Science of the Total Environment 618 (2018) 229–235

Contents lists available at ScienceDirect

Science of the Total Environment

journal homepage: www.elsevier.com/locate/scitotenv

The acute thermal respiratory response is unique among species in a guild of larval anuran amphibians—Implications for energy economy in a warmer future

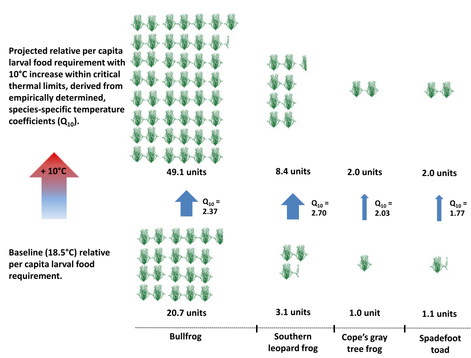
Christopher L. Rowe *, Erin A. Crandall

University of Maryland Center for Environmental Science, Chesapeake Biological Laboratory, PO Box 38, 146 Williams Street, Solomons, MD 20688, USA

HIGHLIGHTS

- Climate warming will alter metabolic expenditures of larval amphibians.
- Metabolic responses to temperature varied among species.
- High temperatures require increased resource consumption to satisfy metabolic costs.
- Ecological changes may result from species-specific energy needs at elevated temperatures.

GRAPHICAL ABSTRACT



ARTICLE INFO

Article history:
Received 8 September 2017
Received in revised form 12 October 2017
Accepted 31 October 2017
Available online xxxx

Editor: Daniel Wunderlin

Keywords:
Bioenergetics
Climate change
Competition
Metabolic rate
Temperature coefficient
Temporary wetland

ABSTRACT

Climate change is bringing about increased temperatures of amphibian habitats throughout the world, where ectothermic larvae will experience elevated respiratory (metabolic) energy demands. We compared the acute, thermal respiratory response ("TRR") of four species of sympatric larval amphibians (*Lithobates sphenocephalus*, *L. catesbeianus*, *Scaphiopus holbrookii*, and *Hyla chrysoscelis*) to determine species-specific differences in the rate at which metabolic energy requirements increase with temperature. The TRR, the slope of the relationship between respiration rate and temperature within critical thermal limits, varied significantly among species such that the absolute, per capita change in metabolic energy requirement as temperature increased was greater for *L. sphenocephalus* and *L. catesbeianus* than for *H. chrysoscelis* and *S. holbrookii*. This was also reflected in the temperature coefficients ($Q_{10,18.5–25.5}$), which ranged from 1.77 (*S. holbrookii*) to 2.70 (*L. sphenocephalus*) for per capita respiration rates. Our results suggest that *L. sphenocephalus* and *L. catesbeianus* will experience a more rapid increase in energetic requirements as temperature increases relative to the other species, possibly magnifying their influences on the resource pool. There is a critical paucity of information on the metabolic responses of most larval amphibians across a range of temperatures, despite that this relationship dictates the magnitude of the priority investment of assimilated energy in respiration, thus shaping the energetic economy of the individual. A broader knowledge of species-specific TRRs, combined with research to determine thermal acclimatory or adaptive potentials over chronic time scales, will provide a framework for evaluating whether asymmetric, climate-mediated differences in energetic demands among species could ultimately influence larval amphibian ecology in a warmer future.

* Corresponding author.
E-mail address: Rowe@umces.edu (C.L. Rowe).

https://doi.org/10.1016/j.scitotenv.2017.10.332

1. Introduction

Climate change will present numerous challenges to wildlife, including, but not limited to altering the thermal environment. Despite commitments by most nations to reduce anthropogenic impacts on the atmosphere by limiting future carbon emissions, a warmer planet appears unavoidable in the future (see IPCC, 2014). Therefore, as we project forward in our efforts to understand the biology and ecology of wildlife, we must consider that the future abiotic environment will be considerably different than it is at present. As increased air/water temperature is a common feature of climate models (IPCC, 2014), we may gain important insights by evaluating animal function under future thermal scenarios (e.g. Dillon et al., 2010). Furthermore, when direct thermal effects are better understood, we can begin to consider more complex, physiological, genetic, and ecological changes in the context of a thermal environment that is substantially altered from current conditions.

In light of a global amphibian decline (see Alford, 2010), investigators have begun to examine the possibility of relationships between climate change and amphibian population status (for example, Li et al., 2013). While climate change will likely bring about alterations in several variables that may influence amphibians (for example, precipitation patterns and wetland hydroperiods, food availability and seasonal phenology of resource abundance, soil moisture levels; see Ficetola and Maiorano, 2016), the underlying cause of these changes is, directly or indirectly, the global increase in temperatures resulting from anthropogenic impacts on atmospheric chemistry (e.g. IPCC, 2014). Evaluations of the effects of increased temperature on amphibian performance are thus a starting point upon which studies of other climate-related variables can be based within the context of the demonstrated thermal effects.

The energetic performance of amphibians, frequently assessed as respiration (metabolic) rates, has been described for numerous species over the past century, but these historical studies most often considered adults rather than larvae and were seldom designed to evaluate energetics across a range of temperatures from which inferences about future conditions can be drawn (see Gatten et al., 1992). The majority of these studies that did include temperature as a variable examined temperature categorically at only a few levels (see Gatten et al., 1992), rather than continuously over a range of temperatures, which would provide predictive power for estimating responses at temperatures near or within the tested range of temperatures. Furthermore, as most historical data for amphibian respiration were derived from studies of adults (Gatten et al., 1992; Rome et al., 1992), there is considerable need for further work evaluating larvae, which frequently occupy small, shallow or temporary pools that may be resource-restricted and are quite susceptible to environmental perturbations such as thermal or climatic changes (e.g. Rowe and Dunson, 1993; Semlitsch and Skelly, 2007). Indeed, conditions in larval habitats determine survival rates, the timing of metamorphosis, and the size of individuals at metamorphosis, ultimately influencing recruitment and population dynamics in some species (Semlitsch et al., 1988; Scott, 1994; Rowe et al., 2003; Scott et al., 2007).

More recent investigations of influences of elevated temperature on larval amphibians have frequently focused on thermal tolerances and critical thermal maxima ("CT_{Max}", see Duarte et al., 2012; Gutierrez-Pesquera et al., 2016). For example, Duarte et al. (2012) described warming tolerances of amphibians from different thermal communities as the extent to which ambient temperatures can increase above current observed maximum temperatures in breeding ponds before reaching the CT_{Max}. They found that temperate larval amphibians had an average warming tolerance close to 10 °C, with a mean CT_{Max} of about 38 °C (Duarte et al., 2012). Although climate models are complex and future temperatures are difficult to predict with precision, current IPCC models for global temperatures in the coming century (IPCC, 2014) do not suggest warming of the magnitude that would be likely to threaten temperate larvae with reaching their CT_{Max}. Therefore, in order to evaluate the immediate or near-term effects of increasing temperatures on temperate amphibian communities, we must examine phenomena that operate within amphibians' critical thermal limits, yet that may still have significant impacts on their physiology and ecology.

With elevated temperature, ectotherms such as amphibians experience increases in their metabolic (respiratory) energy expenditures (Cossins and Bowler, 1987), which may be a direct effect of molecular kinetics (e.g. the Boltzmann factor, Gillooly et al., 2001) or the result of indirect effects on cellular metabolism reflecting evolutionary tradeoffs among structure, function, and stability of proteins (Clarke and Fraser, 2004). Increased metabolic energy expenditures can be detrimental because an individual can harvest and assimilate only a finite quantity of energetic resources from the environment per unit time, and thus it may not be able to satisfy the additional energetic demand due to elevated temperature without subsequent effects on growth or survival (see Congdon et al., 2001; Rowe et al., 2003). Furthermore, under conditions of resource limitation, the negative effects of elevated metabolic costs would be amplified because the total energy available to the individual is restricted. By priority, energy assimilated from the environment must be used to satisfy respiratory requirements for maintenance (underlying physiological and activity costs of survival); residual energy that remains can then be invested in production of somatic or reproductive tissue (see Congdon et al., 2001; Rowe et al., 2003). Increased metabolic expenditures at elevated temperatures require that the individual dedicate a greater proportion of assimilated energy to the respiratory pathway, thereby reducing production potential unless a greater quantity or higher quality of resources can be harvested and assimilated. Asymmetry in the thermal respiratory (metabolic) response (hereafter "TRR") among species will require that individuals of the most thermally-responsive species harvest proportionally greater quantities of resources than less-responsive species under conditions of elevated temperature, perhaps favoring the latter when the shared resource pool is limited (e.g. Tagliarolo and McQuaid, 2015). It is thus possible that differences among species in TRR could have ecological impacts by altering interspecific interactions in resource-limited habitats in response to each species' unique energetic requirements at a given temperature (e.g. Seifert et al., 2014; Tagliarolo and McQuaid, 2015).

As evaluations of metabolic demands of larval amphibians across a range of temperatures within critical limits have been limited to relatively few species (for example, see Niehaus et al., 2011; Kern et al., 2014; Seebacher and Grigaltchik, 2014; Rowe and Funck, 2017), it is not possible to evaluate which species will be energetically favored in a guild and to form hypotheses about how ecological dynamics might respond as the climate warms. Here we provide the first rigorous comparison of TRR within the critical thermal limits among multiple species of larval amphibians that potentially interact in natural habitats. We compared the acute TRR in a four-species guild of larval amphibians of eastern North America to determine 1) whether TRR differs among species and 2) which species experience the greatest increases in metabolic demands as temperature increases. We anticipate that this work will guide future theoretical and empirical examinations of recruitment dynamics and multi-species interactions among larval amphibians with respect to the changing thermal environment. Furthermore our work should motivate research on species-specific thermal acclimatory capacities or adaptations that may influence expression of the TRR when individuals are chronically exposed to elevated temperatures.

2. Material and methods

We used respiration (O_2 consumption) rates as measures of metabolic rate (MR) to evaluate the influence of temperature on four species of larval amphibians that are common in the mid-Atlantic region of North America. These included two true frogs (bullfrogs and southern