Integrative and Comparative Biology

Integrative and Comparative Biology, volume 0, pp. 1–16
https://doi.org/10.1093/icb/icad059

Society for Integrative and Comparative Biology

SYMPOSIUM

Developmental Plasticity in Anurans: Meta-analysis Reveals Effects of Larval Environments on Size at Metamorphosis And Timing of Metamorphosis

Molly A. Albecker[*,†], Sarah McKay Strobel[†] and Molly C. Womack[†,1]

[*]Department of Biology and Biochemistry, University of Houston, 3455 Cullen Blvd, Houston Texas, 77004, USA;
[†]Department of Biology, Utah State University, Logan Utah, 84322, USA

[1]E-mail: molly.womack@usu.edu

From the symposium "Pathways to adulthood: environmental, developmental, and evolutionary influences on the ontogeny of form and function" presented at the annual meeting of the Society for Integrative and Comparative Biology virtual annual meeting, January 16–March 31, 2023.

Synopsis Many anuran amphibians (frogs and toads) rely on aquatic habitats during their larval stage. The quality of this environment can significantly impact lifetime fitness and population dynamics. Over 450 studies have been published on environmental impacts on anuran developmental plasticity, yet we lack a synthesis of these effects across different environments. We conducted a meta-analysis and used a comparative approach to understand whether developmental plasticity in response to different larval environments produces predictable changes in metamorphic phenotypes. We analyzed data from 124 studies spanning 80 anuran species and six larval environments and showed that intraspecific variation in mass at metamorphosis and the duration of the larval period is partly explained by the type of environment experienced during the larval period. Changes in larval environments tended to reduce mass at metamorphosis relative to control conditions, with the degree of change depending on the identity and severity of environmental change. Higher temperatures and lower water levels shortened the duration of the larval period, whereas less food and higher densities increased the duration of the larval period. Phylogenetic relationships among species were not associated with interspecific variation in mass at metamorphosis plasticity or duration of the larval period plasticity. Our results provide a foundation for future studies on developmental plasticity, especially in response to global changes. This study provides motivation for additional work that links developmental plasticity with fitness consequences within and across life stages, as well as how the outcomes described here are altered in compounding environments.

Lay summary We conducted a meta-analysis to identify how six different environments affect mass at metamorphosis and time to metamorphosis in larval anurans. We find that some, but not all, environmental conditions triggered predictable changes in size and timing of metamorphosis, and phylogenetic relatedness rarely explains developmental plasticity variation among species.

Introduction

Complex life cycles are the predominant life history strategy on Earth and are characterized by life cycles that are segmented into distinct stages with unique forms, functions, and ecologies (Wilbur 1980; Werner 1988; Moran 1994). For taxa with complex life cycles, environmental conditions experienced during embryonic and larval life stages can shape phenotypes and survival (West-Eberhard 2003), termed developmental plasticity (Pechenik 2006; Earl and Semlitsch 2013; Collet and Fellous 2019). Environmentally induced phenotypic changes may include growth rates (e.g., cell proliferation) and development (e.g., cell differentiation), which, in turn, can affect the size at metamorphosis and the timing of metamorphosis (Smith-Gill 1983; Rose 2005). Changes in growth,

Advance Access publication June 5, 2023

development, and the duration of early life stages can affect fitness at subsequent life stages, often termed carry-over or latent effects (Pechenik 2006). Thus, understanding how environmental changes affect organismal development is critical for predicting the future impact of global climate change on populations and species.

Anurans (frogs and toads) are the most specious clade of vertebrates, have a complex life cycle, and rank among the taxa most significantly affected by climate change (Hof et al. 2011; Li et al. 2013). Climate change is expected to alter wetland temperatures (Salimi et al. 2021), hydroperiod or drought regimes (i.e., the duration that water remains in a wetland; Walls et al. 2013), salinities (Herbert et al. 2015), and community structure (Gilman et al. 2010). Developmental plasticity has been well documented in response to changes in isolated environmental variables such as temperature (Ruthsatz et al. 2018; Sinai et al. 2022), predators (Relyea 2007), and decreasing water levels (Richter-Boix et al. 2011), but we lack comparisons of how different environmental variables affect growth and development (but see Tejedo et al. 2010; Earl and Whiteman 2015). For instance, reduced temperatures affect larval development rate more than growth (Blouin and Brown 2000), whereas reduced food availability slows growth with limited effects on development (Emerson 1986). However, each of these studies was conducted on a single species, leaving the generalizability of the results unclear. Moreover, it is not known how different environments affect plasticity relative to one another. While the literature clearly shows that food limitation and reduced temperatures affect growth and development, we do not know which has the strongest effect. Although anuran amphibians are a classic vertebrate model system for studying developmental plasticity and complex life cycles, we have limited capacity to establish expectations across different environmental conditions.

Identifying general patterns of developmental plasticity in response to environmental changes is further complicated by species variation. Although interspecific variation in developmental plasticity can decrease our ability to taxonomically generalize, incorporating phylogenetic relatedness, and clade-specific variation may allow us to better predict clade-specific responses in growth and development rates to environmental changes. Species that are more closely related are more likely to have similar life history traits, such as growth rates, development rates, and size at metamorphosis (Richter-Boix et al. 2011; Relyea et al. 2018), which may affect the direction or degree of developmental plasticity of these traits. However, the few studies that have explicitly tested for phylogenetic signal in anuran developmental plasticity have found that phylogenetic signal rarely predict developmental plasticity in response to differing predation pressures (Relyea et al. 2018) or temperatures (Sinai et al. 2022). More comparative studies of developmental plasticity across different environmental conditions are needed to understand when phylogeny can help predict developmental plasticity.

We explored how developmental plasticity alters metamorphic outcomes in amphibians in response to abiotic and biotic environmental conditions that are likely to change in the coming decades with global climate change, such as temperature, salinity, habitat structure, community dynamics, and food availability. Synthesizing the effects of multiple environmental conditions on developmental plasticity will greatly advance our ability to understand amphibian biology and life history, as well as predict the future impacts of global climate change on populations and species (Urban et al. 2014).

Materials and methods

Study selection

We searched the Web of Science database for experimental studies that evaluated metamorphic responses across different larval environments. We conducted the initial search on August 15, 2022. We used the search string, "(stress OR respon* OR polyphen* OR plastic*) AND (develop* OR grow* OR differentiat*) AND (anuran* OR frog OR toad) AND (tadpole* OR larva*) AND metamorph*) and searched abstracts. Initial searches returned 483 hits. Specific exclusion criteria are detailed in the PRISMA diagram (Fig. 1)

Study meta-data

After refining our database, we extracted meta-data from the text, tables, and data repositories, and used WebPlotDigitizer (https://automeris.io/WebPlotDigitizer/) to extract data from figures. We collected meta-data on the taxonomy of study organisms, which environmental parameters of interest (e.g., temperature, predation, etc.) were manipulated, as well as data on the experimental set up including tank size and/or volume, air and water temperatures, type and amount of food provided to tadpoles. We recorded the developmental time point at which experimental animals were collected, the stage or time that the experiment was started, and how each study defined metamorphosis. We collected sample size data that included the number of replicates, treatments, and tadpoles within each experimental unit. Finally, we recorded whether authors collected phenotypic data before metamorphosis or

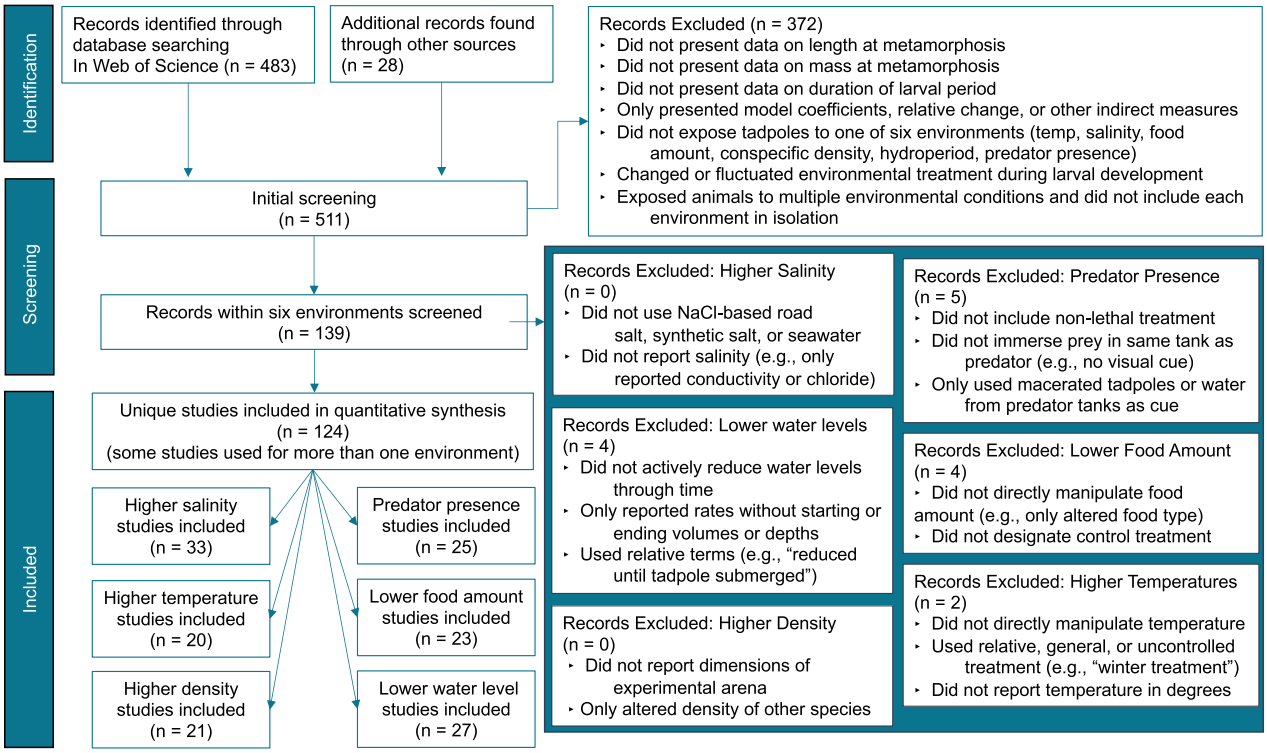

Fig. 1 A PRISMA workflow describing the identification, screening, and inclusion process for the studies included in the meta-analysis. After identifying the pool of studies, studies underwent two screenings: an initial screening that applied to all studies, and then another screening to identify whether the study fit within criteria unique to each environment. Final sample numbers are shown, though the samples for each of the six environmental conditions add up to more than the total number of studies because some studies exposed developing larvae to more than one environmental condition.

after completion of metamorphosis (e.g., measured carry-over effects), in addition to the phenotypic data collected at metamorphosis.

Calculation of effect size

Anurans species demonstrate incredible variation in the size at metamorphosis and the time spent as tadpoles (i.e., duration of larval period). To standardize phenotypic responses across species, we calculated the log odds ratio (LOR) for mass at metamorphosis, length at metamorphosis, and duration of larval period (Chang and Hoaglin 2017; Hamman et al. 2018). LOR is calculated as: $\mathrm{LOR} = \log(\mathrm{phenotype}_{\mathrm{treatment}}/\mathrm{phenotype}_{\mathrm{control}})$ and describes the magnitude and direction of phenotypic change relative to the control treatment. A LOR of 0 is equivalent to an odds ratio of 1, which indicates no difference between treatment and control. A response greater than 0 indicates an increase in length, mass, or larval duration relative to the control, whereas a response less than 0 indicates a reduction in length, mass, or larval duration relative to the control. The further the LOR departs from zero, the greater the magnitude of the effect. Although studies reported length data as either snout-vent length or total length, we combined two different measures of length into a single estimate of length because LORs provide an estimate of relative change compared to control.

To standardize experimental treatments for environmental conditions across diverse studies, we converted each condition to a standardized measure. We calculated the degree of food restriction as the proportion of food relative to the highest food amount within that study. For instance, if the non-restricted treatment received 0.5 grams of rabbit chow daily and the food restricted treatment received 0.25 g daily, the control environment (nonrestricted) was assigned to 0, and the food restricted treatment was 0.5 (50% of what was offered to the control). For salinity exposure studies, all salinity measures were converted to parts per thousand (ppt; or grams of dissolved salt per liter; g/L). Percent seawater was converted to ppt by assuming seawater to be 35 parts per thousand (e.g., 10% seawater is equivalent to 3.5 ppt). Salinity presented as millimole (mMol) was converted to g/L first by multiplying by the molecular weight of NaCl (58.44 g/mol) divided by 1000 (to convert to g/L). Salinity presented as milliosmoles per kilogram (mOsm/kg) was converted to ppt by multiplying the mOsm/kg value by the molecular weight of

sodium chloride and dividing that value by 2000 (1000 ∗ the number of species; NaCl is 2 species). Temperatures were less variable in how they were reported, and we used Celsius scale. Given the range of temperatures across studies, we use a relative measure of warming. Specifically, the lowest temperature was assigned 0, and then warming was assigned as the difference between treatments and the control. For example, a study that exposed tadpoles to 20, 25, and 30C treatments would have relative rise in temperature (Δ temperature) listed as 0, 5, and 10 degrees. Densities were similarly variable across studies. To standardize tadpole densities, we first converted all densities to the number of tadpoles per liter of water. For instance, ten tadpoles held in 500 mL water were converted to 20 tadpoles/liter. We then assigned treatments as differences in the number of tadpoles relative to the control. Using the prior example, the control would again be assigned as 0, and a 25 tadpole/liter treatment would be assigned a 5. We grouped tadpoles into different predator treatments using general taxonomic descriptions to denote predator type. For instance, *Procambarus acutus* (white river crawfish) was classified as "crayfish," and *Anax junius* larva (common green darner) was classified as "dragonfly nymph." Studies that lowered water levels were standardized by calculating the proportional change in water volume or depth from the start to end of the experiment. Nondrying treatments were always assigned 0 (no drying) and ranged to 1 (total dry down). For instance, if a control treatment had 500mL of water, and the drying treatment contained 100mL at the end, the control would equal 0, while the treatment would be 0.8.

Log-odds ratio effect sizes depend on the control, so we defined specific control treatments for each environment. In general, the control was the environment assumed to be the least stressful to tadpoles (with temperature as an exception, in which the control was the lowest temperature treatment included in the experiment). In most cases, the measure of the control was equal to 0 (or in the case of predator presence, no predator). For salinity exposure, the freshwater treatment (0 ppt) was the control. The control for a lower food amount was the treatment with the greatest amount of food provided (e.g., no restriction = 0). To investigate higher temperature effects, we considered the lowest temperature within each treatment as the control (lowest temperature = 0). We assume the lowest density as the control treatment (lowest density per liter = 0). For predator presences, tanks without predators were the control for non-lethal predator presence. Tanks with steady water levels were the control for environments with water levels lowered (no change in water level = 0).

Statistical methods

We conducted all analyses in R version 4.0.3 (R Core Team 2018). Although we collected data on both mass and length, these two phenotypes were shown to be tightly correlated (R^2 = 0.89; Supplemental Fig. 1). More studies reported data on mass than length, so we focused the analyses on mass at metamorphosis and duration of larval period.

To determine whether mass at metamorphosis and duration of larval period varied across the six different environmental conditions, we used log-odds ratio as the response for both mass at metamorphosis and duration of larval period. We used likelihood ratio tests to test whether a model that included the environmental condition as a categorical fixed effect (e.g., "higher temperatures," "predator presence," etc.) fit the data better than a no-effect model. We included study as random effects to account for the variation across studies (see forest plots in Supplemental Figs. 2 and 3). We used linear mixed effects models (package lme4 (Bates et al. 2014) with post-hoc pairwise comparisons to test for differences between environments using *emmeans*() in emmeans package (Lenth 2018). We used false discovery rate (fdr) to adjust *P*-values to account for multiple tests.

The previous tests determined how the type of environmental condition (but not severity) affected responses, so to understand how severity within each condition affected mass at metamorphosis and duration of larval period, we analyzed responses within each environment separately. For these analyses, we employed both phylogeny-based approaches (Bayesian phylogenetic multilevel models) and nonphylogeny-based methods (linear mixed effects models). Results from phylogenetic-based approaches revealed that phylogeny did not account for any variability across any of the models (Supplemental Table 1), so we chose to focus on the results obtained from the linear mixed effects models, which provided greater flexibility in terms of the data that could be incorporated into the analysis and facilitated hypothesis testing.

To construct the linear mixed effects models, we regressed the mass at metamorphosis or the duration of the larval period against each of the environmental conditions. Higher temperatures, higher densities, lower water levels, higher salinities, and lower food amounts were treated as continuous fixed effects, while predator presence was treated as a categorical fixed effect with predator type serving as the level for comparison (e.g., "crayfish," "fish," etc.). We again included study as random effects in these models (Supplemental Figs. 2 and

3). Likelihood ratio tests evaluated whether the model with the environmental condition better fit the data relative to a no-effect model.

Finally, to directly assess the extent that variation in developmental plasticity among species could be attributed to phylogenetic relatedness, we estimated phylogenetic signal in the direction and degree of phenotypic plasticity in response to each environmental change. For each study and treatment, we divided the LOR effect sizes by the severity of each treatment. Since not all species were exposed to the same severity of environmental change treatment, this allowed us to examine the average degree of plasticity among species while accounting for treatment severity variation among studies and species. For these analyses, we further standardized treatments for food and drying as proportional changes between the control and experimental groups (same as above), but temperature, salinity, and density, food amount were adjusted from raw differences to proportional differences (Details can be found in Supplemental Methods 1). For each of the six treatments and the two phenotypic responses (larval duration and metamorph mass), we then estimated phylogenetic signal (as Blomberg's K) using 1000 simulations and conducted a hypothesis test for significant phylogenetic signal with phylosig() in the phytools package version 1.2.0 (Revell 2012). $K > 1$ means that the trait is evolving slower than expected under Brownian motion (BM), so closely related species resemble each other more than expected under BM, while $K < 1$ means closely-related species resemble each other less than expected under BM (Blomberg et al. 2003). We used an existing anuran phylogeny inferred from molecular data via maximum likelihood methods (Pyron 2014) and pruned it to the species within our study using the phytools package version 1.2.0 (Revell 2012) and geiger package version 2.0.10 (Harmon et al. 2008; Pennell et al. 2014). Six species within our dataset were not present in this phylogeny: *Hyperolius spinigularis*, *Nanorana vicina*, *Phrynobatrachus guineensis*, *Pseudophryne australis*, *Ceratophrys stolzmanni*, and *Allopaa hazarensis*. Five of those species were the only members of their genera within our study, so we included them in the analysis by substituting their names for congeners present on the phylogeny: *Hyperolius phantasticus*, *Nanorana parkeri*, *Phrynobatrachus natalensis*, *Pseudophryne bibronii*, and *Ceratophrys cornuta*. The final species that was not present on the phylogeny did not have any congeners in the phylogenetic tree, but multiple molecular studies have found evidence for *Allopaa* being nested within *Nanorana* (Akram et al. 2021; Hofmann et al. 2021) so we substituted *A. hazarensis* for *Nanorana pleskei*. We used the phytools package version 1.2.0 (Revell 2012) for plotting.

Results

Our assembled dataset included data on mass and length at metamorphosis and the duration of larval period from 124 studies across six different environments (Fig. 1). We collected metamorphic data from 27 studies that lowered water levels for developing tadpoles (Supplemental Fig. 4), 23 studies that lowered the amount of food available to the developing larvae (Supplemental Fig. 5), 21 studies that increased the number of conspecific densities (Supplemental Fig. 6), 25 studies that exposed larvae to the nonlethal presence of a predator (Supplemental Fig. 7), 33 studies that increased the salinity (Supplemental Fig. 8), and 20 studies that raised the temperature of the water (Supplemental Fig. 9). These add up to more than 124 studies across environments because some studies exposed larvae to more than one environmental type. Funnel plots indicate a slight asymmetry in mass at metamorphosis indicating that smaller studies with null or negative results may be missing in our dataset (Supplemental Fig. 2) but the duration of the larval period was fairly symmetrical which suggests that studies with null or negative results are present in our dataset (Supplemental Fig. 3).

Does plasticity in mass at metamorphosis and duration of larval period vary among different environments?

Mass at metamorphosis and the duration of larval period were affected by environments (Mass: $\chi^2_5 = 44.6$; $P < 0.0001$; duration: $\chi^2_5 = 92.01$; $P < 0.0001$; Fig. 2). Broadly, each environment, except predator presence and higher salinities, affected mass at metamorphosis and duration of larval period (Fig. 2B). Relative to control conditions, exposure to the treatment condition tended to reduce the mass of individuals at metamorphosis but had varied effects on the duration of the larval period (Table 1). Pairwise comparisons revealed that the effect size differed according to environment (Fig. 2; Table 1). Lower food amounts and higher densities produced smaller metamorphs that experienced longer larval durations (Fig. 2; Table 1). Warmer environments and drying environments produced smaller metamorphs that experienced shorter larval durations. Saltwater exposure and predator presence had variable, non-significant effects on mass at metamorphosis and duration of larval period.

Table 1 Pairwise comparisons between different environmental groups for LOR of mass at metamorphosis (area below black squares) and LOR of duration of larval period (area above black squares). The estimated marginal mean difference between the environmental groups is shown with its corresponding standard error in parentheses. *P*-values corrected using false discovery rate are shown below each estimate. Significant comparisons are shown in bold. Results are averaged across all species.

	Lower water levels	Lower food amounts	Higher densities	Predator presence	Higher salinities	Higher temperatures	Duration of larval period
Lower water levels		**−0.07 (0.013)** **P < 0.0001**	**−0.07 (0.015)** **P < 0.0001**	−0.02 (0.013) P = 0.09	**−0.04 (0.012)** **P = 0.001**	**−0.07 (0.014)** **P < 0.0001**	
Lower food amounts	**−0.077 (0.02)** **P = 0.0015**		0.001 (0.014) P = 0.92	**0.05 (0.013)** **P = 0.001**	−0.024 (0.013) P = 0.08	**−0.14 (0.013)** **P < 0.0001**	
Higher densities	**−0.076 (0.025)** **P = 0.002**	0.03 (0.024) P = 0.34		**0.05 (0.017)** **P = 0.002**	0.03 (0.014) P = 0.08	**0.14 (0.013)** **P < 0.0001**	
Predator presence	**−0.05 (0.02)** **P = 0.03**	**−0.12 (0.02)** **P = 0.0015**	**−0.10 (0.024)** **P = 0.0001**		0.02 (0.013) P = 0.10	**−0.09 (0.014)** **P < 0.0001**	
Higher salinities	−0.03 (0.02) P = 0.19	**0.11 (0.02)** **P < 0.0001**	**−0.008 (0.02)** **P = 0.0017**	−0.021 (0.02) P = 0.34		**0.11 (0.013)** **P < 0.0001**	
Higher temperatures	0.015 (0.022) P = 0.5	**0.09 (0.02)** **P = 0.0001**	**−0.07 (0.03)** **P = 0.02**	−0.04 (0.02) P = 0.11	0.015 (0.02) P = 0.45		
Mass at metamorphosis							

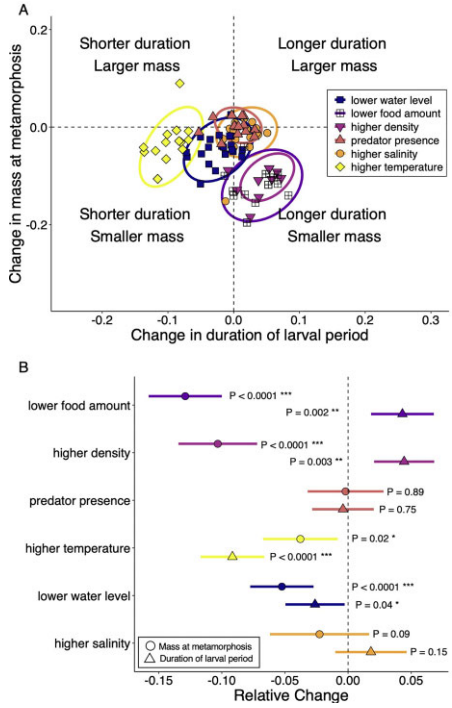

Fig. 2 Environmental effects on mass at metamorphosis and duration of larval period. The mean LOR describing metamorph mass and duration of larval period in different larval environments on based on a meta-analysis of 124 studies (A). Datapoints are predicted averages for different genera encircled by 95% confidence ellipses. In panel A, shape and color indicate each of the six environments. In panel B, the overall effect of each environment on mass at metamorphosis (circles) and duration of larval period (triangles) are shown. Panel B colors match panel A. Points to the right of the dashed line in panel B indicate larger size or longer duration relative to the studies' control conditions, whereas points to the left of the dashed line indicate smaller mass or shorter duration relative to the studies' control conditions. Segments show 95% confidence intervals. *P*-values were estimated using pairwise comparisons with FDR correction.

How does the severity of environmental change affect metamorphic size and timing?

When comparing across studies, the severity of the treatment often affected the degree of developmental plasticity (calculated as LOR). Mass at metamorphosis had a negative relationship with increasing temperatures (see Table 2; Fig. 3A), decreasing water levels (Fig. 3B), lower food amounts (Fig. 3C), and increasing salinities (Fig. 3E). Mass at metamorphosis showed no relationship with increasing tadpole densities (Fig. 3D) or according to the predator identity (Fig. 3F).

Larval period duration had a negative relationship with increasing temperatures (Table 2; Fig. 4A) and decreasing water levels (Fig. 4B). Larval period duration elongated with lower food amounts (Fig. 4C) and increasing salinities (Fig. 4E). Larval period duration varied according to predator identity, with the

Table 2 Model results for analyses testing whether the severity within each environment affected mass at metamorphosis or duration of larval period. Significant tests are bolded.

Environment	Mass at metamorphosis		Duration of larval period	
Higher temperature	$\chi^2_1 = 22.15$	**$P < 0.0001$**	$\chi^2_1 = 58.47$	**$P < 0.0001$**
Lower water level	$\chi^2_1 = 19.1$	**$P < 0.001$**	$\chi^2_1 = 32.25$	**$P < 0.0001$**
Higher density	$\chi^2_1 = 0.012$	$P = 0.91$	$\chi^2_1 = 0.45$	$P = 0.5$
Predator presence	$\chi^2_6 = 10.03$	$P = 0.12$	$\chi^2_6 = 23.9$	**$P = 0.0005$**
Higher salinity	$\chi^2_1 = 18.83$	**$P < 0.0001$**	$\chi^2_1 = 23.23$	**$P < 0.0001$**
Lower food amount	$\chi^2_1 = 92.8$	**$P < 0.0001$**	$\chi^2_1 = 29.13$	**$P < 0.0001$**

greatest reductions in duration of larval period associated with crayfish and turtle predators (Fig. 4F). Increasing densities did not affect larval period duration (Fig. 4D).

Does developmental plasticity vary across the anuran phylogeny?

In total, our meta-analysis included data from 80 species, 39 genera, and 17 families. However, for any given environmental change and developmental phenotype, only 11–26 species were available for comparison (Table 3) and only one species, *Bufo bufo*, had developmental plasticity data available for mass at metamorphosis and duration of larval period for all six environmental treatments (Fig. 5). Species varied in the degree and direction of developmental plasticity in metamorph mass and larval period duration (Fig. 5). However, a significant phylogenetic signal was only found in larval period duration plasticity in response to temperature ($K = 0.419$, $P = 0.036$) and predator presence ($K = 0.295$, $P = 0.044$), as well as in metamorph mass plasticity in response to lowering water levels ($K = 0.574$, $P = 0.037$; Table 3). Even though these values were significant, K values less than one indicate a weak phylogenetic signal. Thus, of the twelve combinations of environmental variables and phenotypes examined here, phylogenetic relatedness explained a small amount of developmental plasticity variation in only three cases.

Discussion

For anuran amphibians, the larval period is an important stage of development that can affect lifetime fitness and population dynamics (Wilbur and Collins 1973; Smith-Gill and Berven 1979; Werner 1988). We conducted a meta-analysis to understand whether developmental plasticity in response to different larval environments produces predictable changes in metamorphic phenotypes. We analyzed data from 124 studies spanning 80 anuran species and six larval environments and observed that mass at metamorphosis and the duration of the larval period depended on the type of environment experienced by larvae and, in some cases, the severity of environmental conditions. We found only weak phylogenetic patterns within the interspecific variation in developmental plasticity. Collectively, our study is the largest synthesis of developmental plasticity in metamorph mass and larval duration to date (but see Tejedo et al. 2010), and our results corroborate and provide additional insights into findings from syntheses that investigated developmental plasticity in response to individual environmental conditions: temperature (Ruthsatz et al. 2018; Sinai et al. 2022), hydroperiod (Richter-Boix et al. 2011), salinity (Hopkins and Brodie 2015), predator presence (Benard 2004; Relyea 2007), and food resources (Tejedo et al. 2010). Our results and collated metadata provide a foundation for future investigations of the environmental effects on early amphibian life stages to contextualize findings across species and experimental designs.

Some, but not all, environmental changes trigger predictable changes to mass at metamorphosis and duration of larval period

Changes in four of the six environmental conditions resulted in consistent directional plasticity in either larval period duration or metamorph mass, but the direction of plasticity differed among the environmental conditions and phenotypes. Limiting food or increasing the density of conspecifics extended the larval period and produced smaller metamorphs, whereas heating the environment or lowering water levels shortened the length of the larval period and produced smaller metamorphs. Accelerated development in response to lowered water levels is consistent with an active response to minimize the risk of desiccation (Schiesari et al. 2006; Richter-Boix et al. 2011). However, the outcomes shown by developing larvae at warmer temperatures, food-restricted environments, or at higher densities are consistent with the passive, biophysical

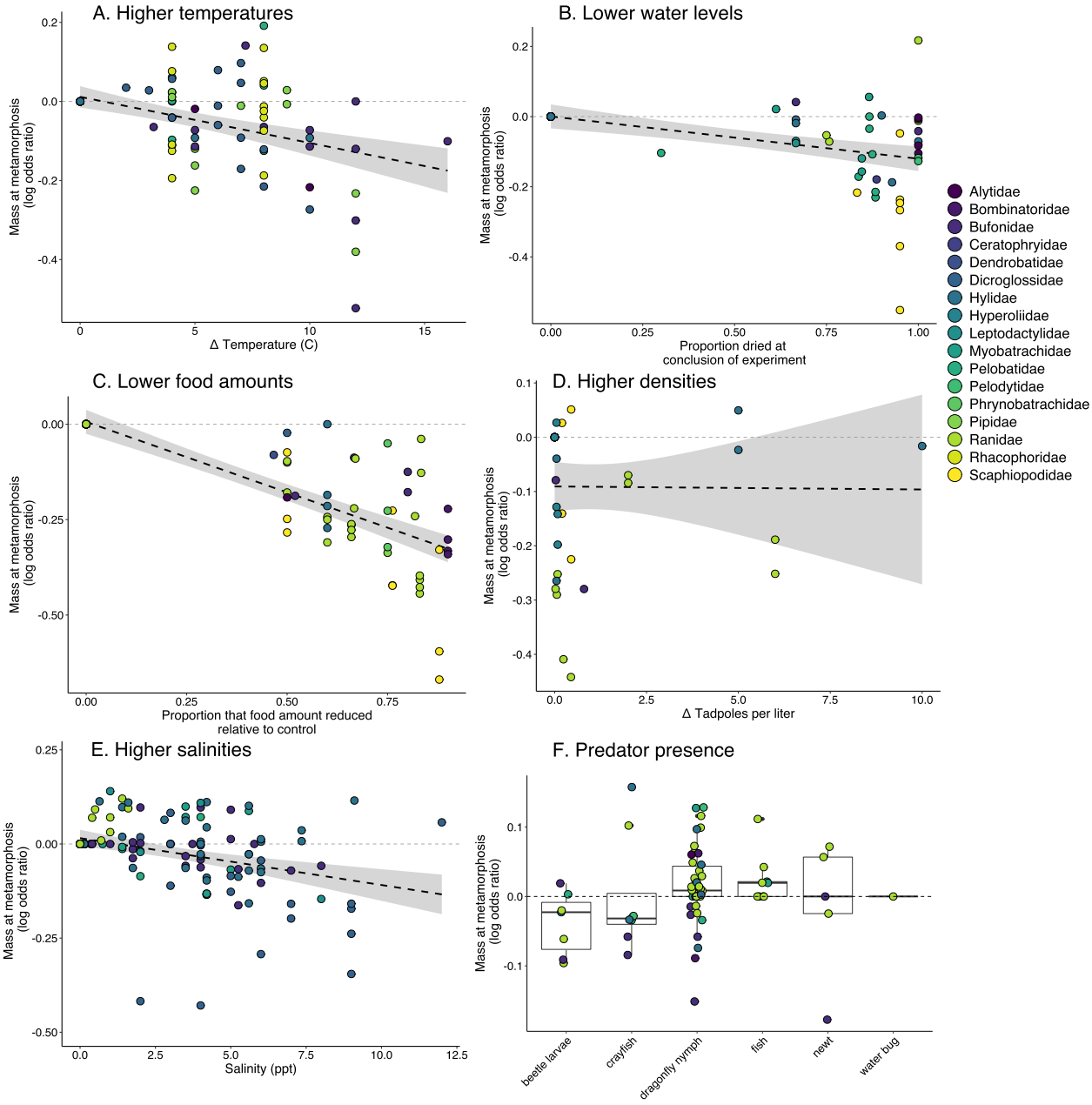

Fig. 3 Mass at metamorphosis for each of the six environments included in the meta-analysis. LOR data are shown along with the model-fit trend line depicting the relationship between phenotype and treatment severity or type (dashed line). Shaded area around the trend line indicates the 95% confidence interval. The x-axis differs in each plot to show change in each environment of the treatment relative to the control. Points are colored according to family and because multiple studies often use the same species, any given species can have more than one point on the plot. Horizontal dashed lines indicate no difference from the control. Mass above zero indicates larger mass at metamorphosis than control treatments whereas mass below zero indicates smaller mass at metamorphosis than control treatments.

consequences of the environment (Ghalambor et al. 2007; Whitman and Agrawal 2009). For instance, higher densities and lower food amounts may have provided insufficient access to resources for both growth and development, whereas thermodynamic processes at warmer temperatures may have accelerated metabolic and developmental pathways (Smith-Gill and Berven 1979).

The results of this study largely support prior meta-analyses, which found that larval duration and metamorph mass decreased with increasing temperatures (Ruthsatz et al. 2018; Sinai et al. 2022). However, our

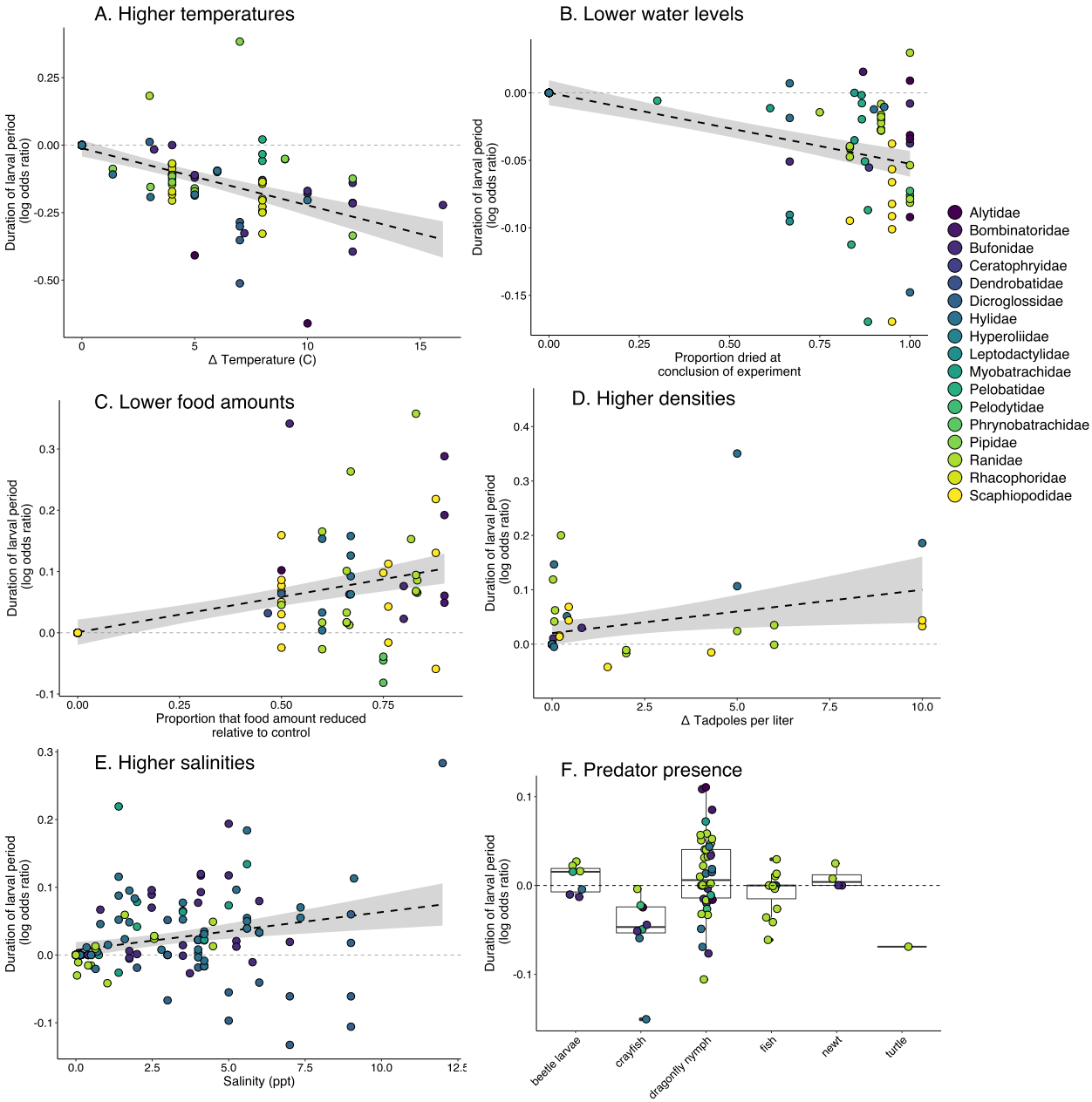

Fig. 4 Duration of larval period for each of the six environments included in the meta-analysis. LOR data are shown along with the model-fit trend line, depicting the relationship between phenotype and treatment severity or type (dashed line). Shaded area around the trend line indicates the 95% confidence interval. Points are colored according to family and because multiple studies often use the same species, any given species can have more than one point on the plot. Horizontal dashed lines indicate no difference from the control. Duration above zero indicates longer larval period than control treatments whereas below zero indicates shorter larval period than control treatments.

study and Ruthsatz et al. (2018) found that temperature affects metamorph mass, whereas Sinai et al. (2022) only found a significant decrease in metamorph snout-vent length, but not mass. Our study also supports prior findings that growth rate is less plastic than larval duration in response to different constant temperatures (Ruthsatz et al. 2018; Sinai et al. 2022). Several studies suggest this could be because tadpoles must reach a minimal size to begin metamorphosis (Wilbur and Collins 1973; Werner 1986; Ruthsatz et al. 2018). However, the fact that metamorph mass is affected more than larval duration by lowering water levels, lowering food rations, and increasing densities casts doubt on this explanation.

Two meta-analyses (Tejedo et al. 2010; Richter-Boix et al. 2011) found that some species in drying habitats had decreased body mass at metamorphosis and, to a lesser degree, increased developmental rates (e.g., shortened the duration of the larval period). Our results

are consistent with this finding and indicate a greater effect of lower water levels on mass than on larval duration (Fig. 2B). Importantly, Richter-Boix et al. generated predictions about expected outcomes given selection on either growth or development. Specifically, if the size at metamorphosis is under stronger selection, increases in developmental rates should be matched or exceeded by increases in growth rates whereas if developmental rates are under stronger selection, increases in developmental rates should occur at the expense of growth (Richter-Boix et al. 2011). In our meta-analysis, we observed reductions in mass at metamorphosis with shortened larval duration in the lower water level and higher temperature environments (Fig. 2), suggesting that accelerating development was prioritized at the expense of growth in these environments, which corroborates prior research (Alford 1999). Given that warming temperatures and changes in drought and hydroperiods are expected to accelerate in the coming decades, it may be that species that exhibit the greatest degree of plasticity in developmental rates may fare better than less plastic species (Levis and Pfennig 2019).

Predator presence altered the timing and size of metamorphosis in variable ways, which corroborates findings from previous syntheses on the effect of predation on larval development. Because the presence of a predator can signal an increase in the risk to the developing larvae (Orrock et al. 2008), tadpoles are expected to balance the presumed trade-off between avoiding consumption and acquiring resources to grow to an optimal size at metamorphosis (Werner 1986; Richardson et al. 2022). Our findings corroborate the findings of two previous predator-focused reviews that found, in contrast to the predictions of optimization-based models, that the presence of non-lethal predators either had no effect or a positive effect on metamorph size or duration of the larval period (Benard 2004; Relyea 2007). These studies noted imbalances in the identity of predators used, which we also observed with dragonfly nymphs as the disproportionately represented predator (Supplemental Fig. 7). Importantly, our findings indicate that less-studied predators, such as crayfish and turtles, could have a large impact on the size and timing of metamorphosis, which has important implications for determining how invasive species, such as rusty crayfish (*Oronectes rusticus*) and red-eared slider turtles (*Trachemys scripta elegans*), may influence native ecosystems through direct or indirect predator interactions.

A previous review of anurans and saltwater suggests that saltwater exposure during larval stages slows growth and disrupts development (Hopkins and Brodie 2015). Our findings confirm that higher salinities tend to reduce mass at metamorphosis (Fig. 3E) and elongate the larval period (Fig. 4E). These effects are likely due to the energetic cost of maintaining homeostasis in osmotically stressful environments. However, given that saltwater is highly lethal to amphibians (Hopkins and Brodie 2015; Albecker and McCoy 2017), we expected that higher salinities would generate stronger responses in developmental plasticity relative to other environments. However, the effects of salinity on metamorph mass and duration of the larval period were mild compared to those in other environments (except for predator presence; Fig. 2). Contrary to our initial expectations, the lack of a response relative to other environments may be due to the high lethality of saltwater. Specifically, the number of data points rapidly declined as salinity increased (Fig. 3E and Fig. 4E). More individuals survived metamorphosis at lower salinities, but there was only a small effect on the size and duration of the larval period at these salinities. Thus, lower salinities incur less mortality and may not be stressful enough to drive strong changes in metamorphic phenotypes.

Previous studies have shown links between the effects of high densities and low food quantities on larval plasticity (Emerson 1986; Tejedo et al. 2000; Relyea and Hoverman 2003; Tarvin et al. 2015), and our findings show that these environments induce similar metamorphic responses (e.g., a longer larval duration and reduced mass at metamorphosis). However, our results contrast with a meta-analysis that investigated the effects of resources on the size and timing of metamorphosis (Tejedo et al. 2010). While Tejedo et al. also observed a larger mass at metamorphosis in higher resource environments, they reported shorter larval durations in resource-restricted environments, whereas we found longer larval durations. Discrepancies may derive from differences in the criteria used to define "resource level" or in the number or identity of studies included (they include data from 17 experiments, whereas we include data from 23). This remains an open area of inquiry, although efforts are underway to unravel the relationship between food availability and anuran development, and how local adaptation can mediate these relationships (Manenti et al. 2023).

Phylogeny is weakly linked to variation in developmental plasticity among species

Our study is the first to phylogenetically examine interspecific developmental plasticity differences in the timing and size of metamorphosis under various environmental conditions. Overall, we found limited evidence that phylogeny influences the degree and direction of developmental plasticity in response to environmental variations. This is consistent with the

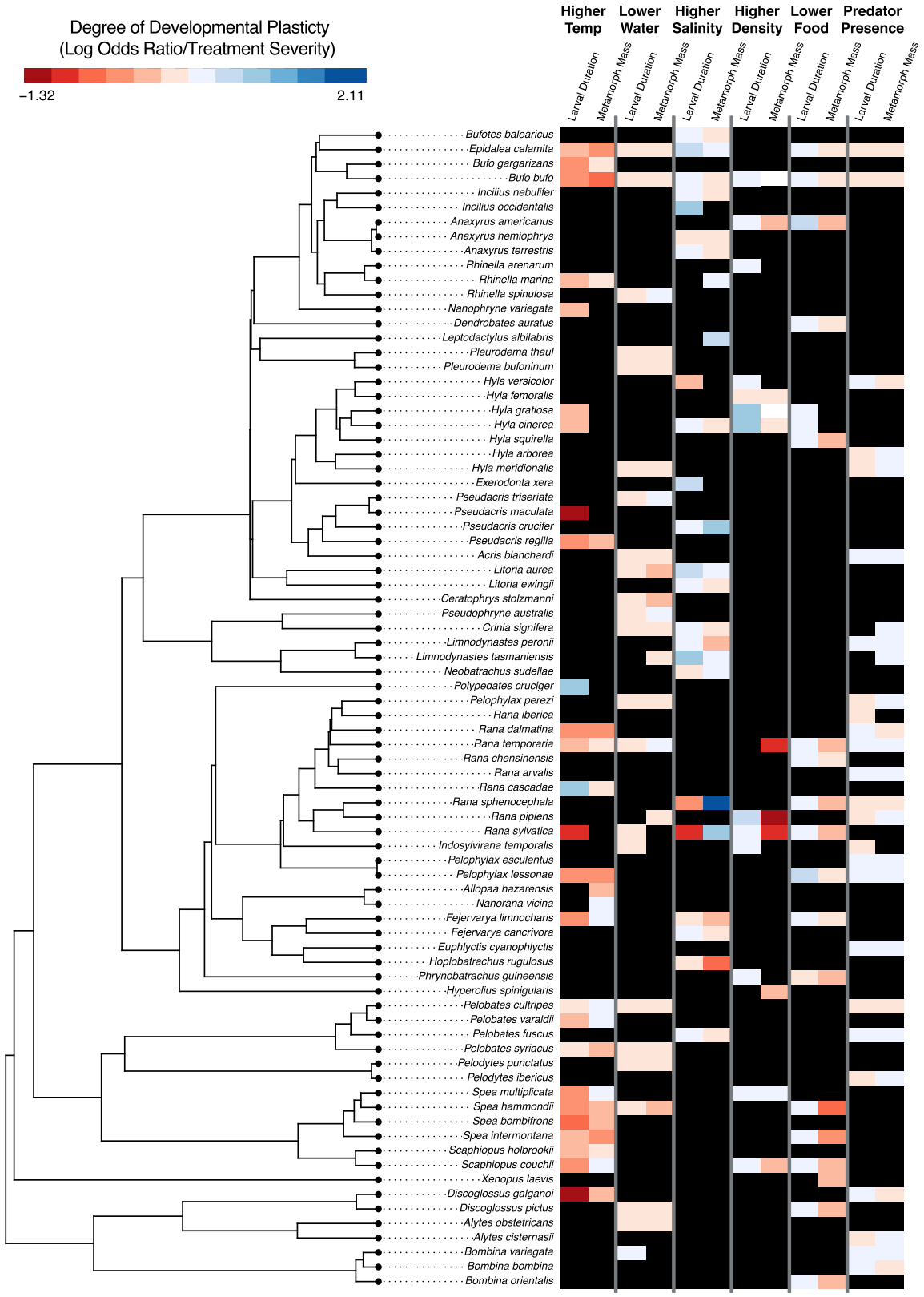

Fig. 5 A phylogenetic heat map showing species' averages in the degree and direction of developmental plasticity (corrected for treatment severity) of larval duration and metamorph mass in response to each of the six environmental treatments. Darker colored matrix cells represent greater averages in the degree of developmental plasticity (corrected for treatment severity), with blue colors indicating longer larval durations and larger metamorphs and red colors indicating shorter larval durations and smaller metamorphs. Black cells indicate that no data are available for that species and treatment.

Table 3 Estimates of phylogenetic signal and results from phylogenetic signal hypothesis test. Significant tests are bolded.

	Phenotype	N (species)	Phylogenetic signal (Blomberg's K)	*P*-value
Higher temperature	**Larval period duration**	**26**	***K* = 0.419**	***P* = 0.036**
	Metamorph mass	22	$K = 0.154$	$P = 0.564$
Lower water level	Larval period duration	23	$K = 0.358$	$P = 0.426$
	Metamorph mass	**22**	***K* = 0.574**	***P* = 0.037**
Higher salinity	Larval period duration	23	$K = 0.319$	$P = 0.373$
	Metamorph mass	23	$K = 0.423$	$P = 0.200$
Higher density	Larval period duration	13	$K = 0.328$	$P = 0.391$
	Metamorph mass	11	$K = 0.237$	$P = 0.842$
Lower food amount	Larval period duration	19	$K = 0.285$	$P = 0.559$
	Metamorph mass	18	$K = 0.517$	$P = 0.124$
Predator presence	**Larval period duration**	**25**	***K* = 0.295**	***P* = 0.044**
	Metamorph mass	25	$K = 0.141$	$P = 0.382$

minimal phylogenetic signal in numerous measures of anuran developmental plasticity in response to predation (Relyea et al. 2018), temperature (Sinai et al. 2022), and developmental plasticity in *Arabidopsis* (Pollard et al. 2001; Pigliucci et al. 2003). We found phylogenetic signal of developmental plasticity was only significant in three cases: larval period duration plasticity in response to temperature and predator presence, and metamorph mass plasticity in response to lowering water levels. Our results contradict Sinai et al. (2022), which found no evidence that phylogenetic relatedness affected plasticity response to temperature in amphibian tadpoles (mostly anurans and some caudate species). However, given that we found a weak but significant phylogenetic signal in the phenotypic response to only a few environmental conditions, our overall results indicate that phylogenetic relatedness is poorly associated with anuran developmental plasticity, at least for these species, phenotypes, and environments.

Interspecific variation in life-history traits may be better than phylogenetic relatedness at explaining species variation in developmental plasticity (Cayuela et al. 2017). For example, species associated with ephemeral habitats can accelerate development more than species associated with permanent habitats when water levels are reduced (Richter-Boix et al. 2011). Additionally, a reduced capacity for developmental rate plasticity in response to temperature has been observed in populations from warmer temperatures (Ruthsatz et al. 2018; Agudelo-Cantero and Navas 2019; Pottier et al. 2022) and latitude (Sinai et al. 2022). Variations in these or other traits that were not included in our study may be important predictors of interspecific variations in developmental plasticity. Future studies that examine developmental plasticity variation while incorporating ecological and life-history traits in a phylogenetic context could directly test whether such traits are more closely associated with developmental plasticity.

We offer a few important caveats that temper our interpretation of the limited phylogenetic differences in developmental plasticity. First, although we provide an important synthesis of developmental plasticity variation, this meta-analysis included only 1% of all 7566 anuran species, 8.5% of anuran genera (39 of 461), and 31% of anuran families (17 of 54; Amphibiaweb, 2023). In most cases, the average developmental plasticity of a species was calculated from a single study, and not all species and genera were exposed to the same experimental conditions (e.g., indoor laboratory conditions versus outdoor mesocosms). Furthermore, species chosen for experimental studies are usually, by design, capable of tolerating laboratory conditions, and often share similar life-history traits (e.g., large clutch size). Thus, despite the notable coverage of genera and families analyzed here, strong biases (including geographic) may exist in the species represented. For example, certain species including *Rana temporaria*, *Epidalea calamita*, and *Rana sylvatica* were represented more commonly than other species (Supplemental Fig. 10). Therefore, we caution against over-generalizing these results to taxa with life histories, geographic distributions, or physiologies distinct from the species within this meta-analysis. Despite these limitations to the interpretation of our phylogenetic results, the collection of experimental data presented here serves as an important springboard for future work interested in developmental plasticity variation among clades and species.

Further research is needed to determine how developmental plasticity affects fitness outcomes

Developmental plasticity may increase fitness and be shaped by selection, in which case it is considered adaptive (Ghalambor et al. 2007; Touchon et al. 2015). For example, the embryos of some tree frog species can hatch early if a predator is detected (Warkentin 2005). In contrast, plasticity in size at metamorphosis or the duration of larval period can have no effect or a negative effect on anuran juvenile and adult life stages (Smith 1987; Altwegg and Reyer 2003; Chelgren et al. 2006; Van Allen et al. 2010; Earl and Whiteman 2015; Tarvin et al. 2015; Bredeweg et al. 2019; Sinsch et al. 2020; Thompson and Popescu 2021; Zeitler et al. 2021). For instance, Gomez-Mestre et al. (2010)exposed two species to different temperatures and food amounts and observed similar effects on metamorph size and larval duration as reported here but found no carry-over effects on post-metamorphic locomotor abilities or performance. Identifying whether plasticity in metamorphic traits confers a fitness benefit or cost is an ongoing area of inquiry, as very few studies have investigated traits beyond metamorphosis. In our assembled dataset, only 26 of the 124 studies (21%) reported data on post-metamorphic performance, morphology, or behavior. However, a 2015 meta-analysis collated data from studies that investigated whether metamorph size and larval duration predicted fitness outcomes (Earl and Whiteman 2015). They reported that, in general, variation in these phenotypes did not clearly predict post-metamorphic fitness, but that size at metamorphosis was a better predictor of fitness than larval duration (Earl and Whiteman 2015). Compensatory growth, in which growth during the juvenile stages can compensate for differences in size at metamorphosis, is common among amphibians and may explain some of the variation in overall fitness (Metcalfe and Monaghan 2001). When placed in the context of our own findings, four of the six environments (higher density, lower food amount, lower water level, and higher temperature) reduced metamorph mass to some degree, which suggests that developmental plasticity in response to these environments may reduce post-metamorphic fitness. However, this remains a conjecture given the unclear role of post-metamorphic compensatory growth and its link to overall fitness. Terminating studies at metamorphosis hampers our ability to parse out the contributions of adaptive and non-adaptive processes and thus remains an important target for future studies, especially for those environmental qualities that will change over the coming century (Li et al. 2013).

Our meta-analysis showed that the environment not only affected the size and timing of metamorphosis, but also the relationship between size and larval duration. For instance, lower water levels caused these metamorphic phenotypes to decouple, such that the mass was smaller (reduced growth), while the duration of the larval period was also shorter (accelerated development; Fig. 2B). Cell differentiation (development) produces opportunities for cell proliferation (growth) (Denver, 1997, 2013). Decoupling growth and development can lead to differences in post-metamorphic morphology due to allometric differences in growth (also called heterochrony; (Emerson 1986; Glennemeier and Denver 2002; Rose 2005; McCoy et al. 2007; Tejedo et al. 2010; Fabrezi 2011; Goldberg et al. 2019); however, the extent to which decoupling these phenotypes affects adult fitness and performance is uncertain. Finally, the differences in development may not be as obvious as those in metamorph size and larval period duration. Whereas most studies assess development relying on external whole-body markers (e.g., Gosner stages, (Gosner 1960), subdermal differences in tissue and organ development, such as gonadal or pronephric tissues, may likewise affect post-metamorphic outcomes (Glennemeier and Denver 2002; McCoy et al. 2007; Fabrezi et al. 2010).

Conclusion

Global climate change is expected to have a significant impact on anurans. The larval life stage can affect lifetime fitness and population dynamics; however, despite an abundance of studies, we lack a collective, comparative understanding of how different environments affect the size and timing of metamorphosis. Our study provides a synthesis of developmental plasticity in response to numerous environmental conditions, showing variation in the degree and direction of developmental plasticity in relation to the type of environmental change as well as the severity of environmental change. We also provide a first look at how phylogenetic relationships affect developmental plasticity across a range of environmental contexts; however, increased phylogenetic representation and intraspecific study replication are needed. Future studies should focus on the fitness consequences of plasticity, both within and across life stages, especially in response to environmental changes associated with global climate change, as well as how interactive effects across multiple environmental conditions alter developmental plasticity.

Acknowledgments

We thank members of the WoLab for thoughtful discussion and insights in the development of this project.

Funding

This work was funded by Utah Agricultural Experimental Station Project (UTA01574) and start up funds from Utah State University awarded to MCW and NSF PRFB 2109599 awarded to SMS.

Supplementary data

Supplementary Data available at *ICB* online.

Conflicts of interest

The authors declare no conflicts of interest.

Data availability

Data and code are available through Dryad archive (https://doi.org/10.5061/dryad.t4b8gtj6s).

References

Agudelo-Cantero GA, Navas CA. 2019. Interactive effects of experimental heating rates, ontogeny and body mass on the upper thermal limits of anuran larvae. J Therm Biol 82:43–51.

Akram A, Rais M, Lopez-Hervas K, Tarvin RD, Saeed M, Bolnick DI, Cannatella DC. 2021. An insight into molecular taxonomy of bufonids, microhylids, and dicroglossid frogs: first genetic records from Pakistan. Ecol Evol 11:14175–216.

Albecker MA, McCoy MW. 2017. Adaptive responses to salinity stress across multiple life stages in anuran amphibians. Front Zool 14:40.

Alford RA. 1999. Ecology: resource use, competition and predation. In: Rw MRA, editors. Tadpoles: the biology of anuran larvae. Chicago Il: University of Chicago Press. p. 240–78.

Altwegg R, Reyer HU. 2003. Patterns of natural selection on size at metamorphosis in water frogs. Evolution 57:872–82.

AmphibiaWeb. 2023. University of California, Berkeley, California. https://amphibiaweb.org (accessed 10 February 2023). Google Scholar

Bates D, Maechler M, Bolker B, Walker S. 2014. Lme4: linear mixed-effects models using Eigen and S4.

Benard MF. 2004. Predator-Induced Phenotypic Plasticity in Organisms with Complex Life Histories. Annu Rev Ecol Evol Syst 35:651–73.

Blomberg SP, Garland T, Jr, Ives AR. 2003. Testing for phylogenetic signal in comparative data: behavioral traits are more labile. Evolution 57:717–45.

Blouin MS, Brown ST. 2000. Effects of temperature-induced variation in anuran larval growth rate on head width and leg length at metamorphosis. Oecologia 125:358–61.

Bredeweg EM, Urbina J, Morzillo AT, Garcia TS. 2019. Starting on the Right Foot: carryover Effects of Larval Hydroperiod and Terrain Moisture on Post-metamorphic Frog Movement Behavior. Front Ecol Evol 7:97.

Cayuela H, Joly P, Schmidt BR, Pichenot J, Bonnaire E, Priol P, Peyronel O, Laville M, Besnard A. 2017. Life history tactics shape amphibians' demographic responses to the North Atlantic Oscillation. Glob Change Biol 23:4620–38.

Chang B-H, Hoaglin DC. 2017. Meta-Analysis of Odds Ratios: current Good Practices. Med Care 55:328–35.

Chelgren ND, Rosenberg DK, Heppell SS, Gitelman AI. 2006. Carryover aquatic effects on survival of metamorphic frogs during pond emigration. Ecol Appl 16:250–61.

Collet J, Fellous S. 2019. Do traits separated by metamorphosis evolve independently? Concepts and methods. Proc Biol Sci 286:20190445.

Denver RJ. 1997. Proximate mechanisms of phenotypic plasticity in amphibian metamorphosis. Am Zool 37:172–84.

Denver RJ. 2013. Neuroendocrinology of amphibian metamorphosis. Curr Top Dev Biol 103:195–227.

Earl JE, Semlitsch RD. 2013. Carryover effects in amphibians: are characteristics of the larval habitat needed to predict juvenile survival? Ecol Appl 23:1429–42.

Earl JE, Whiteman HH. 2015. Are Commonly Used Fitness Predictors Accurate? A Meta-analysis of Amphibian Size and Age at Metamorphosis. Copeia 103:297–309.

Emerson SB. 1986. Heterochrony and frogs: the relationship of a life history trait to morphological form. Am Nat 127: 167–83.

Fabrezi M, Quinzio SI, Goldberg J. 2010. The ontogeny of Pseudis platensis (Anura, Hylidae): heterochrony and the effects of larval development on postmetamorphic life. J Morphol 271:496–510.

Fabrezi M. 2011. Heterochrony in growth and development in anurans from the Chaco of south America. Evol Biol 38:390–411.

Ghalambor CK, McKay JK, Carroll SP, Reznick DN. 2007. Adaptive versus non-adaptive phenotypic plasticity and the potential for contemporary adaptation in new environments. Funct Ecology 21:394–407.

Gilman SE, Urban MC, Tewksbury J, Gilchrist GW, Holt RD. 2010. A framework for community interactions under climate change. Trends Ecol Evol 25:325–31.

Glennemeier KA, Denver RJ. 2002. Developmental changes in interrenal responsiveness in anuran amphibians. Integr Comp Biol 42:565–73.

Goldberg J, Quinzio SI, Cruz JC, Fabrezi M. 2019. Intraspecific developmental variation in the life cycle of the Andean Treefrog (Boana riojana): a temporal analysis. J Morphol 280:480–93.

Gomez-Mestre I, Saccoccio VL, Iijima T, Collins EM, Rosenthal GG, Warkentin KM. 2010. The shape of things to come: linking developmental plasticity to post-metamorphic morphology in anurans. Journal of Evolutionary Biology 23:7.

Gosner KL. 1960. A simplified table for staging anuran embryos and larvae with notes on identification. Herpetologica 16: 183–90.

Hamman EA, Pappalardo P, Bence JR, Peacor SD, Osenberg CW. 2018. Bias in meta-analyses using Hedges' d. Ecosphere 9:e02419.

Harmon LJ, Weir JT, Brock CD, Glor RE, Challenger W. 2008. GEIGER: investigating evolutionary radiations. Bioinformatics 24:129–31.

Herbert ER, Boon P, Burgin AJ, Neubauer SC, Franklin RB, Ardón M, Hopfensperger KN, Lamers LPM, Gell P. 2015. A

global perspective on wetland salinization: ecological consequences of a growing threat to freshwater wetlands. Ecosphere 6:1–43.
Hof C, Araújo MB, Jetz W, Rahbek C. 2011. Additive threats from pathogens, climate and land-use change for global amphibian diversity. Nature 480:516.
Hofmann S, Masroor R, Jablonski D. 2021. Morphological and molecular data on tadpoles of the westernmost Himalayan spiny frog Allopaa hazarensis (Dubois & Khan, 1979). ZooKeys.
Hopkins GR, Brodie JED. 2015. Occurrence of amphibians in saline habitats: a review and evolutionary perspective. Herpetological Monographs 29:1–27.
Lenth R. 2018. Emmeans: Estimated Marginal Means, aka Least-Squares Means. R package. See https://CRAN R-project org/package = emmeans.
Levis NA, Pfennig DW. 2019. Phenotypic plasticity, canalization, and the origins of novelty: evidence and mechanisms from amphibians. In: Seminars in cell & developmental biology Academic Press, United Kingdom.
Li Y, Cohen JM, Rohr JR. 2013. Review and synthesis of the effects of climate change on amphibians. Integr Zool 8:145–61.
Manenti R, Kristensen N, Cogliati P, Barzaghi B, Melotto A, Ficetola GF. 2023. Larval development and poor trophic resource availability: local adaptations and plasticity in a widespread amphibian species. J of Evolutionary Biology.36:529–41,
McCoy KA, McCoy MW, Amick A, Guillette LJ, Jr, St Mary CM. 2007. Tradeoffs between somatic and gonadal investments during development in the African clawed frog (Xenopus laevis). J Exp Zool 307A:637–46.
Metcalfe NB, Monaghan P. 2001. Compensation for a bad start: grow now, pay later? Trends Ecol Evol 16:254–60.
Moran NA. 1994. Adaptation and constraint in the complex life cycles of animals. Annu. Rev. Ecol. Syst. 25:573–600.
Orrock JL, Grabowski JH, Pantel JH, Peacor SD, Peckarsky BL, Sih A, Werner EE. 2008. Consumptive and nonconsumptive effects of predators on metacommunities of competing prey. Ecology 89:2426–35.
Pechenik JA. 2006. Larval experience and latent effects—metamorphosis is not a new beginning. Integr Comp Biol.46:323–33,
Pennell MW, Eastman JM, Slater GJ, Brown JW, Uyeda JC, FitzJohn RG, Alfaro ME, Harmon LJ. 2014. Geiger v2.0: an expanded suite of methods for fitting macroevolutionary models to phylogenetic trees. Bioinformatics 30:2216–8.
Pigliucci, Pollard Cruzan. 2003. Comparative studies of evolutionary responses to light environments in Arabidopsis. Am Nat 161:68.
Pollard H, Cruzan M, Pigliucci M. 2001. Comparative studies of reaction norms in Arabidopsis. I. Evolution of response to daylength. Evolutionary Ecology Research 3:129–55.
Pottier P, Lin H-Y, Oh RRY, Pollo P, Rivera-Villanueva AN, Valdebenito JO, Yang Y, Amano T, Burke S, Drobniak SM et al. 2022. A comprehensive database of amphibian heat tolerance. Sci Data 9:600.
Pyron RA. 2014. Biogeographic analysis reveals ancient continental vicariance and recent oceanic dispersal in amphibians. Syst Biol 63:779–97.
Relyea RA, Hoverman JT. 2003. The impact of larval predators and competitors on the morphology and fitness of juvenile treefrogs. Oecologia 134:596–604.
Relyea RA, Stephens PR, Barrow LN, Blaustein AR, Bradley PW, Buck JC, Chang A, Collins JP, Crother B, Earl J et al. 2018. Phylogenetic patterns of trait and trait plasticity evolution: insights from amphibian embryos. Evolution 72:663–78.
Relyea RA. 2007. Getting out alive: how predators affect the decision to metamorphose. Oecologia 152:389–400.
Revell LJ. 2012. phytools: an R package for phylogenetic comparative biology (and other things). Methods Ecol Evol 3:217–23,
Richardson EL, White CR, Marshall DJ. 2022. A comparative analysis testing Werner's theory of complex life cycles. Functional Ecology 36:1986–2000.
Richter-Boix A, Tejedo M, Rezende EL. 2011. Evolution and plasticity of anuran larval development in response to desiccation. A comparative analysis. Ecol Evol 1:15–25.
Rose CS. 2005. Integrating ecology and developmental biology to explain the timing of frog metamorphosis. Trends Ecol Evol 20:129–35.
Ruthsatz K, Peck MA, Dausmann KH, Sabatino NM, Glos J. 2018. Patterns of temperature induced developmental plasticity in anuran larvae. J Therm Biol 74:123–32.
Salimi S, Almuktar SAAAN, Scholz M. 2021. Impact of climate change on wetland ecosystems: a critical review of experimental wetlands. J Environ Manage 286:112160.
Schiesari L, Peacor SD, Werner EE. 2006. The growth-mortality tradeoff: evidence from anuran larvae and consequences for species distributions. Oecologia 149:194–202.
Sinai N, Glos J, Mohan AV, Lyra ML, Riepe M, Thöle E, Zummach C, Ruthsatz K. 2022. Developmental plasticity in amphibian larvae across the world: investigating the roles of temperature and latitude. J Therm Biol 106:103233.
Sinsch U, Leus F, Sonntag M, Hantzschmann AM. 2020. Carry-over effects of the larval environment on the post-metamorphic performance of Bombina variegata (Amphibia, Anura). Herpetol J 30:3.
Smith DC. 1987. Adult recruitment in chorus frogs: effects of size and date at metamorphosis. Ecology 68:344–50.
Smith-Gill SJ, Berven KA. 1979. Predicting Amphibian Metamorphosis. Am Nat 113:563–85.
Smith-Gill SJ. 1983. Developmental plasticity: developmental conversion versus phenotypic modulation. Am Zool 23:47–55.
Tarvin RD, Silva Bermúdez C, Briggs VS, Warkentin KM. 2015. Carry-over effects of size at metamorphosis in red-eyed treefrogs: higher survival but slower growth of larger metamorphs. Biotropica 47:218–26.
Team, R Core. 2018. R: A language and environment for statistical computing.
Tejedo M, Marangoni F, Pertoldi C, Richter-Boix A, Laurila A, Orizaola G, Nicieza AG, Álvarez D, Gomez-Mestre I. 2010. Contrasting effects of environmental factors during larval stage on morphological plasticity in post-metamorphic frogs. Clim. Res. 43:31–9.
Tejedo M, Semlitsch RD, Hotz H, McEachran JD. 2000. Covariation of Morphology and Jumping Performance in Newly Metamorphosed Water Frogs: effects of Larval Growth History. Copeia 2000:448–58.
Thompson CM, Popescu VD. 2021. Complex hydroperiod induced carryover responses for survival, growth, and endurance of a pond-breeding amphibian. Oecologia 195:1071–81.

Touchon JC, McCoy MW, Landberg T, Vonesh JR, Warkentin KM. 2015. Putting μ/g in a new light: plasticity in life history switch points reflects fine-scale adaptive responses. Ecology 96:2192–202.

Urban MC, Richardson JL, Reidenfelds NA. 2014. Plasticity and genetic adaptation mediate amphibian and reptile responses to climate change. Evol Appl 7:88–103.

Van Allen BG, Briggs VS, McCoy MW, Vonesh JR. 2010. Carry-over effects of the larval environment on post-metamorphic performance in two hylid frogs. Oecologia 164: 891–8.

Walls SC, Barichivich WJ, Brown ME. 2013. Drought, deluge and declines: the impact of precipitation extremes on amphibians in a changing climate. Biology 2:399–418.

Warkentin KM. 2005. How do embryos assess risk? Vibrational cues in predator-induced hatching of red-eyed treefrogs. Anim Behav 70:59–71.

Werner EE. 1986. Amphibian metamorphosis: growth rate, predation risk, and the optimal size at transformation. Am Nat 128:319–41.

Werner EE. 1988. Size, Scaling, and the Evolution of Complex Life Cycles. In: Size-Structured Populations Springer Berlin, Heidelberg. p. 60–81.

West-Eberhard MJ. 2003. Developmental plasticity and evolution. Oxford, England: Oxford University Press.

Whitman DW, Agrawal AA. 2009. What is phenotypic plasticity and why is it important?In: Whitman DW, Ananthakrishnan TN, editors. Phenotypic plasticity of insects Enfield, NH: Science Publishers. p. 1–63.

Wilbur HM, Collins JP. 1973. Ecological aspects of amphibian metamorphosis: nonnormal distributions of competitive ability reflect selection for facultative metamorphosis. Science 182:1305–14.

Wilbur HM. 1980. Complex Life Cycles. Annu Rev Ecol Syst 11:67–93.

Zeitler EF, Cecala KK, McGrath DA. 2021. Carryover effects minimized the positive effects of treated wastewater on anuran development. J Environ Manage 289: 112571.