



Research paper

Local differences of thermal preferences in European common frog (*Rana temporaria* Linnaeus, 1758) tadpoles



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ABSTRACT

Physiological functions of ectotherms and thus their performance depend on environmental temperatures. Many ectotherms are capable of active thermoregulation, e.g. by selecting suitable microhabitats. However, this may be constrained by unavailability of favourable microhabitats or high energetic costs of thermoregulation. Thus, to achieve the optimal performance levels, adaptations to local thermal environments are of great importance. Due to the inability of leaving their aquatic habitat, larval anurans should especially benefit from local thermal adaptations. *Rana temporaria* is a widely distributed European anuran species, inhabiting a range of microhabitats, which makes it an excellent model to study the potential of local thermal adaptation. We raised *R. temporaria* tadpoles from Germany and Croatia under respective natural temperature fluctuations and three constant temperatures (15°, 20° and 25 °C), and tested dependency of their thermal preferences on the developmental stage and temperature regime, and the population origin. Tadpoles of both origins selected higher temperatures towards the end of the developmental period, and their thermal preferences were affected by the developmental temperature. However, regardless of the developmental stage or treatment, tadpoles from warmer Croatia selected higher temperatures than tadpoles from colder Germany. This demonstrates the tendency of adjusting the sensitivity of physiological processes to local thermal conditions.

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1. Introduction

Well-adjusted body temperature is crucial for all organisms, since it affects all physiological functions. Ectotherms are not capable of producing significant quantity of body heat, and are thus dependent on the environmental temperature (Angilletta, 2009; Hillman et al., 2009). However, despite their dependence on external heating (or cooling) sources, many ectotherms are capable of actively maintaining their body temperature within a preferred range (Cowles and Bogert, 1944). Mechanisms involved in active thermoregulation may include morphological, physiological and/or

behavioural processes, such as selection of favourable microhabitat (Brattstrom, 1979; Huey, 1982; Huey and Pianka, 1977; Hutchison and Maness, 1979).

Thermoregulation can enhance performance, and thus, influence fitness (Huey, 1982; Huey and Stevenson, 1979). Therefore, active thermoregulation should be under selection pressure (Angilletta et al., 2002) and organisms usually occur in the environments which best fulfill their temperature needs. However, achieving favourable temperatures is often limited by ecological constraints, such as unavailability of suitable microhabitats. Moreover, active thermoregulation can come at high costs, including energetic budgets, predation pressure, or lost opportunities for feeding or reproduction (Angilletta, 2009; Huey and Slatkin, 1976). These constraints may differ in different environments and, thus, lead to local intra-specific differences in thermal preferences (Angilletta et al., 2002; Huey and Bennett, 1987).

Due to their vulnerability to desiccation, thermoregulation of amphibians is especially challenging (Brattstrom, 1979; Tracy,

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1976). The complex interplay of thermal and hygric requirements and the constraints imposed by the environment have intrigued eco-physiologists for decades (e.g. Hall and Root, 1930; Hillman et al., 2009; Tracy, 1976). The European common frog, *Rana temporaria* Linnaeus 1758; is an explosive breeder, spawning over only a few days in early-spring. It utilizes a variety of permanent and temporary water bodies, such as ponds, puddles, swamps and creeks for reproduction. It occurs from northern Spain to western Siberia, and from northern Scandinavia to northern Greece (Gollmann et al., 2014), and thus is found in a variety of habitats with differing thermal properties. It has been shown that *R. temporaria* exhibits thermoregulatory behaviour, such as basking or selection of favourable microhabitats (Sinsch, 1984; Vences et al., 2002). Strikingly, the literature reports very different thermal preferences of *R. temporaria* adults, in spite of the relatively restricted geographic and climatologically similar central European sites: e.g. 29.6 ± 0.51 °C (Berlin, NE Germany; Strübing, 1954), ca. 10–20 °C (northern Rhineland, NW Germany; Sinsch, 1984), or 19.4 ± 1.7 °C (northern Poland; Köhler et al., 2011). Rühmekorf (1958) reported that temperatures ranging between 21.0 and 26.0 °C are favourable for *R. temporaria* tadpoles.

These differences between populations imply thermal preferences, adjusted to local environmental conditions. Adult frogs can move towards microsites best matching required climatic conditions within its habitat, while larval amphibians can select favourable water temperatures. However, larvae cannot escape their often thermally more homogenous aquatic environments. Thus, adjustments of physiological processes to local thermal environments would be particularly beneficial in the aquatic stage (Seebacher and Franklin, 2005). Herein, we focus on the thermal preferences of *R. temporaria* tadpoles from two geographically distant populations, one from the north of the Alps, Germany, and another from the south of the Alps, Croatia. These populations could exhibit differences in thermal preferences due to adaptations to local climate regimes or react plastically, as a consequence of acclimation to temperatures experienced in their respective environments. We aimed to test if local adaptation, acclimation, or both, direct the thermal preference of *R. temporaria* tadpoles. We raised tadpoles from Germany and Croatia under different constant temperatures, as well as under respective local temperature conditions of each population. We then tested their thermal preferences, across different developmental stages.

We hypothesized that: (i) tadpoles from the warmer Croatia will choose higher temperatures compared to tadpoles from the cooler Germany, due to local adaptation towards higher temperatures; (ii) preferred temperatures will increase towards the end of the larval period, since final developmental stages are particularly vulnerable, due to e.g. decreased mobility (Dupré and Petranka, 1985; Wassersug and Sperry, 1977), and higher temperatures accelerate development (Ultsch et al., 1999); and (iii) tadpoles developing in higher developmental temperatures will select higher temperatures than tadpoles developing in lower temperatures, due to acclimation.

2. Materials and methods

2.1. Study sites

In April 2013, we sampled eggs of 10 freshly laid clutches from a pond (FS06), in Steigerwald, northern Bavaria, Germany (49°55'N, 10°33'E, 409 m asl, see Grözinger et al., 2012, 2014), hereafter referred to as population GER. In March 2014, eggs from 10 clutches were collected from a pond (RJ01) in Medvednica (45°53'N, 16°00'E, 400 m asl), close to Zagreb, Croatia, hereafter referred to as population CRO. Both ponds were permanent and sit-

uated in mixed deciduous forest. The experiments were conducted in the ecological field station of the University of Würzburg in Fabrikerschleibach, Germany (April–June 2013) and in the Zagreb Zoo, Croatia (March–May 2014).

Both study sites belong to the temperate zone; however their climate differs. The climate in CRO is warmer, with an average annual temperature of 10.8 °C. The coldest month is January (average temperature: 0 °C), the warmest month is July (average temperature: 20.9 °C; Maksimir weather station, 45°49'N, 16°02'E; Croatian Hydrometeorological Service). The mean annual temperature in the GER site is 8.2 °C. January is the coldest (average temp: -0.6 °C) and July the warmest month (average temp: 17.4 °C; Ebrach weather station, 49°51'N, 10°30'E; Deutscher Wetterdienst).

2.2. Experimental procedures

2.2.1. Climate chambers and outdoor treatments

After collection, eggs were kept in separate plastic containers filled with original pond water, at a constant temperature of 7–8 °C (similar to the original environmental conditions) for five days. We then assigned them to one of four developmental treatments. Three developmental treatments provided constant temperatures of 15 °C (hereafter referred as T15), 20 °C (T20) and 25 °C (T25), all being within the range of natural temperature variations in both populations. A fourth treatment mirrored the respective local environmental conditions, with natural temperature fluctuations (outdoor treatment, OT). After hatching and reaching developmental stage 25 (after Gosner, 1960: free swimming and feeding), we transferred the tadpoles to the experimental containers.

In each of the climate chamber treatments, we placed six tadpoles each in a single plastic container, filled with 1.2 L of mixed deionized/spring water (pH = 6.5–7.0, conductivity = 150–200 µS/cm). From each population, we kept a total of 120 tadpoles (6 tadpoles × 20 containers) per climate chamber treatment (T15, T20 and T25); thus 360 tadpoles per population. Light conditions in the climate chambers were set to 16:8 L:D h, corresponding to the natural daylight rhythm. The outdoor treatments provided conditions that mimicked the respective natural environments. Here, ten tadpoles were placed into a plastic container with 5 L of the original pond water (GER: pH = 6.9, conductivity = 110 µS/cm, CRO: pH = 7.0, conductivity = 320 µS/cm). To buffer the environmental temperature variability, and ensure that temperature variations resemble those in the natural water sources, the volume in the outdoor treatment containers was higher than in the climate chambers' treatments. Furthermore, the bottom of the container was covered with soil and leaf litter from the original location. Outdoor treatment containers were placed outside in the shade and covered with plastic gauze lids (grid diameter 1 mm) to exclude potential predators. In the outdoor treatments, we kept 300 tadpoles per population (10 tadpoles × 30 containers). In the following, we denote a particular developmental treatment of a particular population using a treatment-population label, e.g. T15-GER for eggs/tadpoles developing at 15°, originating from Germany.

Water quality (temperature, pH, conductivity) was tested regularly. Water in the climate chambers was exchanged two to three times per week, while in the outdoor treatments water was only replaced when necessary (pH out of 6.2–7.5, or CD >370 µS/cm; AL15MultiMeter Instrument; AquaLytic®, Dortmund, Germany). Water temperature in each of the outdoor treatment containers was recorded every 3 h, using a thermologger (Thermochron® iButtons© DS1922L, ±0.5 °C; Embedded Data Systems, Lawrenceburg, Kentucky, USA). All tadpoles were fed *ad libitum* with commercial fish food (TetraTabiMin®; Tetra, Melle, Germany).

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