



Patterns of temperature induced developmental plasticity in anuran larvae

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ABSTRACT

Anurans exhibit plasticity in the timing of metamorphosis and tadpoles show phenotypic plasticity in age and size at metamorphosis as a response to temperature variation. This developmental plasticity to changing thermal conditions is expected to be a primary factor that dictates the vulnerability of amphibians to increasing ambient temperatures such as are predicted in climate change scenarios. We analyzed the patterns of thermal effects on size and age at metamorphosis to investigate whether the intraspecific “temperature-size rule” is applicable over a broad range of anuran species by carrying out a combined analysis based on the data from 25 studies performed on 18 anuran species. Furthermore, we tested whether the thermal background of respective populations impacts the capacity for a plastic response in metamorphic traits. We could confirm this pattern for across-population comparisons. All included populations developed faster and 75% were smaller at the onset of metamorphosis when developmental temperatures were warmer, but the sensitivity of growth and developmental rate to a given temperature change was different. We found that the thermal background of a population influences the sensitivity of metamorphic traits and thus, the capacity for a plastic response in growth and developmental rate. Warm adapted populations were less sensitive to temperature variation indicating a reduced capacity for developmental plasticity and therefore, those species may be more vulnerable to the impacts of climate change. Future studies should include a broader range of rearing temperatures and temperature fluctuations to determine full knowledge of the capacity for developmental plasticity within a species-specific thermal window.

1. Introduction

Species are declining worldwide due to habitat loss, disease, and environmental variation as caused by both natural and anthropogenic global environmental change (Stuart et al., 2004; Strong et al., 2017). In organisms with complex life cycles such as holometabolous insects, marine invertebrates, parasites, most teleost fish, and amphibians changing environmental conditions lead to a plastic response in their timing of metamorphosis (i.e. plastic growth and developmental rate) (Wilbur, 1980; Pechenik et al., 1998; Rudolf and Rödel, 2007; Laudet, 2011). Depending on the taxa, metamorphosis can cause a life-history transition that involves radical changes in habitat, morphology, and physiology. Thus, the timing of metamorphosis is of key importance for the entire life history and population dynamics (Walters and Hassall, 2006; Rudolf and Rödel, 2007). For organisms that live in temporally and spatially heterogeneous environments, phenotypic plasticity in age and size at metamorphosis may provide a means for increasing fitness in later life stages (Schlichting and Pigliucci, 1998; Boorse and Denver,

2004). For example, in amphibians, traits such as short larval period and large size at metamorphosis are assumed to confer greater fitness (Wilbur and Collins, 1973; Beck and Congdon, 2000).

Larval amphibians are especially sensitive to environmental variation due to their life history (Searcy et al., 2015), their highly permeable skin (Yu et al., 2015; Strong et al., 2017), and their limited capacity for habitat selection (Sanzo and Hecnar, 2006; Yu et al., 2015). Amphibians exhibit plasticity in the timing of metamorphosis and tadpoles show phenotypic plasticity in the larval stage in general, but especially in age and size at metamorphosis (Wilbur and Collins, 1973; Newman, 1992; Denver et al., 1998; Boorse and Denver, 2004). Different studies demonstrated a plastic response of metamorphic traits in anuran larvae to changes in environmental conditions such as crowding (Ding et al., 2015), presence of predators (Relyea and Hoverman, 2003; Relyea, 2003), food quality and quantity (Courtney Jones et al., 2015), photoperiod (Laurila et al., 2001), desiccation (Gervasi and Foufopoulos, 2008), water quality (Calich and Wassersug, 2012), and temperature (Vences et al., 2002).

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As amphibians are ectotherms, temperature is one of the major abiotic factors influencing metamorphosis. This can be directly related to the thermal sensitivities of the rate of biochemical and physiological processes that underlie morphogenesis (Smith-Gill and Berven, 1979; Hayes et al., 1993; Denver et al., 1998; Little and Seebacher, 2016). Plasticity in age and size at the onset metamorphosis results from plastic responses of somatic growth of existing tissues and of the developmental rate of new tissues (Newman, 1992; Chambers and Leggett, 1992). These two processes can, to some extent, be decoupled by environmental factors (Zuo et al., 2012; Walters and Hassall, 2006; Gomez-Mestre et al., 2010).

The plasticity in growth and development can be explained by the intraspecific “temperature-size rule” (TSR), which predicts that ectothermic species, including amphibians, reared at relatively lower temperatures display slower growth rates but a prolonged larval period and thus, typically mature later at larger sizes when compared with conspecifics reared at higher temperatures (Atkinson, 1994; Angilletta et al., 2004; Courtney Jones et al., 2015). Walters and Hassall (2006) emphasized that developmental rate is more sensitive to increasing temperatures than growth rate due to differential effects on anabolism and catabolism (von Bertalanffy, 1960; Angilletta and Dunham, 2003). Therefore, a higher temperature affects the development stronger than the growth rate (Gomez-Mestre et al., 2010).

For the TSR an optimal thermal range exists and this is bordered by a suboptimal range in which age and size plasticity does not occur (i.e. extreme conditions at which size decreases significantly) (Walczyńska et al., 2016) and thermal limits, which are usually defined by the critical thermal minimum (CT_{min}) and maximum (CT_{max}) in amphibians (Cowles and Bogert, 1944; Lutterschmidt and Hutchison, 1997; Turriago et al., 2015). The magnitude and direction of the response to temperature is species- and population-specific and depends on the range in thermal tolerance (Freitas et al., 2010). Adaptive shifts in the thermal range of tolerance (i.e. thermal adaptation) can result from biological processes that occur over longer time scales (Angilletta et al., 2002). Pörtner et al. (2006) uses “thermal windows” as an alternative term for the range of thermal tolerance of growth and development for all aquatic taxa but not for anurans which usually have a semiaquatic life-history. However, in most cases a tadpole’s mode of life is entirely aquatic. Therefore, we suggest equally using the term “thermal windows” to describe the range of temperatures suitable for the development of anuran larvae. The thermal window in amphibians is generally related to the geographic and altitudinal distribution of the species (Turriago et al., 2015). In ectotherms, it is relatively broad in temperate species, narrower in tropical species and most narrow in species found only in polar areas (Huey and Kingsolver, 1993; Angilletta et al., 2002; Pörtner and Peck, 2010; Berg et al. 2017). In tadpoles, the width of thermal windows increases from tropical to temperate latitudes due to an increasing cold tolerance (Gutiérrez-Pesquera et al., 2016).

Temperatures beyond this species- or population-specific thermal window proximately cause stress which alters tadpoles’ hormonal balance by activating the neuroendocrine stress axis (Wilbur and Collins, 1973; Berven and Chadra, 1988; Laudet, 2011; Navas et al., 2016). As metamorphosis is a process driven by thyroid hormones (TH), stress hormones may interact with TH resulting in increased TH production (Laudet, 2011; Glennemeier and Denver, 2002) and thus, lead to an increased developmental rate. Consequently, the rate of metamorphosis is in two respects influenced by the ambient temperature: through physiological and endocrine mechanisms which result in plastic responses of growth and developmental rate (Smith-Gill and Berven, 1979; Denver et al., 1998; Courtney Jones et al., 2015).

This considerable impact of temperature on growth and development during the larval stage and therefore, on fitness in later life stages, takes on greater significance in terms of the ongoing global climate change: The frequency of extreme thermal events (temperature peaks beyond CT_{max} of many species, increased desiccation risk, and increased mean annual temperatures) will increase in the future in all

climate zones (Pachauri et al., 2014; Gutiérrez-Pesquera et al., 2016). Rijnsdorp et al. (2009) and Mehner et al. (2011) emphasize that knowledge on the thermal window of organisms is fundamental to understand the response of populations to global warming. Numerous studies on anuran larvae investigated the effect of temperature on growth and developmental rate and thus, on age and size at the onset of metamorphosis. However, these studies refer to the species-specific effect of temperature during the larval period (Smith-Gill and Berven, 1979; Álvarez and Nicieza, 2002; Walsh et al., 2008; Dittrich et al., 2016; Courtney Jones et al., 2015; Gutiérrez-Pesquera et al., 2016). Even if amphibian larvae are generally known to develop at different rates and metamorphose at different sizes within their thermal windows, across-species comparisons, which allow for projections on the impact of climate change, are rare.

In this paper, we examine whether there is a general pattern of thermal effects on age and body size at the onset of metamorphosis in anuran larvae. We perform a combined analysis based on a total of 25 studies from 18 articles published between 1988 and 2016. This analysis aims to examine whether the “temperature-size rule” is not only applicable to intraspecific but also to interspecific comparisons of different anuran species. We specifically investigated (1) the effect of rearing temperature on metamorphic traits within and across all included populations, and (2) how the thermal background of the respective populations impacts the sensitivity of growth and developmental rates to different rearing temperatures. Furthermore, we review the potential consequences of temperature-driven plastic responses in rates of growth and development of pre- and pro-metamorphic larvae to post-metamorphic and adult life stages. This synthesis reveals whether common patterns exist among species-specific thermal effects on metamorphic traits which would allow more robust projections on the impacts of climate change at individual and population level.

2. Material & methods

2.1. Systematic literature review

We did a systematic literature review using ISI Web of Science (ISI WOS, 2017) in January 2017 (searched for: “TOPIC”; search term: (“amphibian larvae” OR “anuran larvae” OR “tadpoles”) AND (“thermal” OR “temperature” OR “environment*” OR “abiotic” OR “biotic” OR “climat* change” OR “climat* shift” OR “acidification” OR “pH” OR “predator” OR “density” OR “desiccation”) AND (“effect*” OR “impact*” OR “cause”) AND (“growth” OR “development*”) AND (rate OR time) AND (“larval time” OR “larval duration” OR “larval period”) AND (development* window OR “thermal window”) AND (“development* plasticity” OR “growth plasticity” OR “plasticity metamorphosis”) AND (“size” OR “time” OR “age”) AND (“metamorphosis”)); Timespan: All years.) (Pullin and Stewart, 2006). The systematic literature review returned 1236 articles into an unfiltered reference library. After examining titles and abstracts, 523 articles were left as possibly relevant in the filtered reference library. Examining the full text of the filtered reference library led to 18 articles accepted in the reference library. The following selection criteria had to be fulfilled by the experimental design of the included studies: (1) experiments were conducted in the laboratory (no field studies), and (2) at least at two different rearing temperatures for the tadpoles. These articles were published between 1988 and 2016 (with 55% of the studies published during the past 10 years) and comprised 25 individual studies representing 25 amphibian populations, which were included as replicated in the analysis. These 25 populations were from 18 species, 12 genera and 7 families according to the Linnean classification.

2.2. Data collection

For each population we extracted results for age (days after hatching to onset of metamorphosis), and size at onset of

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