An Acad Bras Cienc (2024) 96(2): e20230671 DOI 10.1590/0001-3765202420230671
Anais da Academia Brasileira de Ciências | *Annals of the Brazilian Academy of Sciences*
Printed ISSN 0001-3765 I Online ISSN 1678-2690
www.scielo.br/aabc | www.fb.com/aabcjournal

ANIMAL SCIENCE

Effects of temperature on growth, development, and survival of amphibian larvae: macroecological and evolutionary patterns

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Abstract: Temperature affects the rate of biochemical and physiological processes in amphibians, influencing metamorphic traits. Temperature patterns, as those observed in latitudinal and altitudinal clines, may impose different challenges on amphibians depending on how species are geographically distributed. Moreover, species' response to environmental temperatures may also be phylogenetically constrained. Here, we explore the effects of acclimation to higher temperatures on tadpole survival, development, and growth, using a meta-analytical approach. We also evaluate whether the latitude and climatic variables at each collection site can explain differences in species' response to increasing temperature and whether these responses are phylogenetically conserved. Our results show that species that develop at relatively higher temperatures reach metamorphosis faster. Furthermore, absolute latitude at each collection site may partially explain heterogeneity in larval growth rate. Phylogenetic signal of traits in response to temperature indicates a non-random process in which related species resemble each other less than expected under Brownian motion evolution (BM) in all traits, except survival. The integration of studies in a meta-analytic framework allowed us to explore macroecological and macroevolutionary patterns and provided a better understanding of the effects of climate change on amphibians.

Key words: acclimation, metamorphosis, tadpoles, body size, temperature size-rule, climate change.

INTRODUCTION

Most of the ecological and physiological processes of ectotherms can rapidly change in response to their body temperature, leading to alterations in development and behavior (Huey & Stevenson 1979). The intraspecific temperature-size rule (TSR) predicts that ectotherms reared at higher temperatures tend to have faster growth rates, shorter development times, and attain smaller sizes than their conspecifics raised at lower temperatures (Angilletta & Dunham 2003, Atkinson 1994, Ruthsatz et al. 2018, Verberk et al. 2021). Accelerated development and growth can imply physiological and metabolic costs for ectotherms (Gomez-Mestre et al. 2013), and as a result, tadpoles can suffer oxidative stress and experience a significant increase in the activity of antioxidant enzymes (Gomez-Mestre et al. 2013). This oxidative stress could lead to even more severe costs, including reduced longevity and delayed age of sexual maturation (Gomez-Mestre et al. 2013).

However, although we assume that all ectotherms are strongly dependent on environmental temperature, response patterns can be quite contrasting. In amphibians, larval period for *Rhacophorus moltrechti* increases at warmer temperatures and decreases at cooler temperatures (Chang et al. 2014), whereas in *Bufo gargarizans* the opposite occurs, with warmer temperature resulting in a shorter larval period (Ren et al. 2021). Considering the current knowledge gap regarding most amphibian species and their thermal physiology, it is essential to understand whether there are general response patterns to environmental temperature, particularly when assessing which taxa are most vulnerable to the climate change (Katzenberger et al. 2021).

Identifying these response patterns is a complex challenge that requires a multidisciplinary approach, since there are multiple factors that can lead to heterogeneity in temperature responses among species. Some studies show that magnitude and direction of species response to temperature may be related to conservatism in temperature-dependent physiological and life history characteristics, resulting in niche similarity between phylogenetically related species (Araújo et al. 2013, Bodensteiner et al. 2020, Losos 2008). In this case, the greater the degree of relatedness among species fewer phenotypic, ecological, and physiological differences are expected between them (Blomberg et al. 2003, Losos 2008). For amphibians, conservatism in cold and heat tolerance tends to be asymmetric, with greater lability in cold tolerance, which generally varies intra- and interspecifically, while heat tolerance tends to be highly conserved within clades (Araújo et al. 2013).

Throughout the evolutionary process, organisms may also have experienced adaptation to extreme temperatures (Bozinovic et al. 2011, Buckley & Huey 2016, Denny et al. 2009, Kingsolver et al. 2011). Hence, species' thermal tolerance range may limit potential responses to temperature changes (Freitas et al. 2010, Pinsky et al. 2019). The negative impacts of climate change should be more accentuated in climatically specialized species with low adaptive potential (Stillman 2003). Moreover, for species living at environmental temperatures close or above their optimum, any small increase in temperature should disproportionately affect them, leading to sharp declines in thermal performance and Darwinian fitness (Pörtner & Knust 2007, Tewksbury et al. 2008). This is the case of low-latitude ectotherms, which tend to experience relatively higher mean temperatures and lower seasonal variation in environmental temperature (Ghalambor et al. 2006, Huey et al. 2009). If it is confirmed that they present limited acclimation responses (Huey et al. 2009), then adaptative rescue may be less likely to occur than in their higher-latitude counterparts (Souza et al. 2019).

Time required for thermal adaptation, and hence niche evolution, is still poorly understood (Losos 2008). If evolutionary responses and thermal adaptation occur at slower rates than environmental changes (slow niche evolution rate), then species may not be able to persist, particularly in a changing environment (Duarte et al. 2012). However, species that show rapid niche evolution may need relatively few generations to adjust and persist in the current climate change scenario. Moreover, phenotypic plasticity allows organisms to adjust their allocation of resources in response to environmental cues, promoting changes in their traits (Atkinson & Thompson 1987, Denver, 2021). When phenotypic plasticity increases the fitness of organisms and the chance of persistence in a new environment, it can be considered adaptive (Dey et al. 2016, Huang & Agrawal 2016) and, in a longer time scale, it can also represent the climatic niche evolution of a species (Diniz-Filho et al. 2019, Rangel et al. 2018, Wiens et al. 2010).

For amphibian larvae, traits such as development and growth may have potential to exhibit phenotypic plasticity in the face of changing environmental conditions (Kulkarni et al. 2011, Ruthsatz et al. 2018, Tejedo et al. 2010). Here, we explore the effects of acclimation to experimentally induced higher temperatures on tadpole survival, development, and growth, using a meta-analytical approach. Specifically, we evaluate the existence of a latitudinal cline regarding the effects of experimentally increased temperatures on the development and growth of amphibian larvae. We expect that species closely related present similar responses to environmental temperature (Blomberg et al. 2003, Losos 2008), as observed in other physiological traits (Duarte et al. 2012, Gutiérrez-Pesquera et al. 2016), and that these responses follow the temperature-size rule. Considering that extreme local temperatures can drive the evolution of specific thermal windows and thus contributing to species' thermal adaptation (Angilletta 2009, Bozinovic et al. 2011), we also assessed whether species' response to temperature is more related to niche conservatism regarding past climate (Mid Holocene) or to thermal extremes experienced in recent times (since pre-industrial period). This could provide an understanding of whether species have had time to respond to the current climate change scenario, while also assessing their adaptive potential and vulnerability to global warming.

MATERIALS AND METHODS

Data Collection

We performed systematic searches in three databases (Google Scholar, Scopus, and ISI Web of Science) in July 2021, using the following key terms: "larval development" OR "larval growth" OR "larval survival" AND "temperature" OR "thermal stress" AND "tadpoles" OR "larval amphibians" AND "amphibians". Studies that complied with the following eligibility criteria were included in our database: 1) assessed the effect of temperature on development and survival of amphibian larvae, in a laboratory setting, providing data on at least one of the following variables - survival, time to hatching, time to metamorphosis, growth rate, mass, and length; 2) tested at least two constant rearing temperatures, representing contrasting treatments; 3) presented mean, standard deviation or standard error and sample size for the response variables of all treatments.

For each study, we retrieved sampling location where the tadpoles were collected (latitude, longitude, and country), taxonomic classification (species, genus, family and order), following (Frost 2022), life-stage at collection (adult/larva/egg masses), and during trials - when response variables were collected (survival, time to hatching, time to metamorphosis, growth rate, body mass, and total length), and test temperatures (treatment and control). Body mass and total length were used as proxies to size. The variable days to hatch was not used for the calculation of effect size and meta-regression because it was present in only four studies. Studies that presented data for more than one population, species, or collection site (41 of 45 studies included in the meta-analysis) had such information recorded as independent effect sizes. For studies that presented results in graphs, we used GetData Graph Digitizer software (*version 2.26*) to extract the data.

Climatic variables

We evaluated how the development and survival of tadpoles are affected by the current and historical climate in the location where the population was collected using climate data with a spatial resolution of 2.5 arc minutes obtained from the Ecoclimate database (Lima-Ribeiro et al. 2015). This dataset includes simulations for current climate (1950-1999), pre-industrial climate (~1760), and Middle Holocene (6ky) (Lima-Ribeiro et al. 2015). To account for variation between different global circulation models (GCMs) (Varela et al. 2015), we averaged climate projections from three different GCMs: Community Climate System Model (CCSM); National Center for Meteorological Research (CNRM) and Max Planck Institute of Meteorology (MPI). For each period, we extracted maximum environmental temperature and thermal range for the wettest quarter (Supplementary Material - Table SI available at https://doi.org/10.7910/DVN/V1WOKT). The wettest quarter was defined as the three wettest consecutive months and represents the period in which a breeding peak is more likely to occur. Furthermore, we calculated the effect of magnitude of higher temperatures tested in relation to both the maximum environmental temperature and the acclimation temperature. The magnitude in relation to acclimation was calculated by subtracting the temperature used as treatment (high temperatures) from the acclimation temperature, and the magnitude in relation to the environment was calculated by subtracting the temperature used as treatment (high temperature) by the maximum environmental temperature.

Effect size

To obtain an estimate of effect size and sampling variation for each study, we used the standardized mean difference (Cohen's d) for each response variable. We applied a correction for small sample bias (Hedges 1981) and estimated the effect size through the corrected standardized mean difference (Hedges' g). Negative effect sizes indicate a reduction in days to metamorphosis, size, growth rate, and survival of larvae and embryos. We used the *metafor* R package (Viechtbauer 2010) to conduct these analyses.

Meta-analytical random effects model and heterogeneity analysis

For studies that presented more than one individual comparison, either due to the use of more than one population, species or the same control for multiple treatments, we adjusted multilevel phylogenetic meta-analytic models using variation between studies, the relationship between species and the grouping of study-level effect sizes as random effects (Nakagawa & Santos 2012). We used a Brownian motion-process (Lajeunesse 2009) to estimate a variance-covariance matrix that represents the phylogenetic relationships between species.

Heterogeneity in effect sizes was explored through multilevel phylogenetic meta-regressions using absolute latitude, the magnitude of the higher temperatures tested in relation to both the maximum environmental temperature and acclimation temperature and climate data (maximum environmental temperature and thermal range) related to each period (present, pre-industrial and Mid-Holocene) as moderating variables. For this, we generated 19 eligible models for each response variable from the combination of moderating variables with a minimum limit of zero (null model) until the maximum of five variables in a single model (Table SII available at https://doi.org/10.7910/DVN/V1WOKT). As there is a high correlation between the same climate variable in different time periods (present, pre-industrial and Mid-Holocene), we generated models considering the effect of each period separately (Table SIII available at https://doi.org/10.7910/DVN/V1WOKT). Models were then compared using the Akaike Information Criterion corrected for small samples (AICc, Burnham & Anderson 2002) and their respective weights using the R package *MuMIn* (Bartón 2022). The meta regressions are performed using *metafor* R package (Viechtbauer 2010).

Phylogenetic signal

Based on Jetz & Pyron's (2018) amphibian phylogeny (Supplementary Material – Figure S1 available at https://doi.org/10.7910/DVN/V1WOKT), we obtained phylogenetic trees containing only the species with available data for each analysis. We assessed whether trait response to temperature presented a phylogenetic signal by calculating the K statistic from Blomberg et al. (2003). We represented the species' phylogenetic covariance as their phylogenetic relationship, which assumes a Brownian motion of evolution. For each trait, its response was determined as the standardized mean difference (SMD) between treatment (acclimation temperature) and control groups. These analyses were performed using *picante* (Kembel et al. 2010), *ape* (Paradis et al. 2004), and *phytools* (Revell 2012) R packages.

Publication bias

Evidence considered in meta-analytic studies may not be a representative sample of all available data on the subject, leading to inaccurate estimates of effect sizes (Koricheva et al. 2013). For example, significant results are more likely to be published than non-significant results (Møller & Jennions 2001). Hence, we verified the existence of publication bias using both the Egger test, which determines whether the funnel plot is asymmetrical or not (Egger et al. 1997) and the Trim and Fill method ("RO" estimator), which indicates how many missing studies are needed for the funnel plot to be symmetrical and whether the inclusion of these studies alters the significance of the result (Duval & Tweedie 2000). We used the *metafor* R package (Viechtbauer 2010) to conduct these analyses. All analyses were performed using the R software (R core team 2022).

RESULTS

The initial bibliography search returned 24,558 articles from the above-mentioned platforms. We filtered by title and abstract and obtained 196 articles, of which 45 articles were from Web of Science, 51 from Scopus, and 67 from Scholar. After filtering from full text and applying the eligibility criteria, this number was further reduced to 45 articles (Figure 1), resulting in 236 comparisons that evaluated the effect of higher constant temperatures on the survival and development of larvae and embryos of 45 amphibian species (Table SI). Data for Gymnophiona and Caudata is largely underrepresented. The amphibian species belongs to 18 families and is distributed in 16 countries, mainly in the temperate region (Figure 2).

General effects of temperature on biological traits

We found that days to metamorphosis reduces at higher constant temperatures (Hedges g = -4.729, [95% CI: -8.283, -1.176], p = 0.010), whereas no effect was detected on larval survival (Hedges g = 0.432 [95% CI: -0.388, 1.253], p = 0.288), growth rate (Hedges g = 1.026 [95% CI: -2.339, 4.390], p = 0.537) and size (Hedges g = -0.463 [95% CI: -1.179, 0.253], p = 0.202, Figure 3, Table I). Heterogeneity among effect sizes was mostly attributed to between-study variation and less to the grouping of comparisons at study level, with a contribution of the phylogenetic relationship between species only relevant for growth rate (Table II).

Meta-regression

We report the results of the best (lowest AICc) meta-regression model for each trait (Table III). The best model for growth rate indicated that species from high latitudes tend to have a lower growth rate in response to acclimation temperature (Hedges g = -0.221 [95% CI =

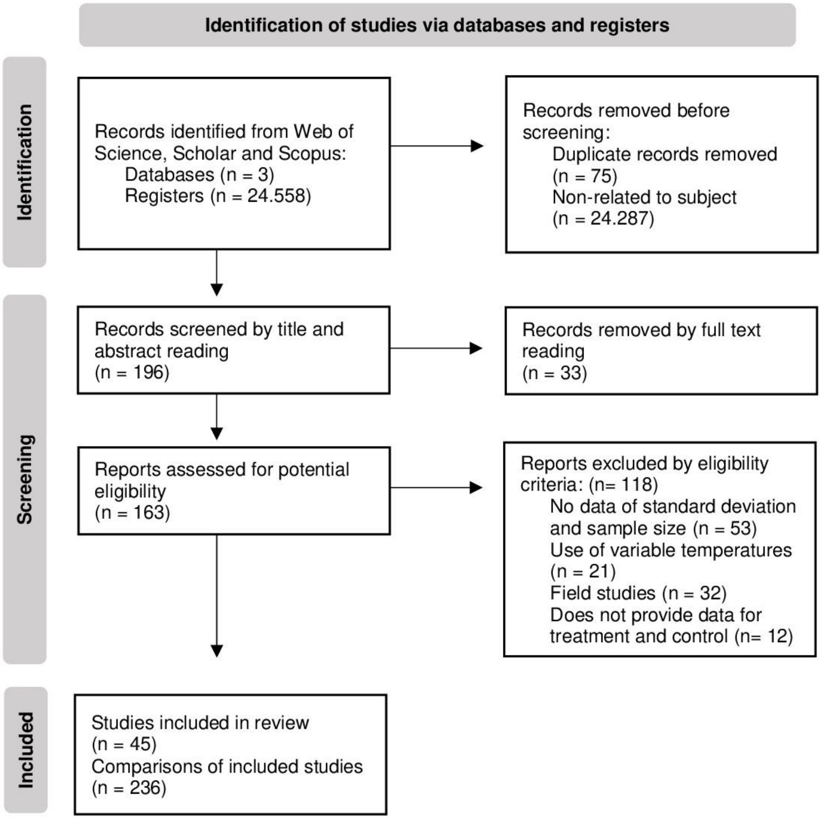

Figure 1. **PRISMA diagram representing the selection process of the studies included in the meta-analysis.**

-0.419, -0.024], AICc = 111, ω = 0.112. Table III), while species from low latitudes tend to have higher growth rate in response to temperature. For the other characteristics, such as size and survival, models with significant moderators can be viewed in Table SII. No moderators were significantly important in explaining changes in days to metamorphosis in response to acclimation temperature (Table III).

Phylogenetic signal

For size ($K = 0.246$, $p = 0.013$), growth rate ($K = 0.375$, $p < 0.001$), and days to metamorphosis ($K = 0.226$, $p < 0.001$), trait response to temperature indicates a non-random process in which related species resemble each other less than expected under Brownian motion (BM) evolution, for the considered phylogenetic tree. However, for survival ($K = 0.813$, $p = 0.380$) we found no support that a non-random process is occurring, thus this trait's response to temperature appears to follow BM evolution (Figure 4, Table IV).

Publication bias

Egger's test indicated that the funnel plot is not symmetrical for studies that assessed days to metamorphosis ($t = 4.717$, $p < 0.001$, df = 57), growth rate ($t = -2.660$, $p = 0.013$, df = 27), and larval size under experimental temperatures ($t = 2.800$, $p < 0.001$, df = 101), suggesting potential publication bias. For studies that assessed survival, the funnel plot was symmetric ($t = -0.211$, $p = 0.835$, df = 23, Supplementary Material - Figure S2 available at https://doi.org/10.7910/DVN/V1WOKT). To achieve funnel plot symmetry, the Trim and Fill method suggests the addition of two studies on the right side for days to metamorphosis, and one on the right side for size, but their inclusion would not change the significance of the effect size (days to

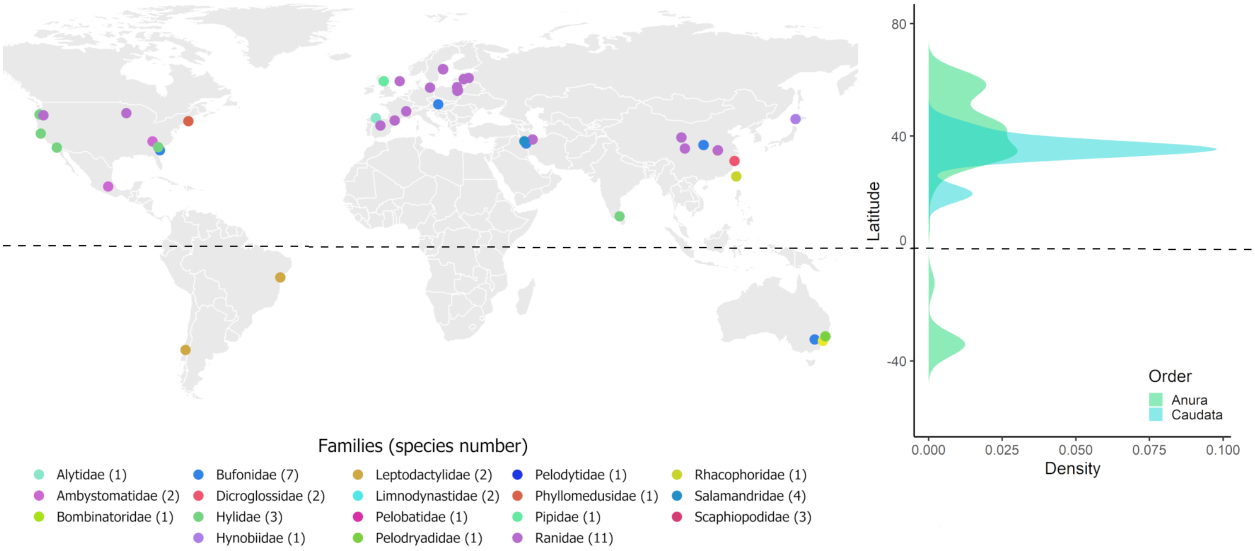

Figure 2. Geographic distribution of studies included in the meta-analysis. The graph represents the density of studies that evaluated the effect of temperature on the development and survival of amphibian larvae.

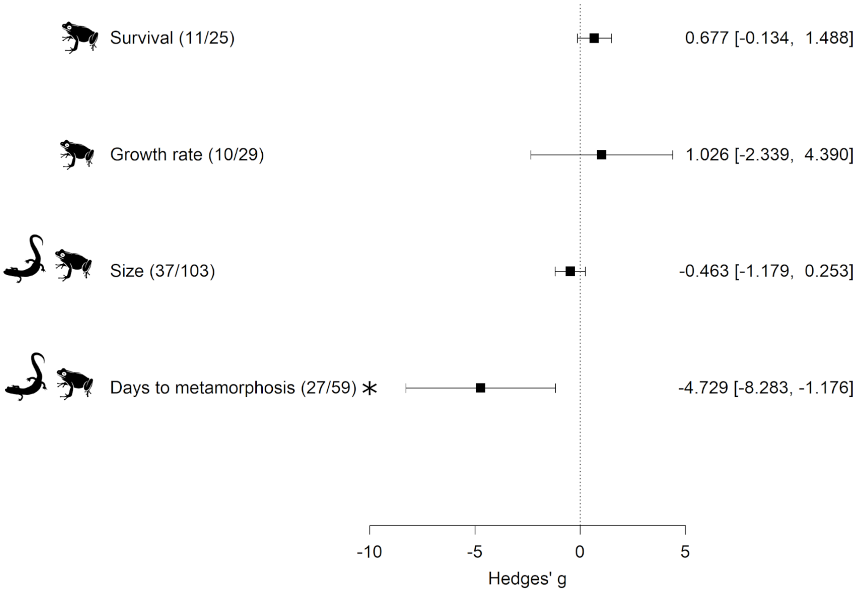

Figure 3. Temperature effect sizes on metamorphic traits of the larval amphibians. Mean g-hedge values and 95% confidence interval are displayed on the right side (asterisks indicate statistical significance). On the left side, the number of studies and individual comparisons for each variable, respectively, are presented. Confidence intervals that touch the dotted line indicate no temperature effect. The variables that have data for Anura and Caudata are those that have stickers from the representatives of the two groups.

metamorphosis, 95% CI = -6.000, -0.690; larval size, 95% CI = -1.182, 0.373). For growth rate, the Trim and Fill method indicates that no study is missing, suggesting a result contrary to that found using the Egger Test.

DISCUSSION

Temperature dictates the rates of several biochemical and physiological processes in amphibians, affecting, for example, the time to metamorphosis and the total length of tadpoles reared under higher temperatures (Angilletta 2009, Goldstein et al. 2017, Khas et al. 2019, McDiarmid & Altig 1999). Our results provide

Table I. Effect of temperature on metamorphic traits. Standardized effect size (Hedges g) of temperature on metamorphic characteristics of amphibian larvae. df = degrees of freedom; SE = Standard deviation.

Variable	Estimate	SE	df	T value	P value	CI 95% lower	CI 95% upper	logLik	AICc
Survival	0.677	0.393	23	1.724	0.098	-0.134	1.488	-38.734	87.573
Growth rate	1.026	1.643	27	0.624	0.537	-2.339	4.390	-65.327	140.393
Size	-0.463	0.361	101	-1.283	0.202	-1.179	0.253	-225.259	458.930
Days to metamorphosis	-4.729	1.775	58	-2.664	0.010	-8.283	-1.176	-170.279	349.312

Table II. Heterogeneity in effect size. Measures of heterogeneity for each metamorphic trait studied. df = degrees of freedom.

Variable	Q	df	P value	T^2 between studies	T^2 cluster-study	T^2 phylogenetic	I^2 total
Survival	83.983	23	< 0.001	0.777	< 0.001	< 0.001	0.777
Growth rate	571.926	27	< . 0001	0.445	0.171	0.374	0.990
Size	804.036	101	< .0001	0.756	0.212	< 0.001	0.968
Days to metamorphosis	858.888	58	< .0001	0.796	0.029	0.169	0.994

evidence that the effects of acclimation to higher temperatures affect the tadpoles development, resulting in reduced days to metamorphosis, whereas growth rate, size and survival were not significantly affected. Previous assessments also indicated that most amphibian populations develop faster at higher temperatures (Tejedo et al. 2010, Ruthsatz et al. 2018). Hence, current literature points that tadpoles’ age at metamorphosis (i.e. time to metamorphosis) is quite labile in response to temperature (Blouin & Brown 2000, Chen et al. 2021, Gomez-Mestre et al. 2010, Ruthsatz et al. 2018, Tejedo et al. 2010).

The rate of development is more strongly impacted by the effect of temperature than the rate of growth (Hayes et al. 1973). This is probably due to the fact that species need a minimum size and a specific threshold of thyroid hormones to achieve metamorphosis, however, probably there is no minimum or maximum larval time before a metamorphosis (Gomez-Mestre et al. 2010, Morey & Reznick 2000). In addition, some authors emphasize that the asymmetric sensitivity in the growth and development rate may be related to the differential effects of temperature on anabolism and catabolism, as they affect the development rate more strongly than the growth rate (Angilletta & Dunham 2003, Gomez-Mestre et al. 2010, Walters & Hassall 2006). Moreover, we observed that growth rate response to acclimation is lower in species that currently experience higher maximum environmental temperatures, suggesting that some species have reduced growth rate lability. These asymmetric responses between days to metamorphosis and growth rate result in the generally observed pattern of tadpoles that are raised at higher temperatures tend to metamorphose earlier but with a smaller body size (Atkinson 1994).

For tadpoles, the main triggers for metamorphosis are thyroid hormones (TH) produced by the thyroid gland (Denver 2021, Laudet 2011, Ruthsatz et al. 2018, Tata 2008). When growing in a stressful environment (e.g. tadpoles growing in a shallow, heated pond about to dry out), the neuroendocrine stress axis is activated by increasing the production of

Table III. Effect of latitude and climatic predictors. Best model for each metamorphic trait according to the lowest AICc. To visualize the complete list of models, see Table SII. df = degrees of freedom, W = weight; SE = Standard error.

Variables	Moderators	Estimate	SE	T value	df	P value	CI 95% Lower	CI 95% Upper	AICc	W
Development time	Intercept	-29.875	30.636	-0.975	43	0.335	-91.659	31.909	286.500	0.524
	Absolute latitude	0.377	0.739	0.510	43	0.613	-1.114	1.867		
	Maximum temperature 1999	0.992	1.230	0.806	43	0.425	-1.489	3.473		
	Thermal Range 1999	-0.304	0.881	-0.345	43	0.732	-2.080	1.472		
	Trail magnitude	-0.300	1.320	-0.228	43	0.821	-2.962	2.362		
	Environmental magnitude	0.794	1.204	0.659	43	0.513	-1.635	3.222		
	Absolute latitude:Maximum temperature 1999	-0.010	0.033	-0.301	43	0.765	-0.076	0.057		
	Absolute latitude:Thermal Range 1999	0.007	0.018	0.368	43	0.715	-0.030	0.044		
	Absolute latitude:Trail magnitude	-0.008	0.035	-0.236	43	0.815	-0.080	0.063		
	Absolute latitude:Environmental magnitude	-0.007	0.031	-0.233	43	0.817	-0.071	0.056		
Size	Intercept	-5.331	10.966	-0.486	83	0.628	-27.141	16.479	387.900	0.552
	Absolute latitude	0.224	0.270	0.830	83	0.409	-0.313	0.762		
	Maximum temperature 1999	0.093	0.375	0.247	83	0.806	-0.653	0.838		
	Thermal Range 1999	-0.090	0.358	-0.250	83	0.803	-0.801	0.622		
	Trail magnitude	0.425	0.516	0.824	83	0.412	-0.601	1.450		
	Environmental magnitude	0.394	0.386	1.021	83	0.310	-0.373	1.161		
	Absolute latitude:Maximum temperature 1999	-0.006	0.010	-0.591	83	0.556	-0.026	0.014		
	Absolute latitude:Thermal Range 1999	0.003	0.009	0.351	83	0.726	-0.014	0.020		
	Absolute latitude:Trail magnitude	-0.013	0.014	-0.944	83	0.348	-0.040	0.014		
	Absolute latitude:Environmental magnitude	-0.012	0.010	-1.174	83	0.244	-0.033	0.008		
Survival	Intercept	-4.420	3.288	-1.344	20	0.194	-11.278	2.439	84.700	0.107
	Absolute latitude	0.077	0.040	1.912	20	0.070	-0.007	0.161		
	Maximum temperature 6ky	0.089	0.091	0.979	20	0.339	-0.101	0.279		
	Thermal Range 6ky	0.025	0.080	0.309	20	0.761	-0.141	0.190		
	Trail magnitude	-0.047	0.039	-1.215	20	0.239	-0.127	0.034		
Growth Rate	Intercept	13.362	6.020	2.220	20	0.038	0.804	25.920	111.000	0.112
	Absolute latitude	**-0.221**	**0.095**	**-2.335**	**20**	**0.030**	**-0.419**	**-0.024**		
	Maximum temperature 6ky	-0.120	0.078	-1.540	20	0.139	-0.283	0.043		
	Thermal Range 6ky	-0.099	0.143	-0.695	20	0.495	-0.398	0.199		
	Environmental magnitude	0.058	0.076	0.771	20	0.450	-0.099	0.216		

stress hormones (Denver 2021). These hormones interact with TH, increasing its production (Denver 2009, 2021, Wilbur & Collins 1973). Thus, increasing temperature can affect the intensity of TH production (Ceusters et al. 1978) and accelerate the arrival of metamorphosis, as demonstrated for the studies included in our review (Blouin & Brown 2000, Chen et al. 2021, Gomez-Mestre et al. 2010).

The acceleration of tadpole's growth and development in warmer environments, potentially shortening the larval period, is a plastic response that demonstrates a remarkable acclimation capacity of the amphibian's larvae.

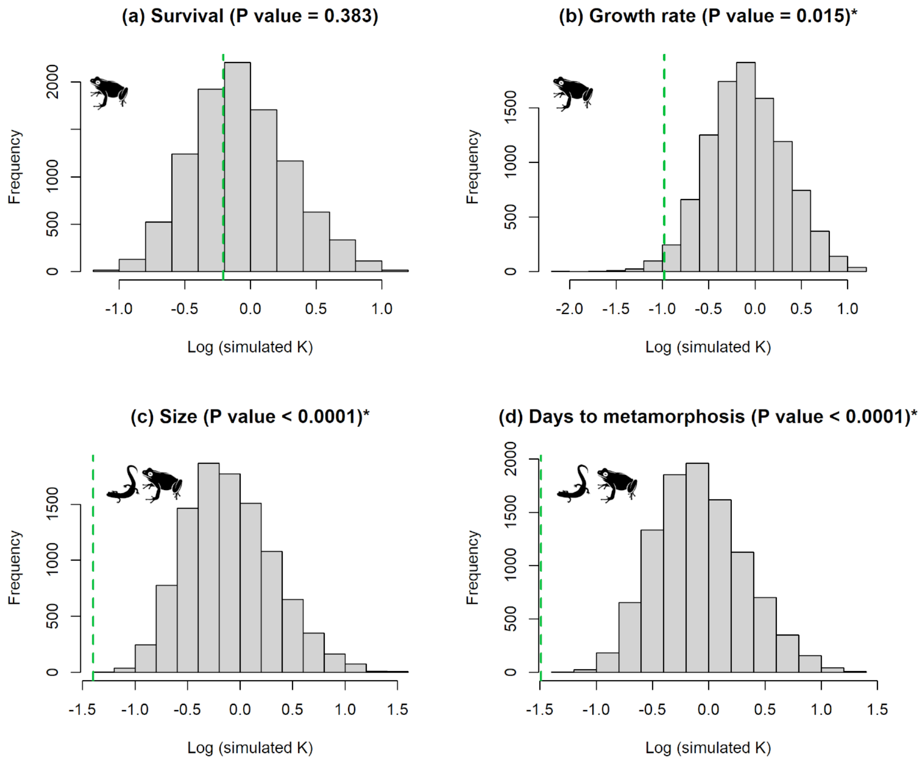

Figure 4. Distribution of expected values in a Brownian motion random evolution model for survival (a), growth rate (b), size (c), and days to metamorphosis(d). Green dashed lines represent observed K values. The variables that have data for Anura and Caudata are those that have stickers of the two groups.

Beyond alterations in growth rate and larval period, organisms can also acclimate their thermal breadth (Angilletta 2009), metabolism, and behavior (Dietz & Somero 1992, Terblanche et al. 2005) in response to higher temperatures. Therefore, thermal acclimation is a type of phenotypic plasticity that occurs within a generation and can help organisms to cope with rising temperatures (Rohr et al. 2018). The plastic response of reduction in body size for tadpoles may be beneficial in some cases, for example, accelerating the acclimation of metabolic rate and thermal tolerance (Rohr et al. 2018). Furthermore, tadpoles that metamorphose into smaller body sizes can escape the risk of desiccation at the pounds (Rohr et al. 2018). However, although plasticity in the time of metamorphosis is a way to persist under a stressful environment, it can result in some physiological and morphological costs for the larvae (DeVore et al. 2021, Gomez-Mestre et al. 2013, Burraco et al. 2022), reducing, for example, the survival rate of juveniles that metamorphose at smaller sizes and affecting sexual selection and adult reproductive success (Burraco et al. 2017, Gomez-Mestre et al. 2013, Hayes et al. 2010).

Temperature can also significantly affect the metabolism of tadpoles through its effects on rates of biochemical reactions, considering that ectotherms' metabolism rate depends mainly on body mass and body temperature (Gillooly et al. 2001). Furthermore, individuals that metamorphose earlier and with smaller body sizes tend to show greater changes in metabolic activity than individuals that metamorphose at a larger size and under a longer larval period (Pough & Kamel, 1984). In addition to an acute effect, temperature may also have chronic effects on tadpoles, particularly if temperature-related metabolic demands surpass the energy intake of organisms, resulting in a "metabolic meltdown" (Huey & Kingsolver 2019). In stressful

Table IV. **Phylogenetic signal for each metamorphic trait.**

Variable	Phylogenetic signal Blomberg's K	P value
Survival	0.813	0.3802
Growth rate	0.375	< 0.0001
Size	0.247	0.0151
Days to metamorphosis	0.226	< 0.0001

environments, such as exposure to warmer temperatures, ectotherms may reduce their metabolic rates (Marshall & McQuaid 2011), and therefore reduce "metabolic collapse", however, growth and reproduction will likely be slower (Huey & Kingsolver 2019).

Despite not observing a general effect of temperature in larvae growth rate, species from higher latitude have a lower growth rate in response to acclimation temperature than their lower latitude counterparts. The asymmetric effect of increasing temperature between regions may be related to the breadth of the organisms' thermal tolerance range (Freitas et al. 2010, Pinsky et al. 2019, Turriago et al. 2015). Species from temperate regions had to adapt to high climatic seasonality throughout their evolution (Buckley & Huey 2016), and therefore should have greater adaptive potential to climate change. On the other hand, ectotherms from low latitude tend to be more adapted to higher temperatures very close to their maximum physiological limits, reducing the likelihood of an evolutionary response (Bozinovic et al. 2011, Ghalambor et al. 2006, Janzen 1967, Sunday et al. 2014). A plethora of studies have demonstrated that the higher sensitivity of tropical species to increasing temperature appears to be comparable among different taxa, such as fish (Vinagre et al. 2016), ants (Diamond et al. 2012), and reptiles (Huey et al. 2009).

Climate change and the extent of its impacts can vary not only based on the likelihood of an evolutionary response for the species, but also with latitude (Root et al. 2003). The adverse effects of climate change are anticipated to be most pronounced in areas where temperature change is most significant (Root et al. 2003, Urban 2015), particularly in the tropics (IPCC 2022). As already known, the tropics are recognized for harboring a rich global diversity of ectotherms, including insects, reptiles, and amphibians, many of which can be highly sensitive to temperature increases (Deutsch et al. 2008, Diamond et al. 2012, Huey et al. 2009, Vinagre et al. 2016). Furthermore, the risk of extinction in response to climate change is expected to be higher in regions that harbor endemic species with small ranges (Urban 2015), such as South America, where 94% of amphibian species are endemic (Bolaños et al. 2008). Despite tropical species often displaying greater sensitivity to temperature changes compared to their temperate counterparts, the literature significantly underrepresents the tropical region, with most studies evaluated in this meta-analysis conducted on temperate species.

For three of the four traits studied (size, growth rate, and days to metamorphosis), response to temperature appears to vary more within related species than among species. This would indicate that adaptive evolution is uncorrelated with phylogeny. Another possible explanation is that some measurement error is lowering K and making closely related species appear less similar than what would be expected under Brownian motion (Blomberg et al. 2003). Since tree topology and branch lengths were obtained from a larger scale phylogeny with > 7000 amphibian species (Jetz & Pyron 2018), it is unlikely that these caused error in estimating K. Regarding the tip data, there are two major concerns. First, not all amphibian clades are well represented in the analysis, with few information for Caudata and none for Gymnophiona. Even within Anura, the most diverse clade, some families are underrepresented while others are not represented at all. This lack of clade representation may be artificially lowering K, as most available data comes from a few anuran families. Second, tested temperatures may differ among studies. Considering that thermal reaction norms usually are asymmetrical and skewed towards lower temperatures (Huey & Kingsolver 1989), the choice of acclimation temperatures may affect the tip data used, even after standardization. This may also explain our results for survival response to acclimation temperatures used for growth and development studies are usually within an optimal temperature range, whereas the negative effects of temperature on survival are more evident at extreme temperatures.

Asymmetry in the funnel plots can be caused by reporting biases, poor methodological quality, true heterogeneity, artefactual or even chance (see Egger et al. 1997 and Sterne et al. 2011 for full discussion). In our case, there is a clear latitude bias (reporting bias) associated with the species included in the available studies. Most of these studies report on temperate species from the northern hemisphere (see Figure 2), which is quite concerning considering that most amphibian species occur in tropical regions, such as the Amazon and the Atlantic Forests (Buckley & Jetz 2007). This indicates that our current understanding of the studied biological traits' response to acclimation temperature is largely based on a few species from regions with relatively low amphibian diversity. Moreover, true heterogeneity may have also contributed to the asymmetry in the funnel plots, as a major proportion of the variation found between studies. Considering that some studies compare more acclimation temperatures than others, perhaps the size of effect differs according to study size (Sterne et al. 2011). However, disentangling the effects of true heterogeneity and publication bias may only be possible in meta-analyses with very large datasets (Peters et al. 2010).

Finally, since we observed that part of the heterogeneity in trait response to temperature may be attributed to latitude (growth rate), perhaps there are other untested factors that may contribute to the observed heterogeneity. All studies included in the review evaluated the effect of constant temperature which does not reflect the daily temperature variation usually found in a natural environment. Moreover, the few studies representing the tropical region evaluated species that inhabit forest zones with more stable climates, but the tropics also hold biomes where daily temperature highly fluctuates (e.g. Caatinga and Cerrado). We also recognize that climatic pattern at large scales data do not accurately reflect the microclimatic variation faced by organisms in their natural environments and may have less explanatory power than microclimatic data (Katzenberger et al. 2018, Sheu et al. 2020, Woods et al. 2015). Despite the current limitations, exploring the existence of general patterns in the experimental response of anuran larvae to temperature using macroecological and macroevolutionary tools can help to achieve a better global understanding of the effects of climate change on species.

Assessing how temperature affects the survival, growth, and development of amphibians has been the focus of many studies over the last century, given that most species in the group have climate-dependent physiological and ecological characteristics. The results confirm that the acclimation to higher temperatures affects the tadpole's development, demonstrating that larvaes that develop at higher temperatures reach metamorphosis earlier. However, our review covers only 45 amphibian species, mostly from temperate regions, and shows a huge underrepresentation for Gymnophiona and Caudata. Therefore, further studies are needed to evaluate the effect of temperature on the development and survival of clades not yet represented. Much still needs to be explored so that we have concrete evidence that allows us to delineate the general patterns of the effect of temperature on these organisms. Only by properly integrating experimental results, ecology, and evolution will we be able to predict the impacts of climate change on biodiversity and try to mitigate some of them.

Data availability

The supplementary tables and figures of this study are available on Harvard Dataverse: https://doi.org/10.7910/DVN/V1WOKT

Acknowledgments

GA-F thanks Paula Caetano for all the discussions about the analyses used in this article. GA-F is also grateful for the Meta Analysis discipline taught by Professor Doctor Juliana de Almeida-Rocha in the post graduate program in Ecology and Biodiversity Conservation at the State University of Santa Cruz. This work was supported by the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior - Brasil (CAPES) [Finance code 001] through a Masters Scholarship to GA-F. DSF received a technological development scholarship from MCTIC/CNPq (Process 465610/2014-5).

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How to cite

ALVES-FERREIRA G, FORTUNATO DS, KATZENBERGER M, FAVA FG & SOLÉ AM. 2024. Effects of temperature on growth, development, and survival of amphibian larvae: macroecological and evolutionary patterns. An Acad Bras Cienc 96: e20230671. DOI 10.1590/0001-3765202420230671.

Manuscript received on June 19, 2023;
accepted for publication on February 23, 2024

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GA-F: conceptualization, data curation, formal analysis, investigation, methodology, software, validation, visualization, and writing—review and editing. DSF: conceptualization, formal analysis, investigation, methodology, software, project administration, supervision, validation, visualization, and writing—review and editing. MK: conceptualization, formal analysis, investigation, supervision, validation, visualization, and writing—review and editing. FGF and MS: project administration, supervision, validation, visualization, writing—review and editing. All authors contributed to the article and approved the submitted version.