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RESEARCH ARTICLE

Climate mediates the trade-offs associated with phenotypic plasticity in an amphibian polyphenism

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Abstract

1. Polyphenisms occur when phenotypic plasticity produces morphologically distinct phenotypes from the same genotype. Plasticity is maintained through fitness trade-offs which are conferred to different phenotypes under specific environmental contexts. Predicting the impacts of contemporary climate change on phenotypic plasticity is critical for climate-sensitive animals like amphibians, but elucidating the selective pressures maintaining polyphenisms requires a framework to control for all mechanistic drivers of plasticity.
2. Using a 32-year dataset documenting the larval and adult histories of 717 Arizona tiger salamanders (*Ambystoma mavortium nebulosum*), we determined how annual variation in climate and density dependence explained the maintenance of two distinct morphs (terrestrial metamorph vs. aquatic paedomorph) in a high-elevation polyphenism. The effects of climate and conspecific density on morph development were evaluated with piecewise structural equation models (SEM) to tease apart the direct and indirect pathways by which these two mechanisms affect phenotypic plasticity.
3. Climate had a direct effect on morph outcome whereby longer growing seasons favoured metamorphic outcomes. Also, climate had indirect effects on morph outcome as mediated through density-dependent effects, such as long overwintering coldspells corresponding to high cannibal densities and light snowpacks corresponding to high larval densities, both of which promoted paedomorphic outcomes.
4. Both climate and density dependence serve as important proxies for growth and resource limitation, which are important underlying drivers of the phenotypic plasticity in animal polyphenisms. Our findings motivate new studies to determine how contemporary climate change will alter the selective pressures maintaining phenotypic plasticity and polyphenisms.

KEYWORDS
climate change, development, life history, metamorphosis, paedomorphosis, polyphenism, salamander

1 | INTRODUCTION

Global climate change has been a hallmark of the anthropocene and has been implicated as inducing evolutionary change. Animal responses to climate change can be attributed to either microevolutionary change or phenotypic plasticity, and it can be difficult to distinguish these processes because they are not mutually exclusive (Charmantier et al., 2008; Gotthard & Nylin, 1995; Karell et al., 2011; Sauve et al., 2019). Trait plasticity should benefit animals under future climate change by increasing adaptive performance to increased environmental stress (Antoniazza et al., 2010; Becker et al., 2018; Richter et al., 2012). However, trait plasticity varies across the animal world, as many species exhibit high degrees of trait conservatism that limit adaptive potential to climate change (Comte et al., 2014; Oostra et al., 2018). While understanding the mechanisms underlying phenotypic plasticity is critical for predicting how animals will respond to future environmental change, further research is needed on how plasticity is maintained by multiple drivers of selection across time and space (Chevin et al., 2013; Fox et al., 2019; Hantak et al., 2021; Merilä & Hendry, 2013).

Phenotypic plasticity occurs when a single genotype produces multiple phenotypes, and that plasticity can be expressed through life history, physiological tolerance, resource use, development and behaviour (Miner et al., 2005). Under natural selection, phenotypic plasticity would be maintained within a species when varying environmental conditions allow for the coexistence of different phenotypes (Becker et al., 2018; Smith & Skúulason, 1996; West-Eberhard, 2003). Indeed, evidence for context-dependent phenotype selection has been well-documented in polyphenisms (Chen et al., 2019; Halali et al., 2021; Hantak et al., 2021; Roskam & Brakefield, 1999), where plasticity produces discrete morphs with distinct trait differences in morphology, habitat and life history (Moran, 1992; Whiteman, 1994). As a result, fitness trade-offs in feeding, growth and reproduction underlie the observed trait differentiation maintaining polyphenisms (Denoél & Joly, 2001; Gross, 1991; Kirk et al., 2023; Laughlin & Messier, 2015; Lejeune et al., 2018). Hence, polyphenisms represent an excellent system for understanding how developmental and selective processes contribute to the evolution of phenotypic plasticity.

Amphibian polyphenisms exhibit high degrees of climate-induced trait plasticity due to their ectothermic and desiccation-intolerant nature. Larval development is highly dependent upon climate for amphibians, as developmental traits like the size and age at metamorphosis are influenced by temperature and water availability (Gomez-Mestre et al., 2013; Laurila et al., 2002; Sinai et al., 2022). Development plasticity is variable for many amphibians due to the energetic demands for achieving metamorphosis at a minimum size-at-age threshold (Altwegg & Reyer, 2003; Werner, 1986). Adult life history traits underlying amphibian polyphenisms also exhibit plasticity in response to temperature and precipitation, such as changes in body size and ages at maturity (Cayuela et al., 2017; Moldowan et al., 2022; Morrison & Hero, 2003; Reading, 2007; Thompson & Popescu, 2021). Furthermore, temperature and precipitation regulate population density, resource productivity and habitat size of amphibians (Ficetola & Maiorano, 2016; Griffiths, 1997; Newman, 1992, 1998; Szèkely et al., 2017), which can also directly and/or indirectly influence life history plasticity and developmental plasticity (Albecker et al., 2023; Edelaar et al., 2017; Kirk et al., 2023).

Emerging research from one amphibian polyphenism, facultative paedomorphosis, has revealed new evidence regarding the complex interactions between climate, habitat and phenotypic plasticity. Facultative paedomorphosis produces two discrete morphs: a terrestrial adult morph that metamorphoses from an aquatic larva and an aquatic adult morph where larval traits are retained (Denoél et al., 2002; Semlitsch et al., 1990; Whiteman, 1994). The trade-offs for each morph have been well-documented, which includes morph-specific life histories that vary along the fast-slow continuum of amphibian life histories (Cayuela et al., 2024; Doyle & Whiteman, 2008; Kirk et al., 2023; Lackey et al., 2019; Moore et al., 2020; Ryan & Semlitsch, 1998). Metamorphosis also provides fitness benefits associated with habitat switching, which includes accessing underutilized resources (Denoél & Joly, 2001; Kirk et al., 2023; Whiteman et al., 1996), escaping density dependence (Whiteman et al., 2012; Wilbur, 1976), and/or avoiding abiotically harsh environments (Denver, 1997; Mathiron et al., 2017). Since growth during larval development remains one of the most well-documented trade-offs of morph outcome (Semlitsch, 1987; Whiteman et al., 2012), we hypothesize that climate will be an important proxy for resource limitation that explains the coexistence of these morphs, as harsh climatic conditions (e.g. cold temperatures and low precipitation) should constrain larval growth (e.g. O'Regan et al., 2014).

Our objective was to evaluate how phenotypic plasticity in a polyphenic population of the Arizona tiger salamander (*Ambystoma mavortium nebulosum*) has responded to annual variation in both climatic effects and density-dependent effects. Using a 32-year mark–recapture dataset documenting the lifetime histories of 191 metamorphic and 526 paedomorphic salamanders, we predict that both abiotic conditions (e.g. climate; Kirk et al., 2023) and biotic conditions (e.g. conspecific densities; Whiteman et al., 2012) underlie the maintenance of this polyphenism. Specifically, we used structural equation models (SEM) to address two questions: (1) whether climate had a direct effect on larval growth and morph outcome, and (2) whether climate had an indirect effect on larval growth and morph outcome, which would be mediated through density-dependent effects (e.g. competition and predation).

2 | MATERIALS AND METHODS

2.1 | Study area and salamander populations

We studied the dynamics of facultative padeomorphosis in a population of Arizona tiger salamanders at the Mexican Cut Nature Preserve (MCNP), which is a system of 60+ subalpine ponds in the West Elk Mountains, USA (3560 m elevation). The subalpine, high-elevation nature of the MCNP results in long overwintering periods and short growing seasons (i.e. June–September). Pond size is positively related to hydroperiod, with smaller ponds having temporary hydroperiods and drying during late summer or early autumn (Wissinger & Whiteman, 1992). Basal food resources are also tied to hydroperiod, with temporary ponds having a unique resource in fairy shrimp (*Branchinecta coloradensis*) and permanent ponds composed mostly of aquatic insects (Balik et al., 2022; Wissinger et al., 1999). Tiger salamanders are cannibalistic, keystone predators in the ponds that influence annual variation in larval salamander and invertebrate densities through top-down effects (Dodson, 1980; Whiteman & Wissinger, 2005; Wissinger et al., 1999, 2010).

To address our study objectives, we used a set of 717 known-age salamanders spanning the period 1988–2014 that have documented larval histories originating from one of the five ponds with well-documented permanent hydroperiods. While these five ponds vary considerably in their habitat (size, microclimate), conspecific densities and life history characteristics of the different morphs (see Table S1), over 98% of all adult salamanders across the 32 years of monitoring have come from these five ponds. We only considered larvae which survived to adulthood with a known morph development (paedomorphic male = 256; paedomorphic female = 270; metamorphic male = 117; metamorphic female = 74), which is representative of the paedomorphic bias documented for this population (Figure S1). For inclusion in analyses, salamanders needed to come from a cohort with at least five known individuals surviving to adulthood and with at least one individual of each morph from that cohort in order to meet our statistical objectives (Gelman & Hill, 2006). The tagging and handling of salamanders were approved by Animal Welfare Committees from Murray State University and Rocky Mountain Biological Laboratory, and fieldwork was permitted by Colorado Parks and Wildlife (HP0339).

2.2 | Climate and density-dependent variables

We evaluated how the environmental conditions experienced by a larva influenced an individual's morph outcome. Hence, climate and density-dependent effects were placed in the context of an individual larva's lifetime prior to reaching adulthood. Larval lifetime specifically refers to the amount of time an individual spent in a sexually immature life stage prior to morph development. For example, when considering a 2-year-old larva, what would be the cumulative number of conspecifics and cumulative magnitude of climatic conditions experienced by that individual during those 2 years of the larval period (e.g. higher lifetime growing degree days (GDD) would indicate a larva which experienced longer summer growing seasons). Thus, all variables were averaged based on the larva's age (e.g. averaged across all larval years; see Figure S2).

We used two density-dependent metrics to describe the variation in conspecific densities that could be associated with biotic interactions for the five permanent ponds (Whiteman et al., 2012; Wissinger et al., 2010): annual larval density and annual cannibal density. Annual larval density (number per m^2) was a pond-specific estimate of larval salamanders (ages 1–3) that was indicative of competition. Average cannibal density (number per m^2) was a pond-specific estimate of salamanders of ages 4 and older, which exert strong consumptive and non-consumptive effects on larval survival and growth (Wissinger et al., 2010). Larval and cannibal densities were estimated across all years from 1988 to 2020 using Lincoln–Petersen mark–recapture models (see Whiteman & Wissinger, 2005).

We used three climate variables to account for variation in growing conditions that larval salamanders experienced. Two variables were atmospheric climate metrics that were calculated over the entire temporal extent of larval cohorts in our study (1988–2014). Both variables were based on remote sensing data provided by the Daily Surface Weather and Climatological database (DAYMET; https://daymet.ornl.gov/), which provides daily estimates of climatic variables for 1 km by 1 km gridded cells based on latitude and longitude. DAYMET has been previously used for determining climate correlates of long-term amphibian demographics (Kirk et al., 2023). The third variable was based on pond temperature data. HOBO temperature loggers were deployed annually in the deepest sections of each pond from 2004 to 2019. Loggers collected hourly temperature data for nearly all years in each of the five ponds with permanent hydroperiods (range: 12–14 years).

The three climate metrics were: the number of GDD, the mass of snowpack levels, and the proportion of the winter and spring seasons that ponds were frozen. Growing degree days have historically been used to quantify plant growing season length, but have more recently become an important metric for quantifying overwintering survival of larval and juvenile ectotherms (McMaster & Wilhelm, 1997). GDD was calculated as:

$$\frac{\text{Daily max air temperature} + \text{Daily min air temperature}}{2} - \text{Base temperature}\left(0^{\circ}\text{C}\right).$$

Negative GDD values were assigned a value of zero and daily GDDs were summed for a given year to serve as a metric of summer growing season length (positive GDDs occur on average from May 30 to October 1 at MCNP). The second metric was a cumulative estimate of snowpack levels (kg/m^2) in the autumn, winter and spring seasons preceding the summer sampling season. Snowpack levels served as a metric for pond volume and hydroperiod. Because these ponds are predominately fed by snowmelt, water levels should affect growth and survival through resource productivity and habitat area (O'Regan et al., 2014; Thompson & Popescu, 2021).

Given that we had pond-level microclimate data, we applied correction factors to each pond for the climatic conditions in a given year to account for spatial variation in the pond temperature variables (see Table S2 for examples and explanations of correction values). GDD for each pond was corrected based on the average summer growing season length of a pond (day of first warming − day of first winter coldspell). Snowpack totals were corrected based on the average overwintering length of a pond (length of time from the first winter coldspell to the day of first warming). The proportion of the winter and spring spent in a coldspell was already pond-corrected since it was the only pond-derived metric. Larval densities and cannibal densities were also adjusted to account for between-pond variation in density-dependent effects (Table S1). Higher values for each density variable indicate an individual experiencing high density-dependent effects during their larval period (e.g. Whiteman et al., 2012). Pond-corrected values were used to account for any environmental variation across ponds and to determine how that environmental variation affects morph product across those different ponds.

The third metric was the proportion of the winter and spring seasons (December 21 to June 20) spent in an overwintering coldspell (i.e. the number of days spent in winter and spring before the DOY when the pond began warming). This was one of 11 pond temperature metrics that we quantified (see Appendix S1), which were extrapolated across all years for the five permanent ponds. Proportion of the winter and spring spent in a coldspell had the highest explanatory power for describing annual climate variation in precipitation (mm/day) and temperature (°C) during the winter and spring seasons (all $R^2 \geq 0.72$). Springs and winters that were cold and wet tended to have later dates of first pond warming (i.e. ponds spent most of the spring and winter frozen), which serves as an indicator for overwintering conditions (i.e. duration that the pond was frozen; Figure S3). Qualitative observational data of ice-off dates from ponds at MCNP strongly correlates to the DOY when the first pond warming occurs ($r = 0.92$; Figure S4).

2.3 | Statistical analysis

We used a piecewise SEM framework to determine the direct and indirect effects of climate and conspecific densities on larval body size and morph outcome. Piecewise SEM builds upon traditional forms of path analysis by allowing for the incorporation of non-normal error distributions, hierarchical mixed effect models and correlation structures (Lefcheck, 2016). We used four mixed-effects models for our SEM analysis (*lmer* and *glmer* functions; R. versions 4.1.2) that were parameterized using the piecewiseSEM package (*psem* function), which allowed us to incorporate random effects and correlation structures that control for temporal autocorrelation present in time-series datasets for amphibian density and climate (e.g. Warren & Bradford, 2010).

Model 1 accounted for all direct effects of larval state (age and body size), climate and density-dependent effects on morph outcome. **Model 2** tested for all indirect effects of climate and density-dependent effects on morph outcome as mediated through larval body size, which was modelled in our SEM models using relative snout–vent length (SVL). Relative SVL was calculated as a larva's absolute (measured) SVL relative to the average SVL of all other larvae from that natal pond in a given year (Moore et al., 2020). Relative SVL was chosen over two other body size metrics (absolute SVL, body condition [BC]) due to higher modelling performance (see Appendix S2). **Model 3** and **Model 4** tested for indirect effects of climate on morph outcome as mediated through density-dependent effects from larval density or cannibal density, respectively. The four models with fixed effects in R syntax are:

Model 1: Morph outcome ~ Relative SVL + Larval Age
+ Lifetime Cannibal Density + Lifetime Larval Density + Lifetime GDD
+ Lifetime Snowpack + Lifetime Coldspells.

Model 2: Relative SVL ~ Larval Age + Lifetime Cannibal Density
+ Lifetime Larval Density + Lifetime GDD
+ Lifetime Snowpack + Lifetime Coldspells.

Model 3: Lifetime Larval Density ~ Lifetime GDD
+ Lifetime Snowpack + Lifetime Coldspells.

Model 4: Lifetime Cannibal Density ~ Lifetime GDD
+ Lifetime Snowpack + Lifetime Coldspells.

Model specified a binomial error distribution for morph outcome (*glmer* function; *cloglog* function due to uneven sample sizes of metamorphs [1] and paedomorphs [0]), whereas all other models assumed Gaussian distributions for relative SVL, lifetime larval density and lifetime cannibal density (*lmer* function). Figure S5 provides a conceptual visualization of the hypothesized pathways for each of the four models in our SEM modelling framework.

To select the best models for SEM, we evaluated the fit and performance of our data with respect to several statistical assumptions. We began by independently testing the assumptions of linear models (normality, heteroscedasticity, dispersion and temporal independence) in each of the four models of our piecewise SEM (following Zuur et al., 2010). Lifetime larval density and lifetime cannibal density were square root transformed to improve assumptions of normality. All variables were standardized and rescaled to *z*-scores (−1, 1) to standardize slope coefficients and to ensure model convergence. Each model included a random intercept term for cohort and a correlation structure for an autoregressive moving average (ARMA) model, which eliminated the presence of temporal autocorrelation in our models (ARMA model order was selected based on the *acf* and *pacf* functions; R v. 4.1.2). Additional random intercept terms for year of larval capture and natal pond were also explored, but models with cohort had better model fit (based on Akaike information criteria [AIC] and log-likelihood tests) and performed better when addressing SEM assumptions (Appendix S2; Tables S3 and S4). Collinearity was low among all fixed effect variables for each model (variance inflation factors were <3; Table S5).

After selecting each of the best models based on the statistical criteria above, we performed a test of directed separation that evaluated the conditional independence of variables to ensure important causal relationships for unspecified pathways were not omitted (Lefcheck, 2016; Shipley, 2009). If all unspecified pathways were non-significant ($p > 0.05$), then all important pathways were correctly accounted for in the model. We evaluated the goodness-of-fit for the SEM models to ensure all accounted pathways adequately fit the hypothesized models (i.e. $p < 0.05$ indicates poor model fit to the data; Shipley, 2009). Preliminary goodness-of-fit tests revealed that models had poor model fit ($p < 0.001$) without accounting for two relationships that were correlative (both $p < 0.001$) but not causative in nature. Hence, because they were not grounded in our initial hypotheses, the effects of larval age on average lifetime cannibal densities and average lifetime larval densities were modelled as correlated errors (i.e. unspecified pathways) in the SEM. Inclusion of both pathways greatly improved the overall model fit and indicated that no important pathways were being excluded. A third correlative pathway was not detected between average lifetime larval density and average lifetime cannibal density.

We report pseudo-R^2 values as our measures of effect size for both fixed effects (marginal-R^2) and combined fixed and random effects (conditional-R^2), which was calculated based on the deviance of the null and fitted models. Model coefficients for Gaussian error distributions were standardized by a 'scaling' parameterization, where coefficients were placed in units of standard deviations of the mean via scaling by the ratio of the standard deviation of the *x* variable over the standard deviation of the *y* variable. Model coefficients were standardized for the binomial error distribution associated with **Model 1** using the latent theoretic approach (Lázaro et al., 2020; Lefcheck, 2016). A fixed effect pathway was considered significant in a given model when $p < 0.05$.

3 | RESULTS

Goodness-of-fit tests (Fisher's $C = 1.06$; $p = 0.587$) and tests of directed separation (all $p > 0.05$) indicated that our final SEM model had adequate fit and were not excluding any important pathways from the hypothesized SEM. Model performance was moderate for **Models 1–3** (marginal-$R^2 = 0.21$–0.32; conditional-$R^2 = 0.30$–0.54), but performance was low for **Model 4** with lifetime cannibal densities (marginal-$R^2 = 0.06$; conditional-$R^2 = 0.20$). **Model 1** indicated a negative effect of larval age (standardized coefficient $= -0.41$; SE $= 0.12$; $p < 0.001$) on morph outcome, and a positive effect of relative SVL on morph outcome (standardized coefficient $= 0.09$; SE $= 0.05$; $p = 0.024$). The probability of becoming a metamorph was thus more likely for younger larvae of a larger size (Figure 1), and this pattern was observed for all three body size metrics (Figure S6; Table S6). There was a main effect of average lifetime cannibal densities on morph outcome, in which metamorphic outcomes declined when larvae experienced high lifetime cannibal densities (standardized coefficient $= -0.26$; SE $= 0.11$; $p = 0.001$). There were no detectable main effects of lifetime larval density (standardized coefficient $= -0.09$; SE $= 0.07$; $p = 0.112$) or climatic factors (all $p \geq 0.250$) on morph outcome.

We found evidence for three potential pathways by which climate and density dependence affect larval body size and morph outcome. The first pathway was associated with **Model 2** and was derived from larval lifetime GDD (Figure 2). There was a direct effect of lifetime GDD on relative SVL (standardized coefficient $= 0.18$; SE $= 0.06$; $p = 0.048$), indicating that longer lifetime summer growing seasons have a positive effect on larval SVL that promotes metamorphic development.

The second pathway was derived from larval lifetime coldspell durations during overwintering periods in **Models 3** and **4** (Figure 2). We observed a direct density-dependent effect on relative SVL from lifetime cannibal density (standardized coefficient $= -0.23$; SE $= 0.03$; $p < 0.001$). While there were no direct effects of lifetime coldspell durations on relative SVL (standardized coefficient $= -0.13$; SE $= 0.07$; $p = 0.154$), there was an indirect effect of lifetime coldspell duration on relative SVL from lifetime cannibal densities (standardized coefficient $= 0.20$; SE $= 0.12$; $p < 0.001$). Larvae experiencing greater lifetime coldspell durations simultaneously experienced higher lifetime cannibal densities that promoted paedomorphic development.

There was also evidence for a third pathway with indirect effects for all three climate variables affecting morph outcome through lifetime larval densities (Figure 2), although lifetime larval densities were not a predictor of relative SVL (standardized coefficient $= <0.01$; SE $= 0.04$; $p = 0.945$). Higher lifetime GDD (standardized coefficient $= -0.43$; SE $= 0.08$; $p < 0.001$), higher lifetime snowpack (standardized coefficient $= -0.21$; SE $= 0.06$; $p < 0.001$) and higher lifetime coldspells (standardized coefficient $= -0.09$; SE $= 0.05$; $p = 0.017$)

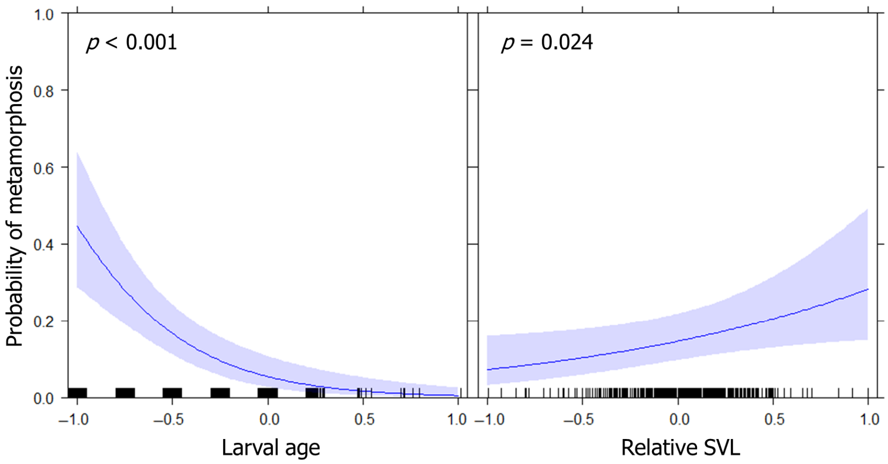

FIGURE 1 Probability of an individual salamander with a known developmental fate developing into a metamorph rather than a paedomorph as a function of larval age (left panel) and relative snout–vent length (SVL) (right panel). Larval age and relative SVL are standardized variables with the mean at 0 and both variables increasing from left to right.

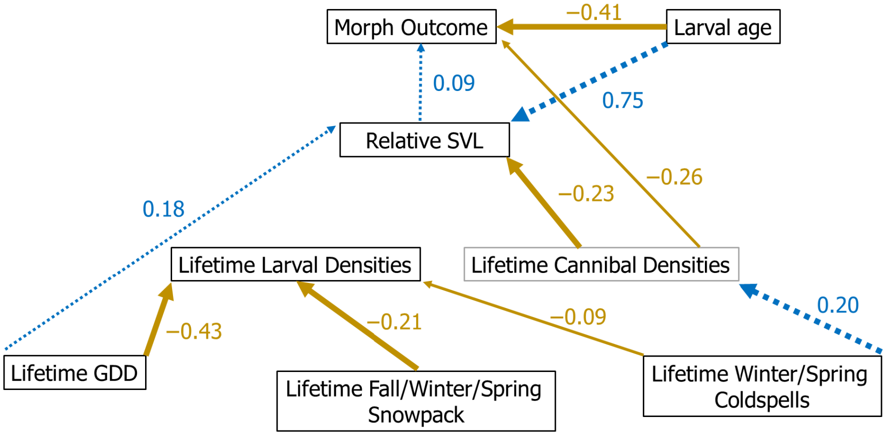

FIGURE 2 Pathways describing the direct and indirect effects of climatic factors and density-dependent factors on morph outcome. Blue dashed lines indicate positive relationships and gold solid lines indicate negative relationships. Arrow weight is based on significance with large-sized arrows having $p < 0.001$ and small-sized arrows having $p < 0.05$.

were all associated with lower lifetime larval densities. SEMs using larval BC as the body size metric revealed a negative effect of lifetime larval densities on body size that supported these indirect effects from a third pathway (Table S6; Figure S6).

4 | DISCUSSION

Polyphenisms are a discrete form of phenotypic plasticity by which trait differentiation provides a means for adapting to environmental variation (Whiteman, 1994). Understanding how plasticity is maintained requires understanding the fitness benefits for each phenotype because under certain environmental contexts, selective processes will favour the fitness of one phenotype over another (Denoél et al., 2007; Moran, 1992; Roff & Fairbairn, 1991; West-Eberhard, 2003). While prior studies have acknowledged these trade-offs, few studies have provided a mechanistic framework that explains how biotic (e.g. competition and predation) and abiotic drivers (e.g. climate) interact to explain the coexistence of multiple phenotypes (Moran, 1992). Our study allowed us to tease apart the different mechanisms underlying the plasticity of an amphibian polyphenism, which included body size/growth rate (Doyle & Whiteman, 2008; Moore et al., 2020), density dependence (Whiteman et al., 2012) and climate (Kirk et al., 2023; Mathiron et al., 2017).

The first driver of plasticity was the direct effect of body size on metamorphosis, which was an intrinsic state-based variable that is highly influenced by environmental conditions for amphibians (Green & Middleton, 2013; Moldowan et al., 2022; Reading, 2007; Wilbur, 1977). Metamorphosis is size-dependent for many amphibians because of the energetic allocation required for achieving morphological and physiological transformation (Laurila et al., 2002; Smith & Berven, 1979; Wilbur & Collins, 1973). Size-dependent determination of life history outcomes has been extensively documented for polyphenisms of amphibians (Doyle & Whiteman, 2008; Moore et al., 2020), fishes (Gross, 1991) and insects (Roff & Fairbairn, 1991; Rowland & Emlen, 2009). Importantly, all three body size metrics considered for our SEM models (BC, absolute SVL, relative SVL) exhibited a similar positive effect on the probability of metamorphosis (Figure S6). Relative SVL was previously identified as a more informative body size predictor of morph selection because it considers the effect of biotic interactions with competitors (Moore et al., 2020), which could explain the lack of an effect from lifetime larval densities in our study. Indeed, larval BC revealed indirect effects of climate on body size as mediated through larval densities (Figure S6), indicating that BC may be a more informative predictor of density-dependent effects by accounting for weight relative to length.

The second set of drivers was from the effects of predation on morph selection, which were mediated through relative SVL. Population densities of the MCNP polyphenism are highly variable and fluctuate between peaks and troughs (Whiteman & Wissinger, 2005; Wissinger et al., 2010; Wissinger & Whiteman, 1992), with years of high cannibal densities frequently corresponding to years of low larval densities (Figure S8; Whiteman & Wissinger, 2005), which highlights the pervasive top-down effect of cannibalism on this population (Wissinger et al., 2010). We observed a direct effect of higher lifetime cannibal densities promoting paedomorphic development, which is supported by pond-level comparisons as ponds with the highest conspecific densities are paedomorphic-biased (Table S1; Whiteman et al., 2012). Adult paedomorphs, which are cannibalistic, indirectly constrain larval body size from non-consumptive effects by inducing ‘a landscape of fear’ (Wissinger et al., 2010; also Grade et al., 2021; Laundre et al., 2001). High conspecific densities also induce intense resource limitation, which prevents many larvae from reaching the size-at-age threshold required for metamorphosis (Newman, 1998; Wilbur, 1976, 1977). Competitive interference has been shown to explain variation in size structure that underlie patterns of morph development in other polyphenisms (Maret & Collins, 1994; Ziemba & Collins, 1999).

The third, and more understudied, driver of plasticity was climate. The first climatic pathway was between growth and temperature, whereby longer lifetime growing seasons also had a direct effect on increased larval size that promoted metamorph development. Hence, warm, long growing seasons ensure larval salamanders reach the conditional threshold for metamorphosis (Morrison & Hero, 2003; Newman, 1998; O'Regan et al., 2014; Wilbur & Collins, 1973), while cold, short growing seasons limit larval growth, and thus promote paedomorphosis. Larvae experiencing cumulatively longer growing seasons also experienced lower lifetime larval densities, which is surprising because longer growing seasons could be associated with better growth conditions (Morrison & Hero, 2003; Newman, 1998). However, longer growing seasons may also induce higher rates of cannibalism and/or metamorphosis. Longer growing seasons and warmer temperatures produce greater size structure in polyphenic populations (see Figure S9; also Ziemba & Collins, 1999; Whiteman et al., 2012), which could be attributable to either higher productivity or increased metabolic activity (O'Regan et al., 2014).

The second climatic pathway was from coldspell duration, where larvae experiencing longer lifetime coldspells simultaneously experienced higher cannibal densities. Overwintering survival is positively related to body size for ectothermic animals, especially during early life stages (Garner et al., 2011; Walsh et al., 2016), so adult survival is likely higher than larval survival during growth-limited periods. Adult paedomorphs could also have higher survival during overwintering periods due to superior competitive abilities, diet plasticity and/or higher energetic reserves (Wissinger et al., 2010). Unfortunately, very little is known about the winter ecology of this subalpine polyphenism and is an emerging area of research (Whiteman H.H. & Thomas S.A., unpublished data). Importantly, a companion study found that paedomorphs experienced an overwintering fitness advantage with respect to adult BC compared with metamorphs (Kirk et al., 2023), which experienced greater energetic losses from overwintering.

A third pathway was observed where low snowpacks and short coldspells corresponded to high lifetime larval densities. Amphibian reproduction dynamics are closely linked to precipitation and water availability (Griffiths, 1997; O'Regan et al., 2014), and both morphs experience fitness benefits from greater water availability because precipitation and water availability is linked to the evolution of both paedomorphosis (Bonett et al., 2013; Whiteman, 1994) and metamorphosis (Denver, 1997; Mathiron et al., 2017). Drought and low precipitation would have negative effects on amphibian growth, fecundity and survival from desiccation risk (Bucciarelli et al., 2020), especially during late summer-early autumn when drying occurs at MCNP (Wissinger & Whiteman, 1992). Furthermore, low precipitation and snowmelt would reduce pond volume, decrease habitat area and limit ecosystem productivity that could all lead to increased competition for resources (Griffiths, 1997; Leip et al., 2000; Shoo et al., 2011). Overall, we hypothesize that lower snowpacks and shorter coldspells promote paedomorphosis from increased larval competition.

5 | CONCLUSIONS

Phenotypic plasticity is an important evolutionary process where survival occurs through local adaptation, which is reflected in the performance of the different phenotypes. While phenotypic plasticity should theoretically increase resilience to climate change (Davis et al., 2017; Richter et al., 2012), the extent to which plasticity is an adaptive response to climate change remains uncertain (Oostra et al., 2018). Importantly, the rate of contemporary climate change experienced by polyphenisms likely differs from the climatic conditions historically responsible for maintaining the coexistence of phenotypes (Evans et al., 2018; Merilä & Hendry, 2013). Future global changes in temperature and precipitation are anticipated to be highly interactive, so predicting the effects of climate change on phenotypic plasticity can be difficult, especially for animals with complex life histories and varying climatic responses (Crozier et al., 2008; Kirk et al., 2023). Hence, we expect that future climate change could disrupt many of the different mechanisms maintaining this high-elevation polyphenism.

The three main outcomes of climate change for any polyphenism would be: (1) a shift in morph frequency, (2) the complete loss of a morph or (3) no change in morph frequency. The first two outcomes would result from changes in the fitness trade-offs associated with each morph (Hantak et al., 2021; Karell et al., 2011; Kirk et al., 2023; Mathiron et al., 2017). For example, when regarding the effects of climate on larval growth, the paedomorphic life history could decline as rising temperatures promote metamorphosis through advanced growth and earlier ages of maturity (Morrison & Hero, 2003; Newman, 1998; O'Regan et al., 2014; Wilbur & Collins, 1973). Increased aridity could also exacerbate the strong density-dependent effects through reduced habitat area and thus promote paedomorphosis (Griffiths, 1997). Increasing aridity could also promote metamorphic development by decreasing hydroperiod length and forcing larva to escape desiccation (Davis et al., 2017; Denver, 1997; Mathiron et al., 2017; Semlitsch, 1987), as pond drying is one of the most important environmental drivers of larval development and metamorphosis (Gomez-Mestre et al., 2013; Laurila et al., 2002). Alternatively, morph frequencies could remain the same due to minimal climatic changes or from additional selective pressures remaining unchanged (Evans et al., 2018; Moore & Ouellet, 2015).

Furthermore, the response of phenotypic plasticity to climate change is also dependent upon life history traits, and the influence of life history may limit the adaptive potential of phenotypic plasticity (Becker et al., 2018; Vedder et al., 2013). Paedomorphs adopt a 'fast' adult life history strategy with early maturity and short lifespans to compensate for the costs of not achieving metamorphosis and the high biotic risks in the aquatic environment (Whiteman, 1994; Wilbur & Collins, 1973). In contrast, metamorphs adopt a 'slow' adult life history strategy with late maturity and long lifespans because larvae made an early and costly energetic allocation to achieve metamorphosis (Kirk et al., 2023; Lackey et al., 2019; Whiteman et al., 1996). Given that life history traits have been shown to be highly responsive to climate change for ectothermic animals, future climate change could alter the adaptive benefits of these 'fast' and 'slow' life histories (see Cayuela et al., 2017; Hoving et al., 2013). Hence, projected changes to polyphenisms from contemporary climate change need to account for multiple trait dimensions on fitness to understand how selection will alter phenotypic plasticity (Laughlin et al., 2021).

Finally, predicting the future impacts of climate change on phenotypic plasticity requires long-term studies on natural populations because the mechanisms of selection vary across time and space (Chevin et al., 2013; Merilä & Hendry, 2013). Prior studies documenting polyphenic changes in response to climate change either involve a snapshot comparison of a few time periods or do not track population-level changes (see Evans et al., 2018; Hantak et al., 2021). Long-term, mark–recapture studies are essential for understanding the influence of climate change on polyphenisms and phenotypic plasticity because such studies provide insight into both individual and generational changes in fitness and life history. Given the potential disruptive effects that climate change can have on certain facets of animal life history (e.g. body size, growth and phenology), our conclusions prompt new research regarding the influence of future climate change on phenotypic plasticity.

AUTHOR CONTRIBUTIONS

Mark A. Kirk and Howard H. Whiteman conceptualized the manuscript. Mark A. Kirk collated the data, performed analyses and wrote the manuscript. All authors contributed to manuscript development and approved the manuscript for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare that they have no conflicts of interest.

DATA AVAILABILITY STATEMENT

The data and code from this publication are available at the Dryad Digital Repository: https://doi.org/10.5061/dryad.6m905qg86 (Kirk & Whiteman, 2024).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Table S1: Descriptive statistics of the five permanent ponds considered for our study.

Table S2: Average growing degree days, average overwintering length, and proportion of the winter and spring durations spent in a cold spell for the five ponds in our study based on water temperature data for limited time periods ($n=98$; 2004–2010, 2012–2015, and 2017–2019).

Table S3: Indicators of performance for the models used in our SEM framework.

Table S4: Model performances for the individual *psem* models based on whether random effects of larval year, cohort, or pond origin were included.

Table S5: Correlation matrix for all state-based variables (larval SVL and larval), density variables (lifetime cannibal and larval densities), climate variables (lifetime GDD, lifetime snowpack totals and lifetime coldspell durations), and random effect variables (only Cohort and Year) used in the SEM framework.

Table S6: Significance of pathways from three body size path analyses.

Figure S1: Distribution of the 717 metamorphic salamanders (left histogram) and paedomorphic salamanders (right histogram) across different cohorts from 1988 to 2014.

Figure S2: Conceptual synthesis of how the climate and density-dependent variables were averaged across an individual larva's lifetime.

Figure S3: Conceptualization of the different metrics calculated for pond temperature analyses.

Figure S4: Relationship between the extrapolated date of first warming based on pond temperature data and the estimated ice-off date based on qualitative observational data for the seven ponds monitored in temperature from 2004 to 2019.

Figure S5: Hypothesized pathways of the four different models in our piecewise SEM modeling framework.

Figure S6: Results from the SEM analysis that were performed based on a larval salamanders absolute SVL (left) and a larval salamanders body condition (right).

Figure S7: Pathway describing the indirect effects of climate on lifetime larval densities on larval body condition and morph outcome.

Figure S8: Annual densities of adult paedomorphic salamanders (age 4+; red line) and larval salamanders (black line) for all ponds across the 32 years of our study.

Figure S9: Relationship between the coefficient of variation (CV) in paedomorphic adult age and paedomorphic adult SVL as a function of the number of growing degree days (GDD) for a given pond in a given year.

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