Journal of Thermal Biology 61 (2016) 55–60

Contents lists available at ScienceDirect

Journal of Thermal Biology

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

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

Panayiotis Pafilis [a,*], Petros Lymberakis [b], Kostas Sagonas [c], Efstratios Valakos [c]

[a] Section of Zoology and Marine Biology, Department of Biology, National and Kapodistrian University of Athens, Panepistimiopolis, Ilissia 15784, Greece
[b] Natural History Museum of Crete, University of Crete, Irakleio, Greece
[c] Section of Animal and Human Physiology, Department of Biology, National and Kapodistrian University of Athens, Panepistimiopolis, Ilissia 15784, Greece

ARTICLE INFO

Article history:
Received 7 June 2016
Received in revised form
23 August 2016
Accepted 23 August 2016
Available online 26 August 2016

Keywords:
Islands
Thermal adaptation
Habitat quality
Lizards
Lacertidae

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 ($E = 0.91$, $\overline{d_e} - \overline{d_b} = 7.6$). 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.

© 2016 Elsevier Ltd. All rights reserved.

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 (Gvozdík, 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 milden the effect of environmental conditions. Island climate is more benign and stable thanks to the

* Corresponding author.
E-mail address: ppafil@biol.uoa.gr (P. Pafilis).

http://dx.doi.org/10.1016/j.jtherbio.2016.08.007
0306-4565/© 2016 Elsevier Ltd. All rights reserved.

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}, $\overline{d_e}$) 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 $\overline{d_e}$) 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 km^2) and Lagouvardos (0.0127 km^2), in the northwestern Cretan Sea (Fig. 1). It is a small-bodied lizard (Snout Vent Length – SVL – for males: 74.50 ± 3.10 mm, SVL for females: 67.50 ± 4.4 mm).

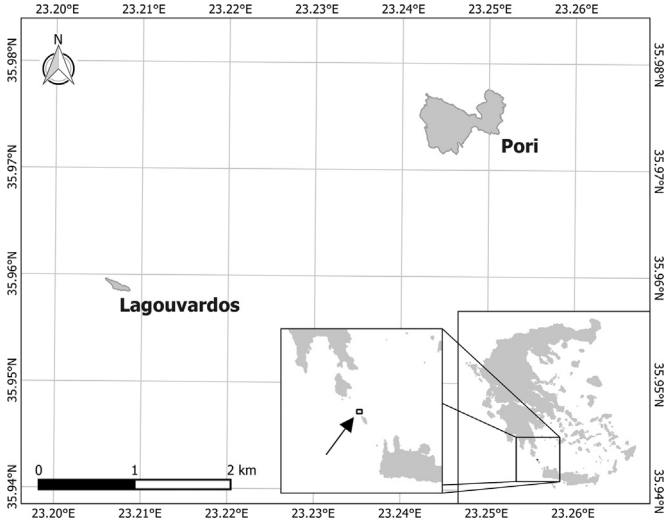

Fig. 1. Map of the two islets hosting *P. levendis* in the northwest Cretan Sea (Greece, NE Mediterranean Basin).

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 kotschyi*), which does not compete with *Podarcis* lizards (Valakos and Vlachopanos, 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_bs of 38 (14 females and 24 males) lizards that were captured in the field. Body temperatures were recorded within 10 s after capture (Veríssimo 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_es 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,

2001; Lutterschmidt and Reinert, 2012). At the one end we left a narrow slot where the logger probes (HOBO U12 4-Channel External Data Logger—U12-008) were plugged in Díaz (1997). The models were placed to cover the different types of microhabitats (in terms of exposure to sunlight) that were available to lizards (Bakken et al., 1985; Huey, 1991). For each model we recorded the condition of exposure (full light [FL] and shade [S]). Operative temperatures were recorded for two consecutive days from 9:00 to 19:00 at 15 min intervals. The thermal heterogeneity of the habitat was quantified as the standard deviation of the mean T_es (Logan et al., 2015).

Before placing the models in the field and to ensure the similarity of the thermal responses between the copper models and the lizards (Hertz, 1992), we performed (three times) a pilot laboratory experiment of cooling and heating rates (Lutterschmidt and Reinert, 2012). A lizard and a model were placed side-by-side under a 150 W lamp. We measured their temperature at 5-min intervals for one hour. After this period we turned off the heat lamp and the cooling phase lasted for another 90 min. We also took temperatures at 5-min intervals with a quick-reading cloacal thermometer. Major axis regression analysis of T_b and T_e (lmodel2 package in R v 2.15.3; R Development Core Team, 2013) suggested a similar thermal response between the lizard and the model (slope $=1.097 \pm 0.038$, intercept $=-2.632 \pm 1.056$; $r^2=0.973$, $N=28$, $P<0.001$).

2.4. Effectiveness of thermoregulation

The effectiveness of thermoregulation was assessed with the formula proposed by Hertz et al. (1993):

$$E = 1 - \left(\overline{d_b}/\overline{d_e}\right),$$

where $\overline{d_b}$ is the mean deviation of field T_b from T_{set} and denotes the accuracy of thermoregulation and $\overline{d_e}$ is the mean deviation of T_e from T_{set} and describes the thermal quality of the habitat. The values of E range from zero (for thermoconformers that select microhabitats randomly and have $\overline{d_b}$ similar to $\overline{d_e}$) to one (for thermoregulators that actively select the appropriate microhabitats where $\overline{d_e}$ is higher than $\overline{d_b}$) (Hertz et al., 1993).

The classical evaluation of the thermoregulation effectiveness (Hertz et al., 1993) largely depends on the values that $\overline{d_b}$ and $\overline{d_e}$ receive. Nonetheless different $\overline{d_b}/\overline{d_e}$ combinations may lead to the same estimation of thermoregulation effectiveness, masking that way the subtle variations of the thermal environment. Thus, we used a complementary method that quantifies the extent of departure from perfect thermoconformity, as proposed by Blouin-Demers and Weatherhead (2001). Positive $\overline{d_b}-\overline{d_e}$ values indicate thermoregulation, zero describes perfect thermoconformity, whereas negative values denote animals that avoid habitats having high thermal quality. The magnitude of the difference between $\overline{d_e}$ and $\overline{d_b}$ provides an index of the effectiveness of thermoregulation (Blouin-Demers and Weatherhead, 2001).

2.5. Statistical analyses

All data were tested for normality (Kolmogorov-Smirnof test) and homogeneity of variances (Levene's test). Whenever parametric assumptions were not met, we performed non-parametric tests. We performed Mann-Witney U-test to examine the differences between the two sexes for T_b and T_{pref} and between models exposed to full light and models that were in shade. Student t-test was used to estimate the differences between T_e and T_{pref}. All test were two-tailed ($\alpha=0.05$). Statistical analysis was performed according to Zar (2010). All analyses were conducted in SPSS (Vs. 23, IBM Corporation).

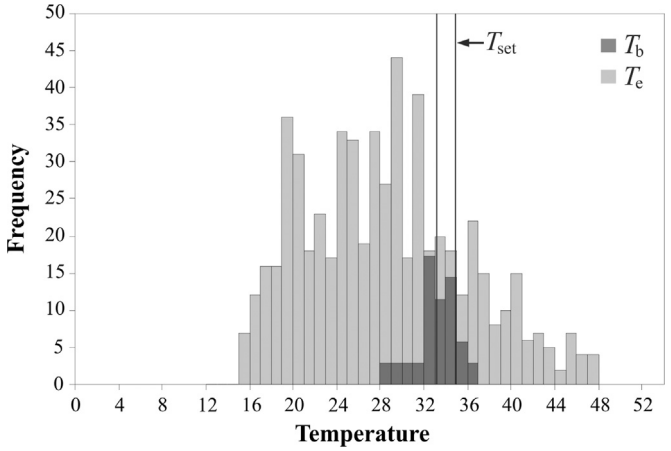

Fig. 2. Plot representing the field body temperature (T_b), operative temperatures (T_e) and set-point temperature (T_{set}) for *P. levendis*.

3. Results

Mean T_b recorded in the field was 32.30 °C for females and 33.58 °C for males. However, no statistically significant difference was found between sexes ($Z=1.401$, $P=0.161$) (Table 2) and thus data were pooled for subsequent analyses. Likewise, T_{pref} did not differ between sexes (males: 34.09 °C and females: 33.77 °C; t-test; $t=1.177$, $df=58$, $P=0.244$) (Table 2) and data were also pooled. The interquartile range of T_{set} for the 50% of all temperatures measured in the laboratory was located from 33.1 to 34.8 °C (Fig. 2). Finally, operative temperatures ranged from 15.62 °C at 9:00 (lowest T_e) to 47.43 °C at 12:30 (highest T_e) (Table 2).

To evaluate the effectiveness of thermoregulation we first calculated $\overline{d_b}$ (0.73 ± 0.26) and $\overline{d_e}$ (7.79 ± 0.21) and then entered them into the Hertz et al. (1993) formula from which a high E value (0.91) arose. The alternative approach we employed (Blouin-Demers and Weatherhead, 2001), corroborated the latter finding and revealed a very high effectiveness of thermoregulation ($\overline{d_e}-\overline{d_b}=7.6$).

To analyse the thermal profile of the habitat we compared the T_e-records during the day based on the solar type. As expected, sun exposed microhabitats were warmer than the shaded ones ($Z=-2.611$, $P=0.009$). Interestingly, T_es from both shaded (24.39 ± 0.62 °C; mean ± StE) and sunny patches (30.87 ± 0.62 °C) were significantly lower than the T_{set} (34.02 ± 0.25 °C) (ANOVA, $F_{2,37}=107.878$, $P<0.001$; Tukey post-hoc test). Field data indicated that the T_es were lower than the 25% quartile of T_{pref} for *P. levendis* for almost 79% of the time. This finding suggests a rather cool thermal environment with low fluctuations (Fig. 2). The thermal heterogeneity of the habitat was calculated to 4.33 °C ($N=12$).

4. Discussion

The analyses of the thermal data offered support to our initial hypotheses. Islet environment had indeed low thermal heterogeneity (with few extreme values and low T_es fluctuations) and low thermal quality (high $\overline{d_e}$), which we expect to further exacerbate during the more difficult summer months (Osojnik et al., 2013), whereas Levendis wall lizard achieved highly effective thermoregulation. According to these findings, it seems that the challenging conditions on Pori islet during spring shaped the thermoregulatory profile of *P. levendis* that deviates from the pattern that other studies reported for insular populations (high thermal quality and low thermoregulatory effectiveness) (Grbac

and Bauwens, 2001; Sagonas et al., 2013a).

In line with our first hypothesis, the operative temperatures on Pori showed little fluctuation, indicating a poor thermal environment: T_es values ranged within a quite narrow thermal window, varying from 15.62 to 47.43 (Fig. 2). The upper T_es limits were much lower than those reported from other east Mediterranean islands (Adamopoulou and Valakos, 2005; Sagonas et al., 2013a, 2013b), and can be compared only to high elevations habitats (Monasterio et al., 2009; Ortega et al., 2016a). The lack of extreme values combined with the low average T_es (Table 2), defined the low thermal heterogeneity on Pori.

Islands are supposed to have a milder climate than mainland, which is reflected in their higher thermal quality (Schwaner, 1989; Grbac and Bauwens, 2001; Sagonas et al., 2013a). However our results sketched out a habitat of low thermal quality (Table 2, Fig. 2), as the thermal quality index (*sensu* Hertz et al., 1993) received high values ($\overline{d_e}$ =7.79), higher than any other east Mediterranean habitat studied so far (Pafilis, 2003; Adamopoulou and Valakos, 2005; Sagonas et al., 2013a, 2013b), exceeding even mainland habitats (Sagonas et al., 2013a; Zamora-Camacho et al., 2015; Ortega et al., 2016a, 2016b). The low thermal quality of continental habitats (high $\overline{d_e}$ values) is usually attributed to the more intense fluctuations of T_es and the higher values of operative temperatures (Sagonas et al., 2013a; Ortega et al., 2016a). This was not the case on Pori islet where the low thermal quality was due to the low T_e readings that define a rather "chilly" habitat (Table 2). We believe that the reason for this finding should be sought to the geographical position of the islet under study. Pori is located in the marine area connecting Aegean and Ionian Seas where no other land mass exists for hundreds of miles in the east-west axis (Fig. 1). As such the islet is exposed to high winds (average wind speed during May: 18 km/h; meteoblue.com) and its low elevation (highest point 129 m) that provides limited protection from the winds, further exacerbates the hard prevailing conditions. Wind intensity is known to affect lizard activity and, consequently, thermoregulation (Scheers and Van Damme, 2002; Maia-Carneiro et al., 2012; Logan et al., 2015). A similar case of low T_e readings has been reported from Aire, an islet in west Mediterranean that also has low elevation (Ortega et al., 2014, Table 1).

For most of the time (79%) operative temperatures were lower than T_{set} (Fig. 2), resulting to the very high $\overline{d_e}$ that was mentioned above. In other words, *P. levendis* has to strive against an unfavorable thermal habitat to achieve body temperatures that would allow physiological functionality. Theory predicts that a thermally challenging environment would dictate a careful thermoregulation and thus *E* would tend to approach one (Hertz et al., 1993, but important deviations have been reported, e.g. Ibargüengoytía et al., 2010). Following this rule, *E* for *P. levendis* received an imposing 0.91, revealing an effective thermoregulator and highlighting the thermal peculiarities of the focal habitat. The complementary approach we used to evaluate thermoregulation (Blouin-Demers and Weatherhead, 2001) confirmed the high effectiveness of temperature regulation and provided the highest value (7.6) reported so far for lacertids, to the best of our knowledge.

Field body temperatures and T_{set} received values within the same range with other insular Mediterranean lacertids (Table 1) (Pérez-Mellado and Salvador, 1981; Castilla and Bauwens, 1991; Grbac and Bauwens, 2001; Adamopoulou and Valakos, 2005; Ortega et al., 2014). T_bs fell within the T_{set} while their diel variation was limited, a finding indicating high precision in thermoregulation (Table 1, Fig. 2) (Hertz et al., 1993). Furthermore, mean d_b was low (0.73), revealing high accuracy in thermoregulation (Hertz et al., 1993). In other words, *P. levendis* is not only an effective, but also a precise and accurate thermoregulator.

Our results do not conform to the high thermal quality of islands and low thermoregulatory effectiveness of insular populations predicted by other studies (Grbac and Bauwens, 2001; Pafilis, 2003; Sagonas et al., 2013a). In fact, our findings suggest that Pori islet is a harsh habitat where lizards have to intensify their thermoregulation efforts. A review of the published literature on *Podarcis* islanders denoted that there is no uniform pattern (Table 1): insular populations may achieve low *E* values (*P. melisellensis* or *P. erhardii*) but also reach high effectiveness in response to habitat particularities (e.g. dunal ecosystems for *P. milensis* and *P. gaigeae*). However, a consistent trend seems to arise from islet populations (first five rows in Table 1). Mediterranean islets demonstrate rather high $\overline{d_e}$ (low thermal quality). In order to deal with such challenging conditions, islet lizards have to thermoregulate effectively to achieve T_b as close as possible to their T_{set}, and this is exactly what they do (*E* values vary from 0.72 to 0.95, Table 1). Thanks to this quite effective thermoregulation islet *Podarcis* afford to survive in unfavorable habitats so as to avoid poor organism's performance (Blouin-Demers and Weatherhead, 2002; Blouin-Demers and Nadeau, 2005).

Mediterranean islets are challenging habitats with limited food resources and low thermal quality (Ouboter, 1981; Brown et al., 1992; Blondel et al., 2010; Sagonas et al., 2013a; Ortega et al., 2014). Lizards living on these islets share a sequence of common features that include high population density (Pérez-Mellado et al., 2008; Pafilis et al., 2009), low predation pressure (Tsasi et al., 2009; Durand et al., 2012), poor food availability (Carretero et al., 2010; Pérez-Cembranos et al., 2016) and strong intraspecific

Table 1
Data on the effectiveness of thermoregulation (E), set-point range (T_{set}) and thermal quality of habitats (mean d_e, the deviation of T_e from T_{set}) for *Podarcis* lizards grouped in islets (rows 1–5), islands (6–11) and mainland (12–16).

Species	Location	E	T_{set}	d_e	Reference
P. levendis	Pori Island, GR	0.91	33.9	7.79	This study
P. gaigeae	Diavates Islet, GR	0.72	34.6	4.8	Sagonas et al., 2013a
P. lilfordi	Aire Islet, ES	0.81	35	11	Ortega et al., 2014
	Colom Islet, ES	0.86			
P. liolepis	Columbretes Islet, ES	0.95	34.2	6.3	Bauwens et al., 1996
P. erhardii	Andros Island, GR	0.66	35.1	6.3	Pafilis, 2003
P. gaigeae	Skyros Island, GR	0.87	33.7	7.2	Sagonas et al., 2013a
P. melisellensis	Cres Island, HR	0.63	33.5	11.05	Grbac and Bauwens, 2001
P. melisellensis	Vis Island, HR	0.83	33.9	6.27	Scheers and Van Damme, 2002
P. milensis	Milos Island, GR	0.95	33.4	3	Adamopoulou and Valakos, 2005
P. muralis	Cres Island, HR	0.81	31.9	9.55	Grbac and Bauwens, 2001
P. peloponnesiacus	North Peloponnese, GR	0.76	34	5.43	Pafilis, 2003
	South Peloponnese, GR	0.75	33.8	6.1	
P. siculus	Athens, GR	0.96	33.8	3.2	Kapsalas et al., in press

Table 2
Values for the thermal parameters ruling thermoregulation. Operative (T_e), body (T_b) and preferred (T_{pref}) temperatures, deviation of T_e from T_{set} (d_e) and deviation of T_b from T_{set} (d_b) for *Podarcis levendis* population at Pori islet. T_e range has been calculated by the mean operative temperatures of each hollow copper model. Means ± standard error; range; sample size.

T_b (°C)	T_{pref} (°C)	T_e (°C)	d_b	d_e
33.2 ± 1.83	33.95 ± 1.06	27.63 ± 1.37	0.73 ± 0.26	7.79 ± 0.21
(29.0–36.4)	(33.7–34.6)	(21.16–35.86)	(0.0–4.1)	(0.0–17.48)
N=38	*N*=12	*N*=12	*N*=38	*N*=12

competition (Pafilis et al., 2008; Cooper et al., 2015). Our results, taken together with those of other studies (Bauwens et al., 1996; Ortega et al., 2014), suggest that effective thermoregulation could be added to the islet characteristics' list. These tiny islands, with their high space homogeneity and low thermal heterogeneity, represent thermally challenging habitats. In order to overcome the environmental obstacles, lizards have to successfully thermoregulate. *Podarcis levendis* achieve indeed an accurate, precise, and effective thermoregulation. Similar studies on more islets within and outside Mediterranean Sea will shed light on the generality of this pattern and also on the possible trade-offs between thermoregulation effectiveness and other islet particularities such as herbivory (Tosini et al., 1994; Carretero, 2004; Vitt et al., 2005).

Acknowledgements

We are grateful to Grigoris Kapsalas for drawing the map. Fieldwork and lab measurements were conducted in accordance with the Greek National Legislation (Presidential Decree 67/81).

References

Adamopoulou, C., Valakos, E.D., 2005. Thermal ecology and activity cycle of *Podarcis milensis* in a sandy coastal area. Isr. J. Zool. 51, 39–52.
Angilletta, M.J., Hill, T., Robson, M.A., 2002. Is physiological performance optimized by behavioral thermoregulation? A case study of the eastern fence lizard, *Sceloporus undulatus*. J. Therm. Biol. 27, 199–204.
Angilletta, M.J., 2009. Thermal Adaptation: A Theoretical and Empirical Synthesis. Oxford University Press, Oxford.
Avery, R.A., 1982. Field studies of body temperatures and thermoregulation. In: Gans, C., Pough, F.H. (Eds.), Biology of the Reptilia, Physiology C, Physiological Ecology. Academic Press, New York, pp. 93–166.
Bakken, G.S., Erskine, D.J., Santee, W.R., 1983. Construction and operation of heated taxidermic mounts used to measure standard operative temperature. Ecology 64 (6), 1658–1662.
Bakken, G.S., Santee, W.R., Erskine, D.J., 1985. Operative and standard operative temperature: tools for thermal energetics studies. Am. Zool. 25 (4), 933–943.
Bakken, G.S., 1992. Measurement and application of operative and standard operative temperatures in ecology. Am. Zool. 32, 194–216.
Bakken, G.S., Angilletta, M.J., 2014. How to avoid errors when quantifying thermal environments. Funct. Ecol. 28, 96–107.
Bartholomew, G.A., 1982. Physiological control of body temperatures. In: Gans, C., Pough, F.H. (Eds.), Biology of the Reptilia, Biology of the Reptilia, Physiology C, Physiological Ecology. Academic Press, New York, pp. 167–211.
Bauwens, D., Hertz, P.E., Castilla, A.M., 1996. Thermoregulation in a lacertid lizard: the relative contributions of distinct behavioral mechanisms. Ecology 77, 1818–1830.
Blouin-Demers, G., Nadeau, P., 2005. The cost-benefit model of thermoregulation does not predict lizard thermoregulatory behavior. Ecology 86, 560–566.
Blouin-Demers, G., Weatherhead, P.J., 2001. Thermal ecology of black rat snakes (*Elaphe obsoleta*) in a thermally challenging environment. Ecology 82, 3025–3043.
Blouin-Demers, G., Weatherhead, P.J., 2002. Habitat-specific behavioural thermoregulation by black rat snakes (*Elaphe obsoleta obsoleta*). Oikos 97, 59–68.
Bogert, C.M., 1959. How reptiles regulate their body temperatures. Sci. Am. 200, 105–120.
Blondel, J., Aronson, J., Bodiou, J.-Y., Boeuf, G., 2010. The Mediterranean Region: Biological Diversity in Space and Time, Second edition. Oxford University Press, New York.
Brown, R., Pérez-Mellado, V., Diego-Rasilla, J., Garcia, J.A., Naranjo, A., Speakman, J. R., 1992. Individual and population energetics of a lizard on a Mediterranean islet. Oecologia 91, 500–504.
Carneiro, D., García-Muñoz, E., Kaliontzopoulou, A., Llorent, G.A., Carretero, M.A., 2015. Comparing ecophysiology traits in two *Podarcis* wall lizards with overlapping ranges. Salamandra 51, 335–344.
Carretero, M.A., 2004. From set menu to a la carte. Linking issues in trophic ecology of Mediterranean lacertids. Ital. J. Zool. 74 (2), 121–133.
Carretero, M.A., Roig, J.M., Llorente, G.A., 2005. Variation in preferred body temperatures in an oviparous population of *Lacerta* (*Zootoca*) *vivipara*. Herpetol. J. 15, 51–55.
Carretero, M.A., Lo Cascio, P., Corti, C., Pasta, S., 2010. Sharing resources in a tiny Mediterranean island? Comparative diets of *Chalcides ocellatus* and *Podarcis filfolensis* in Lampione. Bonn Zool. Bull. 57, 111–118.
Carretero, M.A., 2012. Measuring body temperatures in small lacertids: infrared vs contact thermometers. Basic Appl. Herpetol. 26, 99–105.
Castilla, A.M., Bauwens, D., 1991. Thermal biology, microhabitat selection and conservation of the insulaer lizard *Podarcis hispanica atrata*. Oecologia 85, 366–374.
Clusella-Trullas, S., Terblanche, J.S., van Wyk, J.H., Spotila, J.R., 2007. Low repeatability of preferred body temperature in four species of Cordylid lizards: temporal variation and implications for adaptive significance. Evol. Ecol. 21, 63–79.
Cooper, J.W.E., Dimopoulos, I., Pafilis, P., 2015. Sex, age and population density affect aggressive behaviors in island lizards promoting cannibalism. Ethology 121, 260–269.
Díaz, J.A., 1997. Ecological correlates of the thermal quality of an ectotherm's habitat: a comparison between two temperate lizard populations. Funct. Ecol. 18, 867–875.
Díaz, J.A., Cabezas-Díaz, S., 2004. Seasonal variation in the contribution of different behavioural mechanisms to lizard thermoregulation. Funct. Ecol. 18, 867–875.
Díaz, J.A., Iraeta, P., Monasterio, C., 2006. Seasonality provokes a shift of thermal preferences in a temperate lizard, but altitude does not. J. Therm. Biol. 31, 237–242.
Durand, J., Legrand, A., Tort, M., Thiney, A., Michniewicz, R.J., Coulon, A., Aubret, F., 2012. Effects of geographic isolation on anti-snakes responses in the wall lizard *Podarcis muralis*. Amphibia-Reptil. 33, 199–206.
Dzialowski, E.M., 2005. Use of operative temperature and standard operative temperature models in thermal biology. J. Therm. Biol. 30, 317–334.
Grbac, I., Bauwens, D., 2001. Constraints on temperature regulation in two sympatric *Podarcis* lizards during autumn. Copeia 2001, 178–186.
Gvoždík, L., 2002. To heat or to save time? Thermoregulation in the lizard *Zootoca vivipara* (Squamata: Lacertidae) in different thermal environments along an altitudinal gradient. Can. J. Zool. 80, 479–492.
Hitchcock, M.A., McBrayer, L.D., 2006. Thermoregulation in nocturnal ecthotherms: seasonal and intraspecific variation in the Mediterranean Gecko (*Hemidactylus turcicus*). J. Herpetol. 40, 185–195.
Hertz, P.E., 1992. Temperature regulation in Puerto-Rican *Anolis* lizards: a field test using null hypothesis. Ecology 73, 1405–1417.
Hertz, P.E., Huey, R.B., Stevenson, R.D., 1993. Evaluating temperature regulation by field-active ectotherms: the fallacy of the inappropriate question. Am. Nat. 142, 796–818.
Huey, R.B., Slatkin, M., 1976. Cost and benefits of lizard thermoregulation. Q. Rev. Biol. 51, 363–384.
Huey, R., 1991. Physiological consequences of habitat selection. Am. Nat. 137, 91–115.
Ibargüengoytía, N.R., Medina, S.M., Fernández, J.B., Gutiérrez, J.A., Tappari, F., Scolaro, A., 2010. Thermal biology of the southernmost lizards in the world: *Liolaemus sarmientoi* and *Liolaemus magellanicus* from Patagonia, Argentina. J. Therm. Biol. 35, 21–-227.
Kapsalas, G., Gavriilidi, I., Adamopoulou, C., Foufopoulos, J., Pafilis, P., 2016. Effective thermoregulation in a newly established population of *Podarcis siculus* in Greece: a possible advantage for a successful invader. Acta Herpetol. (in press)
Logan, M.L., Fernandez, S.G., Calsbeek, R., 2015. Abiotic constraints on the activity of tropical lizards. Funct. Ecol. 29, 694–700.
Lutterschmidt, W.I., Reinert, H.K., 2012. Modeling body temperature and thermal inertia of large-bodied reptiles: support for water-filled biophysical models in radiotelemetric studies. J. Therm. Biol. 37, 282–285.
Lymberakis, P., Poulakakis, N., Kaliontzopoulou, A., Valakos, E., Mylonas, M., 2008. Two new species of *Podarcis* (Squamata; Lacertidae) from Greece. Syst. Biodivers. 6, 1–12.
Maia-Carneiro, T., Dorico, T.A., Rocha, C.F.D., 2012. Influences of seasonality, thermal environment and wind intensity on the thermal ecology of Brazilian sand lizards in a restinga remnant. — South American. J. Herpetol. 7, 241–251.
Medina, M., Gutierrez, J., Scolaro, A., Ibargüengoytía, N., 2009. Thermal responses to environmental constraints in two populations of the oviparous lizard *Liolaemus bibronii* in Patagonia, Argentina. J. Therm. Biol. 34, 32–40.
Meiri, S., Bauer, A.M., Chirio, L., Colli, G.R., Das, I., Doan, T.M., Feldman, A., Herrera, F.-C., Novosolov, M., Pafilis, P., Pincheira-Donoso, D., Powney, G., Torres-Carvajal, O., Uetz, P., Van Damme, R., 2013. Are lizards feeling the heat? A tale of ecology and evolution under two temperatures. Glob. Ecol. Biogeogr. 22 (7), 834–845.
meteoblue.com: ⟨https://www.meteoblue.com/en/weather/forecast/modelclimate/antikythera_greece_265080⟩.
Monasterio, C., Salvador, A., Iraeta, P., Díaz, J.A., 2009. The effects of thermal biology and refuge availability on the restricted distribution of an alpine lizard. J. Biogeogr. 36, 1673–1684.
Ortega, Z., Pérez-Mellado, V., Garrido, M., Guerra, C., Villa-García, A., Alonso-Fernández, T., 2014. Seasonal changes in thermal biology of *Podarcis lilfordi* (Squamata, Lacertidae) consistently depend on habitat traits. J. Therm. Biol. 39, 32–39.
Ortega, Z., Mencía, A., Pérez-Mellado, V., 2016a. The peak of thermoregulation effectiveness: thermal biology of the Pyrenean rock lizard, *Iberolacerta bonnali* (Squamata, Lacertidae). J. Therm. Biol. 56, 77–83.
Ortega, Z., Mencía, A., Pérez-Mellado, V., 2016b. Are mountain habitats becoming more suitable for generalist than cold-adapted lizards thermoregulation? PeerJ 4, e2085. http://dx.doi.org/10.7717/peerj.2085.
Osojnik, N., Žagar, A., Carretero, M.A., García-Muñoz, E., Vrezec, A., 2013. Ecophysiological dissimilarities of two sympatric lizards. Herpetologica 69 (4), 445–454.
Ouboter, P.E., 1981. The ecology of the island-lizard *Podarcis sicula salfi*: correlations of microdistribution with vegetation coverage, thermal environment and foodsize. Amphibia-Reptil. 2, 243–257.
Pafilis, P., 2003. Adaptations of Lacertids Based on Their Thermal Biology, Metabolic

Rate and Phylogenetic History (Ph.D. Thesis). University of Athens, Greece.
Pafilis, P., Pérez-Mellado, V., Valakos, E.D., 2008. Post autotomy tail activity in Balearic wall lizard, *Podarcis lilfordi*. Naturwissenschaften 95, 217–221.
Pafilis, P., Meiri, S., Foufopoulos, J., Valakos, E., 2009. Intraspecific competition and high food availability are associated with insular gigantism in a lizard. Naturwissenschaften 96, 1107–1113.
Pérez-Cembranos, A., León, A., Pérez-Mellado, V., 2016. Omnivory of an insular lizard: sources of variation in the diet of *Podarcis lilfordi* (Squamata, Lacertidae). PLoS One 11, e0148947. http://dx.doi.org/10.1371/journal.pone.0148947.
Pérez-Mellado, V., Salvador, A., 1981. Actividad y termorregulación estival de *Podarcis pityusensis* BOSCÀ, 1883 (Saura: Lacertidae) en Ibiza y Formentera. Amphibia-Reptil. 2, 181–186.
Pérez-Mellado, V., Hernandez-Estevez, J., Garcia-Diez, T., Terrassa, B., Ramon, M., Castro, J., Picornell, A., Martin-Vallejo, J., Brown, R., 2008. Population density in *Podarcis lilfordi* (Squamata, Lacertidae), a lizard species endemic to small islets in the Balearic Islands (Spain). Amphibia-Reptil. 29, 49–60.
Piantoni, C., Navas, C.A., Ibargüengoytía, N.R., 2016. Vulnerability to climate warming of four genera of New World iguanians based on their thermal ecology. Anim. Cons. . http://dx.doi.org/10.1111/acv.12255
Porter, W.P., Gates, D.M., 1969. Thermodynamic equilibria of animals with environment. Ecol. Monogr. 39, 227–244.
R Development Core Team, 2013. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna.
Sagonas, K., Valakos, E.D., Pafilis, P., 2013a. The impact of insularity on the thermoregulation of a Mediterranean lizard. J. Therm. Biol. 38, 480–486.
Sagonas, K., Meiri, S., Valakos, E.D., Pafilis, P., 2013b. The effect of body size on the thermoregulation of lizards on hot, dry Mediterranean islands. J. Therm. Biol. 38, 92–97.
Scheers, H., Van Damme, R., 2002. Micro-scale differences in thermal habitat quality and a possible case of evolutionary flexibility in the thermal physiology of lacertid lizards. Oecologia 132, 323–331.
Sears, M.W., Angilletta, M.J., 2015. Costs and benefits of thermoregulation revisited: both the heterogeneity and spatial structure of temperature drive energetic costs. Am. Nat. 185, 94–102.
Schwaner, T.D., 1989. A field study of thermoregulation in black tiger snakes (*Notechis ater niger*: Elapidae) on the Franklin Islands, South Australia. Herpetologica 45, 393–401.
Sfenthourakis, S., Triantis, K.A., 2009. Habitat diversity, ecological requirements of species and the Small Island effect. Divers. Distrib. 15, 131–140.
Sunday, J.M., Bates, A.E., Kearney, M.R., Colwell, R.K., Dulvy, N.K., Longino, J.T., Huey, R.B., 2014. Thermal-safety margins and the necessity of thermoregulatory behavior across latitude and elevation. Proc. Natl. Acad. Sci. USA 111, 5610–5615.
Tosini, G., Jones, S., Avery, R.A., 1994. Effects of feeding on set point temperatures and thermoregulatory behaviour in the lizards *Podarcis muralis* and *Lacerta viviipara*. Amphibia-Reptil. 15, 257–265.
Triantis, K.A., Vardinoyannis, K., Tsolaki, E.P., Botsaris, I., Lika, K., Mylonas, M., 2006. Re-approaching the small island effect. J. Biogeogr. 33, 914–923.
Tsasi, G., Pafilis, P., Simou, C., Valakos, E.D., 2009. Predation pressure, density-induced stress and tail regeneration: a casual-nexus situation or a bunch of independent factors? Amphibia-Reptil. 30 (4), 471–482.
Valakos, E.D., Vlachopanos, A., 1989. Notes on the ecology of *Cyrtodactylus kotschyi* (Reptilia - Gekkonidae) in an insular ecosystem of the Aegean. Biol. Gallo-Hell 15, 179–184.
Van Damme, R., Bauwens, D., Verheyen, R.F., 1986. Selected body temperatures in the lizard *Lacerta vivipara*: Variation within and between populations. J. Therm. Biol. 11, 219–222.
Veríssimo, C.V., Carretero, M.A., 2009. Preferred temperatures of *Podarcis vaucheri* from Morocco: intraspecific variation and interspecific comparisons. Amphibia-Reptil. 30, 17–23.
Vitt, L.J., Caldwell, J.P., Sartorius, S.S., Cooper, W.E., Baird, T.A., Baird, T.D., Pérez-Mellado, V., 2005. Pushing the edge: extended activity as an alternative to risky body temperatures in a herbivorous teiid lizard (*Cnemidophorus murinus*, Squamata). Funct. Ecol. 19, 152–158.
Whittaker, R.J., Fernández-Palacios, J.M., 2007. Island Biogeography: Ecology, Evolution and Conservation, Second edition. Oxford University Press, Oxford.
Zamora-Camacho, F.J., Reguera, S., Moreno-Rueda, G., Pleguezuelos, J.M., 2013. Patterns of seasonal activity in a Mediterranean lizard along a 2200 m altitudinal gradient. J. Therm. Biol. 38, 64–69.
Zamora-Camacho, F.J., Rubiño-Hispán, M.V., Reguera, S., Moreno-Rueda, G., 2015. Thermal dependence of sprint performance in the lizard *Psammodromus algirus* along a 2200-meter elevational gradient: cold-habitat lizards do not perform better at low temperatures. J. Therm. Biol. 52, 90–96.
Zar, J.H., 2010. Biostatistical Analysis. Prentice Hall Inc, Upper Saddle River, New Jersey.

View publication stats