center, One Confluence Way, East Alton, Illinois 62024 USA*
[4]*Department of Biology, Frostburg State University, 101 Braddock Rd, Frostburg, Maryland 21532 USA*
[5]*Warnell School of Forestry and Natural Resources, University of Georgia, 180 E Green St, Athens, Georgia 30602 USA*
[6]*Department of Biology, Loyola University Chicago, 1032 Sheridan Rd, Chicago, Illinois 60660 USA*

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Abstract. Wildlife are faced with numerous threats to survival, none more pressing than that of climate change. Understanding how species will respond behaviorally, physiologically, and demographically to a changing climate is a cornerstone of many contemporary ecological studies, especially for organisms, such as amphibians, whose persistence is closely tied to abiotic conditions. Activity is a useful parameter for understanding the effects of climate change because activity is directly linked to fitness as it dictates foraging times, energy budgets, and mating opportunities. However, activity can be challenging to measure directly, especially for secretive organisms like plethodontid salamanders, which only become surface active when conditions are cool and moist because of their anatomical and physiological restrictions. We estimated abiotic predictors of surface activity for the seven species of the *Plethodon jordani* complex. Five independent data sets collected from 2004 to 2017 were used to determine the parameters driving salamander surface activity in the present day, which were then used to predict potential activity changes over the next 80 yrs. Average active seasonal temperature and vapor pressure deficit were the strongest predictors of salamander surface activity and, without physiological or behavioral modifications, salamanders were predicted to exhibit a higher probability of surface activity during peak active season under future climate conditions. Temperatures during the active season likely do not exceed salamander thermal maxima to cause activity suppression and, until physiological limits are reached, future conditions may continue to increase activity. Our model is the first comprehensive field-based study to assess current and future surface activity probability. Our study provides insights into how a key behavior driving fitness may be affected by climate change.

Key words: activity; Appalachian; climate change; ectotherm; global circulation model; hierarchical model; multivariate adaptive constructed analogs; plethodontid salamander.

INTRODUCTION

Organisms are facing unprecedented challenges as a result of climate change, and predicting behavioral, demographic, and physiological responses dominates current research. Broadly, climate change is expected to increase temperatures and alter periodicity in precipitation (IPCC 2014). Ectothermic organisms, whose physiology and behavior are closely linked to abiotic conditions, are disproportionally impacted by the effects of climate change (Blaustein et al. 2010, Li et al. 2013). Contemporary climate change has already negatively affected many ectotherms (Alford and Richards 1999, Collins and Storfer 2003). For example, freshwater fish experience reduced reproductive output as a result of warmer water temperatures (Ficke et al. 2007, Holt and Jørgensen 2015), and several ectotherms have seen reductions in body size and depressed physiological performance correlated with warming temperatures (Reading 2007, Huey et al. 2009, Sheridan and Bickford 2011, Ohlberger 2013). To estimate wildlife responses to future climate change, we can incorporate the known behavioral and physiological responses of an organism at existing conditions into future climate predictions. Consideration of such biophysical processes has indicated that some organisms may exhibit resilience to change through physiological acclimation and behavioral modification (Kearney et al. 2009, Seebacher et al. 2015, Riddell et al. 2018). Linking relevant species-specific parameters such as physiological traits, behavior, and dispersal ability to climate change

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[7] E-mail: gade.15@buckeyemail.osu.edu

predictions may reveal novel relationships otherwise overlooked. The inclusion of more biological realism into our predictions of climate sensitivity is necessary to estimate the likelihood of persistence and mitigate the impacts of climate change on species.

Determining the distribution and abundance of organisms in relation to environmental variables is a fundamental ecological goal, and developing models to best estimate such patterns is essential for informing conservation and management strategies that account for climate change. Hierarchical binomial mixture modeling has become a staple in ecological research because it can accommodate and partition underlying ecological patterns (i.e., abundance or occupancy) and observational processes that may bias sampling (Royle et al. 2007, Kery and Schaub 2012). Central to many observation processes is "detectability," or the idea that we are unable to perfectly observe all individuals of the focal organism during every survey event. Often, failure to observe a species or individual at a given location does not necessarily indicate its absence, but instead may reflect factors such as observer proximity to the organism, timing (daily or seasonal), general species biology (calling frequency, phenology, etc.), or the environmental conditions driving surface availability.

In addition to addressing bias in estimating other state parameters (e.g., abundance, occurrence, survival), the "detection" process can be biologically relevant for species such as plethodontid salamanders because of its direct link to surface activity, which affects energy intake and overall fitness. Plethodontid salamanders are lungless and rely on highly permeable and moist skin for gas exchange (Feder 1983). Consequently, plethodontids generally require cool and moist conditions to avoid rapid water loss (Feder 1983). Individuals spend significant amounts of time under cover objects or below ground to reduce evaporative water loss (Jaeger 1980, O'Donnell and Semlitsch 2015), and when salamanders do become surface active, it is often for short periods during cool and moist times (McEntire and Maerz 2019). In such a system, the detection component of a binomial mixture model is better capturing surface availability (i.e., the likelihood salamanders will be surface active) instead of the observer's ability to detect an individual. Only when surface active do plethodontids forage, grow, and search for mates. Therefore, surface availability is a reasonable proxy of surface activity, which represents energy intake and subsequently, fitness (Gifford and Kozak 2012, Riddell and Sears 2015, Peterman and Gade 2017, McEntire and Maerz 2019). Evaluating surface activity under predicted climatic change provides a mechanistical understanding of how future climate may affect plethodontid performance and population persistence.

Direct and reliable observations of surface activity in the field are challenging to measure. Previous work in other systems has modeled surface activity indirectly through known physiological limits and/or energy budgets at given abiotic conditions. For example, Buckley (2008) assumed eastern fence lizards (*Sceloporus undulatus*) became active once a minimum temperature was reached, a temperature that was measured in a laboratory. In plethodontids, activity time has been modeled as a function of resistance to water loss at a given temperature and vapor pressure deficit in the atmosphere (Riddell and Sears 2015). Instead of using indirect physiological models to infer activity, it may be possible to use surface availability estimates as a more direct surrogate for surface activity, especially because terrestrial plethodontids are only detectable when surface active, and have inherently low detection levels consistent with their restricted surface activity (Bailey et al. 2004).

The Appalachian region is a global hotspot of salamander species richness and abundance, and members of the Plethodontidae family account for much of the diversity within this region. Given their high abundance and biomass, combined with their role as vital members of the terrestrial food web and contributions to forest nutrient cycling (Davic and Welsh 2004, Best and Welsh 2014, Hocking and Babbitt 2014), and predicted declines with climate change (Milanovich et al. 2010, Sutton et al. 2015), protection and conservation are warranted. Our goal was to determine common weather parameters driving salamander surface activity in the present at a broad scale to inform potential changes in surface activity probability in the future. We used the *Plethodon jordani* species complex as a focal group representative of other Appalachian terrestrial plethodontid species to estimate surface activity probabilities. Originally thought to all be subspecies of *P. jordani*, Highton and Peabody (2000) used allozyme variation to described seven distinct high-elevation isolated species across the Southern Applachian Mountains, each with geographically distinct color variation (Fig. 1). As high-elevation specialists, species of the complex share similar climatic niches and exhibit niche conservatism, providing a unique opportunity to apply data from a subset of species to all species in the complex (Wiens et al. 2010, Riddell et al. 2018, Farallo et al. 2020). Members of the *P. jordani* complex are considered "sky island" species, whereby populations are confined to isolated, but adjacent, mountain peaks (McCormack et al. 2008, Gifford and Kozak 2012). Sky island species are often vulnerable to the effects of climate change because of their genetic isolation, inability to disperse from unsuitable conditions, and narrow physiological tolerances (Kozak and Wiens 2010, Gifford and Kozak 2012, Wiens et al. 2019), underscoring the need for determining responses to climate change as a vital step towards conservation action.

METHODS

Surface activity probability modeling

Data sets description.— Using five independent data sets, we developed a binomial mixture model to estimate abundance while accounting for surface availability

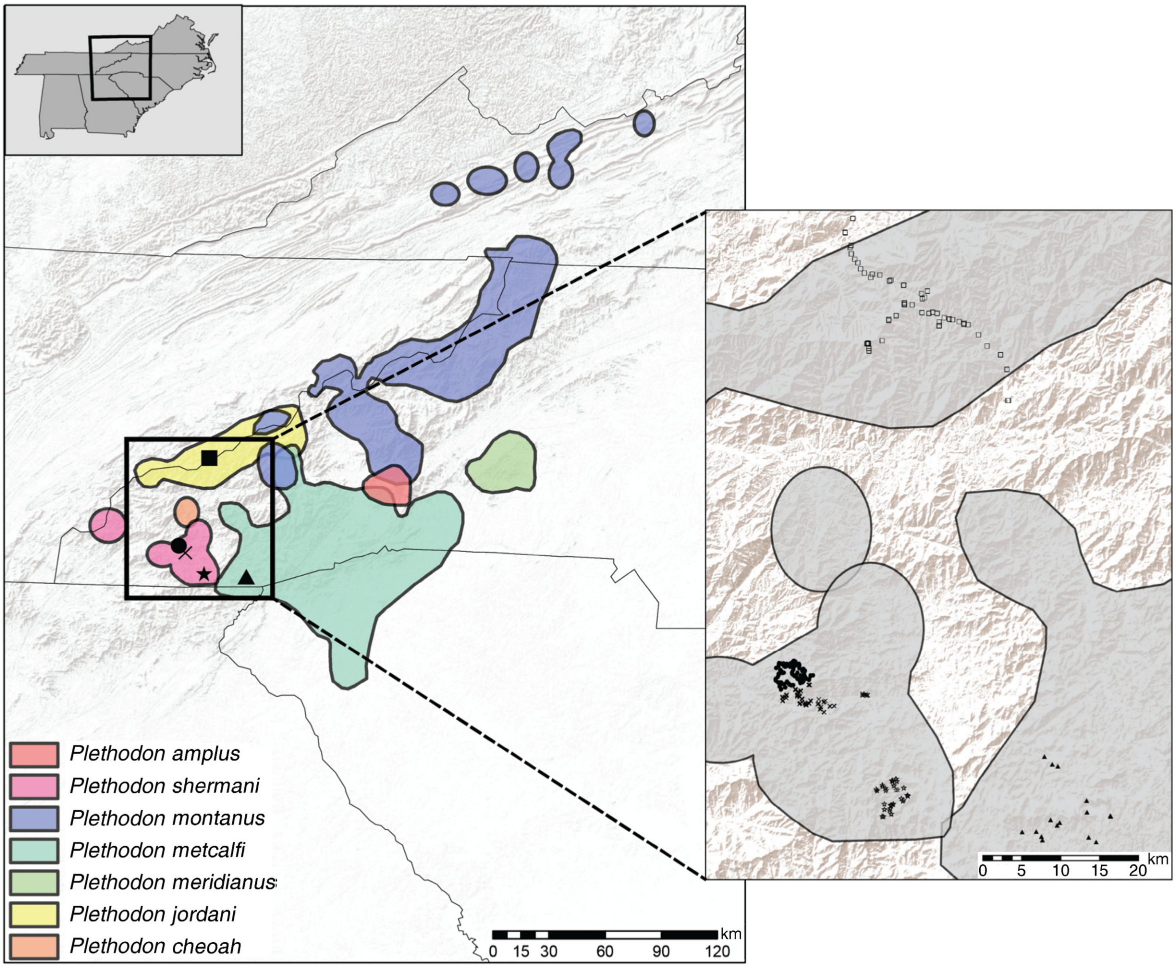

FIG. 1. The geographic ranges for each species of the *Plethodon jordani* complex (from www.iucnredlist.org) with the data sets used to develop the hierarchical model symbolized. Inset map shows every sampling location from each data set. Triangles are data set A, circles are data set B, X's are data set C, squares are data set D, and stars are data set E (in reference to data sets outlined in Table 1).

probability (Royle 2004). Each data set was collected using area-constrained repeated count surveys to estimate abundance across five distinct areas of the Southern Appalachian Mountains (Fig. 1). Surveys occurred between 2004 and 2017, with one data set collected over multiple years and the four others consisting of a single season of observations. The multiyear data set (data set E) used a robust-design survey method (Pollock 1982) with three sampling occasions per season in spring, summer, and fall of 2016 and 2017. Our count data included three of the seven species in the *Plethodon jordani* complex: *P. shermani*, *P. metcalfi*, and *P. jordani*. The data sets were initially collected for other purposes and were adapted for the cross-species assessment in the present study. The specific details of data collection for each data set can be found in Appendix S1: Section S1. Sample plot areas ranged from 9 to 400 m^2 between data sets with 14–195 individual sampling locations in each data set (Table 1).

Surface activity and abundance covariates.—Because of a lack of common survey-level environmental covariates measured across all data sets (see Appendix S1: Table S1), and to ensure consistency between data sets, we downloaded daily weather covariates from Daymet (daymet.ornl.gov) using the *Daymetr* package (Hufkens et al. 2018) in R (version 3.5.1, R Development Core Team 2013). The Daymet data set interpolates local weather station observations to produce a 1 × 1 km gridded weather estimate. To validate that Daymet data were a reasonable surrogate for local, field-collected weather data, we downloaded temperature data from a series of weather stations at Coweeta Hydrologic Lab (CHL), where data set E was collected, and compared it to the Daymet data at CHL from the years 2004–2017. Coweeta Hydrological Lab is within close proximity to all other data sets (Fig. 1), serving as a proxy for the other data sets to validate the Daymet data used in our models.

TABLE 1. Summary of the individual data sets used to develop the global surface activity model.

Data set	Location	Sampling years	Plot area (m^2)	Number of plots	Elevational range (m)	Type of plot	*Plethodon* species
A	35.04, −83.19	2004	400	14	718–1,248	Transect	*Plethodon metcalfi*
B	35.18, −83.59	2012	19.6	136	1,228–1,571	Point	*Plethodon shermani*†
C	35.15, −83.55	2017	9	176	953–1,582	Point	*Plethodon shermani*†
D	35.61, −83.43	2012	100	195	412–2,021	Transect	*Plethodon jordani*
E	35.06, −83.44	2016–2017	25	72	739–1,422	Point	*Plethodon shermani*†

†*Plethodon shermani* is known to hybridize with *Plethodon teyahalee* at intermediate elevations. Counts are inclusive of hybrids.

From Daymet, we extracted daily precipitation (mm), maximum and minimum air temperature (°C), and water vapor pressure (Pa) to point locations of each sampling site in the five data sets (Fig. 1). We averaged the minimum and maximum air temperature and used rolling window analyses to assess the 1-, 2-, and 3-d mean temperature, total number of days since a rainfall event (i.e., dry days), and 1-, 2-, and 3-d total precipitation. We then averaged the 1- and 2-day rolling windows for all weather variables to obtain a corrected 1-d rolling window because all sampling occurred nocturnally, and thus overlapped two calendar days.

For the abundance submodel, we used site-level topographic variables including elevation, slope, topographic position index (TPI), aspect, and stream distance. Variables were derived from a 9-m^2 resolution digital elevation model obtained from EarthExplorer ASTER Global DEM. TPI was calculated as the slope position relative to the surrounding 90 m and aspect was transformed into linear measures of eastness (sine of aspect) and northness (cosine of aspect). Streams were delineated using a flow accumulation layer with a 450-pixel cell threshold, resulting in a drainage area greater than or equal to 0.405 ha (Gade and Peterman 2019). Stream distance was then calculated using the Euclidean Distance tool in ESRI ArcGIS v.10.2 (Redlands, CA).

Model description.—We developed a binomial mixture model for each of the five individual data sets using the same abundance and surface availability covariates in each model. The general expected abundance (λ_{ij}) and surface activity (p_{ijk}) as well as the realized (latent) abundance (N_{ij}) equations are shown below, with i indicating data set, j indicating survey plot, and k indicating sampling occasion. The bracketed ellipses indicate slope terms for the multiple covariates used in the model:

$$N_{ij} \sim \text{Poisson}(\lambda_{ij}) \tag{1}$$

$$\log(\lambda_{ij}) = \alpha 0_i + \alpha 1_i \times x1_{ij} + \alpha 2_i \times x2_{ij} + [\ldots]\log(\text{plot size}) + \varepsilon_j \tag{2}$$

$$\text{logit}(p_{ijk}) = \beta 0_i + \beta 1_i \times x_{ijk} + \beta 2_i \times x2_{ijk} + [\ldots] \tag{3}$$

$$y_{ijk} | N_{ij} \sim \text{Binomial}(N_{ij}, p_{ijk}). \tag{4}$$

We assume that all salamander species are responding to environmental and habitat covariates similarly, so the data-set–level parameters defined above are modeled as drawing from a common distribution. We included hyperparameters to represent an additional hierarchical level and define the global distributions that summarize the data-set–level parameters.

$$\alpha'_i \sim \text{dnorm}(\mu_{\alpha'_i}, \sigma^2_{\alpha'_i}) \tag{5}$$

$$\beta'_i \sim \text{dnorm}(\mu_{\beta'_i}, \sigma^2_{\beta'_i}). \tag{6}$$

We used normally distributed, weakly informative priors with a mean of zero and precision of 0.1 for all priors, global and data-set specific. To accommodate overdispersion in counts, a plot-specific random effect error term, ϵ_j, was included in each data set. An offset term (*log* of the plot area) was also added to account for differences in survey plot sizes between data sets (Eq. 2). We constructed a global model that included all abundance and activity covariates mentioned above and subsequently removed any covariate where <75% of the posterior distribution had the same sign as the mean parameter estimate to create our final model. Temperature (minimum/maximum/average and rolling windows) were correlated; thus we ran separate models including one temperature covariate a time along with the other activity covariates. We analyzed our models in a Bayesian hierarchal framework using the JAGS (v.4.3.0; Plummer 2003) in R using the *jagsUI* (Kellner 2017) in R. All covariates were standardized prior to analysis by subtracting their mean and dividing by the standard deviation. Posterior summaries of the final model were based on 223,300 Markov chain Monte Carlo (MCMC) iterations on four chains thinned at a rate of 10 following an adaptation of 318,000 and burn-in of 210,000. Model convergence was assessed using the Gelman–-Rubin statistic (Rhat < 1.1) and visual inspection of MCMC chain mixing.

Future surface activity.—Using the estimates from the binomial-mixture model described above, which were informed by data from three species of the *P. jordani* complex, we estimated future surface activity for the seven species of the *P. jordani* complex. Species of the complex are closely related and are geographic replacements, as they all inhabit high elevations and share similar climate and physiological requirements (Weisrock and Larson 2006). We incorporated statistically downscaled daily future weather predictions from 10 global circulation models (GCMs) using the multivariate adaptive constructed analogs (MACA) data set (Abatzoglou and Brown 2012) into the global surface availability model we developed above. The MACA method downscales GCMs from a coarse resolution (Appendix S1: Table S2) to a 4-km spatial resolution for the years 2005–2099 at representative concentration pathway (RCP) 4.5 and 8.5. RCP 4.5 represents a stabilized scenario whereby moderate effort is needed to curb emissions and RCP 8.5 represents a scenario where no action is taken to mitigate emissions and greenhouse gas concentration levels increase substantially (Clarke et al. 2007, Riahi et al. 2007). Although 20 GCMs are available in the MACA data set, we selected 10 representative models that (1) incorporated the greatest variation in how the model was developed (using atmospheric chemistry, interactions with biogeochemical processes, etc.), (2) were developed at the finest spatial resolution, and (3) were either recommended by the MACA data set developers and/or were evaluated as “highly credible” from Rupp et al. (2013). Refer to Appendix S1: Table S2 for details on the selected GCMs.

We downloaded daily weather data from the MACA data set to 1,012 unique point locations that spatially encompassed the ranges of the seven *P. jordani* complex species (Fig. 1). Range maps of the species complex were obtained from the IUCN Redlist website.[8] Points were uniformly placed 5 km apart to capture the variation in daily weather variables across the range of the *P. jordani* species complex within the distribution of each species. Data were downloaded from 15 May to 15 August for the years 2020–2099 to represent the peak salamander active season. This time frame was also selected as it is representative of the sampling dates of data sets A–D (Appendix S1: Section S1). We used minimum and maximum temperature, minimum and maximum relative humidity, and the total precipitation at both RCP 4.5 and 8.5. All data were downloaded using the *ClimateR* package in R (Johnson 2019). Similar to the aforementioned methods, we averaged the minimum and maximum temperate and relative humidity and used rolling window analyses to determine the number of dry days and the 1-, 2-, and 3-d average temperature and total precipitation. We averaged 1-d and 2-d rolling windows for temperature and precipitation to obtain a corrected 1-d rolling average. Vapor pressure (VPA) was derived as a function of the minimum daily temperature (T_{mn}) as described in Peterman and Gade (2017) using the following equation:

$$\exp(\mathrm{vpa}) = 6.467 + 0.0657 \times T_{\mathrm{mn}}. \tag{7}$$

All future-climate covariates were rescaled using the mean and standard deviation of the current climate variables that were used to fit the original hierarchical model from the Daymet data set.

We estimated future surface activity probability at each sample point for each day of the 2020–2099 active season using 5,000 random posterior samples generated based on our binomial mixture model for salamander abundance and activity probability. We used the following inverse logit equation to estimate activity:

$$p = \frac{1}{1 + \exp(-1 \times (\alpha\beta0' + \alpha\beta1' \times x1_i + \alpha\beta2' \times x2_i + [\ldots]))}. \tag{8}$$

We made daily surface activity probability predictions at each of the 1,012 locations by averaging 5,000-posterior samples for every day at each site. The daily activity probability estimates at each location were subsequently averaged together by species and year. The final data set included a yearly mean (±SD) activity probability for each of the seven species. To account for the physiological limitations of salamanders, we assumed surface activity was zero if the temperature on any day exceeded 25°C (Peterman and Gade 2017, Caruso and Rissler 2018). We also calculated the coefficient of variation by dividing the mean surface activity by the standard deviation for each species for each year. We then spatially projected the mean surface activity probability for the years 2020, 2050, and 2099 for all species by averaging the activity probability estimates across the year at each point and rasterizing each point to a 5-km resolution.

We assessed the changes in surface activity probability for each species over time using mixed- effect models fit with the *brms* package (Bürkner 2017). In all models, surface activity probability was the response variable; year, RCP, and year × RCP interaction were modeled as predictor variables; and GCM was the random effect. We used a Gaussian distribution with uninformative Student-*t* priors (brms default), run for 3,000 iterations on four chains after a burn-in phase of 1,000 and thinned at a rate of 1. Model fit was assessed using the Gelman-Rubin statistic (Rhat < 1.1). We also projected the change of each weather variable using a mixed-effect model with the weather covariate as the response; year, RCP, and year × RCP interaction as predictor variables, and GCM as the random effect.

RESULTS

Global surface activity model

Across the five data sets, the average individual surface activity probabilities ranged from 0.04 (±0.19) to 0.12 (±0.05). Global surface activity was positively related to 1-d precipitation, 3-d mean temperature, and water vapor pressure. Global surface activity was negatively related to the number of dry days, 3-d precipitation, and 1-d mean temperature (Fig. 2A). Global abundance was related to elevation, stream distance, and

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[8] www.iucnredlist.org

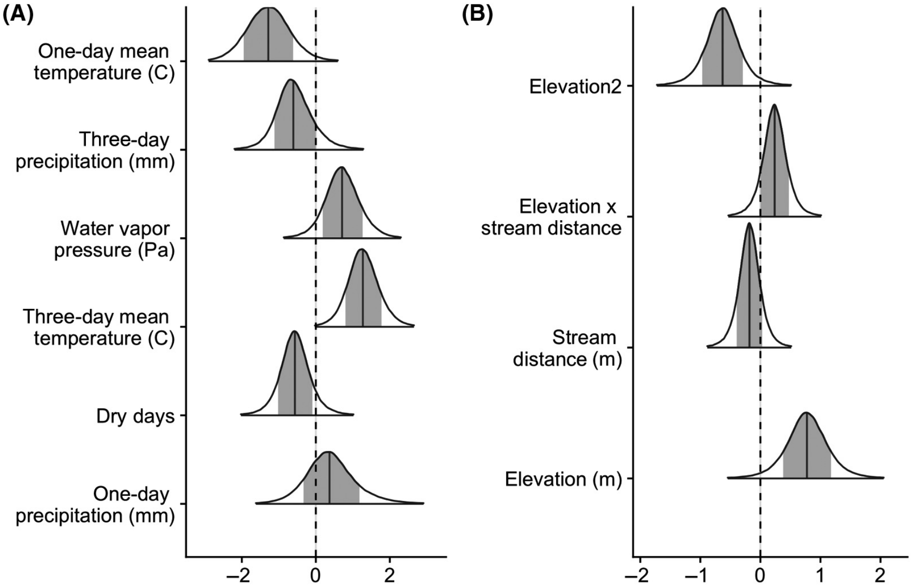

FIG. 2. Mean estimates for (A) surface activity covariates and (B) abundance covariates from the global hierarchical model. Shaded region includes 75% of posterior region.

the interaction of elevation and stream distance (Fig. 2 B; Appendix S1: Table S3). The abundance covariates had greater variation in magnitude and direction between data sets relative to activity covariates, which showed more consistency between data sets (Appendix S1: Fig. S1). Further, the Coweeta weather station data was highly correlated with the Daymet data for the same region from 2004 to 2017 ($r = 0.98$; $P < 0.005$; Fig. 3).

Future surface activity probability

Future projections of surface activity probabilities indicated that mean individual surface activity rates increased with time for all seven species of the *P. jordani complex* (Fig. 4). All species had similar increases in activity probability over time, with *P. metcalfi*, *P. amplus*, and *P. meridianus* estimated to increase by 0.08% per year (Credible Interval (CRI): ±0.001) and *P. cheoah*, *P. jordani*, *P. montanus*, and *P. shermani* were estimated to increase by 0.05% per year (CRI: ±0.001) (Fig. 5). There was no difference in surface activity probability over time between the RCP 4.5 and 8.5 scenarios for all species (average $\beta = 0.001$, CRI: ±0.001). Across all species, the coefficient of variation (CV) in surface activity probability increased over time (Appendix S1: Fig. S2). *Plethodon metcalfi*, *P. amplus*, and *P. cheoah* had a similar increase in CV with $\beta = 0.040$ (CRI: 0.040, 0.050). *Plethodon jordani*, *P. meridianus*, *P. montanus*, and *P. shermani* had similar increases in CV over time with $\beta = 0.05$ (CRI: 0.04, 0.05). The CV for all species did not differ between RCP 4.5 and RCP 8.5 ($\beta = 0.0001$, CRI: ±0.0001). There was no significant interaction between year and RCP for any species. Predicted activity probabilities from models run with the 25°C physiological threshold forcing activity to zero and models without the threshold were highly correlated ($r = 0.97$, $P < 0.001$).

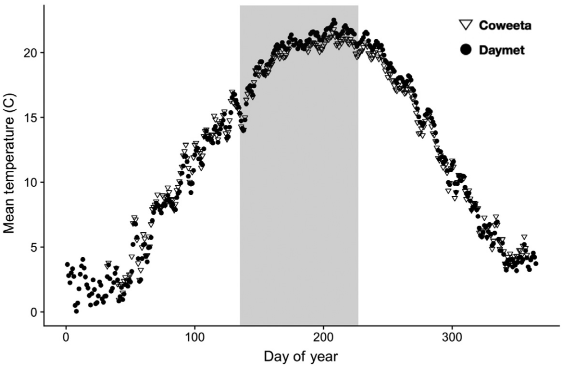

FIG. 3. Mean temperature over time averaged from five weather stations at Coweeta Hydrological Lab (CHL; triangles) and downloaded from the Daymet database (circles) at the same spatial locations of CHL. Data is averaged from the years 2004–2017. The grey shaded region represents the active season time frame we used for future projections of surface activity.

Over the next 80 yr, the MACA data set showed no significant trend in dry days over time ($\beta = 0.09$, CRI: −0.17, 0.34) or between RCPs ($\beta = -323.19$, CRI: −1,117.98, 466.63); 1-d precipitation over time ($\beta = 0.01$, CRI: −0.01, 0.01) or between RCPs ($\beta = 5.91$, CRI: −6.20, 18.15); or 3-d precipitation over time ($\beta = -0.001$, CRI: −0.01, 0.01) or between RCPs ($\beta = 14.48$, CRI: −22.51, 52.33). There was a significant increase of VPA over time ($\beta = 3.25$, CRI: 2.95, 3.55)

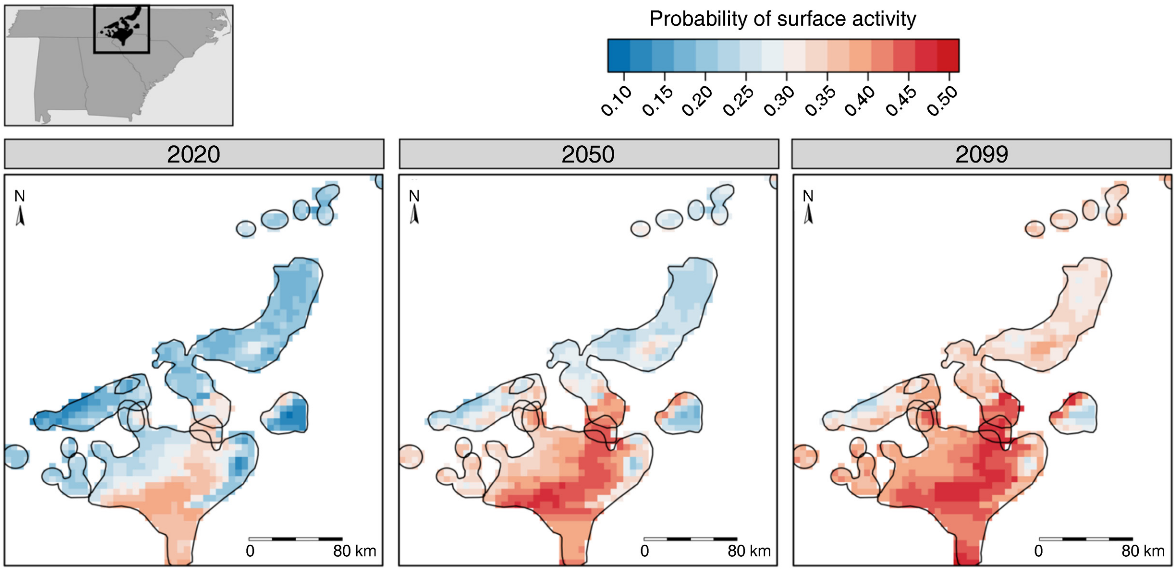

FIG. 4. Average active season surface activity probability across the range of the seven species of the *Plethodon jordani* complex for the years 2020, 2050, and 2099.

and RCP 4.5 was significantly lower than RCP 8.5 (β = −11,446.01, CRI: −12,407.23, −10,478.78). Both 1- and 3-d temperature increased over time (β = 0.03, CRI: 0.02, 0.03 and β = 0.03, CRI: 0.02, 0.03, respectively) and RCP 4.5 was significantly lower than RCP 8.5 (β = −81.3, CRI: −89.17, −73.40 and β = −81.73, CRI: −90.05, −73. 29; Appendix S1: Fig. S3).

DISCUSSION

The threats of climate change are ubiquitous and require immediate attention to understand how species will persist in the future. Our study assessed how surface activity, a fitness-related behavior of terrestrial salamanders, may change over time in the face of global climate change. We developed a model to describe the environmental covariates driving salamander abundance and surface activity probability at a broad scale by integrating five independent data sets. Several previous studies have used hierarchical models to assess similar questions (Dodd and Dorazio 2004; Kéry et al. 2005; Chandler and King 2011; Connette and Semlitsch 2013; Peterman and Semlitsch 2013; Studds et al. 2017; Gade and Peterman 2019), and have found myriad of factors driving abundance and more consistent factors predicting activity probability. For example, independent investigations have found temperature and precipitation to be reliable predictors of activity (Connette et al. 2015, Muñoz et al. 2016, Gade and Peterman 2019). Even across our five data sets, activity covariates maintained more consistent parameter estimates (e.g., covariate "3-d temperature," the parameter estimate ranged from 1.052 to 1.558; Appendix S1: Fig. S1). Surface activity is more likely to be affected by abiotic conditions consistent with the physiological limitations of *Plethodon*. Abundance, alternatively, is affected by both abiotic and biotic factors and often, the site and survey-level nuances, parameters researchers choose to measure in the field, and a priori model decision criteria drive abundance predictors, likely resulting in the greater variance in abundance predictors. Between our five data sets, there were no consistent site-level covariates measured (Appendix S1: Section S1), and our parameter estimates for the abundance covariates significantly varied between each data set (Appendix S1: Fig. S1). Our approach to model and estimate common parameters for both abundance and activity is therefore novel and allows for inferences to be made at broad scales across similar species.

Using our global model parameter estimates, we projected surface activity into the future and found an overall increase in surface activity probability over time, largely coinciding with changes in temperature and VPA. Temperature and VPA had the largest standardized effect sizes in our global model (Fig. 2) and had significant increases over time (Appendix S1: Fig. S3). Both temperature and VPA are key variables relating to plethodontid physiology. Plethodontids are lungless and become surface active during wet and cool nights (Feder and Londos 1984). However, salamander activity appears to increase with increasing temperatures and VPA, a seemingly contradictory result. Southern Appalachian plethodontid salamanders are typically most active during the middle of the summer (Connette et al. 2015) and our sampling window for future projections occurred during the peak activity season when yearly temperatures reach their maximum (Fig. 3). Temperatures likely do not exceed salamander thermal maxima to cause activity suppression, even into the future, which

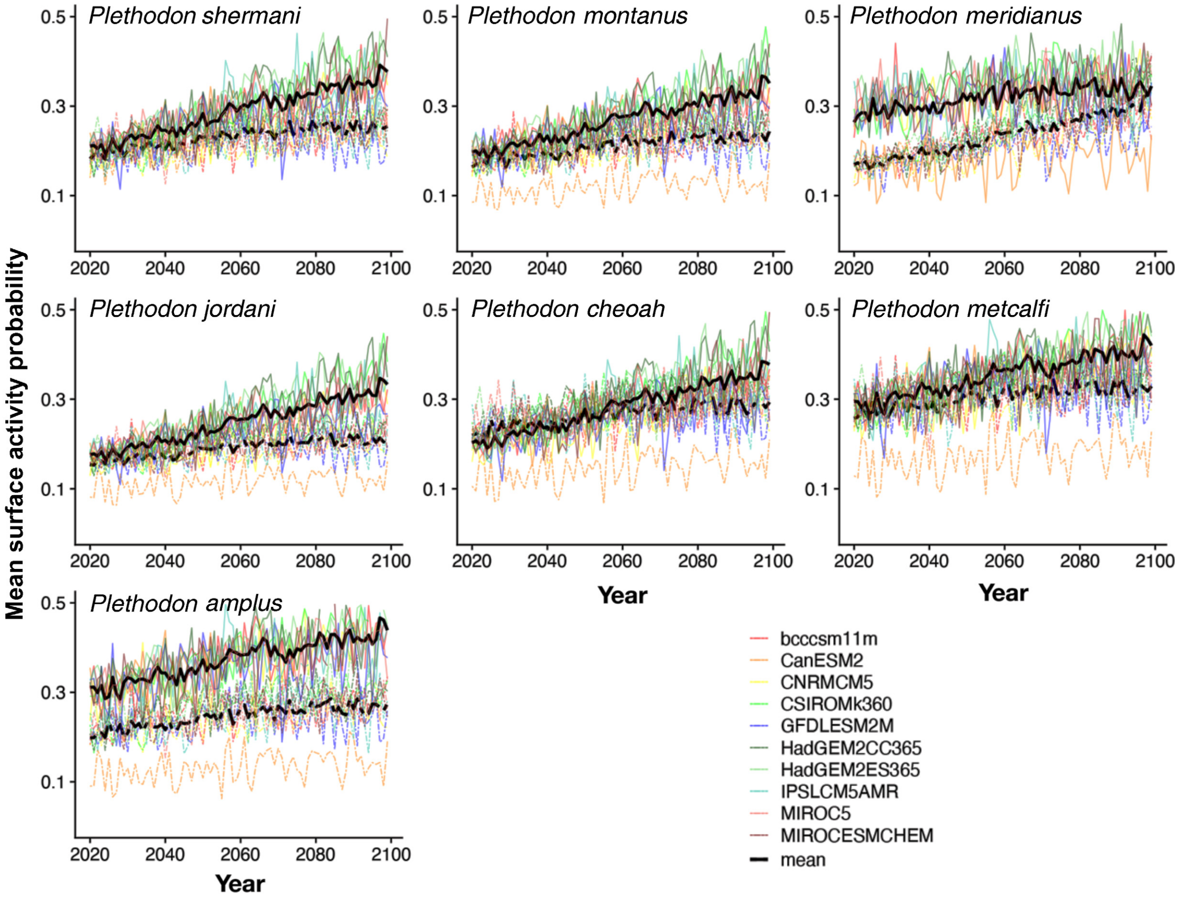

FIG. 5. Mean surface activity probability for the seven species in the *Plethodon jordani* complex for the years 2020–2100. Colored lines represent individual global circulation models (GCMs), with the black line indicating the mean of the 10 GCMs. Dotted lines show representative concentration pathway (RCP) 4.5 and solid lines show RCP 8.5.

is further supported by our high correlation between models that included a 25°C threshold of assumed zero activity and models without the threshold. Clay and Gifford (2017) showed the estimated performance breadth of *P. montanus* ranged from ~17° to 27°C, with 30°C representing the critical thermal maxima of other *Plethodon* species (Spotila 1972). Increased temperatures have also been shown to increase survival probability in *P. montanus*, likely because temperatures never exceeded the species' thermal maxima (Caruso and Rissler 2018). Thus, for high-elevation species with peak activity at the warmest times of the year, future climates might be expected to increase activity until conditions approach and surpass physiological limits.

Globally, ectotherms' current activity times are restricted to the warm summer months, and trends suggest that in temperate regions, there will be an increase of potential surface activity with climate change (Buckley et al. 2012). Our observed increased of activity probability over time is thus likely a warm-season effect. Increases in temperature affect nearly all physiological processes in ectotherms (Rome et al. 1992, Homyack et al. 2010). Warm temperatures increase the metabolic demands of salamanders, which may force more surface activity to maximize foraging opportunities. Connette and Semlitsch (2013) found that salamander surface activity increased in timber harvest plots relative to control plots, which could be a potential result of increased energy demands in the hotter harvest plots. Further, in a lab-based study, Novarro et al. (2018) found that *P. cinereus* had had greater ingestion rates at hotter temperatures, presumably in an attempt to counteract increased metabolic demands. Although Novarro et al. (2018) did not assess activity rates, their results suggest that salamanders would have to increase their surface activity to increase ingestion rates. Further, energy assimilation tends to decrease at higher temperatures, suggesting salamanders will need to increase feeding frequency to maintain energy balances (Clay and Gifford 2017, Fontaine et al. 2018, Huey and Kingsolver 2019). Increased metabolism could also have important population-level demographic consequences. For example, higher metabolism associated with increased temperature has been shown to decrease body sizes and growth rates in

Plethodon (Homyack et al. 2010, Caruso et al. 2014, Muñoz et al. 2016). Reductions in body sizes could lead to delayed maturity or reduced fecundity, ultimately leading to population declines. Thus, although our model predicts greater opportunity for surface activity under future conditions, there may be physiological trade-offs that collectively have negative consequences for salamander populations.

Salamander physiological tolerance and performance appears to be dependent on the climatic history of populations, which often exhibit local adaptation to the experienced background climate (Spotila 1972, Riddell and Sears 2015, Clay and Gifford 2017, Novarro et al. 2018). For example, temperature differentially impacts growth across elevational gradients in *P. montanus* whereby salamanders inhabiting high elevations have increased growth as temperatures increase, and those at low elevation show the opposite growth trend (Caruso and Rissler 2018). The elevational variation in growth rate is likely a result of the conditions experienced at each elevation; higher-elevation temperature increases are within the thermal tolerances of *P. montanus,* whereas low-elevation increases may exceed such tolerances, resulting in decreased growth (Caruso and Rissler 2018). Our modeling framework assesses surface activity probability across the entire range (latitudinal and elevation) of the species complex, combining high- and low-elevation individuals. The average weather conditions across the entire range of the *P. jordani* species complex appear to not exceed the species' thermal maxima, thus explaining why our model predicts continued increases in surface activity probability over the next 80 yr.

Concurrent with increased surface activity probability over time is an increase in variation in our activity probability (Appendix S1: Fig. S2), which corresponds with increased GCM uncertainty. Global circulation models typically have high uncertainty, especially towards the end of the century (Rupp et al. 2013, Northrop and Chandler 2014), with precipitation predictions being more variable than temperature, particularly at the regional scale (Knutti et al. 2008, Northrop and Chandler 2014). We found precipitation to impact surface activity probability in our global model estimates (Fig. 2), supporting previous findings (Connette and Semlitsch 2013, Connette et al. 2015, Muñoz et al. 2016, Caruso and Rissler 2018). Yet, there was no significant trend of precipitation into the future (Fig. 5), thus resulting in no discernable effects on our future surface activity probability estimates. As expected, the RCP 8.5 scenario had greater estimates of changes in VPA and temperature relative to RCP 4.5 (Fig. 5). These scenarios are representative of possible climate futures given emission levels and were specifically included to capture a range of variation in our model. There was no difference in surface activity probability between RCP scenarios, and all species responded with similar rates of increase in surface activity probability. This uniform response across the seven species is not surprising given that members of the *P. jordani* complex exhibit levels of niche conservatism. Mid to high elevations are the cradle of biodiversity for *Plethodon* likely because the climatic conditions experienced here have constrained species to specific climate (elevation) zones for millions of years, leading to greater species accumulation. Geographic isolation and limited dispersal through warmer low elevations has led to species diversification, and resulted in adaptation to the climatic conditions at these elevational regions (Kozak and Wiens 2010).

Our model predicts the probability of a salamander being surface active on a given night into the future, which is related to, but distinct from, the total time a salamander is active during a given night. This distinction is important because the duration of surface activity must be sufficient to fulfill the foraging requirements necessary for growth and survival. Further, mate finding and courtship occur on the forest floor (Jaeger 1980, Feder 1983, Petranka 1998); therefore reproductive opportunities are also tied to surface activity. However, teasing apart the probability of activity and total activity time is challenging. Total season activity has been previously modeled to increase with predicted rainfall (McEntire and Maerz 2019), and total activity time increases with dehydration resistance and water loss thresholds of salamanders, suggesting the importance of wet nights on activity time (Riddell et al. 2018). Our model cannot disentangle these effects. Additionally, discerning between the effects of environmental conditions on surface activity and annual and seasonal cycles is challenging. For instance, we have not observed salamanders at our sites becoming active under suitable conditions outside of their normal active season (J.Maerz, J. Crawford, D. Hocking, et al. *personal observations*). There may be a strong seasonal circadian rhythm to salamander activity that our model cannot detect. Photoperiod circadian rhythm can be a driver of activity initiation and metabolic activity in other urodeles, both of which can be modified by experimentally shifting photoperiod (Adler 1969, Hervant et al. 2000, Maerz et al. 2001). Bird migrations and many mammalian behaviors are strongly influenced by circadian and circannual rhythms (Gwinner 1996, Reppert and Weaver 2002, Albrecht and Eichele 2003). It could, therefore, be possible that the *P. jordani* species complex activity patterns have circadian patterns based on the summer season independent of the proximate environmental conditions.

Understanding surface activity of salamanders has been a long-standing challenge, and previous studies have used agent-based simulations (McEntire and Maerz 2019) and intensive lab-based physiological experiments (Riddell and Sears 2015) to understand and model surface activity. There are also a variety of existing models that attempt to discern future climate change effects on species ranges or biophysical processes (e.g., correlative approaches or mechanistic biophysical models). Our modeling framework is unique in that we adapted an existing framework to understand a targeted behavior—surface activity— directly. Our model is the first comprehensive field-based study to assess surface activity probability at a regional scale and then project activity into the future under climate change scenarios. Our model does, however, have important limitations to consider. Our approach assumes that abundance is constant through time, which may not be wholly representative. There have been numerous studies suggesting declines in amphibians at global scales (Houlahan et al. 2000) and across North America (Grant et al. 2016). Using occupancy models, Grant et al. (2016) found that declines are driven by interacting stressors, including human modification, pesticides, and climate at a local scale. Milanovich et al. (2010) suggested that suitable climate in the Appalachian highlands will significantly decrease, resulting in range contractions and abundance reductions over time. Our future surface activity model does not account for changes in abundance, nor does it account for the interactive and multiplicative stressors amphibians face that may contribute to declines (Blaustein et al. 2010). Our model also uses data from only three out of the seven species in the *P. jordani* complex, and our sampling efforts are somewhat west-skewed geographically (Fig. 1). However, all species of the complex are constrained to similar elevations that experience similar environmental conditions. All of the species had similar projected activity probability in the future (Fig. 5), suggesting our sampling bias does not strongly impact the results for all species in the complex. Finally, our model projects surface activity assuming that salamanders do not modify any behavior or physiology. Short-term lab studies suggest that salamanders have plastic physiological responses with metabolic and water loss suppression during the warmest parts of the year (Riddell et al. 2018). Salamanders may also modify the timing of surface activity to exploit more optimal conditions, a pattern seen commonly in other taxa (Fielding et al. 1999, Tingley et al. 2012, Schuster et al. 2014, Buckley et al. 2015, Muñoz et al. 2016). However, the ultimate demographic consequences of sustained physiological adjustments are unknown. Assessing surface activity cost trade-offs and phenological shifts in activity should be priorities for future studies.

Climate change will favor species with wide thermal tolerances, short generation times, and a range of genotypes among populations (i.e., high adaptive capacity; Ficke et al. 2007). Species of the *P. jordani* complex are unfortunately lacking in all three attributes. They have relatively narrow thermal performance windows (Clay and Gifford 2018), long generation times (Staub 2016), and small and geographically isolated populations with limited gene flow (Highton and Peabody 2000), emphasizing their conservation concern. Our regional, multispecies model demonstrates that temperature, precipitation, and vapor pressure strongly influence surface activity probability, and without physiological or behavioral changes, these salamanders will exhibit higher levels of surface activity during their peak active season under future climate conditions. Our study provides necessary insight into how a key behavior driving fitness of plethodontid salamanders will be affected by climate change.

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Supporting Information

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