

# Effects of hydroperiod on morphology of tadpoles from highland ponds

Thaíse Boelter · Fernanda Marcelia dos Santos · Leonardo Felipe B. Moreira · Cristina Stenert · Martin Reichard · Leonardo Maltchik

Received: 9 June 2020/Accepted: 19 September 2020/Published online: 6 October 2020 © Springer Nature B.V. 2020

**Abstract** Hydroperiod length has been identified as a major driver in community assembly in freshwater systems. Yet we generally lack an understanding of how morphological traits respond to water level decrease under natural conditions. Here, we studied variation in body size and shape in lateral view in tadpoles of *Scinax squalirostris* and *Odontophrynus americanus* inhabiting ponds in superhumid highland plateau in southern Brazil. Hydroperiod did not affect tadpole size in either species. In relation to body shape,

Handling Editor: Télesphore Sime-Ngando.

**Electronic supplementary material** The online version of this article (https://doi.org/10.1007/s10452-020-09799-1) contains supplementary material, which is available to authorized users.

T. Boelter  $\cdot$  F. M. dos Santos  $\cdot$  C. Stenert  $\cdot$ 

L. Maltchik (🖂)

Laboratório de Ecologia e Conservação de Ecossistemas Aquáticos, Universidade do Vale do Rio dos Sinos, UNISINOS, Av. Unisinos, 950, São Leopoldo, Rio Grande do Sul 93022-750, Brazil e-mail: maltchik@unisinos.br

- L. F. B. Moreira Instituto de Biociências, Universidade Federal de Mato Grosso, Cuiabá, Mato Grosso, Brazil
- M. Reichard

Institute of Vertebrate Biology, Czech Academy of Sciences, Brno, Czech Republic

*S. squalirostris* tadpoles from long hydroperiod ponds had shorter tails and deeper tail fins than tadpoles from other hydroperiods. Predator presence was positively associated with hydroperiod, restricting our ability to separate their effects on tadpoles morphology. For *O. americanus*, tadpole shape was not affected by pond hydroperiod. We demonstrated that, in natural environment, the influence of hydroperiod on tadpole morphology might depend on species-specific characteristics, such as behavior and life-history traits. Our results indicate that local context may lead to different effects of hydroperiod, and hydroperiod alone can only partly explain the variation on tadpole shape.

**Keywords** Amphibians · Life history · Araucaria moist forest · Pond drying · Plasticity

M. Reichard

Institute of Botany and Zoology, Faculty of Science, Masaryk University, Brno, Czech Republic

## Introduction

Hydroperiod duration (i.e., the length of aquatic phase) governs dynamics in the wetland abiotic conditions and affects presence, abundance and phenotypic responses of aquatic species (Baber et al. 2004; Székely et al. 2017). Because hydroperiod is often correlated with other aspects of environmental heterogeneity (i.e., pond area, aquatic plant structure, and predator presence), the interpretation of independent effects on community patterns is often hampered (see Knauth et al. 2018; Werner et al. 2007). In tadpoles, individuals of the same species can be found in a variety of freshwater habitats (temporary and permanent ponds, streams, lakes, rice fields, phytotelmata). Although tadpoles can actively select different depths and substrate types (Alford 1999; Melo et al. 2018), they do not have direct choice of the habitat where they occur and rely on breeding-site selection of their parents. Resulting variation in habitat use by tadpoles, along with hydroperiod constraints, can induce phenotype-environment matching whereby individuals develop to maximize their survival and ability to successfully metamorphose (Miner et al. 2005; Michel 2011). Speeding development to reach metamorphosis sooner is an example of plasticity that is directly related to trade-offs with the other aspects of life history. Individuals from populations under disturbances may allocate energy to a functional solution, increasing likelihood of survival in disturbed habitats. However, this reallocation comes at a cost of reducing energy to others functional attributes (Garland 2014; Merilä et al. 2000; Wellborn et al. 1996).

Organisms inhabiting dynamic systems (such as estuaries, floodplains and intermittent ponds) are often subjected to stochastic processes or strong seasonal variations (Ocock et al. 2014; Moreira et al. 2010, 2017; Ramalho et al. 2018). Hence, plasticity in traits related to development and behavior can be an important strategy to face environmental constraints, like water level and predators (Johnson et al. 2015; Amburgey et al. 2016). While factors associated with this plasticity are not well understood, body size and shape clearly respond to environmental variations. For amphibians, plasticity in response to environment was confirmed in controlled laboratory setting (Amburgey et al. 2016), but proven elusive under complex natural conditions (Grözinger et al. 2014). Plasticity may be constrained, for example, by the lack of underlying genetic background to reaction norms (Auld et al. 2010). Amphibians are a group with remarkable differences in life-history strategies, which can be measured by changes in the size and shape of body proportions. Thus, responses to environmental factors, even within species inhabiting the same area, may depend on behavior (Ocock et al. 2014), developmental rates (Rowe and Dunson 1995) or both (Van Buskirk 2000).

Studies with simulated hydroperiod have highlighted that pond drying is an important constraint on amphibian metamorphosis. Hydroperiod has major effect on the age and size at which tadpoles metamorphose, with the two traits not being necessarily correlated (Merilä et al. 2000; Amburgey et al. 2012). When the hydroperiod is long, individuals could delay metamorphosis until achieve larger sizes, so improving post-metamorphic survival (Nylin and Gotthard 1998; Rudolf and Rhödel 2007; Székely 2017). In temporary environments, species often faces a poor growth rate and metamorphosis should be accelerated (even at smaller sizes) to escape from aquatic poor environment conditions (Morey and Reznick 2000; Altwegg and Reyer 2003). However, accelerating development is costly. More rapid larval development in response to environmental stressors reduces survival of tadpoles and post-metamorphic individuals (Amburgey et al. 2016; Brannelly et al. 2019). Negative consequences are more likely detected in natural environments when tadpoles are challenged with a complex interaction between multiple simultaneous stressors-challenges of hydroperiod constraints (i.e., desiccation) and biotic interactions (i.e., predation risk, competition). Tadpole shape variation between individuals of same species is attributed to several factors, such as local abiotic factors, predators, diseases and convergent evolution (Vences et al. 2002; Buskirk 2009; Navarro-Lozano et al. 2018; Sherratt et al. 2018). For example, predator presence may cause a lower relative tail length (Vences et al. 2002), while decreasing water volume can induce shallower body shape and better tadpole swimming performance (Johansson et al. 2010). Trade-offs arising from body shape plasticity are less clear, but may involve the roles of swimming endurance, rapid escape response and maneuverability.

Compelling evidence demonstrates that tadpoles reduce interspecific competition by foraging at

different positions of the water column (Marques and Nomura 2015; Melo et al. 2018), and their body shape is directly related to microhabitat use (Altig and Johnston 1989; Both et al. 2011). For example, benthic tadpoles with dorso-ventrally depressed bodies and low fins are found mostly near the pond bottom. In contrast, nektonic species with deep tail fins and laterally compressed bodies live in open water and move through vegetation (Relyea 2004; Johnson et al. 2008). When pond hydroperiod is truncated tadpole can develop shorter and narrower tail fins (Richter-Boix et al. 2006). Changes in the water depth associated with shape changes might enhance overlap during foraging, which would have implication on interspecific competition (Rogers and Chalcraft 2008).

Here, we assessed natural variation in tadpole morphology of two amphibian species in highland ponds of southern Brazil. We considered changes in body size and shape for larvae of Scinax squalirostris (Hylidae; a nektonic tadpole) and Odontophrynus americanus (Odontophrynidae; a benthic tadpole). Explicitly, we explored whether tadpole size and shape are affected by hydroperiod when controlled by pond identity. We predicted tadpoles of a smaller size in ponds with short hydroperiod. Our prediction is derived from the scenario where tadpoles under drying conditions metamorphosed at a smaller size (Brannelly et al. 2019). For tadpole shape, we predicted that individuals in longer hydroperiods would have increased tail length and wider tail fins. By examining variability within a species, this work contributes to our understanding on how tadpoles allocate resources when faced with a stressor during development. Ultimately, our study may help to elucidate the possible effects of one of the most likely constraints for amphibians under climate change: reduction in the hydroperiod at breeding sites.

## Materials and methods

#### Study area and target species

The study was conducted in the Araucaria moist forest ecoregion, in a landscape formed by a mosaic of grasslands and Araucaria forest patches in the municipality of Bom Jesus, southern Brazil (See Figure S1). The region is a highland plateau (altitude  $\sim 1100$  m), with a temperate superhumid climate (Maluf 2000).

The rainfall distribution is uniform throughout the year, with annual rainfall 1500–1700 mm, without a marked dry season. Annual mean temperature is approximately 14 °C, although freezing temperatures may occur between April and November due to high altitude. Small ponds are common in the region and their hydrological regime is strongly influenced by precipitation and local evaporation. *Odontophrynus americanus* with benthic tadpoles is an explosive spring breeder, while *S. squalirostris* with nektonic tadpoles has continuous breeding activity and may overwinter at larval stage (Maneyro and Carreira 2012). Both species are common in the studied ponds (Knauth et al. 2018).

Sampling design and data collection

Eighteen ponds were sampled for the study (Figure S1). Ponds were < 1.5 ha in area (mean  $\pm$  S.D. 0.49  $\pm$  0.35 ha) and were always located at least 700 m apart. Ponds were assigned to one of three hydroperiod classes in the basis of monthly surveys (from September 2012 to October 2013): (1) six long-hydroperiod ponds, consisting of the ponds that neither desiccated nor reduced their surface area more than 50% of the maximum area recorded over the entire monitoring period; (2) six intermediate-hydroperiod ponds, consisting of the study; and (3) six short-hydroperiod ponds, consisting in those ponds that held water for < 3 months.

We collected tadpoles in three sampling periods (September 2012, November 2012, April 2013). Sampling was performed using a dipnet (30 cm wide, 250  $\mu$ m mesh). Eight sweeps (~ 1 m<sup>2</sup>) were taken per pond; four sweeps along the margins (~ 50 cm from the margin and 30 cm water depth) and four sweeps in the central part of the pond (1 m water depth). We anesthetized all collected tadpoles with benzocaine solution and fixed them in situ in 10% formaldehyde. We also assessed the composition of potential predatory fish were sampled using a 30 cm wide entomological net (frame dip-net) with 250  $\mu$ m diameter mesh. Each sample was represented by a 1 m sweep.

## Geometric morphometrics analyses

Only specimens between Gosner' stages 31 and 35 were measured for morphometric analyses, because it ensured that size was comparable across sites and sampling periods. All individuals with damaged tails were excluded. Size and shape analyses were derived from 86 individual tadpoles (55 *S. squalirostris* and 33 *O. americanus*; see Table S1 for details about sample size by site).

We took digital images of lateral view for each specimen using a digital camera (Canon Rebel T5i; 150 mm lens) mounted to a copy stand. A set of 22 landmarks was digitized from each image (Fig. 1). Of these, 13 landmarks were marked directly: (1) most anterior point of the body; (2) nostril; (3) the center of the eye; (4) most lateral point of the eye; (5) dorsal fin origin; (6) tip of the tail; (7) most anterior point of the proctodeal tube-ventral fin junction; (8) maximum ventral curvature of the body; (10) most posterior point of the oral disk-body junction; (11) most anterior point of the oral disk-body junction; (12) most dorsal point of the caudal musculature-body junction; (13) most anterior point of the axis of the tail myotomes (14) most ventral point of the caudal musculature-body junction. Nine landmarks were set to capture shape and were positioned between direct landmarks: (9) point between landmarks 8 and 10; (15) point of the dorsal tail fin at one-third of the distance between landmarks 5 and 6; (16) point of the dorsal tail fin at two-third of the distance between landmarks 5 and 6; (17) dorsal edge of the tail muscle located at the height of landmark 15; (18) dorsal edge of the tail muscle located at the height of landmark 16; (19) ventral edge of the tail muscle located at the height of landmark 17; (20) ventral edge of the tail muscle located at the height of landmark 18; (21) point located at the margin of the ventral tail fin at the height of landmark 19; (22) point located at the margin of the ventral tail fin at the height of landmark 20 (Fig. 1).

The configuration of landmarks was then digitized using tpsDig2 software, version 2.16 (Rohlf 2010). We applied a Generalized Procrustes Analysis (GPA) to standardize the size and align the configuration of landmark coordinates. Such approach enabled us to separate differences among landmarks configuration in two components—size (as centroid size) and shape (as GPA residuals) (Rohlf and Slice 1990; Cordeiro-Estrela et al. 2006). Alignment, estimation of centroid size and uniform component were performed using the geomorph package (Adams et al. 2019) in the R environment.

### Data analysis

We analyzed relationships between tadpole size and environmental features using linear mixed-effect models (LMM). Hydroperiod class (3 levels) was included in the model as fixed effect, and site identity was included as a random effect. Statistical significance was obtained using ANOVA function which employs a Wald Chi-Square Test. LMMs were computed using the lme4 package (Bates et al. 2015) in R.

We performed a principal component analysis (PCA) to summarize variation in shape space. Then, we used all PCA axes explaining at least 90% of shape variance for further analysis. Relationship between each shape component and hydroperiod was tested with linear mixed models. Fixed effect was



Fig. 1 Landmarks defined for geometric morphometric analysis

hydroperiod class, and site identity was included as a random effect. Ordinations in tangent space were computed using the geomorph (Adams et al. 2019) and Morpho (Schlager 2017) packages in R.

## Results

Five groups of predatory aquatic invertebrates were recorded in the study ponds: dragonfly naiads (Aeshnidae, Coenagrionidae and Libellulidae), water bugs (Belostomatidae) and water scavenger beetles (Hydrophilidae). Predatory fish were recorded in all hydroperiod classes, and all ponds with long hydroperiod had predatory fish. Predatory fish observed in the ponds were Hoplias malabaricus, Cnesterodon brevirostratus, Cnesterodon sp. and Phalloceros caudimaculatus. Table S1 summarizes predator occurrence and number of tadpoles measured by pond.

Neither S. squalirostris tadpole size (Wald  $X^2 = 1.102, d.f. = 2, p = 0.576$ ) nor O. americanus tadpole size (Wald  $X^2$ = 2.785, *d.f.* = 2, *p* = 0.248) displayed a significant relationship with pond hydroperiod. Two of the seven geometric shape components showed associations with pond hydroperiod for S. squalirostris (Table 1; depicted in detail in Figure S2). These two components together account for 6.6% of the variation in shape of S. squalirostris tadpoles. High values of principal component axis 4 (PC4) indicate a short tail and deeper ventral fins (Fig. 2). PC4 explained 4.8% of all shape variation. For PC7 (1.8% of variation), larger values indicate a shorter body and deeper upper fins (Fig. 3). Tadpole shape of O. americanus variation was not related to pond hydroperiod (Table 1).

## Discussion

Our results showed that hydroperiod was important for variation in tadpole morphology, but the effect of pond hydroperiod on naturally occurring variation was small. For S. squalirostris, tadpole shape in lateral view was influenced by hydroperiod. Surprisingly, hydroperiod did not affect tadpole size. Some amphibian species may have not variability in traits related to development. For them, the cost of developing in short hydroperiods can reduce post-metamorphic survival and fitness (Richter-Boix et al. 2011; Brannelly et al. 2019).

Mesocosm experiments had showed that responses in tadpole development vary among species when stressors (i.e., competitors and desiccation risk) are combined (Rowe and Dunson 1995; Boone et al. 2004; Purrenhage and Boone 2009) or not. Past studies coming directly from natural world seldom disentangle correlated effects of pond environmental heterogeneity and hydroperiod. But when these other aspects are explicitly disentangled, the independent effect of hydroperiod is small on amphibian communities (Werner et al. 2007; de Almeida et al. 2015; Valério et al. 2016). In this sense, our results reinforce the idea that hydroperiod alone can only partly explain the variation on tadpole shape. However, other factors might be inter- and counteracting hydroperiod effects. In highland ponds of southern Brazil, there is evidence that aspects of environmental heterogeneity (i.e., pond vegetation cover, aquatic predator composition, water depth) explain tadpole community dissimilarities and are not correlated with hydroperiod (Knauth et al. 2018).

Table 1 Results of mixed-
effect linear models on
measures of morphological
shape (partial warps) in two
tadpole species

	Scinax squalirostris				Odontophrynus americanus	
	Wald $X^2$	р	Estimate (SE)		Wald $X^2$	р
			Intermediate	Long		
PC1	2.354	0.308			0.414	0.812
PC2	0.182	0.912			0.498	0.779
PC3	2.451	0.303			4.788	0.092
PC4	5.680	0.048	0.012 (0.006)	0.018 (0.008)	0.166	0.921
PC5	0.456	0.796			4.454	0.108
PC6	0.883	0.642			2.804	0.246
PC7	17.495	< 0.001	0.014 (0.003)	0.013 (0.004)	0.496	0.783

Estimates are shown only for statistically significant effects



Fig. 2 Box plot illustrating shape component (PC4) and pond hydroperiod for tadpoles of *Scinax squalirostris*. White dots represent mean values. Shape component is illustrated at top

left, with black outline corresponding to high values of the component and gray outline corresponding to the average form



Fig. 3 Box plot illustrating shape component (PC7) and pond hydroperiod for tadpoles of *Scinax squalirostris*. White dots represent mean values. Shape component is illustrated at top

left, with black outline corresponding to high values of the component and gray outline corresponding to the average form

Empirical evidence has indicated that predator presence and reduced hydroperiod can induce more rapid development and metamorphosis at a smaller size (Van Buskirk 2000; Benard 2004; Relyea 2007; Grözinger et al. 2014; Amburgey et al. 2016), which may lead to post-metamorphic costs related to decreased condition and survival. Here, all ponds have invertebrate predators and predatory fish occurrence was highly skewed toward long hydroperiod ponds. The absence of effects of hydroperiod on tadpole size could be attributed jointly to distinct causes: (1) short ponds would not represent constraints for studied species; (2) presence of fish would counterbalance the benefits of more constant water levels. There is reliable information on larval development time for both species (metamorphosis at 2 months in S. squalirostris, and > 2 months in O. americanus (Eterovick and Sazima 2004; Maneyro and Carreira 2012), but only scarce and anecdotic data on variability in larval development time. A more detailed examination of hydroperiods shorter than 3 months may be instructive, because we did not register tadpoles in two ponds that lasting up to 40 days. One could expect that tadpoles from long hydroperiods metamorphosed later and at a larger size than tadpoles from drying ponds (Székely et al. 2017), but this is not always be the case and we have not measured developmental time in our study. But changes in hydroperiod can modify encounter rates with predators, even changing community interactions (Menge and Olson 1990; Gilman et al. 2010). So, the interplay between hydroperiod and tadpoles is additionally complicated by species-specific behavior and local pond characteristics, such as vegetation cover and substrate color. Although it is a challenging task, simultaneous tracking of morphology and behavior may offer a better picture on phenotypic plasticity of tadpoles.

Tadpoles of S. squalirostris had decreased tail length and deeper tail fins in response to longer hydroperiods. Long tail fins may act as a lure and distract predators, deflecting deadly strikes away from the body wall (Johnson et al. 2008). However, the effectiveness of defensive strategies is context dependent (Nomura et al. 2011), with plasticity associated with tail fin being more common in invertebratedominated ponds (Relyea 2007; Johnson et al. 2015). Costly investment to longer tails and its possible tradeoffs with other traits may also lead to departure of tadpole body shape from predicted shape characteristics. Many amphibian species recognize predator cues (visual, chemical, or physical), even during the early larval development (Ferrari et al. 2010; Warkentin et al. 2017). Large part of variation in tadpole shape was not related to pond hydroperiod and could be dependent on other site characteristic, showing flexibility related to local effects mainly on tail length and tail fin width. These results are in line with the idea that tadpoles can fine-tuning their strategies based environmental risk and previous experiences (Mitchell et al. 2016; Eterovick et al. 2020).

## Conclusions

In conclusion, we demonstrated that, in their natural environment, the influence of hydroperiod on tadpole morphology is species-specific, variable and lower than in experimental conditions. Our results indicate that hydroperiod alone can only partly explain the variation in tadpole shape. Although hydroperiod is commonly evoked to explain patterns of amphibian responses to biotic and environmental challenges, we show that local context is important and may lead to different outcomes. Future studies should address synergetic effects of local conditions on morphology and behavior, using a broader selection of tadpole ecotypes (i.e., neustonic, macrophagous, suspension feeder) to fill our current gaps in the understanding of the importance of local conditions on tadpole development.

Acknowledgements This study was funded by CNPq – Conselho Nacional de Desenvolvimento Científico e Tecnológico – (474892/2013-1) and Universidade do Vale do Rio dos Sinos - UNISINOS. We declare that data collection complied with current Brazilian laws (SISBIO 36365-2). All authors read and approved the final manuscript. We have no conflict of interest to declare.

**Data availability** The data for this study can be accessed upon request to the corresponding author.

#### Compliance with ethical standards

**Conflict of interest** The authors declare that there is no potential conflict of interest whatsoever, regarding the publication of this research article.

#### References

- Adams DC, Collyer ML, Kaliontzopoulou A (2019) Geomorph: software for geometric morphometric analyses. Evolution 73:2352–2367
- Alford RA (1999) Ecology: resource use, competition, and predation. In: McDiarmid RW, Altig R (eds) Tadpoles: the biology of anuran larvae. The University of Chicago Press, Chicago, pp 240–278

- Altig R, Johnston GF (1989) Guilds of anuran larvae: relationships among developmental modes, morphologies, and habitats. Herpetol Monogr 3:81–109
- Altwegg R, Reyer HU (2003) Patterns of natural selection on size at metamorphosis in water frogs. Evolution 57:872–882. https://doi.org/10.1111/j.0014-3820.2003. tb00298.x
- Amburgey S, Funk WC, Murphy M, Muths E (2012) Effects of hydroperiod duration on survival, developmental rate, and size at metamorphosis in Boreal Chorus Frog tadpoles (Pseudacris maculata). Herpetologica 68:456–467. https:// doi.org/10.1655/HERPETOLOGICA-D-11-00093
- Amburgey SM, Murphy M, Chris Funk W (2016) Phenotypic plasticity in developmental rate is insufficient to offset high tadpole mortality in rapidly drying ponds. Ecosphere 7:1–14. https://doi.org/10.1002/ecs2.1386
- Auld JR, Agrawal AA, Relyea RA (2010) Re-evaluating the costs and limits of adaptive phenotypic plasticity. Proc R Soc B Biol Sci 277:503–511. https://doi.org/10.1098/rspb. 2009.1355
- Baber MJ, Fleishman E, Babbitt KJ, Tarr TL (2004) The relationship between wetland hydroperiod and nestedness patterns in assemblages of larval amphibians and predatory macroinvertebrates. Oikos 107:16–27
- Bates D, Maechler M, Bolker B, Walker S (2015) Fitting linear mixed-effects models using lme4. J Stat Softw 67:1–48. https://doi.org/10.18637/jss.v067.i01
- Benard MF (2004) Predator-induced phenotypic plasticity in organisms with complex life histories. Annu Rev Ecol Evol Syst 35:651–673. https://doi.org/10.2307/annurev.ecolsys. 35.021004.30000024
- Boone MD, Little EE, Semlitsch RD (2004) Overwintered Bullfrog tadpoles negatively affect Salamanders and Anurans in native amphibian communities. Copeia. https:// doi.org/10.1643/CE-03-229R1
- Both C, Cechin SZ, Melo AS, Hartz SM (2011) What controls tadpole richness and guild composition in ponds in subtropical grasslands? Aust Ecol 36:530–536. https://doi.org/ 10.1111/j.1442-9993.2010.02183.x
- Brannelly LA, Ohmer MEB, Saenz V, Richards-Zawacki CL (2019) Effects of hydroperiod on growth, development, survival and immune defences in a temperate amphibian. Funct Ecol 33:1952–1961. https://doi.org/10.1111/1365-2435.13419
- Cordeiro-Estrela P, Baylac M, Denys C, Marinho-Filho J (2006) Interspecific patterns of skull variation between sympatric Brazilian vesper mice: geometric morphometrics assessment. J Mammal 87:1270–1279. https://doi.org/10.1644/ 05-mamm-a-293r3.1
- de Almeida AP, Rodrigues DJ, Garey MV, Menin M (2015) Tadpole richness in riparian areas is determined by nichebased and neutral processes. Hydrobiologia 745:123–135. https://doi.org/10.1007/s10750-014-2099-7
- Eterovick PC, Sazima I (2004) Amphibians from the Serra do Cipo. PUC Minas, Belo Horizonte
- Eterovick PC, Kloh JS, Figueredo CC et al (2020) Background choice and immobility as context dependent tadpole responses to perceived predation risk. Sci Rep 10:1–9. https://doi.org/10.1038/s41598-020-70274-w

- Ferrari MCO, Manek AK, Chivers DP (2010) Temporal learning of predation risk by embryonic amphibians. Biol Lett 6:308–310. https://doi.org/10.1098/rsbl.2009.0798
- Garland T (2014) Trade-offs. Curr Biol 24:60–61. https://doi. org/10.1016/j.cub.2013.11.036
- Gilman SE, Urban MC, Tewksbury J et al (2010) A framework for community interactions under climate change. Trends Ecol Evol 25:325–331. https://doi.org/10.1016/j.tree.2010. 03.002
- Grözinger F, Thein J, Feldhaar H, Rödel MO (2014) Giants, dwarfs and the environment: metamorphic trait plasticity in the common frog. PLoS ONE. https://doi.org/10.1371/ journal.pone.0089982
- Johansson F, Lederer B, Lind MI (2010) Trait performance correlations across life stages under environmental stress conditions in the common frog, Rana temporaria. PLoS One. https://doi.org/10.1371/journal.pone.0011680
- Johnson JB, Burt DB, DeWitt TJ (2008) Form, function, and fitness: pathways to survival. Evolution 62:1243–1251. https://doi.org/10.1111/j.1558-5646.2008.00343.x
- Johnson JB, Saenz D, Adams CK, Hibbitts TJ (2015) Naturally occurring variation in tadpole morphology and performance linked to predator regime. Ecol Evol 5:2991–3002. https://doi.org/10.1002/ece3.1538
- Knauth DS, Moreira LFB, Maltchik L (2018) Partitioning tadpole beta diversity in highland ponds with different hydroperiods. Freshw Sci. https://doi.org/10.1086/697926
- Maluf JRT (2000) Nova classificação climática do Estado do Rio Grande do Sul. Rev Bras Agrometeorol 8:141–150
- Maneyro R, Carreira S (2012) Guía de anfíbios del Urugay. Ediciones de la Fuga, Montevideo
- Marques NS, Nomura F (2015) Where to live? How morphology and evolutionary history predict microhabitat choice by tropical tadpoles. Biotropica 47:227–235. https://doi.org/ 10.1111/btp.12199
- Melo LSO, Garey MV, Rossa-Feres DC (2018) Looking for a place: how are tadpoles distributed within tropical ponds and streams? Herpetol Notes 11:379–386
- Menge BA, Olson AM (1990) Role of scale and environmental factors in regulation of community structure. Trends Ecol Evol 5:52–57. https://doi.org/10.1016/0169-5347(90)90048-I
- Merilä J, Laurila A, Pahkala M, Räsänen K, Timenes LA (2000) Adaptive phenotypic plasticity in timing of metamorphosis in the common frog Rana temporaria. Ecoscience 7:18–24. https://doi.org/10.1080/11956860.2000.11682566
- Michel MJ (2011) Spatial dependence of phenotype-environment associations for tadpoles in natural ponds. Evol Ecol 25:915–932. https://doi.org/10.1007/s10682-010-9441-y
- Miner BG, Sultan SE, Morgan SG et al (2005) Ecological consequences of phenotypic plasticity. Trends Ecol Evol 20:685–692. https://doi.org/10.1016/j.tree.2005.08.002
- Mitchell MD, Chivers DP, Brown GE, Ferrari MCO (2016) Living on the edge: How does environmental risk affect the behavioural and cognitive ecology of prey? Anim Behav 115:185–192. https://doi.org/10.1016/j.anbehav.2016.03. 018
- Moreira LFB, Machado IF, Garcia TV, Maltchik L (2010) Factors influencing anuran distribution in coastal dune wetlands in southern Brazil. J Nat Hist 44:1493–1507. https://doi.org/10.1080/00222931003632690

- Moreira LFB, Dorado-Rodrigues TF, Ferreira VL, Strüssmann C (2017) An inter-dependence of flood and drought: disentangling amphibian beta diversity in seasonal floodplains. Mar Freshw Res 68:2115–2122. https://doi.org/10. 1071/MF16391
- Morey S, Reznick D (2000) A comparative analysis of plasticity in larval development in three species of spadefoot toads. Ecology 81:1736–1749. https://doi.org/10.1890/0012-9658(2000)081[1736:ACAOPI]2.0.CO;2
- Navarro-Lozano A, Sánchez-Domene D, Rossa-Feres DC et al (2018) Are oral deformities in tadpoles accurate indicators of anuran chytridiomycosis? PLoS ONE 13:1–9. https:// doi.org/10.1371/journal.pone.0190955
- Nomura F, do Prado VHM, da Silva FR et al (2011) Are you experienced? Predator type and predator experience tradeoffs in relation to tadpole mortality rates. J Zool 284:144–150. https://doi.org/10.1111/j.1469-7998.2011. 00791.x
- Nylin S, Gotthard K (1998) Plasticity in life-history traits. Annu Rev Entomol 43:63–83. https://doi.org/10.1146/annurev. ento.43.1.63
- Ocock JF, Kingsford RT, Penman TD, Rowley JJL (2014) Frogs during the flood: differential behaviours of two amphibian species in a dryland floodplain wetland. Aust Ecol 39:929–940. https://doi.org/10.1111/aec.12158
- Purrenhage JL, Boone MD (2009) Amphibian community response to variation in habitat structure and competitor density. Herpetologica 65:14–30. https://doi.org/10.1655/ 08-017R1.1
- Ramalho WP, Machado IF, Vieira LJS (2018) Do flood pulses structure amphibian communities in floodplain environments? Biotropica 50:338–345. https://doi.org/10.1111/ btp.12523
- Relyea RA (2004) Fine-tuned phenotypes: tadpole plasticity under 16 combinations of predators and competitors. Ecology 85:172–179. https://doi.org/10.1890/03-0169
- Relyea RA (2007) Getting out alive: How predators affect the decision to metamorphose. Oecologia 152:389–400. https://doi.org/10.1007/s00442-007-0675-5
- Richter-Boix A, Llorente GA, Montori A (2006) Effects of phenotypic plasticity on post-metamorphic traits during pre-metamorphic stages in the anuran Pelodytes punctatus. Evol Ecol Res 8:309–320
- Richter-Boix A, Tejedo M, Rezende EL (2011) Evolution and plasticity of anuran larval development in response to d, a comparative analysisesiccation. Ecol Evol 1:15–25. https://doi.org/10.1002/ece3.2
- Rogers TN, Chalcraft DR (2008) Pond hydroperiod alters the effect of density-dependent processes on larval anurans. Can J Fish Aquat Sci 65:2761–2768. https://doi.org/10. 1139/F08-177
- Rohlf FJ (2010) tpsDig. Department of Ecology and Evolution, State University of New York, New York

- Rohlf FJ, Slice D (1990) Extensions of the Procrustes Method for the optimal superimposition of landmarks. Syst Zool 39:40–59
- Rowe CL, Dunson WA (1995) Impacts of hydroperiod on growth and survival of larval amphibians in temporary ponds of Central Pennsylvania, USA. Oecologia 102:397–403. https://doi.org/10.1007/BF00341351
- Rudolf VHW, Rhödel MO (2007) Phenotypic plasticity and optimal timing of metamorphosis under uncertain time constraints. Evol Ecol 21:121–142. https://doi.org/10. 1007/s10682-006-0017-9
- Schlager S (2017) Morpho and Rvcg shape analysis in R. In: Zheng G, Li S, Szekely G (eds) Statistical shape and deformation analysis. Academic Press, pp 217–256
- Sherratt E, Anstis M, Keogh JS (2018) Ecomorphological diversity of Australian tadpoles. Ecol Evol 8:12929–12939. https://doi.org/10.1002/ece3.4733
- Székely D, Denoël M, Székely P, Cogălniceanu D (2017) Pond drying cues and their effects on growth and metamorphosis in a fast developing amphibian. J Zool 303:129–135. https://doi.org/10.1111/jzo.12468
- Valério LM, Dorado-Rodrigues TF, Chupel TF et al (2016) Vegetation structure and hydroperiod affect anuran composition in a large neotropical wetland. Herpetologica 72:181–188
- Van Buskirk J (2009) Natural variation in morphology of larval amphibians: phenotypic plasticity in nature? Ecol Monogr 79:681–705
- Van Buskirk J (2000) The costs of an inducible defense in anuran larvae. Ecology 81:2813–2821. https://doi.org/10. 1890/0012-9658(2000)081%5b2813:TCOAID%5d2.0. CO:2
- Vences M, Puente M, Nieto S, Vieites DR (2002) Phenotypic plasticity of anuran larvae: environmental variables influence body shape and oral morphology in Rana temporaria tadpoles. J Zool 257:155–162. https://doi.org/10.1017/ S0952836902000754
- Warkentin KM, Cuccaro Diaz J, Güell BA et al (2017) Developmental onset of escape-hatching responses in red-eyed treefrogs depends on cue type. Anim Behav 129:103–112. https://doi.org/10.1016/j.anbehav.2017.05.008
- Wellborn GA, Skelly DK, Werner EE (1996) Mechanisms creating community structure across a freshwater habitat gradient. Annu Rev Ecol Syst 27:337–363
- Werner EE, Skelly DK, Relyea RA, Yurewicz KL (2007) Amphibian species richness across environmental gradients. Oikos 116:1697–1712. https://doi.org/10.1111/j. 2007.0030-1299.15935.x

**Publisher's Note** Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.