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# The peak of thermoregulation effectiveness: Thermal biology of the Pyrenean rock lizard, *Iberolacerta bonnali* (Squamata, Lacertidae)

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ABSTRACT

We studied, at 2200 m altitude, the thermal biology of the Pyrenean rock lizard, *Iberolacerta bonnali*, in the glacial cirque of Cotatuero (National Park of Ordesa, Huesca, Spain). The preferred thermal range (PTR) of *I. bonnali* indicates that it is a cold-adapted ectotherm with a narrow PTR (29.20–32.77 °C). However, its PTR (3.57 °C) is twice as wide as other *Iberolacerta* lizards, which may be explained by its broader historical distribution. The studied area is formed by a mosaic of microhabitats which offer different operative temperatures, so that lizards have, throughout their entire daily period of activity, the opportunity to choose the most thermally suitable substrates. *I. bonnali* achieves an effectiveness of thermoregulation of 0.95, which makes it the highest value found to date among the Lacertidae, and one of the highest among lizards. Their relatively wide distribution, their wider PTR, and their excellent ability of thermoregulation, would make *I. bonnali* lizards less vulnerable to climate change than other species of *Iberolacerta*. Thanks to its difficult access, the studied area is not visited by a large number of tourists, as are other areas of the National Park. Thus, it is a key area for the conservation of the Pyrenean rock lizard. By shuttling between suitable microhabitats, lizards achieve suitable body temperatures during all day. However, such thermally suitable microhabitats should vary in other traits than thermal quality, such as prey availability or predation risk. Hence, it seems that these not-thermal traits are not constraining habitat selection and thermoregulation in this population. Therefore, future research in this population may study the causes that would lead lizards to prioritize thermoregulation to such extent in this population.



## 1. Introduction

Temperature strongly influences the rate of biochemical reactions (e.g. Pörtner, 2002) and body temperature can have a deep influence in the performance of biochemical procedure (Angilletta, 2009). Environmental temperature varies with latitude (e.g. Sunday et al., 2014), altitude (e.g. Gvozdík, 2002; Zamora-Camacho et al., 2013, 2015), weather (e.g. Hammerson, 1989), seasons (e.g. Díaz et al., 2006; Ortega et al., 2014), microhabitat structure (e.g. Sears and Angilletta, 2015), and even is currently varying as a consequence of climate change (e.g. Parmesan, 2006), and this variation determines the availability of temperatures for organisms. This thermal variation influences two dimensions of thermal biology (Angilletta, 2009), which define the strategies of organisms to deal with environmental thermal heterogeneity: thermal sensitivity (e.g. Huey and Kingsolver, 1989) and thermoregulation (e.g. Hertz et al., 1993). Thermal sensitivity describes the extent to which physiological performance of an organism depends on temperature, from thermal specialists, whose performance is optimal in a narrow temperature range, to thermal generalists, which are able to perform well in a wide range of temperatures. The other dimension of thermal biology is thermoregulation, or the ability to actively regulate body temperature, which ranges from thermoconformers, whose body temperature equals the environment temperatures anytime, to perfect thermoregulators, whose body temperature is practically independent of environmental temperature (see a review in Angilletta, 2009).

Lacertid lizards are effective thermoregulators, which regulate their body temperature mainly shuttling between microhabitats (Arnold, 1987; Castilla et al., 1999). Some studies have addressed thermal biology of lacertid lizards living at high altitudes (e.g. Aguado and Braña, 2014; Martín and Salvador, 1993; Monasterio et al., 2009), although much additional work would be necessary to understand the thermal biology at high altitudes.

There are three factors that make rock lizards one of the most endangered group of reptiles in front of climate change. First, they live at mountaintops, so they do not have a higher and colder place

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to migrate (e.g. Berg et al., 2010). Then, they tend to be cold-adapted, which not only implies that their optimal temperatures would be exceeded sooner than for not cold-adapted ectotherms, but the impact of exceeding the optimal temperatures would be stronger (e.g. Huey et al., 2012). Finally, a faster increase of environmental temperatures and drought is expected throughout the 21st century in the Iberian mountains (Araújo et al., 2006; Maiorano et al., 2013). Moreover, climate warming not only entails hotter habitats for high mountain lacertids, it may provoke the ascension of low-elevation lizards, which may compete with alpine rock lizards (Comas et al., 2014).

We study the thermal biology of the Pyrenean rock lizard, *Iberolacerta bonnali*, which was thought to be a case of strange non thermoregulatory lacertid (Martínez-Rica, 1977). Following the protocol of Hertz et al. (1993), we assess precision of thermoregulation, thermal quality of the habitat, as well as accuracy and effectiveness of thermoregulation. Thus, we will test the hypothesis of thermoregulation (Hertz et al., 1993) for this species. Furthermore, we assess the spatial and thermal heterogeneity of the habitat of *I. bonnali* in order to describe it for future comparisons between other high mountain lizards. Rock lizards live in high mountain isolated habitats (Pérez-Mellado et al., 2009), where they were located after the last glaciation, as other species of *Iberolacerta* (Crochet et al., 2004; Mouret et al., 2011). Given the vulnerability of Pyrenean rock lizards to global warming (see above), together with the fact that their populations are fragmented, small and isolated, *I. bonnali* lizards might have little chances to survive the current climate change. In this framework, this study could be important because it provides useful information in order to ascertain the capacity of these endemic lizards to survive climate warming.

## 2. Material and methods

### 2.1. Studied species and studied area

The Pyrenean rock lizard, *I. bonnali* (Lantz, 1927), is endemic to the Pyrenees mountains, with a fragmented range between 1550 m and 3062 m of altitude (Arribas, 2004; Arribas, 2009). This species belongs to the "Pyrenean group" of *Iberolacerta*, with a different evolutionary history from other species of the genus (Mayer and Arribas, 2003). Mean snout-vent length of the studied lizards is $56.07 \pm 0.64$ mm and mean weight is $4.24 \pm 0.15$ g, lacking sexual dimorphism for body size (unpub. data, $N=38$). They are insectivorous lizards, whose morphology and coloration is similar to the other two species of the "Pyrenean group" (Arribas, 1994). Like other species of the genus, *I. bonnali* is subjected to a short annual period of activity due to snow coverage most of the year (Arribas, 2009, 2010; Martínez-Rica, 1977).

We studied the thermal biology of *I. bonnali* at the glacial cirque of Cotatuero (Huesca, Spain), in the National Park of “Ordesa y Monte Perdido”, at Central Pyrenees. The study area is at 2200 m of altitude, and consists mainly of rocky crops and moist meadows, crossed by several streams. It is a well-preserved and undisturbed area, probably because the access is restricted through a difficult mountain pass that prevents the racking of tourists that is common in the rest of the National Park.

### 2.2. Field sampling

Body temperatures ($T_b$) were sampled between the 9th and the 14th of August of 2013. From 07.00 to 16.00 h GMT, we captured 46 *I. bonnali* adult lizards (23 males and 23 females) by noosing. For each lizard, we measured cloacal temperature ($T_b$) immediately after capture with a Testo® digital thermometer ($\pm 0.1$ °C precision), introducing the thermal probe 0.5 mm into the vent of lizards. We also measured air temperature ($T_a$) 1 cm above the capture point, and substrate temperature ($T_s$) at the capture point. All temperatures were measured shading the thermal probe, in order to avoid a temperature bias due to sun radiation.

We recorded operative temperatures ($T_e$) in the same area of study, simultaneously to $T_b$ sampling in order to assure the same weather conditions. We used copper models as null $T_e$ models (Bakken and Angilletta, 2014). For small ectotherms, hollow copper models of the same length and diameter of lizards match appropriately the temperature of non-thermoregulating individuals, in order to be used as a null hypothesis of thermoregulation (Shine and Kearney, 2001). One thermocouple probe was placed into each hollow model and connected to a data logger HOBO H8 (® Onset Computer Corporation), programmed to take a temperature recording every five minutes. We used 12 data loggers and models, which were randomly placed in different microhabitats: (1) *under rock* ($N=661$), (2) *flat rock in shade* ($N=660$), (3) *grass in shade* ($N=663$), (4) *soil in shade* ($N=659$), (5) *grass in filtered sun* ($N=665$), (6) *flat rock in full sun* ($N=664$), (7) *rock facing North in full sun* ($N=662$), (8) *rock facing South in full sun* ($N=661$), (9) *rock facing East in full sun* ($N=526$), (10) *rock facing West in full sun* ($N=659$), (11) *grass in full sun* ($N=663$), and (12) *soil in full sun* ($N=665$).

Thermal heterogeneity of the habitat was also quantified as the standard deviation of the mean operative temperatures of the data loggers, following Logan et al. (2015). Furthermore, spatial heterogeneity was described by mean values of the proportion of coverage and the frequency of each microhabitat type of 15 lineal transects, 25 m long each.

### 2.3. Preferred temperature range (PTR)

We studied the PTR of *I. bonnali* on the 15th and 16th of August 2013, immediately after the field work to assure similar weather conditions. We captured 24 Pyrenean rock lizards (12 males and 12 females) during the field work days, which were housed on individual terraria, fed daily with mealworms and crickets, and provided with water ad libitum. The thermal gradient was built in a glass terrarium ($100 \times 60 \times 60$ cm$^3$) with a 150 W infrared lamp over one of the sides, obtaining a gradient between 20 and 60 ºC. A value of a selected temperature ($T_{set}$) of a lizard was recorded with a digital thermometer each hour from 08.00 to 18.00 h (GMT), obtaining 143 selected temperature values. The 50% of central values of selected body temperatures was considered as the PTR to assess thermoregulation (Hertz et al., 1993; Blouin-Demers and Nadeau, 2005). The 80% of central values of selected body temperatures or 80% PTR was only used in plots, not in analysis. After the experiment, lizards were released in the same places of capture.

### 2.4. Data analysis

We followed the protocol developed by Hertz et al. (1993) in order to test the null hypothesis of thermoregulation in *I. bonnali*. Thus, we calculated the indexes of accuracy of thermoregulation ($d_b$), thermal quality of habitat ($d_e$) and effectiveness of thermoregulation ($E$). The index of accuracy of thermoregulation ($d_b$) is the average of absolute values of each deviation between $T_b$ and the PTR. Thus, the higher is the value the lower is the accuracy of thermoregulation. The index of thermal quality of the habitat ($d_e$) is the average of absolute values of each deviation between $T_e$ and the PTR. Thus, the higher is the value the lower is the thermal quality of the habitat. Hence, if we compare the deviation of temperatures that lizards would reach without behavioral thermoregulation (i.e. $T_e$) and the actual temperatures of active lizards