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RESEARCH ARTICLE

The role of environmental variation in mediating fitness trade-offs for an amphibian polyphenism

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Abstract

1. Fitness trade-offs are a foundation of ecological and evolutionary theory because trade-offs can explain life history variation, phenotypic plasticity, and the existence of polyphenisms.
2. Using a 32-year mark-recapture dataset on lifetime fitness for 1093 adult Arizona tiger salamanders (*Ambystoma mavortium nebulosum*) from a high elevation, polyphenic population, we evaluated the extent to which two life history morphs (aquatic paedomorphs vs. terrestrial metamorphs) exhibited fitness trade-offs in breeding and body condition with respect to environmental variation (e.g. climate) and internal state-based variables (e.g. age).
3. Both morphs displayed a similar response to higher probabilities of breeding during years of high spring precipitation (i.e. not indicative of a morph-specific fitness trade-off). There were likely no climate-induced fitness trade-offs on breeding state for the two life history morphs because precipitation and water availability are vital to amphibian reproduction.
4. Body condition displayed a contrasting response for the two morphs that was indicative of a climate-induced fitness trade-off. While metamorphs exhibited a positive relationship with summer snowpack conditions, paedomorphs were unaffected. Fitness trade-offs from summer snowpack are likely due to extended hydroperiods in temporary ponds, where metamorphs gain a fitness advantage during the summer growing season by exploiting resources that are unavailable to paeodomorphs. However, paedomorphs appear to have the overwintering fitness advantage because they consistently had higher body condition than metamorphs at the start of the summer growing season.
5. Our results reveal that climate and habitat type (metamorphs as predominately terrestrial, paedomorphs as fully aquatic) interact to confer different advantages for each morph. These results advance our current understanding of fitness trade-offs in this well-studied polyphenic amphibian by integrating climate-based mechanisms. Our conclusions prompt future studies to explore how climatic variation can maintain polyphenisms and promote life history diversity, as well as the implications of climate change for polyphenisms.

KEYWORDS
climate, life history, metamorphosis, paedomorphosis, salamanders, traits

1 | INTRODUCTION

Fitness trade-offs are a conceptual foundation of both ecological and evolutionary theory. Trade-offs reveal the interactive effects between organismal traits and environmental conditions at both the intra- and interspecific levels (Fry, 2003; Stearns, 1989). Fitness trade-offs exist when the performance of traits have contrasting relationships with an environmental gradient (i.e. performance increases for one trait under certain environmental conditions, yet decreases for a second trait under the same environmental conditions). Trade-offs reveal ecological insights into species distributions and resource use and advance our understanding about the mechanisms of evolution and the processes that maintain biodiversity (Laughlin et al., 2021; Walter et al., 2018). Hence, fitness trade-offs have been postulated to explain how diversity is maintained at multiple biological scales across time and space (Agrawal, 2020; Kneitel & Chase, 2004).

Fitness trade-offs are foundational to life history theory, which describes the variation in how organisms allocate energy to growth, development, reproduction and survival (Stearns, 1989; Winemiller & Rose, 1992). Numerous studies have developed organizational frameworks for animal life history traits and consequently reveal generalities in life history trade-offs (Pianka, 1970; Pianka et al., 2017; Winemiller et al., 2015), such as the differences between fast strategies (classic *r*-selected species; early maturity, short lifespans, high reproductive output) and slow strategies (classic *K*-selected species; late maturity, long lifespans, low reproductive output; Cayuela et al., 2016a, 2017; Healy et al., 2019). Trade-offs in reproductive traits have also been well-documented given the energetic difference for reproduction between males and females (Cayuela et al., 2014, 2016b; Grayson et al., 2011; Lackey et al., 2019; Roff & Fairbairn, 1991; Trivers, 1972; Whiteman, 1997). Unsurprisingly, variability and stability of the environment is a primary driver of these life history trade-offs across many animal groups (Cayuela et al., 2017, 2019; Mims & Olden, 2012; Pianka, 1970; Townsend & Hildrew, 1994; Winemiller & Rose, 1992).

Life history traits are evolutionarily selected by environmental pressures that optimize energetic investments. When environmental pressures are highly selective, all organisms tend to adopt a similar set of traits (Balasubramaniam & Rotenberry, 2016; Bears et al., 2009). This concept has been coined environmental filtering and has been well established for life history traits under environmentally harsh conditions (e.g. cold and dry climates; Laughlin et al., 2021; Kirk et al., 2022). However, even though environmental filtering constrains trait diversity, spatial and temporal variability in the environment also promotes life history variation (Cayuela et al., 2016a; Townsend & Hildrew, 1994). Hence, the existence of environmentally mediated fitness trade-offs can provide evidence for the mechanisms that maintain population-level trait diversity, such as phenotypic plasticity and polyphenisms (discrete, alternative morphs; West-Eberhard, 1989, 2003).

Amphibian life history traits are closely linked to climatic variation in temperature and water availability. Variation in amphibian life history traits is influenced by climate across spatial–temporal gradients (Bizer, 1978; Berven, 1982; Morrison & Hero, 2003), which in turn affects the survival and recruitment of different species with unique life history strategies (Cayuela et al., 2017, 2019). In this study, we focus on two fitness parameters linked to amphibian life history that are impacted by climate: breeding state and body condition. Breeding and phenology are well established as being linked to temperature and precipitation (Ficetola & Maiorano, 2016; Reading, 1998; Todd et al., 2011), while numerous studies have documented climate-induced increases and decreases of population-level body size (Caruso et al., 2015; Moldowan et al., 2021; Reading, 2007). However, very little is known about how climate mechanisms influence fitness trade-offs, and whether climate mechanisms are responsible for maintaining phenotypic diversity and polyphenisms (Merilä & Hendry, 2013). For example, fitness trade-offs should be most prominent for polyphenisms when morphs occupy different microhabitats that vary in resources and climate sensitivity (Cayuela et al., 2016a, 2019; Davis et al., 2017; Lejeune et al., 2018; Mathiron et al., 2017; Semlitsch, 1987). Hence, macroclimatic conditions could have differential impacts on the microclimate experienced by each morph, such as the influence of atmospheric temperatures on aquatic versus terrestrial microclimates (Stark & Fridley, 2022).

The objective of our study was to develop an understanding of how environmental variation could explain trade-offs for two fitness metrics (breeding state and body condition) in a polyphenic population of Arizona tiger salamanders (*Ambystoma mavortium nebulosum*). Adult morphs of this polyphenism achieve maturity via facultative paedomorphosis (Denoël et al., 2005; Whiteman, 1994). The two respective morphs, terrestrial metamorphs versus aquatic paedomorphs, vary in life history traits pertaining to development, growth, and reproduction (Bonett et al., 2021; Lackey et al., 2019; Ryan & Semlitsch, 1998; Whiteman, 1997; Whiteman et al., 1996, 2012), while also varying in resource and habitat use (primarily subterranean/terrestrial habitats versus fully aquatic habitats, respectively; Denoël et al., 2007; Lejeune et al., 2018; Whiteman et al., 1994). Using a long-term mark-recapture dataset spanning 1988–2020 on the lifetime histories of 1093 unique tiger salamanders, our primary objective employed a trait-environment modelling approach to test for environmentally induced trade-offs (e.g. seasonal climate variation, density-dependent effects) in fitness for these two morphs. A secondary objective was to evaluate fitness trade-offs between morphs for additional internal state-based variables, such as sex, age, and prior breeding state (e.g. Cayuela et al., 2014, 2016b; Lackey et al., 2019).

We classified two sets of relationships with respect to environmental variation and state-based variables that we could expect for our trait-environment modelling approach. First, similar relationships across the morph (metamorph vs. paedomorph) by sex (male vs. female) combinations would indicate that environmental conditions have a comparable influence on breeding and body condition of each morph (i.e. no fitness trade-offs). Alternatively, contrasting relationships for the morph by sex combinations would be indicative of fitness trade-offs because environmental conditions produce behavioural or habitat-associated differences that increase fitness for one morph and decrease fitness for the second morph (e.g. Laughlin et al., 2021). We assume that contrasting relationships would provide evidence that environmental variation plays an important role in the maintenance of this polyphenism.

2 | MATERIALS AND METHODS

2.1 | Study area and salamander surveys

We evaluated our objectives about environmentally induced fitness trade-offs using a 32-year mark-recapture dataset of adult Arizona tiger salamanders (*Ambystoma mavortium nebulosum*) at a system of high-elevation ponds in the West Elk Mountains, Colorado, USA (39.02°N, 107.06°W). While the Mexican Cut Nature Preserve (MCNP) contains 60+ ponds of varying hydroperiod, most salamander activity occurs in only eight ponds (Lackey et al., 2019). Five ponds have permanent hydroperiods and four of those ponds have paedomorphs present. Three ponds lack paedomorphs and only metamorphic development occurs because of more temporary hydroperiods (i.e. late summer/early autumn drying in occasional years induces high mortality; Whiteman et al., 1996; Wissinger & Whiteman, 1992). Due to the MCNP's subalpine nature (3640 m elevation), these ponds have short growing seasons (ice-free from early June to early October). Permanent and temporary ponds have different invertebrate communities and ecosystem processes, which are largely attributable to hydroperiod and the presence of salamanders (Balik et al., 2021; Wissinger et al., 1999). Adult salamanders prey upon invertebrate communities in ponds of both hydroperiods and are also cannibalistic. Hence, salamanders serve as the top predators of these ponds and regulate populations through top-down effects (Wissinger et al., 1999, 2010).

Adult salamanders of this population are facultatively paedomorphic and exhibit two distinct life history morphs. Paedomorphic adults develop as slow-growing larvae that retain their larval morphology in sexual maturity because they do not achieve a minimum conditional threshold required for metamorphosis by their third year. In contrast, metamorphic adults reach that conditional threshold within the third year of their life and transform into a terrestrial morphology (Whiteman et al., 2012). Paedomorphic adults thus require permanent aquatic habitats and reside in their natal ponds. Metamorphic adults reside in subterranean habitats during overwintering periods but migrate to both permanent and temporary ponds to breed and forage during the summer growing season (Whiteman et al., 1994, 1996).

Mark-recapture monitoring began in 1988 and remains ongoing, and we report on data through 2020. Since 1990, larval and adult salamanders at these ponds have been sampled on almost a daily basis from June–August of every year. Both larval and adult salamanders during this period have been given unique identification marks either in the form of toe clips or passive integrated transponder (PIT) tags inserted into the body cavity (11 and 12.5 mm; Biomark Inc.). Salamanders were caught either by hand or using dipnets and identified by their unique identification mark. Each adult had the following biological data recorded: snout-vent length (SVL; distance from the snout to the end of the cloaca), total length (TL), mass, sex and breeding state (both based on visual inspection of the cloaca; see Appendix 1), capture date, pond of capture, and cohort. Cohorts were assigned to individuals based on their birth year, which was determined during larval captures and based on age-frequency distributions. After processing, all salamanders were returned to the location where they were captured and adult salamanders were often captured multiple times in a given year (see Whiteman et al., 2012 for further details).

2.2 | Measures of salamander fitness

Our study consisted of adult lifetime capture histories for 1093 uniquely marked salamanders which had a total of 4351 annual documentations. Salamanders for this analysis were required to have known cohort dates, which ranged from 1988 to 2016. The distribution of morph by sex combinations for adult salamanders was: paedomorphic male = 442; paedomorphic female = 346; metamorphic male = 182; metamorphic female = 110. This 28% versus 72% split is representative of the paedomorphic bias documented for this population, and our data are representative of recruitment patterns to adulthood with the biggest representations from the 1988 (15%) and 2000 cohorts (30%; Lackey et al., 2019). There were also nine females and 19 males that metamorphosed later in life after first breeding as a paedomorph (i.e. after the third-year threshold reported above; this intermediate morph represented 2.5% of the dataset, which is similar to the <3% reported by Whiteman et al., 2012).

The first metric we used for individual fitness of a salamander was their breeding state. An individual salamander of either morph was classified as being in a breeding state for a given year based on detection at the ponds with the presence of a swollen cloaca (sensu Lackey et al., 2019). The presence of a swollen cloaca was used as our marker for breeding because presence and absence at the ponds relates to both breeding state and detectability of the two morphs (see Appendix 1 for more details on breeding state). The second metric we used for individual fitness of a salamander was their body condition (BC) in a given year, which was calculated as mass divided by SVL and represents a measure of plumpness relative to body size (i.e. high condition corresponds to high energetic reserves). Body condition predicts total fat reserves and clutch size better than other body size metrics (Lackey et al., 2019), and our trait-environment models revealed similar results when SVL was used instead of BC. The BC of an adult salamander in a given year was based on the date of first capture for that salamander (i.e. the post-overwintering, early-summer condition of salamanders).

2.3 | Climate data

Macroclimatic conditions for the 1988–2020 mark-recapture period were based on remote sensing data provided by the Daily Surface Weather and Climatological database (DAYMET; https://daymet.ornl.gov/). DAYMET provided daily atmospheric estimates of climate variables for 1 km by 1 km gridded cells based on the latitude and longitude of MCNP. We obtained daily estimates of three climate variables: minimum air temperature (°C), precipitation (mm/day), and snowpack coverage (kg/m^2). We focused on minimum temperatures rather than maximum temperatures because of high collinearity ($r = 0.97$) and minimum temperatures performed better in exploratory models than maximum temperatures. We averaged the three climate variables into four 'seasonal climatic periods' that we hypothesized would be important to high elevation amphibian ecology (see Table S4). The climatic variables in a given season of a given year were merged with the mark-recapture histories of all 1093 uniquely marked salamanders based upon capture year. All seasonal climate variables reference the period prior to the annual capture of a unique salamander ($t - 1$).

To assess how climate affected breeding state and body condition, we defined four seasonal climatic periods. First, we defined climate during prior summer conditions (defined as June 21–September 20). Summer represents the primary season of growth and activity for all salamanders in the MCNP which is critical for amphibian development and survival. We could also expect delayed or carryover effects given the short growing seasons and long overwintering periods of high-elevation environments. The second seasonal period was based on prior Autumnal conditions (September 21–December 20), which represents an important transition between the active summer season and the dormant overwintering period. The third and fourth seasonal periods were prior Winter (December 21–March 20) and prior Spring (March 21–June 20) conditions. Winter and spring represent periods of brumation (i.e. dormancy and inactivity) due to heavy snow and deep freezes, which can affect survival, growth, breeding state and recruitment. We also calculated the standard deviation (SD) of these seasonal climate variables to evaluate relationships with climate variability (e.g. average spring precipitation vs. consistency of Spring precipitation), resulting in a total of 24 macroclimate predictors (see Table S4 for climate variable list and associated hypotheses).

2.4 | Statistical analyses

We evaluated whether environmental conditions have similar (not indicative of trade-offs) or contrasting (indicative of trade-offs) fitness-related responses in the four morph by sex combinations (paedomorph male, paedomorph female, metamorph male, metamorph female) using a trait-environment modelling approach with generalized linear mixed-effects models (NLME, LME4, and GLMMTMB packages; R version 4.1.2, R Development Core Team, 2021; following Laughlin et al., 2021; Kirk et al., 2022). Two separate trait-environment modelling approaches were evaluated for each fitness metric because of different error distributions for each response. While breeding state was modelled as a binomial distribution (0 = pond presence with non-swollen cloaca, 1 = pond presence with swollen cloaca), BC was modelled with a Gaussian (normal) distribution. However, both models used the same information-theoretic framework for model selection to evaluate relationships between seasonal climate variables, internal state-based covariates, additional environmental covariates, and any control variables. Hence, we selected a set of candidate models a priori to identify the 'best' model to address our hypotheses for environmental variation and fitness.

Candidate models for both fitness response variables included (1) additive effects of average and SD for single climate variables within a given seasonal period (e.g. average and SD of only Spring precipitation) and (2) additive effects of average and SD for all three climate variables within a given seasonal period (e.g. average and SD of Spring precipitation, Spring minimum temperature, and Spring snowpack). We also tested for lag effects in all seasonal climatic variables for both fitness models to better evaluate delayed or carryover effects from prior years on breeding status and body condition (Bredeweg et al., 2019). We thus included another candidate set of climatic conditions for seasonal variables 2 years prior to the summer sampling season ($t - 2$) and 3 years prior to the summer sampling season ($t - 3$; age threshold at which larvae develop into paedomorphic adults; Whiteman et al., 2012). Finally, we included a candidate model with no climatic variables to determine if climate improved model performance over models with only internal state-based variables, other environmental covariates, and control variables. The approach resulted in a total of 49 models to evaluate (i.e. four climate variable models replicated across four seasonal periods across three time-lag periods, plus one null model).

In addition to climate variables, all models considered three important internal state-based variables (salamander age, breeding state in the prior year, BC), two environmental covariates (annual density of metamorphs, annual density of adult paedomorphs), and two control variables (day-of year that a salamander was caught, whether a breeding event occurred before or after the first known breeding event; see Appendix 2). Unique salamander identities, cohorts (birth years of salamanders; 1988–2016), and capture year (1990–2020) were initially considered as random effects, which controlled for pseudoreplication and temporal autocorrelation in our models. However, cohort explained very little variance in the models, and ΔAIC and loglikelihood values indicated that the most parsimonious and highest performing models had only random effects for unique identifier and year. All remaining variables were treated as fixed effects. As an example, a seasonal climate model for the effects of only spring precipitation on breeding state with all internal state-based variables, environmental covariates and control variables would have the following R-based syntax:

$$\begin{aligned}&\text{Breeding}\,(0,1)\%\text{Spring Precip}^{*}\text{Morph}-\text{sex}+\text{Spring Precip. SD}^{*}\text{Morph}-\text{sex}\\&+\text{Bred prior year}^{*}\text{Morph}-\text{sex}+\text{Age}^{*}\text{Morph}-\text{sex}+\text{BC}^{*}\text{Morph}-\text{sex}\\&+\text{Annual metamorph density}^{*}\text{Morph}-\text{sex}+\text{DOY}^{*}\text{Morph}-\text{sex}\\&+\text{After first breeding}+(1\mid\text{Identifier})+(1\mid\text{Year})\end{aligned}$$

We tested for significant relationships using maximum likelihood estimation, which was determined from the interactive terms in each model. Using linear contrasts (EMMEANS package; R v. 4.1.2), we tested for pairwise differences in the slopes of the statistical interactions for each morph-sex combination to identify what specific morph- and sex-based differences exist. An information theoretic approach was used to identify the 'best' models from the a priori set of 49 candidate models for seasonal climate variables (Burnham & Anderson, 2002). 'Best' models were evaluated based on Akaike information criterion (AIC), with lower AIC scores and higher model Akaike weights (w_i) indicating higher model likelihoods. We limit our interpretations to only candidate models with $w_i > 0.1$ and with ΔAIC values <2. We also report an evidence ratio (*ER*; Burnham et al., 2011), which is calculated as the w_i of the top ranked model divided by the w_i of the second ranked model. The *ER* provides a likelihood comparison of hypotheses associated with the top model to the hypotheses associated with second ranked model.

All continuous predictors were transformed and normalized to *z*-scores (range: −1 to 1) to standardize slope coefficients and improve model convergence. To ensure a similar comparison of effect sizes between the two fitness models due to their different error distributions, we calculated a pseudo-R^2 for the binomial breeding models based on a comparison of the observed model likelihood to the corresponding likelihood of a null model. Model coefficients were transformed to odds ratios (OR) for the breeding state models to report changes in the probability of a breeding state with climate variables, internal state-based variables, or environmental covariates. We followed standard data exploration practices to ensure that assumptions of normality, heteroscedasticity, dispersion, temporal autocorrelation, and collinearity (all variance inflation factors [VIF's] < 3.0) were not violated for our linear models of fitness metrics (following Zuur et al., 2010). All main effects and interactive effects were considered significant at $p < 0.05$.

3 | RESULTS

3.1 | Breeding state: Top models for climate

There were two top-performing models for breeding state and climate. The 'best' model included all summer seasonal climate variables from 3 years prior ($w_i = 0.53$), which performed only slightly better than the second ranked model with spring precipitation variables from the prior year ($w_i = 0.43$, ΔAICc = 0.44; Table 1). The *ER* of 1.23 indicates a similar level of support for both models and both models had similar predictive performance (both fixed effects pseudo-$R^2 = 0.44$; Table 1).

For the 'best' model, paedomorphic females (negative slopes) and paedomorphic males (positive slopes; $p = 0.018$) was the only morph by sex combination significantly different from each other for interactions with the variation in summer temperatures 3 years prior (Figure 1a). Metamorphic males (negative slopes) and paedomorphic females differed (positive slopes; $p = 0.004$), and paedomorphic males (negative slopes) and paedomorphic females (positive slopes; $p = 0.002$) differed for summer snowpack 3 years prior (Figure 1b). Males of both morphs appeared more likely to breed in a given year when the summer 3 years prior had less snow and more thermal variability, while paedomorphic females appeared more likely to breed in a given year when the summer 3 years prior had more snow and less thermal variability.

For the second-ranked model, there was a significant main effect of average precipitation in the preceding Spring ($\beta = 1.73$, $p = 0.022$), but no significant pairwise differences in the four morph by sex combinations (all $p \geq 0.687$). For every unit increase in average spring precipitation, there was a 5.6% increase in breeding probability (Figure 1c). There were no significant main effects or interactive effects observed with spring precipitation variability (all $p \geq 0.604$).

3.2 | Breeding state: Internal state-based variables and environmental covariates

Among state-based variables, there was a significant main effect of breeding in the prior year on current breeding status. All individuals were less likely to breed following a prior breeding event ($\beta = -1.30$, $p < 0.001$; Table S5). However, females of both morphs exhibited a non-linear decline in the probability of breeding back-to-back, which

TABLE 1 List of the top ranked models for breeding state and body condition. R^2 is based on the variation explained by fixed effect variables (marginal-R^2). While we only discussed models with $w_i > 0.1$, we also report the next best model with $w_i < 0.1$, which serves as a comparison of strength for the top-ranked models.

Fitness metric	Lag	Model	Deviance	R^2	AIC_c	ΔAIC_c	w_i
Breeding	*t*-3	All summer variables	3115.6	0.43	3218.8	0	0.53
	t-1	Spring precipitation	3148.7	0.44	3219.3	0.44	0.43
	t-2	All summer variables	3121.6	0.44	3224.9	6.04	0.03
BC	*t*-1	Summer snowpack	−14,302	0.11	−13,987.7	0	1.00
	t-2	Spring snowpack	−14,236	0.09	−13,925.2	62.46	0

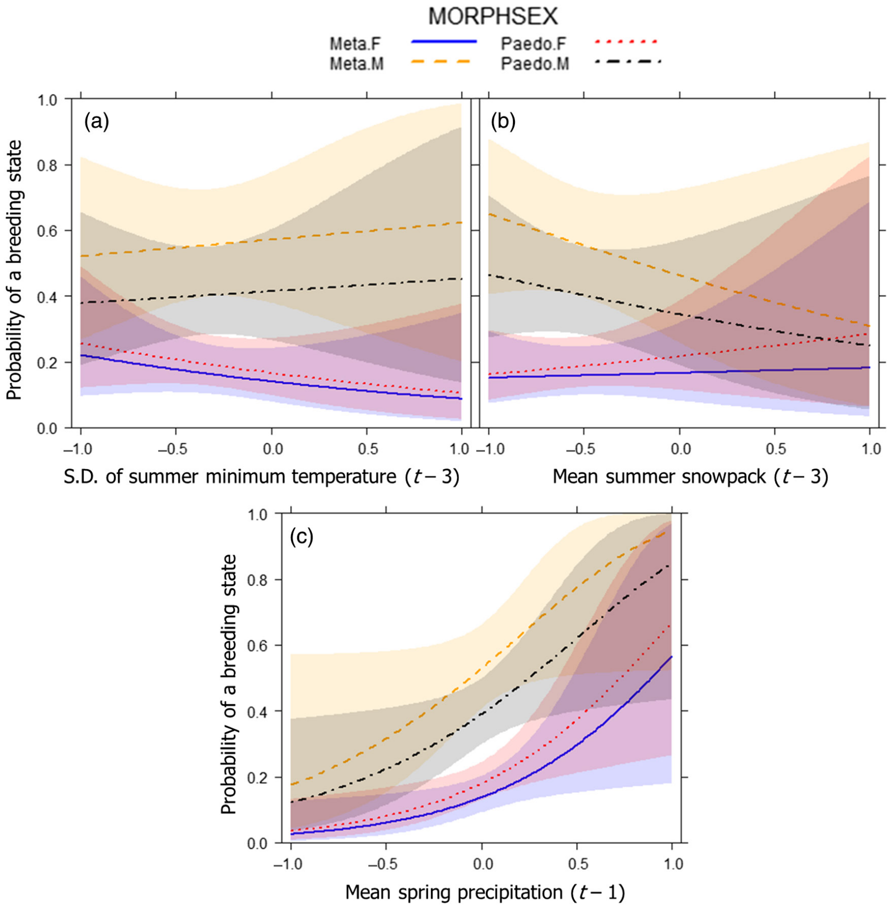

FIGURE 1 Trait by climate interactions for the effects of (a) the standard deviation (SD) of summer minimum temperatures for a 3-year time lag, (b) the mean summer snowpack for a three-year time lag and (c) the mean spring precipitation of the prior year on the probability of metamorphs (blue solid lines and gold dashed line for females and males, respectively) and paedomorphs (red dotted line and black dashed-dotted lines for females and males, respectively) being in a breeding state each year (i.e. present at the ponds with a swollen cloaca). Shading indicates 95% confidence intervals.

were more pronounced than the linear declines for males (Figure S2). Paedomorphic male and paedomorphic female ($p < 0.001$), and metamorphic male and paedomorphic female ($p = 0.038$) were the only morph by sex combinations to significantly differ in breeding probability.

There were also significant main effects and interactive effects with salamander age on breeding state. The probability of breeding decreased with age for all sex by morph combinations at a rate of 0.54% for each unit increase in age ($\beta = -0.61$, $p = 0.031$; Table S5). However, paedomorphs were always more likely to breed at earlier ages than metamorphs of the same sex, whereas metamorphs always had higher breeding probabilities than paedomorphs at older ages. Hence, paedomorphs exhibited an exponential decline in breeding with age, while metamorphs exhibited a linear decline (Figure 2a). Morph-based differences were indeed the only slope comparisons that were significantly different (all $p \leq 0.004$) for breeding probability.

There was no main effect of BC on breeding probability ($\beta = 0.20$, $p = 0.703$; Table S5), despite all morphs, except metamorphic females, exhibiting higher breeding probabilities with increased BC. There were also no significantly different slopes for the morph by sex combinations (all $p \geq 0.085$). Generally, BC had a stronger effect on paedomorph breeding status than it did for metamorphs, considering that low condition metamorphs have higher breeding probabilities than low condition paedomorphs (Figure 2b). These exponential (paedomorphs) versus linear (metamorphs) patterns between BC and breeding are strikingly similar to the morph-based patterns of age on breeding.

There was a significant main effect of DOY ($\beta = -4.00$, $p < 0.001$; Table S5), with the probability of breeding decreasing as the summer sampling season progressed (Figure 2c). Significant pairwise differences in morph by sex combinations were also observed for metamorphic males and metamorphic females ($p < 0.001$), metamorphic females and paedomorphic females ($p < 0.001$), and metamorphic males and paedomorphic males ($p < 0.001$). Males of both morphs had higher probabilities of being in a breeding state later in the season than did females. Finally, there were no significant main effects ($\beta = 0.28$, $p = 0.534$; Table S5) or interactive effects (all $p \geq 0.227$) for annual metamorph density on breeding state.

3.3 | BC: Top model for climate

The top model for BC was easily the best model ($w_i = 1.00$) and included summer snowpack conditions of the prior year. While the model had weak performance (fixed effects $R^2 = 0.11$; Table 1), we observed contrasting relationships for significant main effects of both preceding year average summer snowpack ($\beta = 0.02$, $p = 0.031$; Table S6) and preceding year summer snowpack variability ($\beta = 0.03$, $p < 0.001$) that is indicative of climate mediated trade-offs (Figure 3). The pattern was most clear for summer snowpack variability, where all between morph slope comparisons were significantly different

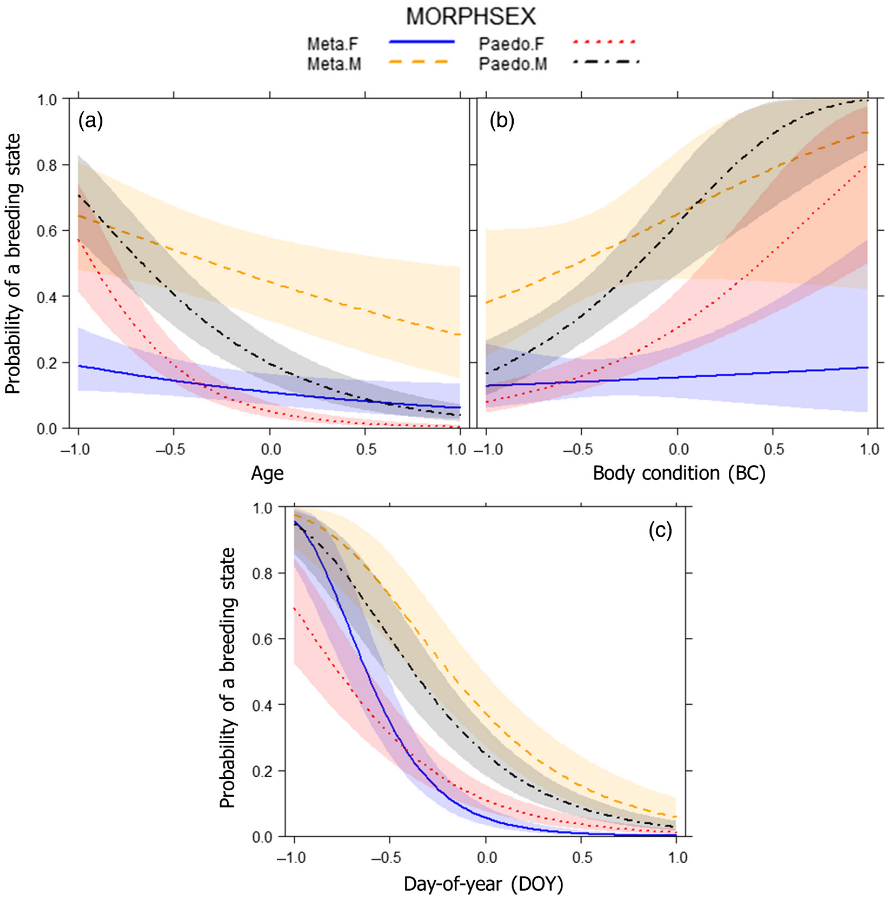

FIGURE 2 Trait by state-based and environmental interactions for the effects of (a) salamander age, (b) salamander body condition (BC) and (c) day-of-year (DOY) when the salamander was captured on the probability of metamorphs (blue solid lines and gold dashed line for females and males, respectively) and paedomorphs (red dotted line and black dashed-dotted lines for females and males, respectively) being in a breeding state each year (i.e. present at the ponds with a swollen cloaca). Shading indicates 95% confidence intervals.

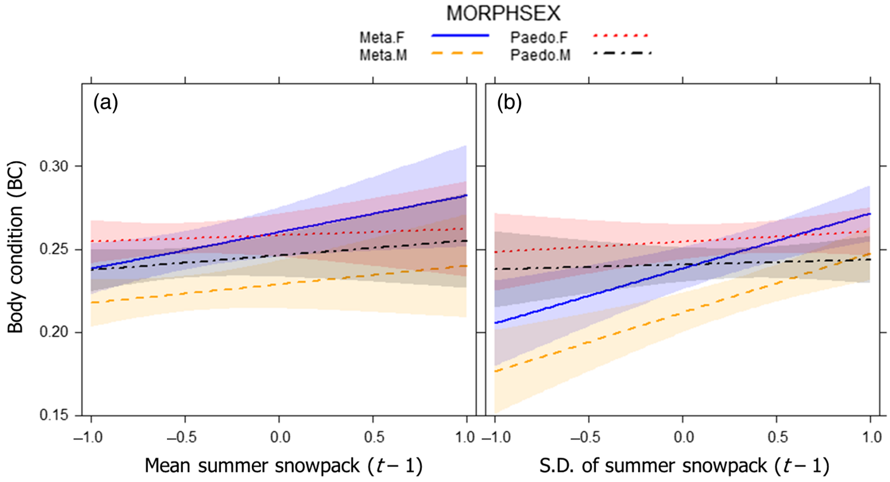

FIGURE 3 Trait by climate interactions for the effects of (a) mean summer snowpack in the prior year and (b) standard deviation (SD) of summer snowpack in the prior year on the body condition of metamorphs (blue solid lines and gold dashed line for females and males, respectively) and paedomorphs (red dotted line and black dashed-dotted lines for females and males, respectively). Shading indicates 95% confidence intervals.

(all $p < 0.001$) and within morph comparisons were non-significant (both $p > 0.669$). Only metamorphic female and paedomorphic female slopes varied for average summer snowpack ($p = 0.005$; all other pairwise comparison p's ≥ 0.076).

3.4 | BC: Internal state-based variables and environmental covariates

There was a significant main effect of age for all morphs ($\beta = 0.04$, $p < 0.001$; Table S6), with older individuals achieving higher BC (Figure 4a). The only pairwise difference in slopes was between the males of each morph ($p = 0.004$; all other pairwise comparison p's ≥ 0.055). There was a near significant relationship between BC and breeding state ($\beta = 0.01$, $p = 0.051$; Table S6), where all morphs exhibited a weak and identical pattern of increased BC when in a breeding state (Figure S3; all pairwise comparison p's > 0.983). Not only was there a significant main effect of DOY with increasing BC over the course of the summer sampling period ($\beta = 0.06$, $p < 0.001$; Figure 4b), but all between-morph comparisons of slopes were significantly different (all $p < 0.001$). Metamorphs experienced greater increases in BC by the end of the summer sampling period

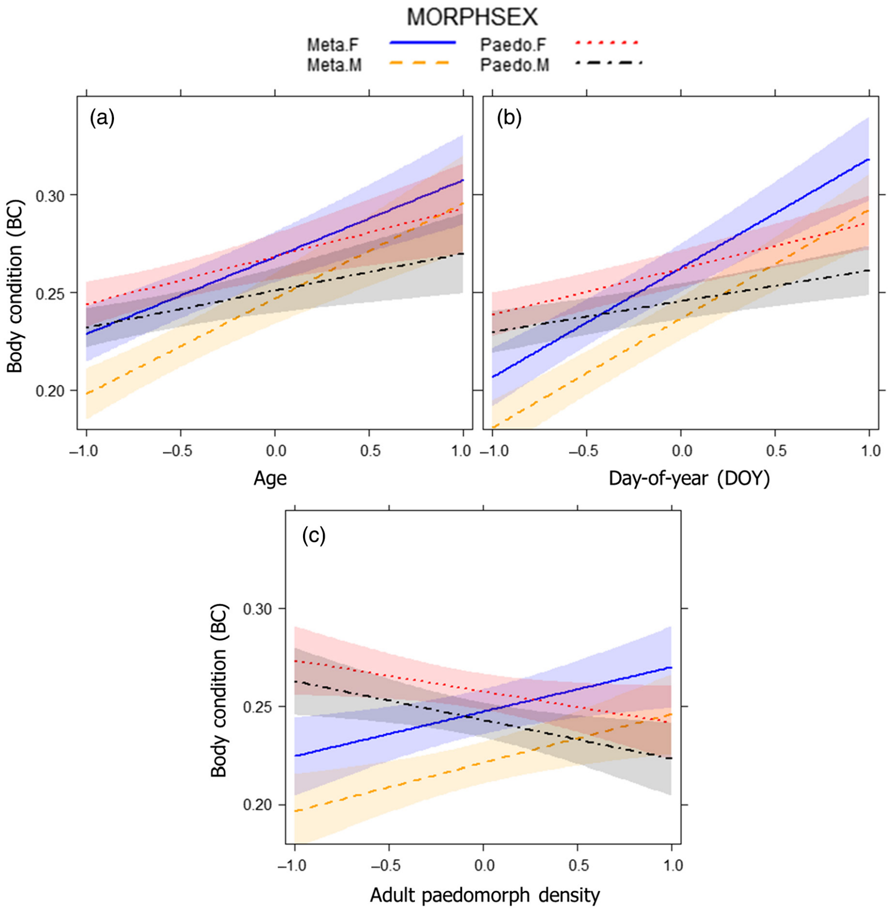

FIGURE 4 Trait by state-based variable and environment interactions for the effects of (a) salamander age, (b) day-of-year (DOY) when the salamander was captured and (c) adult paedomorph densities (age 4+) on the body condition of metamorphs (blue solid lines and gold dashed line for females and males, respectively) and paedomorphs (red dotted line and black dashed-dotted lines for females and males, respectively). Shading indicates 95% confidence intervals.

compared with paedomorphs. However, paedomorphs had higher BC early in the summer sampling period (Figure 4b). The effects of total breeder density were also present as both main effects ($\beta = 0.02$, $p = 0.011$) and interactive effects. Significant pairwise comparisons indicated slope differences that were again solely morph-based (all $p < 0.001$). While paedomorphs declined in BC with increased breeder density, metamorphs increased in BC with higher breeder density (Figure 4c).

4 | DISCUSSION

Our study provides important insight on how fitness trade-offs can underlie the evolution and maintenance of phenotypic diversity by highlighting when life history strategies are favourable or unfavourable under specific environmental contexts. We documented intrinsic life history trade-offs between paedomorphic adults (relatively short-lived, early reproduction, strong condition-dependent breeding, better adult condition early in life) and metamorphic adults (relatively long-lived, late reproduction, weak condition-dependent breeding, better adult condition later in life). These trade-offs are associated with a fast-slow continuum (see Healy et al., 2019), which have been well-documented in animals (e.g. Cayuela et al., 2016a; Lackey et al., 2019; Pianka, 1970; Ryan & Semlitsch, 1998; Winemiller & Rose, 1992). The specific life history trade-offs between fast and slow strategies are related to investment differences across life stages pertaining to growth, reproduction, and developmental pathway.

Our characterization of paedomorphosis as a fast life history strategy is consistent with the negative relationship between larval growth rate and size at metamorphosis along elevation gradients (i.e. slow growth imposes body size constraints for achieving metamorphosis; Bizer, 1978), which could explain why paedomorphosis dominates in cold, high-elevation environments (Sprules, 1974). Certain life history traits associated with fast strategies in fishes and amphibians have been shown to be more adapted to conditions of high environmental stress (Cayuela et al., 2016a; Kirk et al., 2022; Mims & Olden, 2012). Hence, environmental filtering from climate may constrain growth during key developmental periods (e.g. metamorphosis; see also Walter et al., 2018) and thus limit adopting a slow life history strategy (Cayuela et al., 2017; Lowe et al., 2021). An alternative mechanism for explaining the fast life history strategy adopted by paedomorphs is from growth limitations induced by density-dependent effects (Ryan & Semlitsch, 1998; Whiteman, 1994; Whiteman et al., 2012; Wissinger et al., 2010).

Interestingly, the lifetime fitness advantage favours metamorphs (i.e. slow strategy) as they achieve the highest body condition and highest survival later in life (Lackey et al., 2019; Mathiron et al., 2017; Whiteman et al., 1996, 2012). Timing and body size at metamorphosis can affect survival and body size in adulthood, which reveals the importance of early life growth on post-metamorphic fitness (Altwegg & Reyer, 2003; Schmidt et al., 2012). While that advantage comes with a cost early in life through an energetic investment (Ryan & Semlitsch, 1998; Smith & Berven, 1979; Wilbur & Collins, 1973), metamorphs experience that advantage later in life by escaping density-dependent resource availability and exploiting alternative food resources in temporary ponds (Denoël et al., 2007; Whiteman et al., 1994). In contrast, the body condition of paedomorphs was always lower in years of higher breeder densities because paedomorphs are functionally trapped in permanent ponds. Metamorphosing and adopting a migrant life history strategy has been shown to be beneficial when density-dependent effects are high (Grayson et al., 2011). Overall, our results support the "best of a bad lot" mechanism for explaining the predominance of paedomorphosis in this polyphenic population (Whiteman et al., 2012), which likely results from a combination of climate and density-dependent mechanisms (i.e. cold temperature and high competition limit growth through resource limitation).

Sex-based fitness trade-offs have also been well-documented for amphibian polyphenisms (Lackey et al., 2019; Mathiron et al., 2017; Whiteman, 1997; see also Appendix 3). While both sexes showed a lower probability of breeding after being in a breeding state the prior year, females of both morphs were more likely to be in a non-breeding state by the end of the summer period. Females are more likely to always reproduce when in a breeding state given their greater reproductive investment (Trivers, 1972), which also explains why female amphibians are more likely to "skip" reproduction when environmental conditions are less than optimal (Cayuela et al., 2014, 2016b). Evidence also suggests that metamorphosis can be biased towards males given the energetic investment required for transformation (i.e. the male-escape hypothesis; Mathiron et al., 2017). Given the extremely low probabilities we observed for females breeding in consecutive years (Figure S2), our results support the contention that high elevation climates limit reproductive investment (Berven, 1982; Hautier et al., 2009).

Our study provides an important and novel contribution to the ecological and evolutionary understanding of fitness trade-offs by examining the influence of climatic factors on the maintenance of polyphenisms. Spring precipitation had a positive effect on the breeding state for all morph by sex combinations providing evidence of a shared fitness benefit from climatic conditions. Laughlin et al. (2021) concluded that similar fitness relationships are more likely observed than contrasting fitness relationships, especially under climatically stressful conditions (e.g. cold and arid), supporting our contention here (see Appendix 4). The observation of a three-year lag effect from summer climate on sex-based trade-offs in paedomorph breeding could be related to either delayed effects that are associated with the long durations between being reproductively active or carryover effects from the larval state. While evidence indicates that both mechanisms are prominent for paedomorphs, summer climate was the most common seasonal period for affecting morph fitness (Appendix 3).

However, trade-offs in body condition revealed morph-specific fitness advantages. Metamorphs experience a fitness advantage from heavier summer snowmelts, which extend the hydroperiod of temporary ponds and provide a longer growing season for exploiting high-quality fairy shrimp (*Branchinecta coloradensis*) populations (Denoël et al., 2007; Whiteman et al., 1994, 1996). A prior study showed that climatic factors affect long-term metamorph presence more than long-term paedomorph presence (Denoël et al., 2019), further suggesting that climate affects the two morphs differently. While the over-summer growth advantage to metamorphs is consistent with their ability to escape density dependent effects in permanent ponds, the overwintering benefit to paedomorphs was surprising. We initially hypothesized that long overwintering periods would negatively influence paedomorph fitness because of low dissolved oxygen and increased hypoxia, which leads to high overwinter kills (Table S4; Bradford, 1983; Berman et al., 2019). Instead, terrestrial habitats for metamorphs may have relatively lower resource production than the energy-rich aquatic habitats with high rates of cannibalism (Wissinger et al., 2010), which could explain the overwintering advantage for paedomorphs (Schriever et al., 2014). Hence, we hypothesize that other microhabitat trade-offs exist that could explain the maintenance of this polyphenism.

Physiological mechanisms associated with the microclimate of different habitats (e.g. terrestrial/subterranean versus aquatic) likely influence fitness trade-offs. Thermal variability in overwintering habitats induces energetic costs for ectothermic animals, especially in terrestrial habitats where freeze tolerant behaviours are highly adaptive (Costanzo et al., 1993; Fitzpatrick et al., 2020; Layne & Lee, 1995). If density-dependent effects were stronger, and/or resources were more limiting in subterranean habitats (Berven, 2009), then the synergistic effects between these two factors could reveal why metamorphs had lower condition than paedomorphs following overwintering periods. Strong density-dependent effects are well documented in the aquatic habitats (Whiteman et al., 2012), so resource limitation could also induce density-dependent effects in subterranean habitats. Interactions between energy demand and fitness benefits in the two habitat types are currently being explored in microclimatic studies (sensu Reider et al., 2022).

Both morphs are adapted to survive the extreme high elevation climate. Both experience wide seasonal variation in the thermal environment (Heath, 1975), and near-zero temperatures for extended overwintering periods. Overwintering periods can even increase reproductive success and survival in temperate, high-elevation amphibians (Calatayud et al., 2021; Kissel et al., 2019). Many animals exhibit adaptive behaviours to tolerate extreme cold and hypoxia (Berman et al., 2019; Fitzpatrick et al., 2020; Layne & Lee, 1995; Reider et al., 2021), which could include freeze tolerance and/or freeze avoidance behaviours to endure the prolonged overwintering periods. Behavioural thermoregulation would reduce the abiotic stress from climate in overwintering periods and provide further evidence regarding how density-dependent and climatic mechanisms interact to produce fitness trade-offs in this polyphenism.

The observed fitness trade-offs in this polyphenism could be altered by future climate change (see Appendix 5). While the sensitivity of amphibians to climate change is well-documented and many species are predicted to endure negative fitness consequences (e.g. Caruso et al., 2015; Moldowan et al., 2021; Reading, 2007), animal responses to climate change are highly trait-dependent (Pacifici et al., 2017). Even though trait-based studies indicate that climate change will favour certain life history strategies, we lack an understanding of how climate change will alter the specific mechanisms that maintain the trade-offs underlying life history diversity (Both & Visser, 2005; Lancaster et al., 2017). Given the rapid acceleration of contemporary climate change, our work motivates future studies to understand the role of climate variation for explaining the existence and maintenance of polyphenisms, and whether life history diversity promotes climatic resilience (see Davis et al., 2017).

In conclusion, our long-term mark-recapture dataset on an amphibian polyphenism has provided novel insight on foundational concepts in life history theory, fitness trade-offs and how selective pressures act differently on life history traits (Fry, 2003; Stearns, 1989). Our results indicate that the selective pressures and fitness trade-offs that maintain polyphenisms are multi-dimensional, which occur through biotic interactions (e.g. fish introductions reducing paedomorphosis; Davis et al., 2017; Denoël et al., 2019) and/or environmental filtering (e.g. increased aridity reducing paedomorphosis; Mathiron et al., 2017; Semlitsch, 1987). We provide evidence for both mechanisms in the form of density-dependent effects and climatic effects. Our work provides valuable insight into tradeoff theory by highlighting how temporal (e.g. climate change) and spatial (e.g. aquatic vs. terrestrial habitats) mechanisms maintain the existence of phenotypic plasticity.

AUTHOR CONTRIBUTIONS

Mark A. Kirk and Howard H. Whiteman conceptualized the manuscript; Mark A. Kirk collated the data, performed data analyses and wrote the manuscript; and 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

Salamander trait data, climate data and the R code associated with the analyses in this publication are available online at the Dryad Digital Repository https://doi.org/10.5061/dryad.z612jm6h9 (Kirk, 2023).

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SUPPORTING INFORMATION

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

Appendix 1. Defining the fitness metric of breeding state.

Figure S1. Relationship between breeding state and a climate variable associated with Spring precipitation. Note how the climatic relationship documented here is the same as our results in the manuscript (Figure 1c).

Table S1. Comparison of the top models under three different modeling assumptions (#1: all morph absences are included and assumed as non-breeding; #2: only metamorph absences are included and assumed as non-breeding; #3: all morph absences are excluded and breeding is defined based solely on the presence at the ponds with non-swollen cloaca). Only models with $w_i > 0.1$ are shown. Note how all approaches selected the same top-ranked models (models with the climate variable in Figure S1). Ultimately, we selected assumption #3 as our modeling approach because it produced lower model deviances and higher log-likelihoods, it allowed for the inclusion of important co-variates that we wanted to account for (DOY and BC), and it performed the best when evaluating the assumptions of normality and temporal autocorrelation in linear models.

Table S2. Comparison of parameter estimates and *p*-values when using the top-ranked model (Model ID 2a; Table S2) under two of the three different modeling assumptions (#1: all morph absences are included and assumed as non-breeding; #3: all morph absences are excluded and breeding is defined based solely on the presence at the ponds with non-swollen cloaca). Bolded values indicate significant relationships ($p < 0.05$). Note how the coefficient and *p*-values are similar for all fixed effect variables shown except for the main effect of climate axis #2, which is now only marginally significant (highlighted in red). Hence, it appears that a type II error is present when assuming non-captures equate to a non-breeding state because of either misidentifying individuals in a given year or due to low sampling effort in a given year.

Table S3. Pairwise comparisons of different morph-sex combinations and whether they differ significantly from each other in response to PCA axis #2 under two of the three modeling assumptions (#1: all morph absences are included and assumed as non-breeding, #3: all morph absences are excluded and breeding is defined based solely on the presence at the ponds with non-swollen cloaca). Bolded values indicate significant differences in morph-sex responses to PCA axis #2 ($p < 0.05$).

Table S4. Full list of the 12 macroclimate variables summarized for all years of the mark-recapture database (1988–2020) that were downloaded from the atmospheric DAYMET database. Average and standard deviation were calculated for each macroclimatic variable; resulting in a total of 24 variables. The expected effects of each climate variable on amphibian fitness and an example of a potential climatic tradeoff for the two life history morphs are described, and citations are provided to support these examples; including for the high elevation salamander polyphenism in this study (see 5, 6, 7, 19, 23).

Appendix 2. Explanation and justification of covariates in our trait-environment models.

Figure S2. Trait by state-based variable interaction for the effect of an individual's breeding state in the previous year (1 = had a swollen cloaca in the previous year) on the probability of metamorphs (blue and gold lines for females and males, respectively) and paedomorphs (red and black lines for females and males, respectively) being in a breeding state for the current year (i.e., present at the ponds with a swollen cloaca).

Figure S3. Trait by state-based variable interaction for the effect of an individual's current breeding state (0 = did not have a swollen cloaca) on the body condition of metamorphs (blue and gold lines for females and males, respectively) and paedomorphs (red and black lines for females and males, respectively).

Appendix 3. Sex effects, Delayed effects, and Carryover effects.

Figure S4. Significant main effects for the third ranked model of two years prior summer climate variables on current breeding state (Table 1). All main effects were significant with similar responses (all $p < 0.003$). Greater summer thermal variability, greater summer snowpack, higher summer precipitation, and more summer snowpack variability during the summer growing season two years prior corresponds to a breeding state for all morph-sex combinations in the current year.

Appendix 4. Relationships between precipitation, ice-off, and breeding migrations.

Figure S4. Relationships between first metamorphic female arrival (top panel) and first observed paedomorphic female breeding (bottom panel) with qualitative observations on the date of first ice-off from the co-author (H.H. Whiteman) using 23 years of data.

Table S5. Main effect variable significance for breeding state models. Bolded values are significant ($p < 0.05$).

Table S6. Main effect variable significance for body condition models. Bolded values are significant ($p < 0.05$).

Appendix 5. Expected climate change impacts on life history tradeoffs for this amphibian polyphenism.

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