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Demographic consequences of climate variation along an elevational gradient for a montane terrestrial salamander

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Abstract

Climate change represents a significant threat to amphibians. However, for many species, the relationship between demography and climate is unknown, which limits predictive models. Here, we describe the life history variation of *Plethodon montanus* using capture–recapture data over a period of 4 years, along an elevational gradient to determine how survival and growth vary with climate, and how these relationships vary with elevation. We used a hierarchical model to estimate asymptotic size and growth rate and a spatial Cormack-Jolly-Seber model to estimate the probability of capture and survival and dispersal variance. We found that during the active season, growth and survival rates are both positively affected by precipitation; however, while survival was positively affected by temperature at all elevations, higher temperatures led to a decrease in growth at lower elevations, while at higher elevations the opposite was true. During the inactive season, we found reduced growth rates, whereas survival was lower compared with the active at lower elevations but was higher at higher elevations. Increased inactive season temperatures resulted in decreased survival while we found that temperature, amount of snow, and elevation interacted to influence survival. At low elevations, which were warmer, survival decreased with increasing snowfall but at higher elevations, survival generally increased with increasing snowfall. Our results demonstrate that understanding how the environment can affect salamander demography to develop mechanistic models will require knowledge of the actual environmental conditions experienced by a given population as well as an understanding of the overall differences in climate at a given site.

KEYWORDS

capture–recapture, growth, life history, MCMC, *Plethodon*, survival

1 | INTRODUCTION

Amphibians are one of the most endangered vertebrate taxa (Hoffman et al., 2010; IUCN, 2016; McCallum, 2007) and face multiple onslaughts including emerging infectious diseases, habitat loss, invasive species and climate change (Blaustein et al., 2010; Grant et al., 2016; Hoffman et al., 2010). Currently, at least 41% of the approximately 6,500 recognized amphibian species are considered threatened (Hoffman et al., 2010; IUCN, 2016), and at least 50% of all salamander species are currently listed as "critically endangered", "endangered", or "vulnerable" (IUCN, 2016). Trends in declining salamander populations have recently become both taxonomically and geographically widespread (e.g., Adams et al., 2013; Rovito, Parra-Olea, Vásquez-Almazán, Papenfuss, & Wake, 2009; Spitzen-van der Sluijs et al., 2013). These declines are especially concerning because salamanders represent a significant portion of the total forest biomass and function as keystone predators (Burton & Likens, 1975; Milanovich & Peterman, 2016).

Given that many populations are already experiencing declines, future changes in climate represent a

compounding threat to amphibian populations (Milanovich, Peterman, Nibbelink, & Maerz, 2010; Sutton et al., 2015; Caruso, unpublished data). Recent evidence suggests that contemporary changes in climate have already affected amphibian life history traits (e.g., Reading, 2007; Caruso, Sears, Adams, & Lips, 2014; but see Connette, Crawford, & Peterman, 2015). In addition, warmer temperatures result in metabolic depression (Catenazzi, 2016) and slower growth rates of salamanders (Muñoz, Hesed, Grant, & Miller, 2016), which can negatively affect fitness. Under future climate change, populations may become further isolated to higher, cooler elevations (Bernardo, Ossola, Spotila, & Crandall, 2007; Bernardo & Spotila, 2006; Gifford & Kozak, 2012; Lyons, Shepard, & Kozak, 2016). Current model predictions of how changes in climate may affect salamander distributions are generally limited to correlative models (e.g., Milanovich et al., 2010; Sutton et al., 2015; Caruso, unpublished data), which do not take into account metrics of demographic vital rates (i.e., survival, growth and reproduction) as they are lacking for many species. Therefore, current models likely underestimate the effects of future changes in climate (Buckley et al., 2010; Urban et al., 2016).

Demographic vital rates can vary across spatial gradients, and these rates are driven by the biotic (e.g., competition) and the abiotic (e.g., temperature) environment. Lower quality environmental conditions can limit a species' distribution, while higher quality environments allow for persistence (Gaston, 2003). In general, poleward range limits are thought to be set primarily by abiotic factors and equatorward limits by biotic interactions (Schemske, Mittelbach, Cornell, Sobel, & Roy, 2009). Contrastingly, correlative niche models suggest that amphibian ranges may be more limited at the warmer range edges by the abiotic environment (Cunningham, Rissler, Buckley, & Urban, 2016). Although data for montane salamander species are sparse, physiological constraints (Bernardo & Spotila, 2006; Gifford & Kozak, 2012; Lyons et al., 2016) and results of reciprocal transplant experiments (Cunningham, Rissler, & Apodaca, 2009; Caruso, unpublished data) support this trend. However, detailed sampling of vital rates across multiple populations distributed across a species' range is time-consuming and labor-intensive; therefore, few studies on salamanders have used this information to inform models of range limits and shifts.

As global climates continue to shift, demographic vital rates have become increasingly important to characterize the health of natural populations and to develop informed population models (Buckley et al., 2010; Caswell, 2000; Coulson, Gaillard, & Festa-Bianchet, 2005; Pauly, 1995; Sarrazin & Legendre, 2000; Tenhumberg, Tyre, Shea, & Possingham, 2004; Urban et al., 2016). Unfortunately, vital rates and life history traits are unknown for many plethodontid species, adding further uncertainty to their potentially bleak future

(e.g., Milanovich et al., 2010). Even when such studies are done, sampling biases such as unobservable ecological states, imperfect and variable detection and measurement error can distort vital rate estimates of natural populations (Connette et al., 2015; Connette & Semlitsch, 2015; Eaton & Link, 2011; Kéry & Royle, 2016; Kéry & Schaub, 2012; Leberg, Brisbin, Smith, & White, 1989; Royle & Dorazio, 2008; Schwarz & Runge, 2009). Capture–recapture (CR) methods offer a solution for accounting for these biases; individual observable ecological states can be tracked, while uncertainty in these states can be modeled (Kéry & Royle, 2016; Kéry & Schaub, 2012). Survival is often a focus of CR studies, as understanding survival, its variation (both temporal and spatial), and the abiotic and biotic factors that drive this variation, are necessary to understanding the underlying spatial and temporal variation in population growth (Lebreton, Burnham, Clobert, & Anderson, 1992; Sæther & Bakke, 2000). Similarly, growth is useful for understanding population demographics because larger body size in many species, especially amphibians, is associated with higher fitness (e.g., Berven, 1981; Semlitsch, 1985; Verrell, 1982). Both survival and growth estimates can be improved using CR methods. Survival can be modeled by accounting for capture probability and dispersal (Lebreton et al., 1992; Schaub, Gimenez, Schmidt, & Pradel, 2004; Schaub & Royle, 2014), while estimating measurement error and the variation in growth within and among individuals can improve growth estimates (Eaton & Link, 2011; Link & Hesed, 2015).

In this study, we collected 4 years of CR data for *Plethodon montanus* at five sites along an elevational gradient and used hierarchical models to explore the relationship between demography and climate. The objectives of our study were to (a) determine how demographic vital rates (growth and survival) vary along an elevational gradient and among seasons, (b) determine how environmental conditions (temperature and precipitation) affect variation in growth and survival and (c) determine how the relationship between both survival and growth and environmental conditions varies along the elevational gradient and among seasons. We hypothesized that *P. montanus* vital rates would be driven by climate, whereby warmer and drier conditions would decrease both survival and growth and that lower elevation populations, by virtue of being warmer and drier, will show reduced survival and growth compared to those at higher elevations.

2 | MATERIAL AND METHODS

2.1 | Locations and sampling

We established five sites along an elevational gradient within the range of *P. montanus* in Pisgah National Forest in

2013: Spivey Gap (996 m), Iron Mountain Gap (IMG; 1,134 m), Hughes Gap (1,231 m), Big Butt Trail (1,300 m) and Carver's Gap (CG; 1,464 m). These sites were chosen to minimize the differences among sites in leaf litter depth, aspect, canopy coverage and number of surface retreats while establishing an elevational gradient within distribution of *P. montanus*.

Within each site, we delineated 1–150 m^2 plot (10 × 15 m). Starting in 2014, we established a grid (25–2 × 3 m sections) within the plot to determine the location of each individual salamander within 0.5 m. Although surveys differed in number of people, effort and type (i.e., diurnal and nocturnal), salamanders were processed similarly regardless of survey type, amount of effort, or number of surveyors. We captured all salamanders encountered and measured their body size from the snout to the posterior margin of the vent snout-vent length (SVL). We marked *P. montanus* using Visual Implant Elastomer (Northwest Technology Inc., Shaw Island, Washington) tags, which have minimal effects on fitness and low incidence of tag loss (Bailey, 2004). After all salamanders were processed on a particular sampling occasion, we released all individuals back to the original point of capture. See Appendix S1, Supporting Information for additional detail about sampling and site characteristics.

2.2 | Site- and survey-specific climate

First, we defined two seasons based on our sampling; the active season (i.e., when salamanders were typically active and when we conducted surveys—27 May to 13 October) and the inactive season (14 October to 26 May). Next, for the length of our study, we obtained daily temperature and precipitation data from the DAYMET database (http://www.daymet.org; Thornton, Running, & White, 1997) as covariates in our growth and survival models. We defined temperature for both the active and inactive season as the mean maximum temperature (°C) during the sampling interval, while we defined precipitation for the active season as mean precipitation (mm) and for the inactive season as the mean snow water equivalent (SWE; mm) during the sampling interval.

2.3 | Asymptotic size and growth

To test the degree to which growth is driven by climate, we used a hierarchical model to estimate the effects of season, elevation, temperature and precipitation on growth rates. Our model estimates the expected size of the *i*th individual at the *t*th time (ES$_{i,t}$) using the von Bertalanffy growth curve, parameterized for unknown ages (Fabens, 1965) as a function of its expected size at the previous measurement time (TS$_{i,t-1}$), elevation-specific asymptotic size (a_{elev}), active [$k(A)_{i,t}$] and inactive [$k(IA)_{i,t}$] season growth rates scaled for 365-day increments and the interval between captures

(number of days) during the active [$\Delta t(A)_{i,t}$] or inactive [$\Delta t(IA)_{i,t}$] seasons (Equation (1)).

$$ES_{i,t} = ES_{i,t-1} + (a_{elev} - ES_{i,t-1})$$
$$\times \left(1 - e^{-k(a)_{i,t} \times \frac{\Delta t(A)_{i,t}}{365} - k(i)_{i,t} \times \frac{\Delta t(IA)_{i,t}}{365}}\right).$$
(1)

The logarithm of active and inactive season growth rates were subsequently defined by season-specific intercepts [$\alpha_{k(A)}$, $\alpha_{k(IA)}$], as well as covariates for elevation [$\beta elev_{k(A)}$, $\beta elev_{k(IA)}$], temperature [$\beta temp_{k(A)}$, $\beta temp_{k(IA)}$], precipitation [$\beta precip_{k(A)}$], SWE [$\beta swe_{k(IA)}$], the interaction between elevation and temperature [$\beta et_{k(A)}$, $\beta et_{k(IA)}$], precipitation [$\beta ep_{k(A)}$], or SWE [$\beta es_{k(IA)}$], the interaction between active temperature and precipitation [$\beta tp_{k(A)}$] or SWE [$\beta tsw_{k(IA)}$], and the interaction between elevation, temperature and precipitation [$\beta etp_{k(A)}$] or SWE [$\beta etsw_{k(A)}$; Equation (2)].

$$\log(k(A)_{it}) = \alpha_{k(A)} + \beta elev_{k(A)} + \beta temp_{k(A)} + \beta precip_{k(A)}$$
$$+ \beta et_{k(A)} + \beta ep_{k(A)} + \beta tp_{k(A)} + \beta etp_{k(A)}$$
(2)
$$\log(k(IA)_{it}) = \alpha_{k(IA)} + \beta elev_{k(IA)} + \beta temp_{k(IA)} + \beta swe_{k(IA)}$$
$$+ \beta et_{k(IA)} + \beta es_{k(IA)} + \beta tsw_{k(IA)} + \beta etsw_{k(IA)}.$$

Finally, our measurements of a given individual (SVL$_{i,t}$) are described by independent normal random variables with a mean of the expected size (ES$_{i,t}$) and an estimated standard deviation (σ_{SVL}; i.e., measurement error). Therefore, using this hierarchical model we estimated 22 parameters. For further model details and code, see Appendix S2.

2.4 | Growth analysis

To evaluate our growth models, we assigned vague normal priors (mean = 0; variance = 100) to all growth rate covariates, uniform priors for elevation specific asymptotic size (min = 50, max = 80) and a vague Gamma prior (shape and rate = 0.001) to the parameter $\frac{1}{\sigma^2_{SVL}}$ (i.e., precision). All continuous covariates were first scaled and centered prior to model fitting. We fit the model using Markov chain Monte Carlo (MCMC), generating three chains, each with 500,000 iterations. We used an adaptation phase of 1,000, discarded 350,000 burn-in iterations and used a thinning rate of 50, retaining 3,000 iterations from each chain to estimate posterior distributions (9,000 total samples).

2.5 | Capture, dispersal and survival

To test the degree to which survival is driven by climate, we used a spatial Cormack-Jolly-Seber (s-CJS) model (Schaub & Royle, 2014) to estimate the effects of season, elevation, temperature and precipitation on survival while accounting for variation in capture probability and dispersal.

For each individual, we modeled survival to each primary period after its initial capture. Therefore, an individual's ecological state during the primary period where it is first captured and marked is known (i.e., equal to one). For subsequent primary periods, the ecological state of the ith individual at the tth primary period ($z_{i,t}$) is described by a Bernoulli distribution where the probability of success (i.e., the individual is alive, given that it was alive previously) is the product of the probability of survival of the ith individual to the tth primary period ($\phi_{i,t}$) and the ecological state of the ith individual at the previous primary period ($z_{i,t+1}$). Our observation process is likewise described by a Bernoulli distribution where the probability of success (i.e., finding the ith individual, at the tth primary period and ttth secondary period, given that it is alive and within the bounds of the study area) is the product of the capture probability ($p_{i,tt,t}$), ecological state ($z_{i,t}$) and spatial state ($r_{i,tt,t}$) of the ith individual, at the tth primary period and ttth secondary period (Kéry & Schaub, 2012; Schaub & Royle, 2014).

To account for the fact that some individuals emigrated and thus represent apparent survival (Schaub & Royle, 2014), we included each individual's spatial location within each study site and estimated dispersal from subsequent recaptures. The spatial state ($r_{i,tt,t}$) of the ith individual, at each ttth secondary period and tth primary period, is given a value of one if the location in the x- and y-axes ($Gx_{i,tt,t}$ and $Gy_{i,tt,t}$, respectively) of that individual, at that time is within the study area, while the spatial state receives a value of zero if that individual, at that time is outside the study area. Because we sampled secondary periods within primary periods (2013–2014), we first describe the primary period center of activity in the x- and y-axes ($Gx_{i,t}$ and $Gx_{i,t}$, respectively). The initial primary period center of activity of the ith individual, at the tth primary period is described by a uniform distribution, which is bounded by the lower and upper bounds of the x- and y-axes of the plot area (i.e., an individual must be within the study area to be marked). For subsequent primary periods ($t+1$), the center of activity of the ith individual is normally distributed where the mean is the center of activity at the previous primary period in the x- and y-axes and two estimated precision parameters ($\frac{1}{\sigma^2_{Gxt}}, \frac{1}{\sigma^2_{Gyt}}$). Finally, the spatial location of the ith individual at the ttth secondary period and tth primary period is also normally distributed, where the mean is the center of activity during the tth primary period and two estimated precision parameters ($\frac{1}{\sigma^2_{Gxtt}}, \frac{1}{\sigma^2_{Gytt}}$). We, therefore, estimated four parameters for the dispersal portion of our model.

We modeled the logit of the capture probability ($p_{i,tt,t}$) for the ith individual, at the tth primary period and ttth secondary period as a function of an intercept (α_p), survey type (diurnal or nocturnal; βsurv$_p$), effort (1 or 2; βeff$_p$), number of people (1 or 2; βpers$_p$), linear and quadratic terms for Julian day (βjday$_p$ and βjday^2_p, respectively), site (βsite$_p$) and random intercepts for individuals (ε_i) and primary period ($\gamma_{i,t}$; Equation (3)).

$$\text{logit}(p_{i,tt,t}) = \alpha_p + \beta\text{surv}_p + \beta\text{eff}_p + \beta\text{pers}_p + \beta\text{jday}_p \\ + \beta\text{jday}^2_p + \beta\text{site}_p + \varepsilon_i + \gamma_{i,t}. \quad (3)$$

Therefore, for capture probability, we estimated 12 total parameters (i.e., 10 for the fixed effects and one for the precision component for each of the two random intercepts). Finally, we modeled the logit of survival ($\phi_{i,t}$) of the ith individual at the tth primary period as a function of an intercept (α_ϕ), size (last SVL measurement; βsize$_\phi$), elevation (βelev$_\phi$), season (βseason$_\phi$), temperature, precipitation and SWE during the active [βtemp$_{\phi(A)}$, βprecip$_{\phi(IA)}$] and inactive [βtemp$_{\phi(A)}$, βswe$_{\phi(IA)}$] seasons, as well as interactions between active temperature and precipitation [βtp$_{\phi(A)}$], inactive temperature and SWE [βtsw$_{\phi(IA)}$] elevation with season (βese$_\phi$), active season temperature and precipitation [βet$_{\phi(A)}$, βet$_{\phi(IA)}$], inactive temperature and precipitation and SWE [βep$_{\phi(A)}$, βesw$_{\phi(IA)}$], elevation, active temperature and precipitation [βetp$_{\phi(A)}$], and elevation inactive temperature and SWE [βetsw$_{\phi(IA)}$; Equation (4)].

$$\text{logit}(\phi_{i,t}) = \alpha_\phi + \beta\text{size}_\phi + \beta\text{elev}_\phi + \beta\text{season}_\phi + \beta\text{temp}_{\phi(A)} + \\ \beta\text{temp}_{\phi(IA)} + \beta\text{precip}_{\phi(A)} + \beta\text{swe}_{\phi(IA)} + \beta\text{tp}_{\phi(A)} + \beta\text{tsw}_{\phi(IA)} + \\ \beta\text{ese}_\phi + \beta\text{et}_{\phi(A)} + \beta\text{et}_{\phi(IA)} + \beta\text{ep}_{\phi(A)} + \beta\text{esw}_{\phi(IA)} + \beta\text{etp}_{\phi(A)} + \\ \beta\text{etsw}_{\phi(IA)}. \quad (4)$$

We, therefore, estimated 17 parameters for survival. For further model details and code, see Appendix S2.

2.6 | Survival analysis

To evaluate our survival models, we first scaled and centered all continuous predictor variables. We assigned uniform priors (min = 0, max = 10) to all spatial variance estimates. For fixed parameters, we assumed vague normal priors (mean = 0; variance = 100), and random intercepts ($\gamma_{i,t}$ and ε_i) were given normal priors, which had estimated precision parameters from a uniform distribution (min = 0; max = 10). We fit the model using MCMC, generating three chains, each with 800,000 iterations. We used an adaptation phase of 1,000, discarded 500,000 burn-in iterations and used a thinning rate of 50, retaining 6,000 iterations from each chain to estimate posterior distributions (18,000 total samples).

All analyses were performed in program R, version 3.3.1 (R Core Team, 2016). We used the *jagsUI* package (Kellner, 2017) to call JAGS (Plummer, 2003), from program R for MCMC analyses. We examined traceplots of parameters for adequate mixing among chains and the $\hat{R}$ statistic (Gelman, Carlin, Stern, & Rubin, 2004) to evaluate model convergence (see Appendix S3), and we evaluated parameter significance based on the overlap of 95% highest posterior density (HPD) with zero.

3 | RESULTS

Over 190 diurnal ($n = 58$; 31%) and nocturnal ($n = 132$; 69%) surveys, we captured 2,962 salamanders representing nine species ($P.\ montanus = 2,413$, 81%; nontarget species = 549, 19%). We marked a total of 1,343 individuals, and recapture events constituted 1,070 (44%) of our total captures of *P. montanus* captures; we recaptured 559 (42%) individuals at least once (range = 1–15 times). Recapture rates generally increased throughout the duration of this study, and average recapture rates were at least 40% during the final year of this study at all sites (Appendix S1).

3.1 | Growth

We used animals that were captured at least twice for all growth analyses, which included 1,586 total measurements (544 unique individuals), with a range of 92–728 measurements per site (36–215 unique individuals per site). Although the highest elevation site (CG) had one of the largest asymptotic size estimate (mean = 62.1 mm), this size was similar to the asymptotic size estimate for IMG (62.2 mm), which is approximately 300 m lower in elevation, while the remaining three sites had smaller asymptotic sizes (Figure 1a). During the active season, we found significant effects of average precipitation [$\beta\mathrm{precip}_{k(A)}$; 95% HPD = 0.10, 0.52] and the interaction between average temperature and elevation [$\beta\mathrm{et}_{k(A)}$; 95% HPD = 0.09, 0.36; Figure 1b]. At all sites, increased precipitation was associated with higher growth rates at all sites, whereas the

relationship between temperature and growth rate varied along the elevational gradient; higher temperatures at lower elevations resulted in lower growth rates while the opposite was observed at higher elevations (Figure 2a). Average growth rates during the inactive season were considerably lower [$\alpha_{k(IA)}$; 95% HPD = −28.74, −6.68] than those during the active season [$\alpha_{k(A)}$; 95% HPD = 0.11, 0.37] and inactive season growth rates were not significantly influenced by climate (Figure 1c).

3.2 | Dispersal and capture

Dispersal variance estimates from s-CJS models were similar for primary and secondary seasons with values of approximately one in both the *x*- and *y*-axes (Figure 3a). Therefore, we would expect that 95% of an individual's movements in the *x*- and *y*-axes would be found within approximately 2 m from their previous point of capture. Individual variation in capture probability (σ_ε) was lower (95% HPD = 0.00, 0.19) than primary period variation (σ_γ; 95% HPD = 0.67, 1.06), and we found that survey type ($\beta\mathrm{surv}_p$; 95% HPD = 2.00, 2.42), the amount of effort ($\beta\mathrm{eff}_p$; 95% HPD = 0.76, 1.94) and the number of people ($\beta\mathrm{pers}_p$; 95% HPD = 0.45, 1.24) significantly explained capture probability (Figure 3b). Capture probability was higher during nocturnal surveys and those that had two people and an increased effort (Figure 3b).

3.3 | Survival

We found that survival was significantly affect by size ($\beta\mathrm{size}_\phi$; 95% HPD = 1.26, 1.62), elevation ($\beta\mathrm{elev}_\phi$; 95%
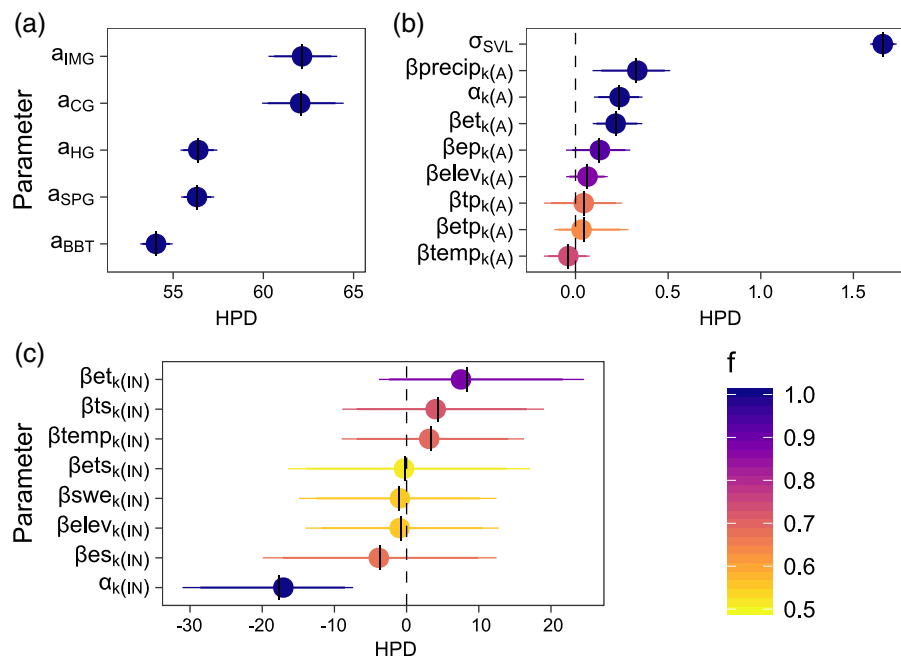

FIGURE 1 Highest posterior density for growth model with (a) asymptotic size, (b) active season parameters and measurement error and (c) inactive season parameters. Points represent median estimates and vertical lines represent mean estimates; thick lines show 90% HPD, while thin lines show 95% highest posterior density (HPD). Color scale denotes the proportion of the posterior sample that has the same sign as the mean estimate (f)
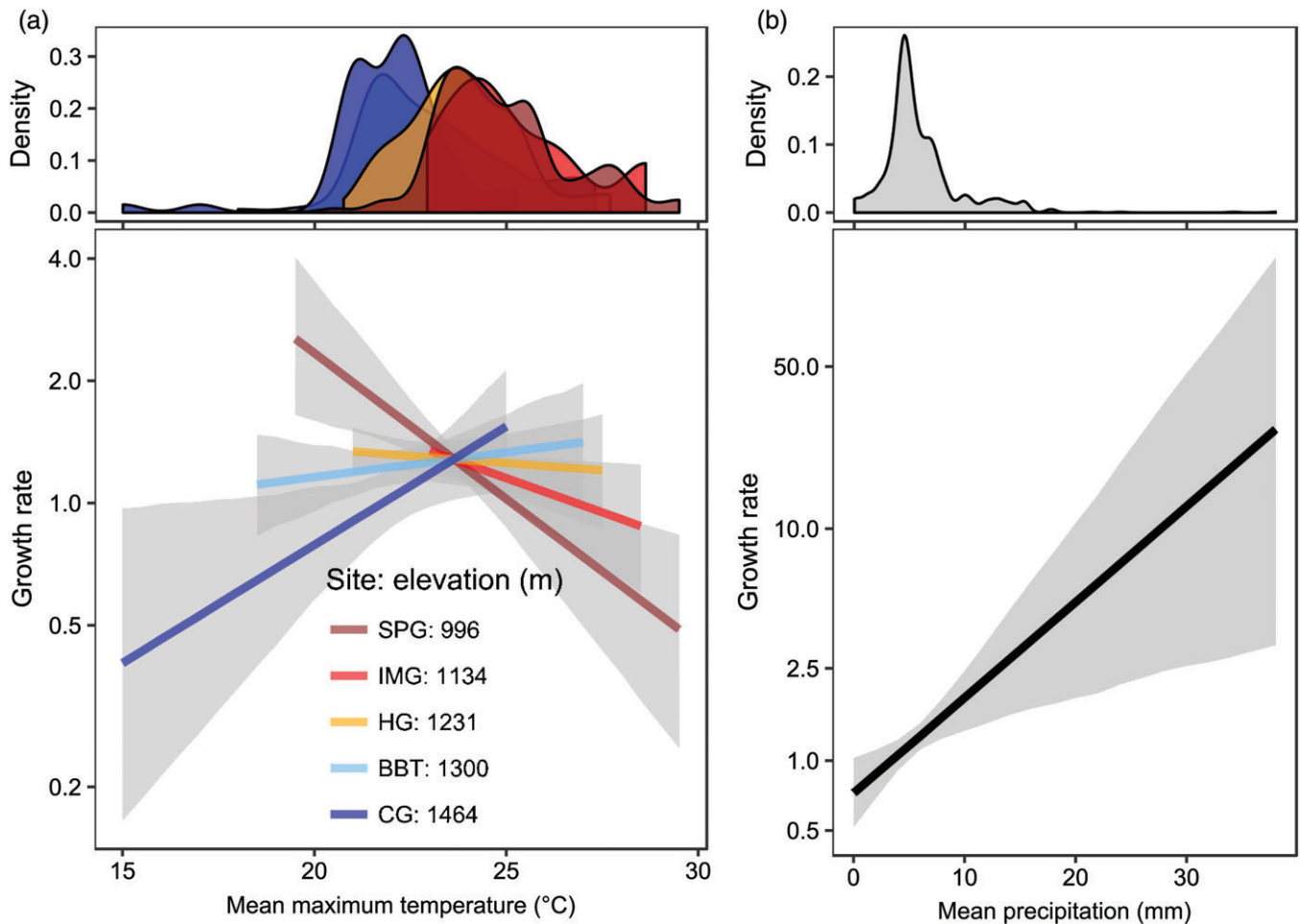
FIGURE 2 Relationship between growth rate with (a) active season temperature and elevation and (b) precipitation. Colors denote site elevation, lines show median predicted relationship, while the gray-shaded ribbon shows the 95% highest posterior density (HPD). The top portion of each panel shows the density distribution of (a) elevation-specific mean maximum temperature and (b) mean precipitation at all sites. Predicted relationships were limited to the actual range of climate experience by (a) each site or (b) at all sites

HPD = −0.67, −0.11) and season (βseason$_\phi$; 95% HPD = −3.33, −1.61) and the interaction between season and elevation (βese$_\phi$; 95% HPD = 1.19, 4.41; Figure 3c). Survival increased with increased SVL, during the active season was lower at high elevations compared to low elevations but was higher at higher elevations compared with lower elevations during the inactive season (Figures 3c, 4 and 5). During the active season, both temperature [βtemp$_{\phi(A)}$; 95% HPD = 0.24, 0.90] and precipitation [βprecip$_{\phi(A)}$; 95% HPD = 0.19, 0.97] positively influenced survival; increased precipitation and higher temperatures were associated with higher survival (Figure 4a,b). However, during the inactive season, we found that survival was significantly influenced by temperature [βet$_{\phi(IA)}$; 95% HPD = 1.98, 5.85; Figure 3c], the interaction between average SWE and elevation [βesw$_{\phi(IA)}$; 95% HPD = −1.20, −0.10; Figure 3c], the interaction between average SWE, temperature and elevation [βetsw$_{\phi(IA)}$; 95% HPD = 1.38, 5.37; Figure 3c]. Survival decreased with increasing temperature at all elevations, and the relationship between survival and SWE was temperature dependent across elevations (Figure 5). At lower elevations, where

inactive season temperatures were warmer than higher elevations, survival decreased with increasing SWE; however, at higher elevations, survival increased with increasing SWE except at lower temperatures (Figure 5).

4 | DISCUSSION

We present 4 years of CR data to provide a detailed account of how survival and growth of *P. montanus* varies along an elevational gradient and with climate. We found that survival and growth of *P. montanus* is influenced by climate and importantly that the relationship between either survival or growth and climate can vary along an elevational gradient. Our results suggest that *P. montanus* exhibits variation in life history along this elevational gradient, likely resulting from the differences in abiotic environment experienced by those populations. Therefore, understanding how the environment can affect salamander populations, via survival and growth of individuals, may require more than just knowledge of the actual environmental conditions experienced by
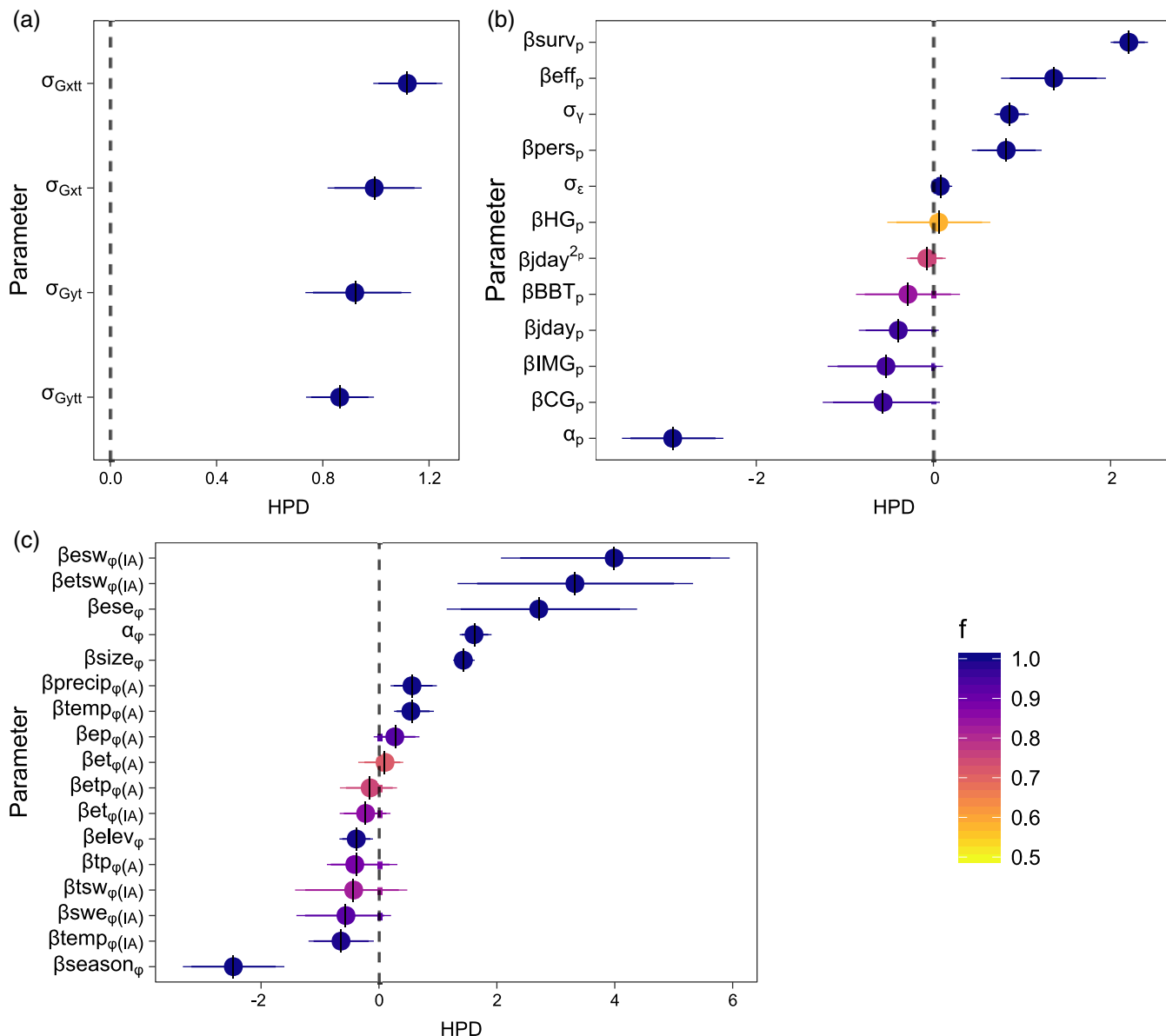
FIGURE 3 Highest posterior density for spatial Cormack-Jolly-Seber (s-CJS) model with (a) dispersal parameters, (b) capture parameters and (c) survival parameters. Points represent median estimates and vertical lines represent mean estimates; thick lines show 90% highest posterior density (HPD), while thin lines show 95% HPD. Color scale denotes the proportion of the posterior sample that has the same sign as the mean estimate (f)

a given population but also understanding the overall differences in climate at a given site.

4.1 | Dispersal

Previous studies have found small home ranges and low dispersal in other species of terrestrial plethodontids (Kleeberger & Werner, 1982; Mathis, 1991; Merchant, 1972; Muñoz et al., 2016). Our observations for *P. montanus* are consistent with these patterns. Dispersal and subsequent immigration can buffer sink populations from declines even when climate negatively affects demographic vital rates and population growth (Brown & Kodric-Brown, 1977; Dias, 1996; Pulliam, 1988; Tavecchia et al., 2016). Unfortunately, montane salamanders, such as *P. montanus,* are also physiologically restricted at lower elevations, and tracking suitable climate would likely be limited

through warmer valleys and across latitudes, which may exacerbate population isolation and range contractions (Bernardo & Spotila, 2006; Kozak & Wiens, 2006). The low dispersal observed for *P. montanus* and other terrestrial plethodontids (Cabe, Page, Hanlon, Aldrich, & Marsh, 2007; Liebgold, Brodie III, & Cabe, 2011; Marsh, Thakur, Bulka, & Clarke, 2004; Ousterhout & Liebgold, 2010; Peterman & Semlitsch, 2013) likely further increases their risk of population decline under future climate change.

4.2 | Active season

We found that increased precipitation is associated with higher growth rates across the elevational gradient (Figure 2b). It has been well established that rainfall can influence surface activity of plethodontid salamanders
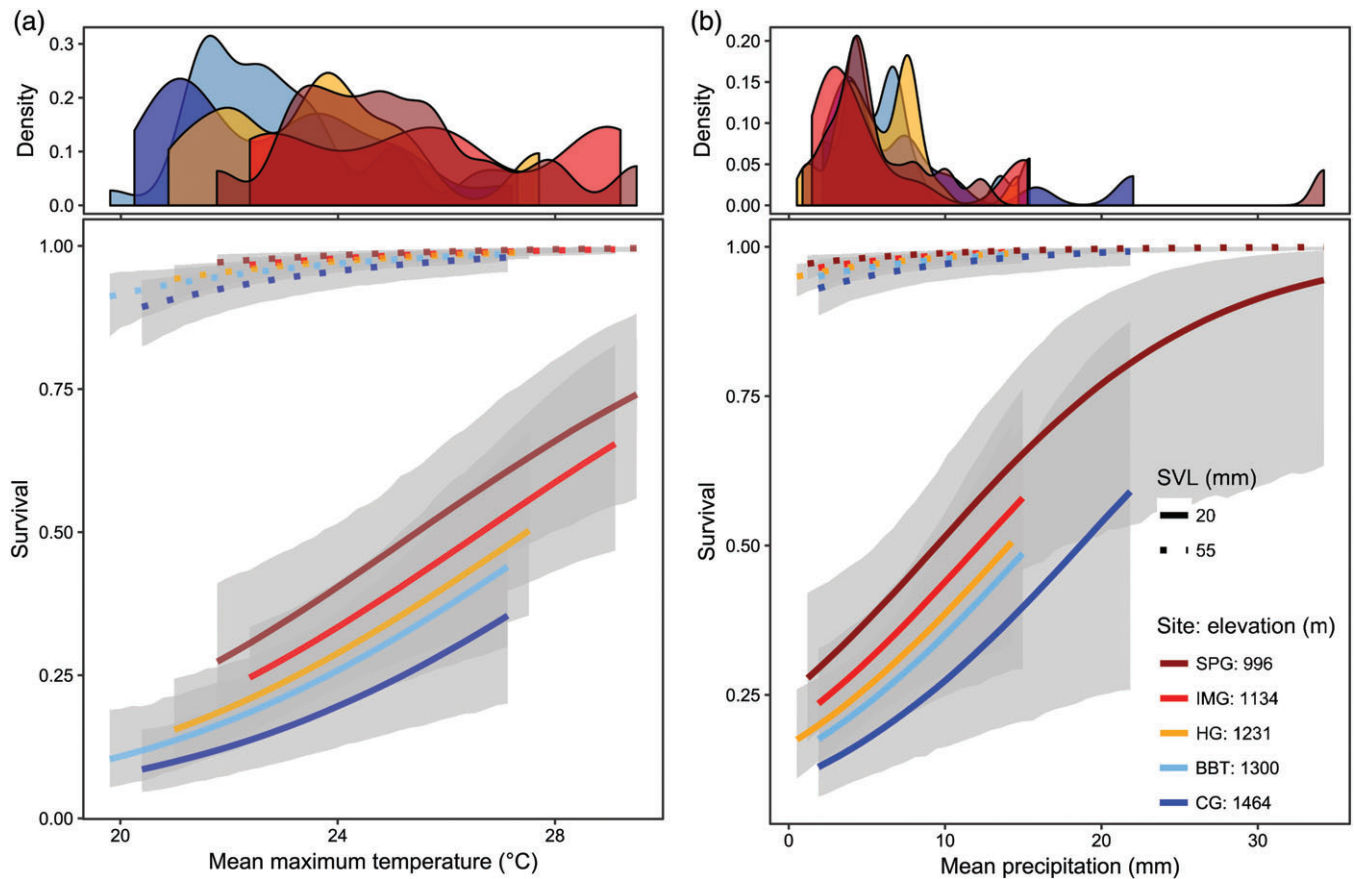
FIGURE 4 Relationship between survival with (a) active season temperature and (b) precipitation. Colors denote site elevation, lines show median predicted relationship, while the gray-shaded ribbon shows the 95% highest posterior density (HPD). Solid lines denote individuals with a body size of 20 mm, while dotted lines represent 55 mm to show the variation in survival over the range of sizes. The top portion of each panel shows the density distribution of elevation-specific (a) mean maximum temperature and (b) mean precipitation. Predicted relationships were limited to the actual range of climate experience by each site

(Bendik & Gluesenkamp, 2013; Connette et al., 2015; Petranka & Murray, 2001), which require moist conditions due to their high rates of evaporative water loss (Spight, 1968; Spotila, 1972; Spotila & Berman, 1976). Conditions, such as increased precipitation allow for a greater surface activity window and subsequently increased foraging time (Feder & Londos, 1984) or may increase the encounter rates of salamanders with their prey (Jaeger, 1978, 1980); both of which would likely increase the total number of prey captured and would lead to increases in growth rates, assuming other environmental conditions are equal (e.g., temperature; Catenazzi, 2016). Higher precipitation was also associated with an increase in survival across the elevational gradient (Figure 4b). While salamanders are able to find and take advantage of moist microhabitats in seemingly unfavorable habitats (e.g., Yanev & Wake, 1981); reductions in rainfall can eventually have negative consequences on salamander fitness. Reduced rainfall can limit surface activity (Connette et al., 2015), and dehydration can cause a decline in locomotor performance (Feder & Londos, 1984), both of which can reduce foraging success or opportunities, which would decrease energy intake and likely result in lower survival.

Temperature sensitivity in various aspects of growth rates (e.g., rates of assimilation and digestion) has been previously demonstrated in plethodontids (e.g., Bobka, Jaeger, & McNaught, 1981; Clay & Gifford, 2017; Fitzpatrick, 1973; Muñoz et al., 2016). In our study, the effect of temperature on growth rates of *P. montanus* varied along the elevational gradient; higher temperatures resulted in lower growth rates at low elevations and higher growth rates at high elevations (Figure 2a). The range of average temperatures experienced by these populations may explain this pattern, at least in part; high elevation populations generally experienced temperatures lower than those experienced by low elevations (Appendix S1; Figure 2a). Indeed, Clay and Gifford (2017) found a similar pattern, in which energy assimilation under laboratory conditions in *P. montanus* steadily increased with increasing temperatures but rapidly dropped after reaching an optimum (22.8°C for high elevations and 22.6°C for low elevations) similar to the average temperature at which the growth rate temperature relationship in our study (23.5°C) changed from positive (lower temperatures) to negative (higher temperatures; Figure 2a). Survival, on the other hand, was affected by temperature similarly across our elevational gradient; higher temperatures were associated with higher
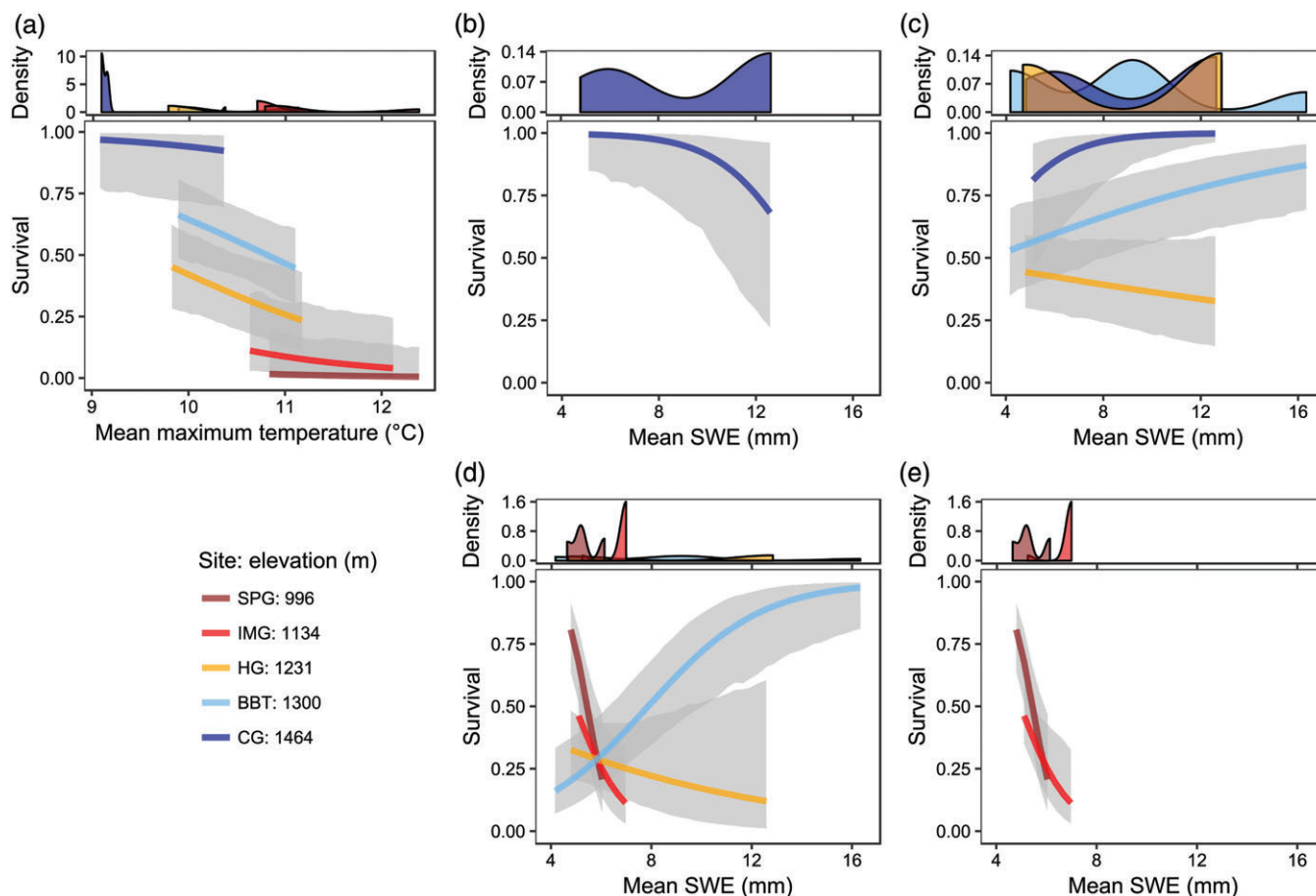
FIGURE 5 Relationship between survival with (a) inactive season temperature and snow water equivalent (SWE) at (b) 9.1°C, (c) 10.1°C, (d) 11.1°C and (e) 12.1°C to demonstrate the interaction between SWE and temperature. For all figures, predicted relationships are for the mean body size (39.5 mm SVL). Colors denote site elevation, lines show median predicted relationship, while the gray-shaded ribbon shows the 95% highest posterior density (HPD). The top portions of each panel show the density distribution of elevation-specific (a) mean maximum temperature and (b–e) mean SWE. Predicted relationships were limited to the actual range of climate experience by each site

rates of survival (Figure 4a). While high temperatures can invariably lead to death in plethodontids, temperatures experienced by our populations never reached higher than 30°C, which is lower than the critical thermal maximum of similar species (Spotila, 1972). Increased temperature can have a positive influence on terrestrial salamander endurance and speed (Else & Bennett, 1987; Johnson, Johnson, & Shaffer, 2010), which may allow them to more readily escape predation. Moreover, under extended warmer conditions, plethodontids may reduce surface activity (Spotila, 1972), which would result in a reduction in encounters with potential surface predators. If higher temperatures increased survival via a reduction in surface activity, we would also expect populations to show a reduction in growth rates due to reduced foraging opportunities, which is supported in our growth analyses (Figure 2a).

4.3 | Inactive season

Our results suggest a disparity in growth at all elevations and in survival at lower elevations during the inactive season compared with the active season (Figures 1 and 3). Low growth rates during the inactive season are likely due to the extended periods of inactivity and lower prey availability. However, temperatures above freezing during the inactive season allow salamanders to be active on the surface (e.g., Catenazzi, 2016). Salamanders that experience warmer inactive season conditions, which allows for an increase in surface activity, would likely have greater metabolic expenditure compared with individuals that are in habitats with colder temperatures and hibernate throughout the inactive season (Catenazzi, 2016). Therefore, we would expect that salamanders that are active during warmer winter conditions and that are not able to find the necessary food sources to compensate for this increased activity would result in a decrease in body condition and ultimately lower survival (Catenazzi, 2016; Reading, 2007; Sinclair et al., 2013). This hypothesis is supported by our survival results; we found that warmer temperatures during the inactive season, especially at lower elevations results in a decreased survival compared to colder temperatures and higher elevations (Figure 5a).

During the inactive season, we found that temperature and SWE interacted with elevation to influence survival for *P. montanus* (Figure 4). At high elevations, survival was high and increased with increasing SWE, except at lower

temperatures, whereas at lower elevations, survival was lower and decreased with increasing SWE (Figure 5b,e). We suggest two mechanisms by which increases in the amount of snow at higher elevations could increase survival. First, salamanders may have increased survival in areas with more snowpack throughout the winter because of their reduced surface activity, which leads to a reduction in the number of encounters with surface predators (Turbill, Bieber, & Ruf, 2011). Alternatively, survival may increase with an increase in snowfall because snow acts as a soil insulator (Decker, Wang, Waite, & Scherbatskoy, 2003), and less snowpack can lead to more variable and colder soil temperatures (Bale & Hayward, 2010; Brown & DeGaetano, 2011; Groffman et al., 2012; Henry, 2008). Therefore, hibernating salamanders in areas with more snowpack would have a greater buffer from subzero temperatures (Decker et al., 2003).

Importantly, predictions of salamander population growth under future climate change that only account for responses to the active season conditions may underestimate losses. Warming is predicted to be unequal among seasons, winter months will likely see a greater increase in temperatures than the other seasons (Xia et al., 2014). For logistic reasons, studies of terrestrial plethodontids have typically focused on the active season (i.e., when individuals are available for capture). Therefore, determining the effect of winter conditions on salamander demography (e.g., survival) through the experimental manipulation of temperature or snowpack would improve mechanistic predictive population models (Sanders-DeMott & Templer, 2017).

5 | CONCLUSIONS

Future climate change is predicted to be a major challenge for Appalachian salamanders (Catenazzi, 2016; Milanovich et al., 2010; Sutton et al., 2015; Caruso, unpublished data). Yet, mechanistic population growth models are lacking, due, in part, to the paucity of demographic data for many species. Through surveying multiple populations along an elevational gradient, this study was not only able to estimate survival, growth and their variation with relevant climatic factors but also demonstrate that the relationships between salamander demography and climate vary with elevations. This spatial variation in demographic vital rates, and their relationship with relevant climatic factors, is necessary to model population growth and develop conservation strategies (Buckley et al., 2010; Caswell, 2001; McLean, Lawson, Leech, & van de Pol, 2016; Urban et al., 2016). Furthermore, our study demonstrates the importance of climate variation in life history strategies in *P. montanus* likely resulting from both the overall environmental differences in our elevational gradient as well as the variation in climate experience by these populations over the course of this study.

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SUPPORTING INFORMATION