



Intraspecific geographic variation in thermal limits and acclimatory capacity in a wide distributed endemic frog



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ABSTRACT

Intraspecific variation in physiological traits and the standard metabolic rate (SMR) is common in widely distributed ectotherms since populations at contrasting latitudes experiences different thermal conditions. The climatic variability hypothesis (CVH) states that populations at higher latitudes presents higher acclimation capacity than those at lower latitudes, given the wider range of climatic variability they experience. The endemic four-eyed frog, *Pleurodema thaul* is widely distributed in Chile. We examined the variation in maximum and minimum critical temperatures (CT_{max} and CT_{min}), preferred temperature (T_{Pref}), SMR and their acclimatory capacity in two populations from the northern and center of its distribution. All the traits are higher in the warmer population. The capacity for acclimation varies between traits and, with the exception of CT_{max} and T_{Pref} , it is similar between populations. This pattern could be explained by the higher daily thermal variability in desert environments, that increases plasticity to the levels found in the high latitude population. However, we found low acclimatory capacity in all physiological traits, of only about 3% for CT_{min} , 10% for CT_{max} and T_{Pref} , and 1% for SMR. Thus, despite the fact that *Pleurodema thaul* possess some ability to adjust thermal tolerances in response to changing thermal conditions, this acclimatory capacity seems to be unable to prevent substantial buffering when body temperatures rise. The low acclimatory capacity found for *P. thaul* suggests that this species use behavioral rather than physiological adjustments to compensate for environmental variation, by exploiting available micro-environments with more stable thermal conditions.

1. Introduction

Environmental temperature (T_A) is by far the abiotic factor that has the largest impact on the physiology and ecology of most of the planet's biodiversity (Angilletta, 2009). Thus, the projected rise in T_A under climate change scenarios (IPCC, 2014) is a serious threat to biodiversity, most notably so for ectotherms (Angilletta, 2009; Deutsch et al., 2008; Stillman, 2003; Sunday et al., 2011). Most functional traits of ectothermic species (e.g. growth, reproduction, physiology) change as T_A does, a relationship that can be described by a thermal performance curve (Angilletta, 2009; Huey and Berrigan, 2001). This curve can be described by three parameters: (1) a minimum critical temperature (CT_{min}), which represents the T_A below which performance is at a minimum, (2) a maximum critical temperature (CT_{max}), which represents T_A above which performance is also at a minimum, and (3) an optimum temperature, which represents T_A at which performance is maximized. These parameters have been used to describe mechanistically the variation of thermal performance among natural

populations of ectotherms, and the evidence indicates that these traits usually co-vary along geographic clines (e.g. latitude), reflecting the ability of ectotherms to adapt, at least in part, to their environments (Fangue et al., 2006; Klok and Chown, 2003; Lardies et al., 2004a).

Given the actual rate of global warming (IPCC, 2014), ectotherms with low dispersion capacities are at higher risk of demographic collapse unless they are capable of physiological and/or behavioral adjustments or evolutionary adaptation (Calosi et al., 2008; Chevin et al., 2010; Davis et al., 2005; Hoffmann and Sgrò, 2011). The lack of evidence for rapid adaptive evolution in amphibians in response to the increase in T_A in the last decades (Urban et al., 2014) suggests that phenotypic plasticity of physiological traits will be key for the success of populations coping with new thermal scenarios (Bozinovic et al., 2011; Ruiz-Aravena et al., 2014). This is of concern as amphibians are not only particularly sensitive to climate change (Kerby et al., 2010), but have already experienced declines and extinctions worldwide (Blaustein and Kiesecker, 2002; Gibbons et al., 2000; Houlahan et al., 2000; Stuart et al., 2004). Even when it is known that land-use change

Abbreviations: T_A , Environmental temperature; CVH, Climatic variability hypothesis; ARR, Acclimation response ratio; CT_{min} , Minimum critical temperature; CT_{max} , Maximum critical temperature; T_{Pref} , Preferred temperature; SMR, Standard metabolic rate

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is the principal driver of those declines, global warming can reinforce their effect, and that of emerging infectious diseases (Bacigalupe et al., 2017; Hof et al., 2011; Sodhi et al., 2008). Also, there is consistent literature indicating that the climate change has driven changes in the distribution and abundance of amphibians (D'Amen and Bombi, 2009; Lawler et al., 2006, 2010; Ochoa-Ochoa et al., 2012).

For amphibians, as for other ectotherms, the plasticity of thermal tolerance limits is usually correlated to the magnitude of variation in T_A they experience (Addo-Bediako et al., 2000; Calosi et al., 2010; Ghalambor et al., 2006; Naya et al., 2011; but see Sørensen et al., 2016). Therefore, it is expected that populations at higher latitudes require broader tolerance limits and acclimation capacity than individuals inhabiting lower latitudes, given the wider range of climatic variability (i.e. seasonality) they experience, according to the climatic variability hypothesis (CVH, Calosi et al., 2010; Chown et al., 2004; Ghalambor et al., 2006; Janzen, 1967; Naya et al., 2011; Stevens, 1989). In addition, a negative correlation has been found between thermal acclimation and heat resistance in *Drosophila* spp. (Berrigan and Hoffmann, 1998; Cavicchi et al., 1995) and in *Escherichia coli* (Leroi et al., 1994), which combined with a positive covariation of the acclimation capacity of CT_{max} and CT_{min} , with latitude in marine intertidal crabs (Stillman, 2003; Somero, 2010), suggest that the higher CT_{max} of low latitude species is related to its low plasticity (Stillman, 2003; but see Calosi et al., 2008). This reinforces the idea that lower latitude species are at a higher risk from climate change (Deutsch et al., 2008; Dillon et al., 2010; Huey et al., 2009; Sinervo et al., 2010). For amphibians, the rate and range of thermal acclimation has been determined for fifty-three species from a wide variety of habitats, latitudes and altitudes in North and Central America (Brattstrom, 1968). In turn, Brattstrom shows that: (1) there is little geographic variation in CT_{max} within a species, except for those with widespread distribution, (2) tropical anurans have broader acclimatory capacities than temperate species and (3) species with reduced geographic ranges have poor acclimatory capacities. Recently, it was determined for 22 species of frogs inhabiting an altitudinal gradient in the Andes at southern Peru, that specimens living at high elevations exhibits lower CT_{min} and CT_{max} , and a wider thermal breath, even when this last relation was statistically non-significant (von May et al., 2017). Although other studies have evaluated intraspecific geographic patterns in thermal tolerance in several ectotherms groups (e.g. Fanguie et al., 2006; Hoffmann et al., 2003; Kuo and Sanford, 2009; Storch et al., 2009), to date, the relationship between thermal limits and their acclimatory capacity for amphibians across latitude at the intraspecific level remains poorly understood.

The metabolic rate of an organism is linked to its pattern of energy use and as such represents a holistic measure of the 'pace of life' (Gillooly et al., 2001). However, there are two contrasting patterns of geographic variation for ectotherms' metabolic rates (Bozinovic et al., 2011; Burton et al., 2011). One body of evidence indicates that populations at lower latitudes, experiencing warmer temperatures throughout the year, exhibit higher metabolic rates than their conspecifics at higher - colder latitudes (Angilletta, 2001; Lardies et al., 2004b; Peck, 2002). On the other hand, the metabolic cold adaptation hypothesis (MCA) states that at equivalent environmental temperatures, the metabolic rate of ectothermal species and populations from cold climates is greater than that of their warm-climate relatives (Addo-Bediako et al., 2002; Gaston et al., 2009; Jacobsen and Brodersen, 2008). This compensation for low T_A has been thought of as a general evolutionary adaptation of terrestrial ectotherms from high latitudes or altitudes (Chown and Gaston, 1999; Gaston et al., 2009). An increase in metabolic rates with raising T_A implies that at the warmer edge of the geographical distribution of an ectotherm species, populations will be at higher risk of extinction (Dillon et al., 2010). However, if the metabolic rate covaries negatively with T_A , as it is predicted by the MCA hypothesis, we should expect higher risk of extinction in all areas within an ectotherm's actual geographical range of distribution.

Therefore, intra-specific comparisons in species widely distributed, can provide a mechanistic understanding to guide conservation strategies to support wildlife that is prone to be in danger of local extinction as a consequence of the future thermal regimes (Wikelski and Cooke, 2006).

Here we determine the plasticity and geographic variation of CT_{min} , CT_{max} , T_{pref} and metabolic rate, in the four-eyed frog, *Pleurodema thaul* (Lesson, 1827), a small amphibian endemic to Chile and Argentina with a distributional range that spans more than 2500 km from the Atacama Desert (27°S) to Aysen (45°S) (Vidal et al., 2009) and from the Pacific coast up to 2700 m.a.s.l (Correa et al., 2007). Along its range in Chile, *P. thaul* inhabits a wide variety of biomes, from the northern arid territories to the southern *Nothofagus* forest, being the most common frog in the country (Díaz-Páez and Ortiz, 2003). From its large distributional range, we selected two populations that inhabit highly contrasting T_A conditions: Carrera Pinto, at the northern limit of the distribution in a small oasis in the Atacama Desert and El Caulle, about 1500 km south of Carrera Pinto, located near the center of its range.

2. Materials and methods

2.1. Study organism and laboratory maintenance

Ninety individuals of *P. thaul* were collected in November 2012 at Carrera Pinto (27°06'S, 69°53'W), an oasis in the Atacama Desert where the northernmost population of this species has been reported (Correa et al., 2007). Forty individuals were collected in December 2014 from El Caulle (40°39'S, 72°10'W), a location 1500 km south of Carrera Pinto and approximately in the center of the current distribution of the species (Fig. 1a). For the metabolic rate assays, we captured 72 individuals from the warmer population in October 2014, and 42 from the colder population in December 2015.

All specimens were transported to the Universidad Austral de Chile (Valdivia) within 2–3 days of collection. Following capture, each animal was marked by toe clipping and maintained in the laboratory at a temperature of 20 ± 1 °C and with a photoperiod of 12 h: 12 h, D:L. Animals were housed in terrariums ($N = 8$, 15,000 cm³) provided with a cover of moss and vegetation and a small reservoir filled with water. Specimens were fed once a week with mealworms (*Tenebrio molitor* larvae) and Mazuri® (St. Paul, Minnesota, USA) gel diets. We were not able to identify for certain the sex of all individuals, but we verify to not use gravid females in any of the experimental trials. All the measurements were conducted according to current Chilean law and the protocols we use were approved by the Committee on the Ethics of Animal Experiments of the Universidad Austral de Chile.

2.2. Exposure to laboratory temperatures

After three weeks at maintenance conditions, animals were exposed to the experimental temperatures of 10 and 20 °C. These temperatures reflect the annual mean and maximal thermal conditions at Carrera Pinto (mean: 13.1 °C, max: 19 °C; Fig. 1b) and El Caulle (mean: 10.9 °C, max: 20 °C; Fig. 1c). In a split cross design (e.g., included statistically as a random factor, see Section 2.4), the 90 individuals from Carrera Pinto were randomly assigned to one of two temperatures of acclimation for two weeks, at either 10 °C or 20 °C. After measuring traits, animals were exposed to the second temperature, and again the thermal traits were measured after two weeks of acclimation. The 40 animals captured in El Caulle were exposed first at 10 °C and then at 20 °C for two weeks before the physiological measurements were performed. To measure the standard metabolic rate (SMR), after three weeks at maintenance conditions, the animals captured in Carrera Pinto and El Caulle were randomly assigned to one of the acclimation temperatures (10 °C or 20 °C) and were maintained in these conditions for two weeks before metabolic assays were performed. From each population and acclimation treatment, the SMR of half of the animals was measured at 20 °C and the other half was measured at 30 °C.

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