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Thermal biology of *Liolaemus* lizards from the high Andes: Being efficient despite adversity

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ABSTRACT

We studied the efficiency of thermoregulation in four high elevation *Liolaemus* species in the Andes of Salta, Argentina; *Liolaemus irregularis*, *Liolaemus multicolor*, *Liolaemus albiceps* and *Liolaemus yanalcu*. One of the species, *L. irregularis*, shows a broad distribution being in allopatry in some localities and in sympatry with *L. albiceps*, *L. multicolor* and *L. yanalcu* at different sites. Together with this variation in assemblages, the degree of phylogenetic relatedness is different with *L. irregularis* being most closely related to *L. albiceps* than to the other two species (*L. multicolor* and *L. yanalcu*). We measured body (T_b), microenvironmental (T_a, T_s), and operative temperatures (T_e) in the field, and preferred body temperature (T_{pref}) in laboratory for each one of the species of assemblages. Three out of the four species showed a high thermoregulatory efficiency except for *L. yanalcu*, a moderate thermoregulator. The species studied here show high T_b in the field compared to most of the recorded *Liolaemus* species. However, the T_{pref} values were similar to other *Liolaemus* species. No evidence of thermal niche segregation between species in sympatry was observed. Our results suggest that the species studied here, despite living at high elevation and harsh climatic conditions are able to behaviorally or physiologically thermoregulate to achieve T_bs close to their T_{pref}, probably because of low predation risk and perhaps low levels of competition.

1. Introduction

One important aspect for ectotherms is their thermoregulatory efficiency, particularly in variable climates where temperature is a key factor. Temperature has a great impact on ectotherms affecting, physiological, behavioral and life history traits such as, reproductive timing (Zug et al., 2001; Labra and Bozinovic, 2002), reproductive mode (Shine, 2004), growth rate, survivorship (Huey, 1982), locomotion (Hertz et al., 1983; Angilleta et al., 2002) and diet (Espinoza et al., 2004). Additionally, the global increase in temperature has been suggested as a potential threat for lizards at a global scale (Sinervo el al., 2010). Incorporating thermal data from different types of environments may consequently help to disentangle the importance of thermal trends and their effects at local and global scales for lizard faunas. Geographic distribution gradients of elevation and latitude may result in different availability of thermal resources (Van Damme et al., 1987) and consequently affect thermal characteristics of lizards from different habitats (Andrews, 1998) at inter and intraspecific levels (Avery, 1976; Andrews, 1998; Huey et al., 2003).

Field and laboratory studies show that the accuracy of temperature regulation can be influenced by competition and predation (Huey, 1982). For example, interspecific competition in *Anolis* lizards show that the ranges of body temperature can vary, being broader in allopatric species than those of species sympatric with other *Anolis* species (Lister, 1976). On the other hand, a narrowly fixed body temperature due to a narrow thermoregulation may be maladaptative for a species, particularly if heat sources or microhabitats are rare or scattered thus imposing limitations on thermoregulation (Sears, 2005).

Since different species have different ranges it is likely that they may have different thermal requirements, where species with wider geographic ranges are expected to show a wider tolerance and conversely species with narrow distributions expected to be thermal specialists (Huey and Kingsolver, 1989; Addo-Bediako et al., 2000; Cruz et al., 2005). Therefore, different species may have a different susceptibility to global warming (Sinervo et al., 2010), depending on aspects such as distributional range, region where the species occurs, its physiology, among others. Additionally, in case of sympatric species, the degree of relatedness (phylogenetically or morphologically) may affect their interactions for limiting resources (Losos, 2000). Thus, a species with a wide

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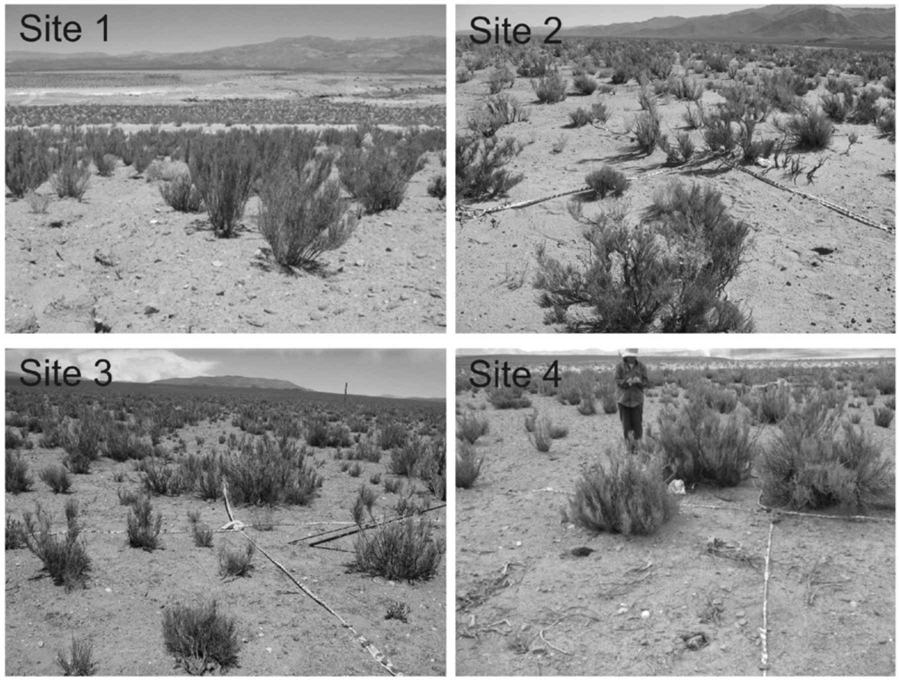

Fig. 1. Photographs of each one of the study sites (1–4). Notice the homogeneity of the environment.

geographic range contacting several congeneric species will have different interaction intensities with each sympatric species. The outcome of these interactions may be related to factors such as phylogenetic distance, aggressiveness, body size, among others.

High elevation environments are thermally challenging, mostly because adequate thermal microhabitats may be scarce. The high elevation Puna habitat of Argentina (above 3500 masl) is a very simple type of habitat with few bushes and bare soil dominating the landscape (Fig. 1), air temperature varies between day and night in a dramatic fashion with hot days (above 30 °C) and nights with temperatures below zero (Cabrera, 1994).

In the Puna habitats several *Liolaemus* species occur. This genus includes more than 230 species (Lobo et al., 2010) that may be found in wet temperate or cold forests to extremely dry deserts, and from sea level to 5100 m above sea level (Cei, 1986; 1993; Aparicio and Ocampo; 2010), showing a great variability of habitat use and presumably a variable ecology. Studies on *Liolaemus* lizards showed both, intra and interspecific differences in daily activity patterns and the type of substrates used (Marquet et al., 1989; Carothers et al., 1997, 1998; Verrastro and Bujes, 1998; Labra et al.; 2001). Additionally, several species differ in their body temperatures in relation to climatic conditions (Halloy and Laurent, 1987; Rocha, 1991, 1995a, b; Labra, 1998; Labra et al., 2001; Ibargüengoytía and Cussac, 2002; Fernández et al., 2011). In the case of *Liolaemus*, reproductive mode is apparently related to elevation, where viviparity is predominant at high elevations (Schulte et al., 2000). Thermal tolerance may be also related to either high elevation or latitude (Cruz et al., 2005). At least one species (*L. lutzae*) was suggested to be threatened by an increase in temperature as a consequence of global warming (Sinervo et al., 2010). Thus, thermal characteristics of the environment may lead to different responses and consequences. Thermal biology of *Liolaemus* species, is labile across their geographic distribution (Rodríguez-Serrano et al., 2009; Moreno Azócar et al., 2012) and thermal tolerances vary in direct relation to the thermal variability of the environments they inhabit (Cruz et al., 2005). However, other studies found that members of the family Liolaemidae show little or no relationship between thermal biology or resting metabolic rates when compared to the environment they inhabit (Cruz et al., 2009, 2011). Given these divergent results for different species, a mixture of adaptive and non-adaptive responses (Labra et al., 2009; Bonino et al., 2011, Moreno Azócar et al., 2012) may be expected.

The thermal biology of high elevation *Liolaemus* species has been seldom studied (but see Halloy and Laurent, 1987; Labra et al., 2001; Cruz et al., 2005). Here we study the thermoregulatory ability and thermal interactions of four species of *Liolaemus* living at high elevation in the Puna of Northwestern Argentina's Salta province; *Liolaemus irregularis*, *Liolaemus multicolor*, *Liolaemus albiceps* and *Liolaemus yanalcu*. The distribution of these species is of particular interest because *L. irregularis* shows a broad distribution being in allopatry in some localities. Yet this species shares its environment with *L. albiceps*, *L. multicolor* and *L. yanalcu* at different sites. Moreover, the degree of phylogenetic relatedness is different among these species, with *L. irregularis* and *L. albiceps* being sister species (Abdala, 2007) and *L. irrgularis* being phylogenetically closer to *L. multicolor* than it is to *L. yanalcu* (Lobo et al., 2010).

Here, we examine and compare the thermal biology in allopatry and sympatry of *L. irregularis* and its interactions with congeneric species with different degrees of phylogenetic relatedness. The main questions we want to answer are: (a) are these species inhabiting the high elevations of the Puna habitat efficient thermoregulators? (b) does the thermal biology reflect the phylogenetic relatedness of species? and (c) is there a relationship between thermal plasticity and distributional ranges in the Puna *Liolaemus* lizards? Additionally, we discuss our results relative to data available for other members of the genus.

2. Materials and methods

2.1. Study area and materials

The species studied here inhabit and are typical of the Puna habitat, which is a high elevation desert located in Northwestern