



# Thermal sensitivity of cold climate lizards and the importance of distributional ranges

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## ABSTRACT

One of the fundamental goals in macroecology is to understand the relationship among species' geographic ranges, ecophysiology, and climate; however, the mechanisms underlying the distributional geographic patterns observed remain unknown for most organisms. In the case of ectotherms this is particularly important because the knowledge of these interactions may provide a robust framework for predicting the potential consequences of climate change in these organisms. Here we studied the relationship of thermal sensitivity and thermal tolerance in Patagonian lizards and their geographic ranges, proposing that species with wider distributions have broader plasticity and thermal tolerance. We predicted that lizard thermal physiology is related to the thermal characteristics of the environment. We also explored the presence of trade-offs of some thermal traits and evaluated the potential effects of a predicted scenario of climate change for these species. We examined sixteen species of *Liolaemus* lizards from Patagonia representing species with different geographic range sizes. We obtained thermal tolerance data and performance curves for each species in laboratory trials. We found evidence supporting the idea that higher physiological plasticity allows species to achieve broader distribution ranges compared to species with restricted distributions. We also found a trade-off between broad levels of plasticity and higher optimum temperatures of performance. Finally, results from contrasting performance curves against the highest environmental temperatures that lizards may face in a future scenario (year 2080) suggest that the activity of species occurring at high latitudes may be unaffected by predicted climatic changes.

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## 1. Introduction

A species' geographic range is considered the fundamental unit of macroecology (Brown et al., 1996; Gaston, 2003; Whitton et al., 2012) and can vary in relation to many different factors (such as climate, competition, diseases, resource types and abundances). Ectothermic animals constitute the vast majority of terrestrial biodiversity (Wilson, 1992) and are expected to be sensitive to climatic variations, making them an interesting group to test the relationships between climatic variables and the distribution of species throughout time and space. The occurrence of these organisms in physiographically variable environments can be explained by different aspects; for example, behavioral regulation, physiological

plasticity or genetic differentiation among populations (Hertz et al., 1983). Therefore, discerning the role of physiological or behavioral plasticity in the context of climatic change is an important task. To appropriately address these alternatives in species with different geographic ranges, first we need to elucidate species distribution patterns and geographic variation in physiological traits. Then, we need to derive the mechanisms or characteristics underlying the ecological and evolutionary patterns observed (Gaston et al., 2009; Naya et al., 2012). Recent studies explicitly relate physiological traits of species and their geographic distribution ranges (e.g., Buckley, 2008, 2010; Kearney and Porter, 2009). Additionally, since the recognition of rapid and recent global climate change (Solomon et al., 2007), numerous studies have emphasized the potential risks and responses of species facing climate change (e.g., Parmesan et al., 1999, 2000; Huey and Tewksbury, 2009; Huey et al., 2010; Sinervo et al., 2010; Hanna, 2012).

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One of the hypotheses related to species distribution across environmental gradients is the climatic variability hypothesis (Gaston and Blackburn, 2000), which states that the range of climatic fluctuation experienced by terrestrial animals increases with latitude and/or elevation (and their combinations) and implies broader tolerance ranges and acclimation ability for species persisting in these sites (Gaston and Chown, 1999; Cruz et al., 2005; Ghalambor et al., 2006; Deutsch et al., 2008; Naya et al., 2012 and citations therein). Direct evidence supporting the climatic variability hypothesis has been obtained during the last fifty years (Brattstrom, 1968; Brett, 1970; Snyder and Weathers, 1975; van Berkum, 1988; Addo-Bediako et al., 2000; Cruz et al., 2005; Naya et al., 2012). Thus, there is support for predicting an association between a flexible thermal physiology and climatic variability.

Thermal tolerance capability and thermal sensitivity are strongly linked to physiological performance and environmental conditions (Hertz et al., 1983; Crowley, 1985). Thermal tolerance is the body temperature range within which an organism can survive or recover (Carothers et al., 1997; Cruz et al., 2005). Thermal sensitivity, often described as a curve, is the extent to which physiological capabilities are influenced by variation in thermal conditions within the tolerance range (Crowley, 1985; van Berkum, 1988; Hochachka and Somero, 2002; Pörtner, 2002; Gunderson and Leal, 2012). These performance curves have an area generally depicted as a left-skewed Gaussian bell curve (Huey and Kingsolver, 1989; Angilletta, 2006; Bulté and Blouin-Demers, 2006) and are described by several key parameters: the thermal optimum ( $T_o$ ; temperature at which maximum performance is reached); the optimal temperature range (known as B95); the thermal performance breadth (also known as B80); the thermal limits, referred to as the critical thermal minimum and the critical thermal maximum; and the maximal performance (Hertz et al., 1983; Angilletta, 2009). Running ability is frequently used as a performance measurement strongly related to thermal physiology (Hertz et al., 1983; Crowley, 1985; Huey and Bennett, 1990; Garland and Losos, 1994; Bauwens et al., 1995) and may have potential consequences on fitness (Wright, 1932; Arnold, 1983; Huey and Bennett, 1987), although this is not fully demonstrated.

Understanding the relationship between thermal physiology and climate requires a better knowledge of an individual's maximum performance as it depends on its optimum temperature (Angilletta et al., 2010). Barcroft (1934) and Hochachka and Somero (1973) argue that genotypes adapted to higher temperatures have greater performance ability than cold-adapted ones, since higher temperatures accelerate chemical reactions ("hotter is better"). On the other hand, Clarke (2003), Frazier et al. (2006) and Angilletta et al. (2010) suggest that biochemical adaptation may compensate the effects on thermodynamic performance, assuming that species adapted to low temperatures may present the same levels of performance compared to species adapted to high temperatures, thus turning the discussion about thermal physiology controversial.

Another interesting question is whether an organism with broad thermal tolerance has an evolutionary advantage over species with narrower thermal tolerance. Physiological and biomechanical theory suggests that design characteristics necessary for maximizing the performance of different traits can be difficult to reconcile in one phenotype (Vanhooydonck et al., 2001). Thus, theoretical models in this field are based on the assumption that the "jack of all trades is master of none" (MacArthur, 1972; Huey and Slatkin, 1976; Pianka, 1978; Huey and Hertz, 1984). Then, the performance curve of ectotherms (level of performance at different temperatures) can be viewed as a reaction norm and may allow identification of trade-offs (compromises) between the breadth

(plasticity) and the maximum level of specialization (performance; Angilletta et al., 2003).

In the present study we attempt to explore the issues expounded above in Patagonian lizards. Patagonia is characterized by a rigorous climate with strong winds and low temperatures (Páruelo et al., 1998). We studied 16 species of Patagonian Liolaemini, a species-rich clade with 257 recognized species of *Liolaemus* (Abdala and Quinteros, 2014) and nearly 40 *Phymaturus* species (Lobo et al., 2013; Avila et al., 2014). These 16 species vary considerably in the size of their distribution ranges: from microendemic species that are known only from the type locality or very few localities covering a small area (e.g., *Liolaemus kolengh*), to widespread species covering areas larger than 150,000 km<sup>2</sup> (e.g., *Liolaemus fitzingerii* and *Liolaemus elongatus*). Our aim was to evaluate the effect of their thermal tolerance and sensitivity given their distinct geographic ranges and phylogenetic relationships in an attempt to elucidate evolutionary patterns of ecophysiological traits.

In this framework we expected to find that (i) species with broader distribution ranges, where climatic fluctuations are present, will show broader thermal tolerance and performance curves compared to species with restricted distributions (Cruz et al., 2005); (ii) genotypes adapted to higher temperatures have greater performance ability than cold-adapted ones ("hotter is better"; Barcroft, 1934; Hochachka and Somero, 1973); (iii) species with broad plasticity levels have lower levels of performance (trade-off between performance level and amplitude indicators (Huey and Bennett, 1987; Garland et al., 1991; Bauwens et al., 1995; Bonino et al., 2011); and (iv) physiological thermal characteristics indicative of thermal breadth should be directly related to environmental thermal amplitude and the area occupied, rather than to mean environmental temperature in accordance with the climatic variability hypothesis (Gaston and Blackburn, 2000). We also explore the potential effects of predicted climate change based on performance breadths and future climatic predictions.

## 2. Materials and methods

### 2.1. Study animals

We studied 16 Liolaemini lizard species with very distinct geographic range sizes (see Table S1 in the supplementary online Appendix): *Liolaemus baguali*, *Liolaemus ceii*, *Liolaemus coeruleus*, *Liolaemus elongatus*, *Liolaemus fitzingerii*, *Liolaemus gallardoi*, *Liolaemus hatcheri*, *Liolaemus kingii*, *Liolaemus kolengh*, *Liolaemus magellanicus*, *Liolaemus multimaculatus*, *Liolaemus shitan*, *L. sp.* (a new and unnamed species), *Liolaemus zullyi*, *Liolaemus xanthoviridis* and *Phymaturus tenebrosus*. Distribution area estimates for each species were obtained through minimum convex polygons from our own collection data, as well as georeferenced data from the literature and museum collections for each studied species (see Table S2 in the supplementary online Appendix).

In all, 319 lizards were collected from different Patagonian localities (covering Neuquén, Río Negro, Chubut and Santa Cruz provinces in Argentina; see Table S1) and the Buenos Aires coast during different field trips between February 2009 and March 2010. After capture, the lizards were transported to the laboratory in cloth bags with moist material to avoid stress and desiccation. In the laboratory, the lizards were released in glass terraria (1.2 m × 0.6 m, subdivided into five lanes of 1.2 m × 0.12 m) where a thermal gradient (20–40 °C) was provided by three infrared lamps of 150 W at one end, so they were able to select their preferred temperature and be fed. Lizards were offered live crickets (*Achaeta domestica*), tenebrio larvae (*Tenebrio molitor*), flower buds and water ad libitum. Lizards that lost 20% or more of their original weight were not included in the experiments.

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