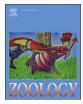
## ARTICLE IN PRESS

### Zoology xxx (xxxx) xxx-xxx



Contents lists available at ScienceDirect

# Zoology



journal homepage: www.elsevier.com/locate/zool

## Physiological differences in preferred temperatures and evaporative water loss rates in two sympatric lacertid species

Marco Sannolo<sup>a,b,\*</sup>, Frederico M. Barroso<sup>a,c</sup>, Miguel A. Carretero<sup>a</sup>

<sup>a</sup> CIBIO, Research Centre in Biodiversity and Genetic Resources, InBIO, Universidade do Porto, Campus de Vairão, Rua Padre Armando Quintas, Vairão, 4485-661, Vila do Conde, Portugal

<sup>b</sup> Departamento de Biologia, Faculdade de Ciências da Universidade do Porto, R. Campo Alegre, s/n, 4169-007, Porto, Portugal

<sup>c</sup> College of Medical, Veterinary and Life Sciences, Graham Kerr Building, University of Glasgow, Glasgow, G12 8QQ, Scotland, UK

## ARTICLE INFO

Keywords: Lacertidae Podarcis Sister species Thermal ecology Water balance Preferred temperature

## ABSTRACT

Sister species living in sympatry offer the opportunity to study the degree of divergence in their ecological, physiological and life-history traits. It has been hypothesized that closely related species with overlapping distribution should differ in their niche to reduce competition for resources. Furthermore, the investigation of sympatric species may shed light on how they may coexist without outcompeting each other. In the present study, we assess the degree of physiological divergence in two sympatric lacertid lizards, *Podarcis bocagei* and *Podarcis guadarramae lusitanicus*. These species share a Pliocenic ancestry and overlap at a both geographical and ecological scale. We assessed their thermal preferences and water loss rates, two physiological traits considered stable across congeneric species. We found that the two species differ in both traits, with *P. bocagei* selecting higher temperature than *P. g. lusitanicus* and losing more water than the latter at and above its preferred temperature. The results also showed that for both species body size has a relevant impact on thermal and hydric traits, with bigger individuals losing proportionally less water and selecting higher temperatures. These results, combined with previous evidence, suggest that physiological mechanisms, ecological preferences and morphology probably allow these two species to overlap in their distribution while selecting different microhabitats and thus decreasing possible competition between them.

## 1. Introduction

Closely related species with sympatric distribution offer the opportunity to study the extent of divergence in their ecology, physiology and life-history traits (Connell, 1983). It has been hypothesized that closely related species belonging to the same ecological guild and living in sympatry should differ to reduce competition (Schulter, 1994). Alternatively, specific combinations, or assemblages of species are expected to exclude one another (Diamond, 1975).

Patterns of divergence in sympatric species are common and encompass a large variety of taxa. For example, interspecific competition and competitive exclusion appear to be relevant in shaping ant communities (Andersen and Patel, 1994), and niche partitioning might be a powerful force segregating fish species in terms of ecological and morphological space (Wikramanayake, 1990). In amphibians, the degree of character displacement can be associated with the intensity of competition between tadpoles of closely related species sharing the same ponds (Pfennig and Murphy, 2002). Depending on the case, either genetic or non-genetic changes can lead to reduced competition through niche shift associated with phenotypic plasticity or character displacement (Pfennig and Murphy, 2002; Price et al., 2003).

Lizards represent an excellent model to study adaptation, competition, niche shift and habitat segregation. For example, *Anolis* lizards from the Caribbean islands have been intensively investigated in this regard on each island, either one or more *Anolis* species are present, with different species assemblages on each island (Roughgarden, 1995). If several species live on the same island, they segregate into different ecomorphs that evolved several times independently (Losos, 1990). It has also been shown that sympatric lizards differ in scale morphology, likely the result of adaptation to different climatic niches (Wegener et al., 2014). Thus, in *Anolis* lizards, interspecific competition has driven the evolution of morphology, behavior, and physiology, shaping the species composition on each island to reduce niche overlap among species (Losos, 1994).

Lizards are also excellent model organisms to investigate thermal adaptation, with seminal studies dating back to the first decades of the

\* Corresponding author at: CIBIO, Research Centre in Biodiversity and Genetic Resources, InBIO, Universidade do Porto, Campus de Vairão, Rua Padre Armando Quintas, Vairão, 4485-661, Vila do Conde, Portugal.

E-mail address: up201410160@fc.up.pt (M. Sannolo).

https://doi.org/10.1016/j.zool.2017.12.003

Received 24 July 2017; Received in revised form 12 December 2017; Accepted 19 December 2017 0944-2006/ © 2017 Elsevier GmbH. All rights reserved.

previous century (Bogert, 1949). An overwhelming amount of evidence has been collected regarding the thermal ecology of many species, as well as the relationship between environmental temperature, body temperature and fitness (Cossins and Bowler, 1987; Angilletta, 2009). Ectotherms rely on external sources of heat to raise their body temperature and many of them actively thermoregulate (Angilletta, 2009). One of the most important themes in thermal biology is related to the concept of the preferred temperature (T<sub>pref</sub>) that represents a range of temperatures, usually narrow, within which most physiological functions are performed nearly at their maximum (Huey and Stevenson, 1979). For lizards, it has been hypothesized that  $T_{pref}$  should be either an evolutionary labile or static trait, depending on the view and the history of the considered group. The labile hypothesis focuses more on local adaptation, while the static one stresses the evolutionary rigidity of T<sub>pref</sub>, considering it an umbrella parameter for many physiological functions (Hertz et al., 1983). On the other hand, thermal ecology is strongly intertwined with water balance. For instance, it has been shown that dehydrated lizards tend to prefer lower body temperature (Crowley, 1987). However, for a long time most studies on lizards focused solely on the thermal aspect of their ecology.

The current state of knowledge on water balance, evaporative water loss (EWL) rates and the effect of temperature on the hydric status of lizards is poor, particularly if compared with the amount of studies focused solely on lizards' thermal biology. For example, in desertdwelling lizards, differences in EWL were shown to be attributable to habitat selection (Dmi'el, 2001), while in Anolis lizards it has been found that species living in drier and warmer climates tend to have fewer dorsal scales, probably to reduce cutaneous water loss (Wegener et al., 2014). However, there is surprisingly little evidence regarding physiological differences among sympatric lizards, especially from temperate climates. García-Muñoz and Carretero (2013), for example, showed that Algyroides marchi and Podarcis hispanica select similar temperatures but are characterized by different water loss rates, possibly associated with different microhabitat selection. To our knowledge, EWL has never been studied at various temperatures for sympatric sister taxa of lizards.

Podarcis wall lizards have been used as model species to investigate many aspects of reptile biology, from evolution (Harris and Arnold, 1999; Herrel et al., 2008) to morphology and life-history traits (Bauwens and Diaz-Uriarte, 1997; Kaliontzopoulou et al., 2012). Conversely, the thermal and hydric ecology of Podarcis species has been investigated in some species but little is known on the relation between thermal ecology and water balance, with studies usually focusing on the thermal preferences of a single species (Ji and Braña, 1999). Regarding EWL rates, information is even more scarce, with data available only for a few species, showing that, in general, either congeneric or heterogeneric species living in sympatry differ in their relative EWL (García-Muñoz and Carretero, 2013; Osojnik et al., 2013; Carneiro et al., 2015). Podarcis species of the Iberomaghrebian clade are an intriguing case to study ecophysiology, due to their high level of genetic diversity coupled with a complex pattern of evolutionary and biogeographical history (Carretero, 2008; Kaliontzopoulou et al., 2011).

In the present study, we examined these two ecophysiological traits, T<sub>pref</sub> and EWL, using two sister taxa of lacertid lizards, *Podarcis bocagei* and *P. guadarramae lusitanicus (sensu Geniez et al., 2014)*. These two species were once included into the *Podarcis hispanica* species complex, from which several lineages have been elevated to species or subspecies level (Harris and Sá-Sousa, 2002). Most of the forms in the complex show an allopatric or parapatric distribution, while *P. bocagei* and *P. g. lusitanicus* are largely sympatric in their distribution range in northwestern Iberian Peninsula (Kaliontzopoulou et al., 2011; Geniez et al., 2014). These two species are characterized by one of the closest genetic distances among the recognized species pairs within the complex (Kaliontzopoulou et al., 2011). In contrast with this phylogenetic proximity, recent studies highlighted how these two closely related species differ substantially in morphological traits and microhabitat use

(Kaliontzopoulou et al., 2012; Gomes et al., 2016). In particular, *P. bocagei* is more robust and seems associated with a more grounddwelling life style in comparison with *P. g. lusitanicus*, which has a more compressed head, associated with a more saxicolous life-style. Furthermore, the former is restricted to Atlantic climate, while the latter occurs both in Atlantic and Mediterranean areas (Loureiro et al., 2008). This mixture of phylogenetic affinity, coupled with overlap in their distribution and divergence in microhabitat use and morphology, makes this two-species system a good candidate to investigate the existence of a divergence in physiological traits directly linked to thermal and hydric biology.

In this context, we expected that (i) if the labile view of  $T_{pref}$  is found in the study system, the two species should differ in thermal preferences due to current or past adaptive processes, even though they are sister taxa; (ii) if instead one of the two species selects for higher temperatures, it should also lose more water, assuming a trade-off between thermal preference and the rate of evaporative water loss,; (iii) considering species distribution, climate affinity, and microhabitat use, *P. g. lusitanicus* would be more resistant to water loss than *P. bocagei*.

### 2. Methods

## 2.1. Individual sampling and housing

Lizards were collected by noosing near Moledo, a coastal locality in northern Portugal (41°50 N, 8°52 W) where the two species live in syntopy. To avoid the effects of reproduction, body condition and ontogeny on T<sub>pref</sub> and EWL, only males with intact tails were captured (Carretero et al., 2005). Samplings took place during August and September 2015. To avoid recaptures across sampling sessions, we applied photo-identification using I<sup>3</sup>S Classic (Van Tienhoven et al., 2007; Sacchi et al., 2016; download at http://www.reijns.com/i3s/). Lizards were brought to the lab where their snout-vent length (SVL) and head height (HH) were measured to the nearest 0.01 mm using a digital calliper and their body mass was measured to the nearest 0.0001 g using a precision balance (Sartorius M-Pact AX224; Sartorius AG, Goettingen, Germany). All measurements were taken by the same person (MS). Lizards were housed in individual terraria (40 cm  $\times$  25 cm  $\times$  25 cm) for two days before experimentation. During this period, lizards had ad libitum access to water and shelter, but no food was given to prevent digestion from affecting T<sub>pref</sub> and EWL (Van Damme et al., 1991). During captivity, lizards were exposed to a natural light cycle regime with daytime air temperature set at 27 °C, and nighttime air temperature set at 20 °C. By the end of the experiment, all lizards were released at the point of capture.

## 2.2. Preferred temperature

We individually exposed 37 P. bocagei and 32 P. g. lusitanicus to gradients (  $\pm$  20–50 °C) thermal by putting them in  $100\ \text{cm} \times 30\ \text{cm} \times 40\ \text{cm}$  acrylic terraria provided with a 150 W infrared lamp at one end. A thin layer of sand (~5 mm) acted as a substrate. Room temperature was kept at 20 °C by an air conditioning system to guarantee the establishment of the gradient inside the terraria. Individuals were granted 24 h of habituation to experimental conditions before the experiment started. Then, every hour, for nine repetitions (10:30-18:30), we measured cloacal temperature with a contact thermometer (Hibok 18, precision: 0.1 °C) fitted with a k-type thermocouple probe. We limited each contact with lizards to 10-15 s to prevent them from changing body temperature during the readings. This procedure might cause some stress to the lizards, but we believe it represented the best option, considering that the use of infrared thermometers or trailing thermocouples attached to the cloaca is not feasible on small species (Trullas et al., 2007; Carretero, 2012). To prevent the lizards from losing water during the experiment, possibly altering the pattern of  $T_{pref}$  (Crowley, 1987), a cup of water was provided in the Download English Version:

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