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Journal of Thermal Biology

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

The impact of insularity on the thermoregulation of a Mediterranean lizard

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ARTICLE INFO

Article history:

Received 28 March 2013

Accepted 4 August 2013

Available online 9 August 2013

Keywords:

Islands

Thermal preferences

Thermal quality

Predation pressure

ABSTRACT

The overall biology of ectotherms is strongly affected by the thermal quality of the environment. The particular conditions prevailing on islands have a strong effect on numerous features of animal life. In this study we compared mainland and island populations of the lizard *Lacerta trilineata* and hypothesized that insularity would affect the thermoregulatory strategy. Continental habitats were of lower thermal quality, experiencing more intense fluctuations and had higher values of operative temperatures. Nevertheless mainland lizards selected for higher body temperatures in the lab and showed more effective thermoregulation during summer than their island peers. Lizards achieved similar body temperatures in the field in both types of habitat, underlining the importance of predation as a potential factor to mainland lizards that failed to reach their higher thermal preferences. Both island and mainland populations of *L. trilineata* have been adapted to their thermal environment, supporting the labile view on the evolution of thermal physiology for this species.

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1. Introduction

The thermal environment and the habitat use have an important effect on ectotherms, affecting body temperature, and consequently the overall fitness of an organism (Cowles and Bogert, 1944; Porter and Gates, 1969). In order to achieve a thermal equilibrium with their environment, reptiles have to adjust their temperatures, mainly through behavioral mechanisms (Avery, 1982; Stevenson, 1985). The ability to thermoregulate effectively and maintain body temperature within a narrow range is of pivotal importance for reptiles since the majority of behavioral and physiological processes are temperature dependent (Bauwens et al., 1995; Angilletta, 2001; Shine, 2004).

Environmental temperatures represent a decisive feature in lizard biology (Medina et al., 2009; Meiri et al., 2013). However the temperature of a given environment does not imply a solid, unique thermal strategy to all species dwelling there. Different species exploit in a clearly distinct way the thermal microhabitats when in sympatry (Adolph, 1990; Scheers and Van Damme, 2002). On the other hand not all populations of a single species share the same thermoregulation pattern throughout the species range. Body temperatures may fluctuate considerably along altitudinal or

latitudinal gradients (Van Damme et al., 1989; Qualls and Shine, 2000; Kiefer et al., 2005).

Three variables are used traditionally to sketch out the thermal profile of ectotherms (Huey and Slatkin, 1976; Hertz et al., 1993): the body temperatures (T_b) that animals achieve in the field; the operative temperatures (T_e) that a non-thermoregulating animal reach under natural conditions, representing environmental temperatures; and the set-point range (T_{set}), the temperature that animals achieve under laboratory conditions with no physiological or ecological restrictions. The interactions among these values are responsible for the thermal strategy that an organism will eventually adopt. Body temperatures may be seen as the result of the compromise between the thermal utopia that is T_{set} (expressing thermoregulation under ideal conditions) and the environmental constrains as described by T_e (passive thermoregulation with minimal accuracy).

Intraspecific variation in thermoregulation has been well assessed in mainland lizards (e.g. Gvozdik and Castilla, 2001; Díaz and Cabezas-Díaz, 2004; Ibargüengoytia et al., 2008). Many researchers have also focused on the thermal biology of insular species, producing a growing body of literature (e.g. Bauwens et al., 1990; Adamopoulou and Valakos, 2005; Vasconcelos et al., 2012). However the comparison between the thermal strategies of continental and island populations of a single species remains largely understudied.

The biology of island species deviates in many ways from that of their mainland kin. Terms such as the Island Syndrome (Adler and Levins, 1994) or the Island Rule (Van Valen, 1973;

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Lomolino, 2005) have been coined to outline the impressive adaptations of island life. Insular lizards differ in numerous traits such as body size (Meiri, 2007; Meiri et al., 2011), life history (Pafilis et al., 2011; Novosolov et al., 2013), antipredatory tactics (Pérez-Mellado et al., 1997; Pafilis et al., 2008), digestive efficiency (Herrel et al., 2008; Vervust et al., 2010), diet (Van Damme, 1999) etc. Environmental conditions on island are different than those prevailing on mainland (MacArthur and Wilson, 1967; Whittaker and Fernández-Palacios, 2007). We anticipated that these differences would induce changes in the thermal physiology of island populations compared to the mainland ones.

The Balkan green lizard (*Lacerta trilineata*) lends itself to a comparative approach of thermoregulation. Its distribution covers the greater part of the Balkan Peninsula (Schmidtler, 1997), while in Greece it is found throughout the mainland as well as in the majority of the islands (Valakos et al., 2008). To clarify whether the particular environmental conditions of the islands affect the thermal profile of this lizard, we compared two mainland and two insular populations, on a short-term scale during the summer. We formulated two hypotheses and one question: First, we presumed that island habitats would provide a less challenging thermal environment and, consequently, T_{es} would achieve lower values and lizards would avoid overheating. Thanks to the buffering effect of the surrounding sea, island climate is in general milder than the one of the neighboring mainland areas (Schwaner, 1989). We thus expected less temperature fluctuations with fewer extreme values. Second, we anticipated that the lizards of the thermally benign island habitats would be less effective thermoregulators. Lizards that live in thermally invariable habitats tend to dedicate less energy to active thermoregulation and tend to shift to a certain extent of thermoconformity (Hertz et al., 1993; Shine and Madsen, 1996). The question we posed refers to the thermal preferences: what happens with T_{set} ? Two conflicting aspects have been identified by Hertz et al. (1983). According to the “static” view (thermal physiology is evolutionary conservative), preferred body temperatures should be identical in both mainland and island populations (Bogert, 1949). The “labile” view (thermal physiology responds readily to directional selection), contrariwise, predicts that T_{set} may vary in response to fluctuations in environmental temperatures (Huey, 1982). Consequently T_{set} in island lizards should narrow down due to the more stable environment they inhabit.

2. Materials and methods

2.1. Study sites and species

L. trilineata is a large-bodied lizard, second only to *Timon lepidus* among European members of Lacertidae, with a snout-vent length (SVL) ranging from 80 to 170 mm and body mass up to 145 g (Arnold, 1987; Valakos et al., 2008). In Greece it ranges in most of the habitats but typically in meadows and scrublands, cultivated areas, open deciduous woodlands as well as on stone walls.

Fieldwork was conducted during May and June 2012 in four areas on mainland (Karditsa at Thessaly and Stymphalia Lake at Peloponnese) and island Greece (Skyros and Andros islands) (Fig. 1). Both islands have the typical Mediterranean type vegetation with maquis and phrygana as dominant habitats. The climate in the two islands is milder than in continental areas (Kotini-Zabaka, 1983). Andros' air temperature (T_{air}) ranges from 10.0 °C in winter to 25.5 °C in summer, whereas the values for Skyros are 9.9 °C and 25.3 °C, respectively. To the contrary, the climate in the mainland sites is more severe with more extreme values: winter T_{air} at Karditsa averages at 3.5 °C and during summer at 30.1 °C.

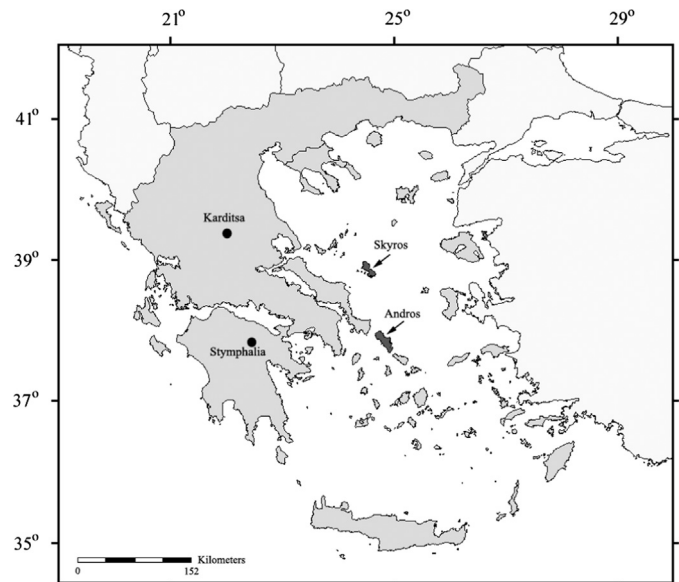


Fig. 1. Map of Greece at East Mediterranean Sea. Arrows and dots denote the four sampling locations.

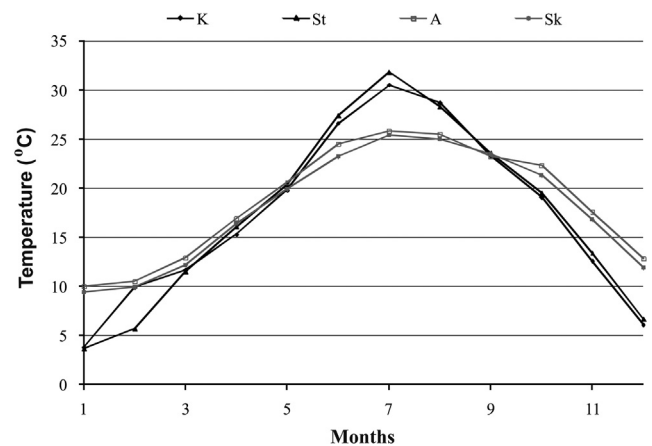


Fig. 2. Monthly means of air temperature for the last 30 years, in the four under studied locations. K, Karditsa; St, Stymphalia; A, Andros; Sk, Skyros.

Stymphalia plateau, located in 600 m altitude, has a harsh and rainy winter (T_{air} 7.0 °C) and a warm summer (T_{air} 32.8 °C). Monthly means of temperature for the last 30 years were obtained from the National Meteorological Service of Greece (http://www.hnms.gr/hnms/greek/index_html) (Fig. 2).

All lizards were collected in accordance with the Greek National Legislation (Presidential Decree 67/81) and were brought to the laboratory facilities of the Biology Department at the University of Athens. Lizards were individually housed in vitreous terraria (80 cm × 30 cm × 40 cm) on a substrate of sand where stones were provided as hiding places. The animals were held at 30 °C under a controlled photoperiod (12 light: 12 dark; fluorescent tube lighting) while additional incandescent lamps (60 W) allowed animals to thermoregulate behaviorally for 8 h/d. Lizards had access to water ad libitum and were fed every other day with adult crickets (*Acheta domestica*) and mealworms (*Tenebrio molitor*), coated with a powder containing vitamins and minerals supplements (TerraVit Powder, JBL GmbH & Co. KG). All animals were released into the field by the end of the study.

2.2. Field measurements (T_b and T_e)

We sampled T_b of 74 adult male individuals that were captured by noose in the four populations under study (28 from the islands and 46 from mainland). Immediately after capture T_b s were recorded with a Weber quick-reading cloacal thermometer (T-4000, Miller & Weber, Inc., Queens, NY) to the nearest 0.1 °C. SVL (in mm) of each individual was measured using a digital caliper (Silverline 380244, accurate to 0.01 mm). Lizards with SVL longer than 80 mm were considered adults (Pafilis and Valakos, 2008).

The operative temperatures (*sensu* Bakken, 1992) were estimated using 16 hollow copper models placed in a variety of sites so as to cover as many microhabitats as possible (Huey, 1991; Dzialowski, 2005). For each model we took into account its exposure to sunlight (defining three different regimes, full light [FL], semi-light [SL] and shade [S] and substrate type (two different categories, ground [G] and rock [R]). Thus six different combinations of microhabitats were available to lizards: FL-G (3 models), FL-R (3 models), SL-G (3 models), SL-R (3 models), D-G (2 models) and D-R (2 models). The number of models placed in each of the above combinations was determined based on the proportion of these microhabitats in the area.

Models approximated the shape and size of the study species (Bakken, 1992). In order to replicate the thermophysical properties of *L. trilineata*, models were painted green (radiative properties) and filled with approximately 3 ml of water (heat capacity) (Bakken, 1992; Grbac and Bauwens, 2001; Lutterschmidt and Reinert, 2012). Models were closed at both ends, except for a narrow slot, and then connected to 4 data loggers (HOBO U12 4-Channel External Data Logger–U12-008) each with four thermocouples (Díaz, 1997). Micro-environmental temperatures were recorded every half hour from 8:00 to 19:00 for two consecutive days. All field trips took place within May and June (during early hours in the morning) and temperature measurements were taken only when weather conditions were favorable for *L. trilineata* (Castilla and Bauwens, 1991; Pafilis and Valakos, 2008).

In order to ensure the similarity of the thermal responses between the non-thermoregulating model and the lizard (Hertz, 1992), we conducted (thrice) a laboratory experiment of heating and cooling rates (Lutterschmidt and Reinert, 2012). We placed a lizard and a water-filled model side by side and allowed them to attain an initial temperature of 15 °C. A heat source (150 W lamp) was placed 60 cm above the terrarium, providing heat for 45 min. After this period the heat lamp was turned off and a cooling phase of 90 min initiated. During this period (140 min in total) model and lizard temperatures were recorded with a Weber quick-reading thermometer at 5 min intervals. Regression analysis of T_b on T_e suggested that the models had a strong association with the living lizards' T_b ($r=0.985$, $N=168$, $P < 0.001$).

2.3. Lab measurements (T_{set})

Experiments to determine the mean and range of preferred body temperatures (T_{pref}) were carried out in 74 adult males in a purpose-built terrarium (150 × 45 × 45 cm). Two heating lamps (100 W and 60 W) suspended above one end and two ice bags were placed against the wall at the other end of the terrarium (Van Damme et al., 1986) providing a smooth thermal gradient, ranging from 10 °C to 50 °C. Preferred temperatures were measured during summer only (Grbac and Bauwens, 2001; Gvozdik and Castilla, 2001). The body temperatures of lizards were measured every hour for a 5 h period with a cloacal Miller–Weber thermometer, starting 30 min after lizards were first released into the terrarium. We measured the set-point range (T_{set}) as the central 50% of all body temperatures selected in the laboratory (Huey, 1982; Hertz et al., 1993).

2.4. Effectiveness of thermoregulation

The effectiveness of thermoregulation (i.e. the ability of an animal to maintain its body temperature closer to the T_{pref} rather than T_e s) was calculated using two different approaches. We used the classical formula proposed by Hertz et al. (1993): $E=1 - (\bar{d}_b/\bar{d}_e)$, where \bar{d}_b denotes the accuracy of thermoregulation and is the mean deviation of field T_b from T_{set} and \bar{d}_e , that describes the thermal quality, is the mean deviation of field T_e from T_{set} . However this method encompasses an inherent bias since a variety of different \bar{d}_e and \bar{d}_b combinations may conclude in the same values of E , thus eliminating the differences of the thermal environment that animals might face. To circumvent this problem we applied a complementary approach proposed by Blouin-Demers and Weatherhead (2001) where the difference between \bar{d}_e and \bar{d}_b quantifies the extent of departure from perfect thermoconformity.

In the first case (Hertz et al., 1993) thermoconformers select microhabitats randomly, exhibiting similar \bar{d}_b and \bar{d}_e , and E tends to 0, while thermoregulators actively seek for the appropriate microhabitat, show higher \bar{d}_e than \bar{d}_b and E tends to 1. In the second case (Blouin-Demers and Weatherhead, 2001) positive values of $\bar{d}_e - \bar{d}_b$ describe animals that thermoregulate, zero represents animals demonstrating perfect thermoconformity, and negative values stand for animals that avoid thermally favorable habitats. The magnitude of the difference ($\bar{d}_e - \bar{d}_b$) represents an index of the effectiveness of thermoregulation.

2.5. Statistical analyses

Parametric tests were used after applying the Kolmogorov–Smirnov and Lilliefors normality tests on the data set. We performed a one-way analysis of variance (ANOVA) to examine the differences among *L. trilineata* populations for all variables (T_b , T_{set} and T_e), coupled with a post-hoc Tukey HSD test (Zar, 2010). In addition, we performed analysis of covariance (ANCOVA) to evaluate the effect of SVL on T_b s and T_{set} . Paired *t*-test was used to estimate the differences between field and selected body temperatures for each individual.

To generate the 95% confidence intervals for effectiveness of thermoregulation (E) between mainland and island lizards, we used the bootstrap resampling method (1000 times) proposed by Hertz et al. (1993). The values of \bar{d}_e , \bar{d}_b and E were calculated based on random sampling (with replacement) from the distribution of T_e s, T_b s and T_{set} at each population. Bootstrap resampling was carried out in R (v. 2.12.2). The rest of the statistical analyses were conducted using PASW-18.0 (SPSS Inc. 2010).

3. Results

3.1. Body size

Since body size may influence the effectiveness of thermoregulation (Sagonas et al., 2013), we assessed the SVL within and among the four populations under study to detect possible differences. According to the analysis, no statistically significant difference was found (ANOVA, $F_{3,70}=2.44$, $P > 0.05$, Table 1).

3.2. Field measurements (T_b and T_e)

Field body temperatures were pooled in two groups, one for the insular and another for the mainland populations, since they did not differ statistically (ANOVA, islands: $F_{1,26}=1.34$, $P > 0.05$, mainland: $F_{1,44}=0.60$ $P > 0.05$).

Table 1

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 the four *Lacerta trilineata* populations. Also values for snout-vent length (in mm). Means \pm standard deviation; range; sample size. Results of the one-way ANOVA for all the above mentioned parameters.

Location	Population	SVL (mm)	T_b ($^{\circ}$ C)	T_e ($^{\circ}$ C)	T_{pref} ($^{\circ}$ C)	d_e ($^{\circ}$ C)	d_b ($^{\circ}$ C)
Islands	Andros (A)	12.73 \pm 1.54 (10.4–16.1) N=14	31.32 \pm 1.63 (28.5–33.6) N=14	36.33 \pm 4.68 (30.6–49.5) N=16	33.11 \pm 1.03 (31.1–34.7) N=14	3.21 \pm 3.66 (0.0–15.89) N=32	1.17 \pm 1.06 (0.0–4.13) N=28
	Skyros (Sk)	13.75 \pm 2.13 (8.7–15.3) N=14	31.92 \pm 1.09 (29.9–33.8) N=14	36.22 \pm 4.17 (32.0–46.9) N=16	32.91 \pm 0.86 (31.2–34.6) N=14		
Mainland	Stymphalia (St)	12.15 \pm 1.88 (9.2–17.4) N=24	31.94 \pm 1.65 (28.7–35.0) N=24	39.65 \pm 7.20 (31.1–54.4) N=16	34.12 \pm 1.13 (31.5–36.3) N=24	5.58 \pm 5.51 (0.0–19.25) N=32	1.54 \pm 1.19 (0.0–4.8) N=46
	Karditsa (K)	12.73 \pm 1.51 (10.7–16.2) N=22	32.30 \pm 1.54 (29.5–34.5) N=22	38.76 \pm 6.17 (30.2–51.1) N=16	34.23 \pm 1.26 (32.4–36.4) N=22		
ANOVAs		$F_{3,70}=2.44$ $P=0.07$	$F_{3,70}=1.18$ $P=0.32$	$F_{3,60}=6.63$ $P=0.0042$	$F_{3,70}=6.34$ $P=0.0007$	$F_{1,62}=4.07$ $P=0.048$	$F_{1,72}=1.30$ $P=0.25$
Groups		{A,Sk,St,K}	{A,Sk,St,K}	{A,Sk}{St,K}	{A,Sk}{St,K}	{Isl}{Main}	{Isl, Main}

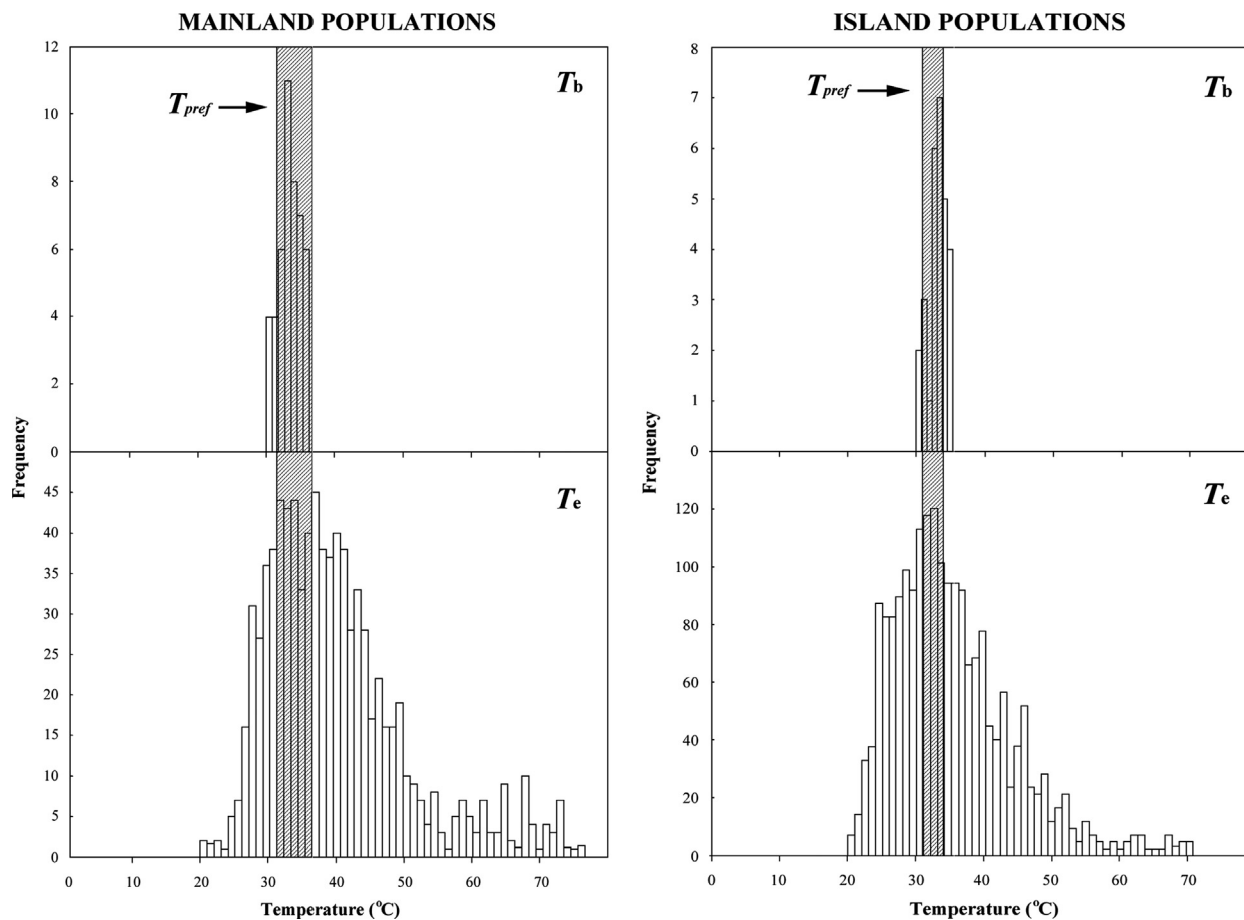


Fig. 3. Distribution of the mean active body temperature in the field (T_b) and the mean operative environmental temperature (T_e) in *Lacerta trilineata*, grouped for island and mainland populations. Grey diagonal lines indicate the preferred temperature range (T_{pref}) measured under laboratory conditions.

Mean lizards' body temperatures were slightly lower in island than in mainland populations (Fig. 3), though no statistically significant difference was found (T_b range: Island=28.5–33.8 vs. Mainland=28.7–35.0, ANOVA, $F_{3,70}=1.18$, $P>0.05$, Table 1). Even when T_b values were pooled in the two afore-mentioned groups, no differences were detected (t -test, $t=-1.33$, $df=72$, $P>0.05$)

Data for operative temperatures of insular and mainland populations were pooled in pairs since they did not differ statistically (ANOVA, islands: $F_{1,30}=0.01$, $P>0.05$, mainland: $F_{1,30}=0.14$, $P>0.05$, Fig. 3). Mean T_e s were significantly higher in the mainland sites (T_e range: Island=30.6–49.5 vs. Mainland=30.2–54.4, ANOVA, $F_{3,60}=6.63$, $P<0.05$; post-hoc Tukey HSD test, Table 1). In addition, in order to take into account

Table 2
Values for the operative temperatures (T_e) in the three different solar microclimates in all four locations. Means \pm standard deviation; range; sample size. Results of the one-way ANOVA and pairwise comparison (Tukey HSD test) for the available thermal microhabitats.

Location	Population	Shade (S) ($^{\circ}$ C)	Semi-light (SL) ($^{\circ}$ C)	Full-light (FL) ($^{\circ}$ C)
Islands	Andros (A)	28.33 \pm 3.93 (18.96–33.92) N=108	34.43 \pm 4.92 (24.47–45.91) N=162	40.57 \pm 8.99 (25.06–68.08) N=162
	Skyros (Sk)	29.55 \pm 6.11 (21.50–35.30) N=108	33.52 \pm 8.32 (22.10–56.60) N=162	40.18 \pm 12.19 (22.40–69.80) N=162
Mainland	Stymphalia (St)	29.27 \pm 3.32 (21.55–35.84) N=108	35.88 \pm 5.10 (25.56–47.43) N=162	47.36 \pm 13.75 (23.63–75.80) N=162
	Karditsa (K)	30.55 \pm 5.05 (19.16–36.17) N=108	36.45 \pm 5.98 (25.07–48.60) N=162	44.88 \pm 11.63 (23.63–71.80) N=162
ANOVAs		$F_{3,428}=1.62$ $P=0.18$	$F_{3,644}=7.45$ $P<0.001$	$F_{3,644}=14.12$ $P<0.001$
Groups		{A,Sk,St,K}	{A,Sk}{St,K}	{A,Sk}{St,K}

the thermal heterogeneity of the habitats, we further analyzed the T_e -records during the day based on the six solar/substrate combinations, on which the models were placed. The pairwise comparison revealed that only the exposure to sunlight (and not the type of substrate) affected significantly T_e s (two-way ANOVA, all $P<0.05$). Therefore, in the rest of the analyses, we grouped the six distinct combinations into three. Significant differences were revealed in all four locations (ANOVA, all $P<0.05$, Tukey HSD test, $P<0.05$, Table 2).

3.3. Set-point temperature range (T_{set})

Preferred body temperatures differed significantly between island and mainland populations (ANOVA, $F_{3,70}=6.34$, $P<0.05$, Table 1) with insular lizards achieving lower T_{pref} than their mainland peers. T_{set} for islands ranged from 32.63 $^{\circ}$ C to 33.63 $^{\circ}$ C ($N=28$) and for mainland varied from 33.50 $^{\circ}$ C to 35.13 $^{\circ}$ C ($N=46$). Post-hoc analysis (Tukey HSD test) indicated the existence of two distinct groups, one including the insular and another containing the mainland populations (Table 1). Consequently island and mainland populations were grouped in pairs for further analyses (Fig. 3).

Mean T_{pref} was higher than the mean T_b in both island (paired t -test, Andros: $df=13$, $t=2.98$, $P<0.05$, Skyros: $df=13$, $t=2.69$, $P<0.05$) and mainland populations (paired t -test, Stymphalia: $df=23$, $t=6.29$, $P<0.05$, Karditsa: $df=21$, $t=3.90$, $P<0.05$).

3.4. Effectiveness of thermoregulation (E)

We found statistically a significant difference between the mean deviation of T_e from T_{set} (\bar{d}_e) on mainland and insular lizards (5.58 vs. 3.21 $^{\circ}$ C, $F_{1,62}=4.07$, $P<0.05$ Table 1). Though the mean deviation of field body temperature from T_{set} (\bar{d}_b) was higher on mainland than on the islands (1.54 vs. 1.17 $^{\circ}$ C, $F_{1,72}=1.30$, $P>0.05$, Table 1), no significant difference was detected. On the islands the majority of T_b s were lower than the minimum T_{set} (68%, $N=19$) and only 10% ($N=3$) were higher than the maximum T_{set} (Fig. 3). Likewise, more T_b s were lower than the minimum T_{set} (72%, $N=33$) on the mainland populations, whereas no lizard achieved T_b higher than T_{set} (Fig. 3).

Following the formula by Hertz et al. (1993) we used \bar{d}_e and \bar{d}_b to evaluate the effectiveness of thermoregulation on the islands ($E=0.64$) and mainland ($E=0.72$). Additionally, we used the index $\bar{d}_e - \bar{d}_b$ proposed by Blouin-Demers and Weatherhead (2001) to quantify the extend of deviation from perfect thermoconformity, for the islands ($\bar{d}_e - \bar{d}_b = 2.04$) and mainland ($\bar{d}_e - \bar{d}_b = 4.04$). Bootstrap resampling revealed significant difference in E between

island and mainland populations (E values for mainland were higher than those for the islands; 963 times based on 1000 permutations, $P<0.05$).

4. Discussion

The comparison between the mainland and the island populations of *L. trilineata* yielded differences in almost all the parameters of thermoregulation that were examined. Though all lizards were active thermoregulators, island lizards were characterized by lower effectiveness of thermoregulation during summer. Mainland lizards on the other hand achieved higher body temperatures in the lab. The last finding, coupled with the more challenging mainland environment, advocates the labile view regarding the evolution of the thermal strategy of *L. trilineata*. We have to stress that we pay special attention to focus on biotopes as similar as possible in terms of vegetation, geology and morphology to minimize their effect. Thus, our results should be attributed mainly on the particular features of insularity, both physical (e.g. restricted temperature variation) and ecological (e.g. predation relaxation).

Our first hypothesis regarding the thermal quality of the islands was confirmed. Operative temperatures were higher on mainland and showed greater variation due to more extreme values (Table 1, Fig. 3). According to Hertz et al. (1993) a mean d_e equal to zero describes a thermally ideal habitat since a lizard would always achieve T_b within T_{set} , whereas habitats with \bar{d}_e close to the unit are of lower thermal quality. In our study \bar{d}_e was considerably lower on the islands (Table 1), revealing the higher thermal quality of insular habitats. To the contrary the higher \bar{d}_e of the mainland is indicative of thermally poorer environment. Mainland areas have a severe climate and experience intense intra-annual variability contrary to the dry and more stable climate of the islands, especially in Mediterranean (Kotini-Zabaka, 1983; Whittaker and Fernández-Palacios, 2007).

In terms of microhabitats, the type of substrate was insignificant and thus we focus on the sun light exposure. Only models placed in semi-light positions achieved suitable thermal conditions for lizards. Records from the shade models achieved T_e s within T_{pref} only during a relatively short period of the day, whereas T_e s for the fully exposed models were higher than T_{pref} for the longer part of the day (Table 2). Thus lizards, especially in mainland where T_e variations are greater, have to constantly move across microhabitats during the day to maintain T_b close to their T_{pref} . (Grbac and Bauwens, 2001).

The effectiveness of thermoregulation on mainland was higher, in line with our second hypothesis. Though all populations adopted the strategy of active thermoregulation, mainland lizards have a higher E (0.72) than their island kin (0.64). E tends to approach one when \bar{d}_b is smaller than \bar{d}_e and, consequently, animals have to thermoregulate carefully (Hertz et al., 1993). Mainland lizards, living in a challenging habitat, have to exert a more effective thermoregulation to achieve T_b as close as possible to their T_{set} and thus their E is closer to one.

The second approach we applied to assess thermoregulation patterns (*sensu* Blouin-Demers and Weatherhead, 2001), confirmed the higher effectiveness of the mainland lizards. Island and mainland animals had positive values of $\bar{d}_e - \bar{d}_b$ (2.04 and 4.04, respectively), and this underscores the active character of thermoregulation in both cases. However the respective value for mainland populations was almost twofold higher over that of the insular populations. The higher the magnitude of the difference ($\bar{d}_e - \bar{d}_b$) is, the more effective thermoregulation appears (Blouin-Demers and Weatherhead, 2001). This complimentary index highlights in a striking way the extent of thermoregulation exerted by the mainland lizards, a finding that otherwise would be masked by the small difference between the two E values. Hertz et al. (1993) acknowledged this possible source of biases and proposed to directly examine \bar{d}_b and \bar{d}_e alongside E in order to fully understand the patterns of thermoregulation.

The preferred temperatures differed between mainland and island populations. Mainland lizards achieved higher temperatures under laboratory conditions, showing a preference to higher thermal optima (Clusella-Trullas et al., 2007). Our results support the labile view, according to which T_{set} depends on the particular conditions of the habitat, in accordance with previous studies on lacertid thermal physiology (Scheers and Van Damme, 2002). T_{set} may change with season, sex, age, reproductive status and body size (Andrews et al., 1999; Carretero et al., 2005; Veríssimo and Carretero, 2009; Sagonas et al., 2013). Herein, we showed that insularity has an impact on preferred temperatures as well.

Body temperatures that lizards achieved in the field did not differ between mainland and island populations. Despite the differences in the thermal quality of the two types of habitat and the higher thermal preferences of the mainland lizards, both categories maintained their body temperature within the same narrow range (Table 1). However our findings on T_{set} and T_e plead for higher T_b in mainland lizards: animals that live in a “warmer” habitat and have higher thermal preferences should select for higher body temperatures in the field. We believe that the reason for this discrepancy lies in predation, one of the most important features affecting thermoregulation under natural conditions (Case, 1982; Crowder and Magnuson, 1983).

Predation pressure on lizards is notably relaxed on Mediterranean islands (Pérez-Mellado et al., 1997; Pafilis et al., 2008). Snakes, the most specialized saurophagous predators (Pafilis et al., 2009a), do not range in all Aegean islands. Andros and Skyros lack *Malpolon monspesulanus* and *Vipera amodytes*, respectively (Valakos et al., 2008). Furthermore mammalian predators such as the red fox (*Vulpes vulpes*), the wild boar (*Sus scrofa*) and even the ground squirrel (*Spermophilus citellus*) which has been reported to attack *L. trilineata* (Koshev, 2010), are absent from both islands. In other words island lizards are less affected by predation pressure when thermoregulating (Meiri et al., 2013), whereas mainland individuals have to deal with a much more intense predation regime and, in their effort to avoid possible predators, cannot afford to bask to their thermal optima (Case, 1982). We believe that this could be the reason for the observed difference between body temperatures and T_{set} . However we have to stress out that without data on behavior (e.g. basking frequency,

shuttling frequency) it is hard to clearly resolve this issue and thus more detailed studies are required. Also, as insular biota differ in numerous ways from their mainland counterparts (e.g. higher population densities, competition relaxation, different reproductive strategies, food availability), the observed differences could be attributed as well to other factors besides predation.

The mean deviation of field body temperatures from T_{set} revealed no significant difference. \bar{d}_b represents an index of how closely T_b s match the set point range and defines the accuracy of thermoregulation (Hertz et al., 1993). High \bar{d}_b describes low accuracy while lower values represent high accuracy. Both mainland and island lizards achieved low values of \bar{d}_b (1.54 vs. 1.17, respectively, Table 1), which means that both populations thermoregulate with accuracy.

To sum up, it appears that insularity has an effect on thermal strategies. Insular lizards thermoregulated less effectively because of the more benign, in terms of thermal quality, environment and have lower thermal preferences. Thanks to their more relaxed thermoregulatory pattern, island animals may spend more time on reproduction or foraging (Huey and Slatkin, 1976; Case, 1982; Díaz, 1994). Mainland lizards on the other hand, showed the opposite pattern of thermoregulation with higher effectiveness as result of the more demanding environment. Under these conditions an effective and accurate thermoregulation is a prerequisite to avoid poor organism's performance (Blouin-Demers and Weatherhead, 2002; Blouin-Demers and Nadeau, 2005). Predation regime seems to restrict the ability to achieve body temperatures closer to the set-point range. Future comparative studies that will include closely related species of both mainland and island origin will offer the necessary ground for unraveling the detailed repertoire of thermal and behavioral adaptations.

Acknowledgements

The present study was supported by a research grant from the “Kapodistrias” program of the National and Kapodistrian University of Athens. We also wish to express our gratitude to the anonymous reviewers for comments that significantly improved an earlier version of the manuscript.

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