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The particularities of a remote islet shape the thermoregulatory profile of an endemic Mediterranean lizard



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ABSTRACT

Environmental temperatures considerably affect the reptilian ability for thermoregulation and harsh climatic conditions may impose a highly effective body temperature regulation to lizards. Such demanding conditions are more common to extreme mainland habitats (e.g. deserts or mountains). To the contrary, islands have more benign climate conditions thanks to the thermal buffering effect of the surrounding sea. However, this favorable effect may be eliminated in small size islets where the scarcity of thermal shelters and exposure to high winds create challenging conditions. Here we investigate the impact of a tough islet habitat on the thermoregulation of *Podarcis levendis*, a lacertid lizard endemic to two rocky islets in the north Cretan Sea, Greece. To evaluate the thermoregulatory effectiveness of *P. levendis* we measured operative and body temperatures in the field and the preferred body temperatures in the lab. Analyses of the thermal data revealed an accurate, precise, and effective thermoregulator, achieving very high thermoregulation values ($E = 0.91$, $\bar{d}_e - \bar{d}_b = 7.6$). This high effectiveness comes to compensate living in an inhospitable habitat as the operative temperatures denote ($d_e = 7.79$). Our findings, together with the limited published literature, suggested the lack of a general pattern for all insular lizards and indicated a possible deviation for islet habitats.

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1. Introduction

As ectotherms, reptiles are not capable of producing and using metabolic heat for thermoregulation, at least to a sufficient extent, and thus resort to the behavioral regulation of body temperature as they rely on environmental heat sources (Bogert, 1959; Bartholomew, 1982). Through behavioral thermoregulation ectotherms (and among them reptiles) attempt to deal with the environmental conditions in order to conduct metabolic processes on which fitness depends, as the rate and performance of biochemical procedures are temperature dependent (Porter and Gates, 1969; Pörtner, 2002; Angilletta, 2009). Reptiles should carefully navigate through the thermal mosaic of their environment by exploiting the favorable environmental temperatures (close to their thermal optima), and avoiding exposure to extreme thermal conditions (Avery, 1982). The typical strategy of thermoregulators to achieve this is to change microhabitats depending on their given temperature at a given time-frame, though among thermoconformers (i.e. burrowing species), critical temperatures

plays the decisive role (Huey and Slatkin, 1976; Angilletta et al., 2002). Species living under challenging environmental conditions master this 'shuttle game' and are able to thermoregulate with effectiveness and hence colonize even unfavorable habitats, though may be unable to attain their optima (Hertz et al., 1993; Gvoždík, 2002; Monasterio et al., 2009; Ortega et al., 2016a).

Among the factors that define a thermally unfavorable habitat, environmental temperatures, the most influencing factor in reptilian thermal biology, hold a central role (Medina et al., 2009; Angilletta, 2009; Meiri et al., 2013). Environmental temperatures may vary in response to several factors such as seasonality, weather, or microhabitat structure (Díaz and Cabezas-Díaz, 2004; Díaz et al., 2006; Ortega et al., 2014; Sears and Angilletta, 2015) and are mainly affected, among others, by latitude and altitude (Gvoždík, 2002; Zamora-Camacho et al., 2013; Sunday et al., 2014; Zamora-Camacho et al., 2015). Habitats in high elevation and high latitude are characterized by challenging thermal conditions, and reptiles, mostly lizards, have to be quite effective thermoregulators (Ortega et al., 2016a; Piantoni et al., 2016).

While such extreme climate parameters are not rare in mainland, insularity seems to milder the effect of environmental conditions. Island climate is more benign and stable thanks to the

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buffering effect of the surrounding sea and, as a result, insular habitats have higher thermal quality (Schwaner, 1989; Whittaker and Fernández-Palacios, 2007; Sagonas et al., 2013a). Island lizards take advantage of the favorable insular climate and may afford a less effective thermoregulation compared to their mainland peers (Grbac and Bauwens, 2001; Pafilis, 2003; Sagonas et al., 2013a). However small islets may deviate from this pattern due to particular features. For instance, islets have low habitat heterogeneity because of their small size (Triantis et al., 2006; Sfenthourakis and Triantis, 2009). Also, most islets usually have low elevation and thus are more exposed to sea winds. Thus, the beneficial sea effect could be minimized.

Here we aimed to assess whether the particularities of a tough insular habitat (Pori islet, Cretan Sea) exposed to high winds impose a distinct thermoregulatory pattern on the lizards living therein (*Podarcis levendis*). To that end, we measured field body temperatures (T_b), the set-point range (T_{set}) deriving from the preferred temperatures that animals achieve under laboratory conditions, and operative temperatures (T_e) that a non-thermoregulating animal reaches under natural conditions and represent environmental temperatures (Huey and Slatkin, 1976; Hertz et al., 1993). Using these thermal parameters, we evaluated the standard index of thermoregulation effectiveness and the thermal quality (defined as the deviation of T_e from T_{set} , \bar{d}_e) of the habitat (Hertz et al., 1993). We made three hypotheses. First, we presumed that islet environment would have low thermal heterogeneity, expressed as low fluctuations in the operative temperatures and less extreme values. Second, we hypothesized that contrary to the alleged high thermal quality of the islands, Pori islet would have low thermal quality (high \bar{d}_e) due to its exposure to high winds. Third, we anticipated that the thermoregulation effectiveness of *P. levendis* should be high in response to the (presumed) low thermal quality of the habitat.

2. Material and methods

2.1. Study system

Levendis wall lizard (*Podarcis levendis*, Lacertidae) was recently elevated to species level, separating from the Erhard's wall lizard (*P. erhardii*) (Lymberakis et al., 2008). The species distribution is restricted to only two islets, Pori (0.317 km²) and Lagouvardos (0.0127 km²), in the northwestern Cretan Sea (Fig. 1). It is a small-

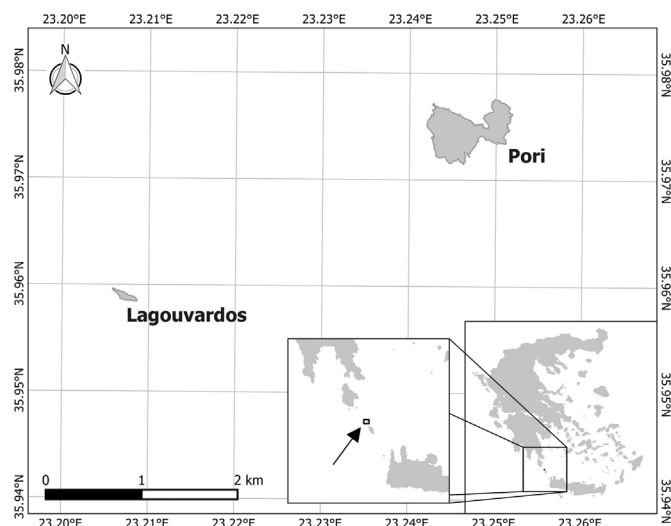


Fig. 1. Map of the two islets hosting *P. levendis* in the northwest Cretan Sea (Greece, NE Mediterranean Basin).

bodied lizard (Snout Vent Length – SVL – for males: 74.50 ± 3.10 mm, SVL for females: 67.50 ± 4.4 mm).

The vegetation of the islet comprises sparse phrygana shrubs, with wild olive trees (*Olea oleaster*) and lentiscs (*Pistacia lentiscus*) as dominating species, and thorny burnet (*Sarcopoterium spinosum*) and tree spurge (*Euphorbia dendroides*) as the main undergrowth species. Pori islet is surrounded by steep, mostly bare cliffs and has a maximum altitude of 120 m. Its eastern side is dominated by low shrubs with openings of bare soil and rocks, whereas in the western side there is also sparse maquis vegetation. The islet host only one more terrestrial reptile, the Kotschy's gecko (*Mediodactylus kotschy*), which does not compete with *Podarcis* lizards (Valakos and Vlachopoulos, 1989).

In May 2010, a field trip took place on Pori islet. Lizards (24 males and 14 females) were captured by noose and were transferred to the laboratory facilities of the Department of Biology at the University of Athens. In the lab, we sexed lizards (on the basis of femoral pores and hemipenis presence, but also on secondary features such as head size and copulation marks) and then recorded SVL to the nearest 0.01 mm with a digital caliper (Silverline 380244) and body mass to the nearest 0.01 g using a digital scale (Ohaus, Scout-TM).

Animals were individually housed in vitreous terraria (80 × 30 × 40 cm) containing sand and bricks (used as shelters), had access to water ad libitum and were fed every other day with mealworms (*Tenebrio molitor*), coated with a multivitamin powder (TerraVit Powder, JBL GmbH & Co. KG). Temperature in the animal house was 25 °C. Each terrarium had a controlled photoperiod thanks to fluorescent tube lighting (12 light: 12 dark), while additional incandescent lamps (60 W) allowed lizards to thermoregulate for 8 h per day.

2.2. Lizard temperatures (T_b and T_{set})

We took T_b s of 38 (14 females and 24 males) lizards that were captured in the field. Body temperatures were recorded within 10 s after capture (Verissimo and Carretero, 2009; Osojnik et al., 2013) with a quick-reading cloacal thermometer (T-4000, Miller & Weber, Inc., Queens, NY, accurate to 0.1 °C).

We measured T_{pref} in 12 adult lizard (7 males and 5 females; the limited sample size is due to the strict protection status of the species by the Hellenic Law and the particularly hard access to the islet) in a specially designed terrarium (100 × 25 × 25 cm) that had two ice bags at one end and two heating lamps (100 W and 60 W) at the other end, thus providing a thermal gradient ranging from 10 to 50 °C (Van Damme et al., 1986). Before starting taking measurements, we allowed lizards to acclimate for an hour (Hitchcock and McBrayer, 2006; Sagonas et al., 2013a, 2013b; Carretero, 2012; Carneiro et al., 2015). Preferred temperatures were recorded every hour for a 5 h period (acclimation period lasted from 9:00 am to 10:00 am; T_{pref} were recorded between 10:00a.m. and 3:00p.m.) with a quick-reading cloacal thermometer. Females were not gravid, since this would affect T_{pref} (Carretero et al., 2005). Set-point range (T_{set}), an index of the thermal optima of organisms (Carretero et al., 2005; Clusella-Trullas et al., 2007), was estimated as the central 50% of all T_{pref} (Hertz et al., 1993).

2.3. Operative temperatures (T_e)

In order to estimate T_e s we used 12 hollow copper models built to mimic the conductive and reflective properties of *P. levendis* (Bakken et al., 1983; Bakken, 1992; Dzialowski, 2005; Bakken and Angilletta, 2014). Models (length: 70 mm, diameter: 12.2 mm) were closed at both ends and filled with 2.5–3 ml of water to replicate the heat storage capacity of lizards (Grbac and Bauwens,

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