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Living in sympatry: The effect of habitat partitioning on the thermoregulation of three Mediterranean lizards

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ABSTRACT

The ability for effective, accurate and precise thermoregulation is of paramount importance for ectotherms. Sympatric lizards often partition their niche and select different microhabitats. These microhabitats, however, usually differ in their thermal conditions and lizards have to adapt their thermoregulation behavior accordingly. Here, we evaluated the impact of habitat partitioning on the thermal biology of three syntopic, congeneric lacertids (*Podarcis peloponnesiacus*, *P. tauricus* and *P. muralis*) from central Peloponnese, Greece. We assessed thermoregulation effectiveness (E) using the three standard thermal parameters: body (T_b), operative (T_e) and preferred (T_{pref}) temperatures. We hypothesized that the microhabitats used by each species would differ in thermal quality. We also predicted that all species would effectively thermoregulate, as they inhabit a thermally challenging mountain habitat. As expected, the partition of the habitat had an effect on the thermoregulation of lizards since microhabitats had different thermal qualities. All three species were effective and accurate thermoregulators but one of them achieved smaller E values as a result of the lower T_b in the field. This discrepancy could be attributed to the cooler (but more benign) thermal microhabitats that this species occupies.

1. Introduction

Sympatry between closely related animal species is often accompanied by resource partitioning in one or more niche dimensions, mainly including shifts in activity time, dietary preferences and space use (De León et al., 2014; Murray et al., 2016; Schoener, 1974b). Niche separation allows species to relax or even minimize interspecific competition (Albrecht and Gotelli, 2001; MacArthur and Pianka, 1966). However, resource partitioning does not necessarily involve competitive exclusion, but could rather reflect species-specific ecological preferences (Carrascal et al., 1992; Dias and Rocha, 2007; Vrcibradic and Carlos Frederico, 1996).

Competition in lizard assemblages is well documented and has been mainly attributed to territoriality and mating success (Lailvaux et al., 2012; Yasui, 1998), access to food resources (Carretero et al., 2006; Stamps, 1977) and behavioral dominance hierarchies (Pafilis et al., 2009; Stamps, 1977). To minimize interspecific interactions, sympatric lizard species can often partition their niche and differentiate their habitat use (Corbalán et al., 2013; Harmon et al., 2007; Huey and Webster, 1976; Van Damme et al., 1990). However, the partition of space, especially in structurally rich environments with high thermal heterogeneity, often results in great differences in the environmental temperatures experienced by lizards (Martín-Vallejo et al., 1995; Ortega et al., 2016a; Van Damme et al., 1990).

In contrast to endotherms, lizards do not use metabolic heat to control their body temperature but thermoregulate behaviorally, mainly by actively selecting the more suitable thermal microhabitats (Cowles and Bogert, 1944). Environmental temperatures are one of the most important abiotic determinants of lizard biology (Medina et al., 2009; Meiri et al., 2013) and may differ considerably among the numerous microhabitats that arise from habitat partitioning (Žagar et al., 2015). To overcome problems associated with variable environmental temperatures and maintain their body temperature within a narrow optimal range, lizards have to demonstrate behavioral and physiological flexibility (Angilletta, 2009; Hertz et al., 1983). In other words, lizard species that share the same habitat have to either differentiate their thermal preferences or select different microhabitats (Murray et al., 2016; Scheers and Van Damme, 2002).

The study of the ectotherm thermal physiology requires the estimation of three main metrics (Bakken, 1992; Hertz et al., 1993):

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(i) the actual body temperatures (T_b) that active animals achieve in the field, (ii) the body temperatures that animals achieve when no ecological or other physical constraints exist (the so called preferred temperatures, T_{pref}, usually quantified using the set-point range, T_{set}), and (iii) the temperatures that a non-thermoregulating animal would reach in the field (operative temperatures, T_e). These three features provide simple and reliable information to assess the thermal quality of the habitat and to evaluate the effectiveness, precision and accuracy of the thermoregulation that an ectotherm may achieve (Hertz et al., 1993).

The purpose of this study is to clarify how coexistence and habitat partitioning affect thermoregulation effectiveness. To this end, we evaluated the above-mentioned thermal parameters in three lacertid lizards (*Podarcis peloponnesiacus*, *Podarcis tauricus* and *Podarcis muralis*) that live syntopically in a very restricted mountain habitat in Peloponnese, Greece. The three species belong to the same genus, have distinctive microhabitat preferences (Buttle, 1988; Valakos et al., 2008) and demonstrate a clear niche segregation at the study site (Mayer and Beyerlein, 1999). We formulated two hypotheses. First, we presumed that the thermal quality of the different microhabitats arising from niche partitioning would differ, despite the small size of the focal site. Vegetation cover, exposure to sun or to wind, slope and substrate affect the thermal conditions of microhabitats (Campbell and Norman, 1998; Ortega et al., 2016b; Scheers and Van Damme, 2002), so we expected that their thermal quality would be different. Second, we anticipated that all three species would be effective thermoregulators as mountain lizards have been repeatedly reported to achieve very effective thermoregulation in response to the challenging climate conditions at high altitudes (Monasterio et al., 2009; Ortega et al., 2016a, 2016c; Piantoni et al., 2016; Zamora-Camacho et al., 2013).

2. Material and methods

2.1. Study system

Fieldwork was carried out on May 15th and 16th 2015 in a narrow site in the proximity of Lake Doxa (Feneos plateau, Peloponnese, Greece; Fig. 1). Lake Doxa is located at 900 m above sea level (asl) and is surrounded by high mountains (up to 2374 m) covered with fir, black pine (*Pinus nigra*) and oak (*Quercus coccifera*) tree forests. The climate is typical temperate, with harsh, snowy and rainy winters (mean T_{air} 1 °C) and warm summers (mean T_{air} 31.7 °C). The focal habitat was a narrow strip of land (100 m in length and 20 m in width) lying to the northwestern outskirts of the lake, comprising of stony terrains with rock faces, small field openings with short annual and perennial herbaceous vegetation, and mixed ground with stony small slopes semi-covered by plane trees (*Platanus occidentalis*).

Feneos plateau is well known for its rich reptile fauna, which includes 28 species (Koppitz, 2014; Mayer et al., 1990). It is the only area in Europe where seven lizards of the family Lacertidae occur in sympatry (Mayer and Beyerlein, 1999). We studied three small-bodied (snout to vent length from 60 to 85 mm), heliothermic and insectivorous lacertid lizards (Valakos et al., 2008). The three species differ considerably in their habitat preferences. The common wall lizard (*P. muralis*, Fig. 2a) frequents rocky areas and screes, usually in shady and rather humid spots (in the southern part of its distribution), and is an excellent climber, even in steep cliffs (Arnold and Ovenden, 2002). The Peloponnesian wall lizard (*P. peloponnesiacus*, Fig. 2b) is endemic to Peloponnese (but see Hedman et al., 2016). It climbs on small walls, stones, fallen tree trunks and low rocks, selecting habitats with rocky substrate and sparse scrub vegetation (Arnold and Ovenden, 2002). Finally, the Balkan wall lizard (*P. tauricus*, Fig. 2c) is a mainly terrestrial species than can be found in flat, open areas and grasslands (Böhme et al., 2009). The separation of the three species in the study site is clear: *P. peloponnesiacus* occurs on stony low slopes and big stones embedded in the ground, *P. tauricus* is found almost exclusively in the open grassland that extends from the aforementioned stony terrains to the lake, while *P. muralis* lives only in the rocky faces in a well shaded area by the plane trees opposite the area of *P. tauricus* and *P. peloponnesiacus* (for a detailed description see Pafilis, 2003).

Lizards were captured by noose in the field (samples sizes in Table 1). We immediately measured their body temperatures (see below) and then transferred them to the laboratory facilities of the Department of Biology at the University of Athens. Animals were housed individually in vitreous terraria (25×35×15 cm) with sand and artificial shelters and were held at 30 °C under a controlled photoperiod with fluorescent tube lighting (12 light: 12 dark). Additional incandescent lamps (60 W) allowed lizards to thermoregulate behaviorally for 8 h/d. Lizards had access to water *ad libitum* and were fed every other day with mealworms (*Tenebrio molitor*), coated with a powder containing vitamin and mineral supplements (TerraVit Powder, JBL GmbH & Co. KG). At the end of the experiment lizards were released back in the field.

2.2. Field temperatures (T_b and T_e)

On May 15th and 16th 2015, we captured a total of 231 adult lizards of both sexes belonging to the three focal species (samples sizes in Table 1) and within the same time frame the T_es were recorded. Body temperature (T_b) was measured to the nearest 0.1 °C, using a quick-reading cloacal thermometer (T-4000, Miller & Weber, Inc., Queens, NY) immediately and no later than 10 s after capture (Osojnik et al., 2013; Veríssimo and Carretero, 2009). Body length (snout-vent length; SVL) was measured with a digital caliper (Silverline 380244, accurate to 0.01 mm).

We estimated the operative temperatures of non-regulating lizards (Bakken, 1992) by using 72 hollow, electroformed copper models, connected to four data loggers (HOBO U12 4-Channel External Data Logger-U12-008; Díaz, 1997). Models approximated the size, shape and color of the focal lizards, were closed at both ends and filled with 2–3 ml of water to replicate the heat storage capacity of the lizard (Bakken, 1992; Bakken and Angilletta, 2014; Lutterschmidt and Reinert, 2012). Operative temperatures were recorded for two consecutive days from 10:00 to 19:00 at 30 min intervals. To sketch out the thermal profile of the habitat used by each species, we placed the models (samples sizes in Table 1) randomly in the main types of microhabitats available to lizards (Dzialowski, 2005; Huey, 1991). The definition of the microhabitats preferred by each species followed the extensive work done in the area by one of the authors (Pafilis, 2003). Nine different microhabitats were categorized based on their exposure to sunlight [full light (FL; models placed in open areas such as on rocks, litter or grass, soil), semi-light (SL; models placed on sites were exposure to sun might change during the day) and shade (S; models placed on plant roots, inside bushes, below rocks/stones or inside stone crevices)] and the type of substrate [litter (L), soil (S) and rock (R)]. The number of models placed in each of the above combinations was determined based on the availability of these microhabitats (personal observations in the field; for sample size see Supplementary material Table S1 and Table 2) in the area that each species occupies.

To ensure the similarity of the thermal responses between models and lizards (Hertz, 1992) we tested their cooling and heating rates (Lutterschmidt and Reinert, 2012). A lizard and a water filled model were placed side by side under the same heat source (a 150 W lamp) and allowed to attain an initial temperature of 15 °C. We measured their temperature for 45 min. After this period we turned off the heat lamp and the cooling phase began for another 90 min. A Weber quick reading thermometer was used to measure model and lizard temperatures for a total period of 135 min, every 5 min. Regression analysis of T_b and T_e suggested that the thermal responses of the models fit well with our study species (regressions statistics ± SE; for *P. muralis*: slope=1.114 ± 0.030, intercept=−2.061 ± 0.842; r^2=0.991, N=28, $P < 0.001$, for *P. peloponnesiacus*: slope=1.063 ± 0.035, intercept=−1.717

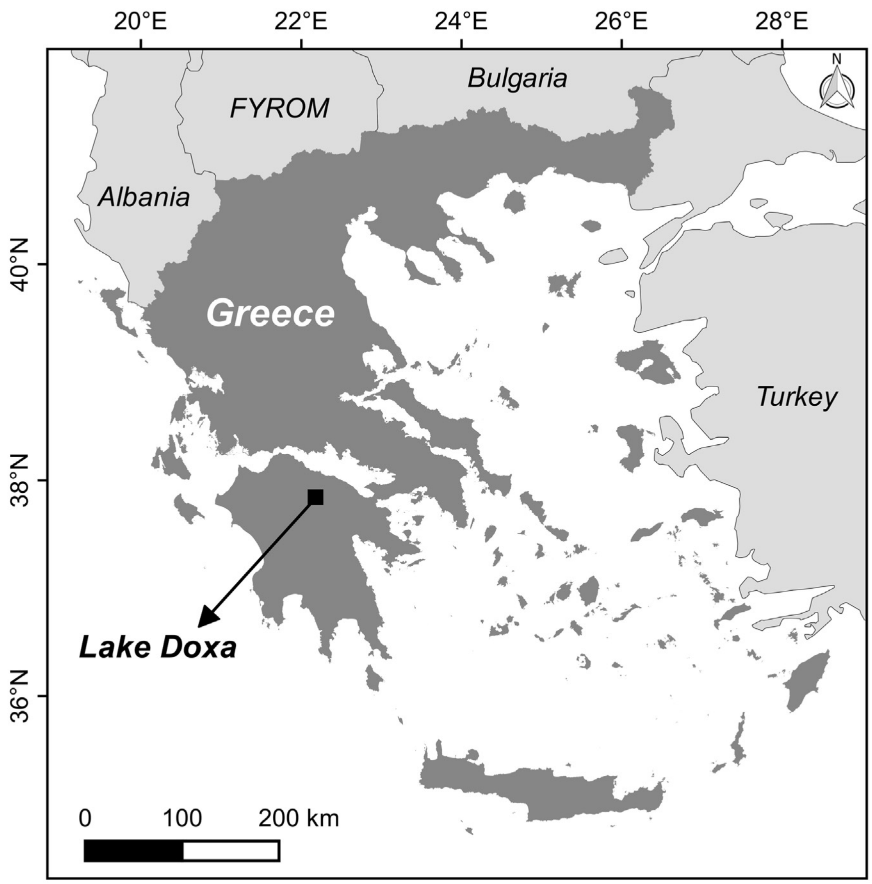

Fig. 1. Location of lake Doxa at Feneos plateau, northern Peloponnese, Greece.

± 1.012; r^2=0.972, N=28, $P < 0.001$, and for *P. tauricus*: slope=1.114 ± 0.031, intercept=−2.163 ± 0.869; r^2=0.980, N=28, $P < 0.001$).

2.3. Lab measurements (T_{pref} and T_{set})

Lizards were kept in the lab from May 16th to June 27th and laboratory experiments took place from May 26rd to June 9th. We estimated the set-point temperature ranges (T_{set}) of each species from the interquartile range (middle 50%) of the preferred body temperatures (T_{pref}) of each individual (Hertz et al., 1993) (samples sizes in Table 1) and then used the average values to find the upper and lower limits of T_{set}. To determine the T_{pref} one lizard at a time was placed in a specially designed terrarium (100×25×25 cm). To ensure a smooth thermal gradient ranging from 15 to 60 °C, we placed two ice bags against the wall at the one end and two heating lamps (100 W and 60 W) at the other end of the terrarium (Van Damme et al., 1986). Prior to the experiment we allowed lizards to acclimate for an hour in the terrarium (Carneiro et al., 2015; Carretero et al., 2005). The T_{pref} were measured every hour for a five-hour period with a cloacal Miller–Weber thermometer (Sagonas et al., 2013a). The acclimation period lasted from 9:00 a.m. to 10:00 a.m.; T_{pref} were recorded between 10:00 a.m. and 3:00 p.m. To preclude the effects of gravidity on the T_{pref} we did not collect gravid females (Carretero et al., 2005).

2.4. Effectiveness of thermoregulation

The effectiveness of thermoregulation (i.e. the ability of lizards to maintain their body temperature close to the T_{pref}) was estimated using two indices. First, we used the classical index proposed by Hertz et al. (1993): $E=1-(\overline{d_b}/\overline{d_e})$, where $\overline{d_b}$ denotes the accuracy of body temperatures and is the mean absolute deviation of field-active T_{b} from T_{set}, and $\overline{d_e}$ describes the thermal quality of the habitat, and is obtained by the mean deviation of T_{e} from T_{set}. E values range from zero (thermoconformers that select microhabitats randomly in their environment) to one (thermoregulators that actively select appropriate microhabitat) (Hertz et al., 1993). Other studies, however, suggested that the E index, despite its recognized value, includes certain innate biases, since different $\overline{d_b}/\overline{d_e}$ combinations may lead to the same E, (for details see Blouin-Demers and Weatherhead, 2001, 2002). We therefore used, additionally to the index of Hertz et al. (1993), the index ($\overline{d_e}$-$\overline{d_b}$) proposed by Blouin-Demers and Weatherhead (2001) that circumvents the aforementioned problems. The magnitude of the difference ($\overline{d_e}$-$\overline{d_b}$) is a measure of how much an animal departs from thermoconformity, and, like E, represents an index of the effectiveness of thermoregulation. Positive values arise when animals actively thermoregulate, zero represents animals demonstrating perfect thermoconformity, and negative values describe animals that avoid thermally favorable habitats.

2.5. Statistical analyses

We conducted parametric tests after confirming the normality and heteroscedasticity of the data. We used analysis of variance (ANOVA) to assess the differences in body length (SVL) between species and *t*-test between sexes. To test for sex-related effects on the accuracy of thermoregulation within species, we performed independent *t*-tests using the field body temperatures and T_{set} as dependent variables and sex as the independent variable. ANOVA was also used to test for differences between species in all the metrics of the thermoregulatory effectiveness (T_{b}, T_{e}, T_{set}, $\overline{d_b}$, $\overline{d_e}$), and to assess the differences in T_{e} between the nine microhabitats (the interaction between the substrate type and the exposure to sun) for each species and between species. ANOVAs with statistically significant differences were followed by post-hoc Tukey *HSD* tests.

Fig. 2. a) Common wall lizard (*Podarcis muralis*), b) Peloponnese wall lizard (*Podarcis peloponnesiacus*), c) Balkan wall lizard (*Podarcis tauricus*).

To compare the effectiveness of thermoregulation between species, we used a bootstrap resampling method (repeated 1000 times) to generate the 95% confidence intervals (Hertz et al., 1993) for both indices (E and $\overline{d_e}$-$\overline{d_b}$). We applied Tukey *HSD* post hoc test to adjust the confidence intervals for multiple comparisons for the effectiveness of thermoregulation. We considered that two species were significantly different from one another if one of them had values of thermoregulatory effectiveness higher than 98.9% (i.e. the 95% adjusted) of the paired comparison. All statistical analyses were carried out in R 3.2.3 (R Development Core Team, 2015).

3. Results

3.1. Field measurements (SVL, T_b and T_e)

Body length showed significant sexual dimorphism for all species, with males being larger than females for *P. peloponnesiacus* (84.91 ± 2.31 vs. 80.40 ± 2.11; t=9.30, df=83, $P < 0.001$) and *P. tauricus* (76.75 ± 3.49 vs. 73.48 ± 2.56; t=5.04, df=87, $P < 0.001$), while the opposite pattern was observed for *P. muralis* (68.08 ± 2.14 vs. 70.04 ± 3.10; t=−2.82, df=55, P=0.007). Furthermore, the comparison of SVL indicated significant differences between species for both males (ANOVA; $F_{2,119}$=379.64, $P < 0.001$) and females (ANOVA; $F_{2,106}$=142.74, $P < 0.001$), with *P. peloponnesiacus* being the largest, followed by *P. tauricus* and *P. muralis*.

Sex had no effect on T_bs (*P. peloponnesiacus*: t=−0.29, df=83, P=0.771; *P. tauricus*: t=0.22, df=87, P=0.823; *P. muralis*: t=−1.32, df=55, P=0.193), even when SVL was taken into account (*P. peloponnesiacus*: $F_{1,82}$=0.21, P=0.648; *P. tauricus*: $F_{1,86}$=1.69, P=0.200; *P. muralis*: $F_{1,54}$=2.06, P=0.156). Therefore, data on T_b were pooled for the subsequent analyses. Mean T_bs differed significantly between species (ANOVA; $F_{2,228}$=10.28, $P < 0.001$), with *P. tauricus* achieving the highest body temperatures and *P. muralis* the lowest (Tukey *HSD* post hoc test; Ps < 0.05; Table 1 and Fig. 3). Likewise, when SVL was used as a covariate, these differences remained (ANCOVA; $F_{2,227}$=11.13, $P < 0.001$; Tukey *HSD* post hoc test).

Exposure to sunlight (ANOVA; for all species $P < 0.05$; Supplementary Table S1) but not substrate type (ANOVA; for all species $P > 0.05$; Supplementary Table S1) significantly affected T_e. As such, the T_es from the different substrate types were pooled together and the nine microhabitats (the effects of exposure to sunlight and substrate type) were grouped into three (based only on the exposure to sunlight) for each species examined. ANOVA among these microhabitats showed that operative temperatures of the three microhabitats were higher for *P. peloponnesiacus* and *P. tauricus* compared to those of *P. muralis* (Table 2). The comparison of the average operative temperatures in the field revealed substantial differences in the thermal quality of the habitats used by the different species (ANOVA; $F_{2,2733}$=29.34, $P < 0.001$). Post-hoc analysis (Tukey *HSD* test) clearly indicated that *P. muralis* occupied cooler habitats (36.6 °C) compared to *P. peloponnesiacus* and *P. tauricus* (both T_e ~40 °C) (Table 1 and Fig. 3). Operative temperatures showed high fluctuations during the day for all species, ranging from 19.0 to 67.5 °C for *P. tauricus*, from 19.0 to 66.2 °C for *P. peloponnesiacus* and from 23.6 to 60.0 °C for *P. muralis*.

3.2. Lab measurements (T_{pref} and T_{set})

We found no differences in the preferred body temperature ranges between sexes (for all species *P. peloponnesiacus*: t=−1.03, df=45, P=0.308; *P. tauricus*: t=−0.001, df=15, P=0.999; *P. muralis*: t=0.49, df=20, P=0.627), even when SVL was taken into account (*P. peloponnesiacus*: $F_{1,44}$=0.47, P=0.497; *P. tauricus*: $F_{1,14}$=0.22, P=0.648; *P. muralis*: $F_{1,19}$=0.46, P=0.505), and thus we pooled the data. Though *P. tauricus* selected slightly higher body temperatures in the laboratory (33.26 ± 1.47 °C) than *P. peloponnesiacus* (32.82 ± 1.34 °C) and *P.*

Table 1
All estimated metrics for assessing thermoregulation effectiveness for the three species and body length (SVL). Also, the two complimentary indices of thermoregulation effectiveness (Blouin-Demers and Weatherhead, 2001; Hertz et al., 1993) are given. Mean ± standard deviation, range (in parenthesis) and sample size (*N*; in parenthesis the number of males – first – and females). Operative (T_e) and body (T_b) temperatures, deviation of T_e from T_{set} (d_e) and deviation of T_b from T_{set} (d_b). *Pt* refers to *P. tauricus*, *Pp* to *P. peloponnesiacus* and *Pm* to *P. muralis*. For operative temperatures the number of copper models is also provided in parenthesis.

Species	SVL	T_b (°C)	T_{pref} (°C)	T_e (°C)	d_b (°C)	d_e (°C)	d_e-d_b	*E*
P. peloponnesiacus	82.89 ± 3.16 (76.0–88.4) *N*=85	32.59 ± 2.81 (26.5–8.0) *N*=85 (47+38)	32.82 ± 1.34 (28.1–34.7) *N*=47 (24+23)	39.41 ± 7.82 (19.0–66.2) *N*=1064 (*28*)	1.55 ± 1.55 (0.0–5.6) *N*=85	7.57 ± 5.77 (0.0–32.5) *N*=1064	6.02	0.80
P. tauricus	75.10 ± 3.46 (68.2–84.5) *N*=89	33.20 ± 2.11 (27.0–36.7) *N*=89 (44+45)	33.28 ± 1.47 (30.7–35.8) *N*=17 (6+11)	39.39 ± 7.71 (19.0–67.5) *N*=1064 (*28*)	0.84 ± 1.08 (0.0–.3) *N*=89	7.15 ± 5.40 (0.0–33.12) *N*=1064	6.32	0.88
P. muralis	68.98 ± 2.77 (63.4–77.5) *N*=57	31.28 ± 2.57 (24.6–35.8) *N*=57 (31+26)	32.61 ± 1.13 (30.6–35.1) *N*=22 (16+6)	36.68 ± 7.67 (23.6–60.0) *N*=608 (*16*)	1.15 ± 1.65 (0.0–6.7) *N*=57	4.94 ± 5.96 (0.0–25.9) *N*=608	3.80	0.76
Statistics	$P < 0.001$	$P < 0.001$	P=0.312	$P < 0.001$	P=0.004	$P < 0.001$	$P < 0.001$	$P < 0.001$
GROUPS	{*Pm*}{*Pp*}{*Pt*}	{*Pm*}{*Pp,Pt*}	{*Pm,Pp,Pt*}	{*Pm*}{*Pp,Pt*}	{*Pt,Pm*}{*Pp,Pm*}	{*Pm*}{*Pp,Pt*}	{*Pp,Pt*}{*Pm*}	{*Pt*}{*Pp,Pm*}

muralis (32.61 ± 1.13 °C), ANOVA showed that these differences were not statistically significant ($F_{2,83}$=1.18, *P*=0.312; Table 1), even after correcting for SVL ($F_{2,82}$=1.88, *P*=0.159). Set-point temperatures were rather similar for the three species (*P. peloponnesiacus*: 32.05–33.7 °C, *P. tauricus*: 32.33–34.38 °C and *P. muralis*: 31.31–34.01 °C) and received values in a narrow temperature window. We found no differences in the T_{set} among the species (ANOVA; $F_{2,83}$=1.13, *P*=0.327; Fig. 3).

The difference between T_b and T_{set} revealed that *P. peloponnesiacus* and *P. tauricus* were able to maintain their body temperature with consistency within the set-point range (*t*-test; *P. peloponnesiacus*: *t*=1.09, *df*=130, *P*=0.28 and *P. tauricus*: *t*=0.81, *df*=104, *P*=0.42). In contrast, mean T_b was significantly lower than T_{set} for *P. muralis* (*t*-test; *t*=3.22, *df*=77, *P*=0.002).

3.3. *Effectiveness of thermoregulation*

We detected no effects of SVL on T_b or on T_{pref}, a finding indicating that SVL does not affect *E* in the focal species. Though the mean deviation of T_b from T_{set} ($\overline{d_b}$) differed significantly among the species (ANOVA; $F_{2,228}$=5.43, *P*=0.005), these differences stemmed from the comparison between *P. tauricus* and *P. peloponnesiacus* (Tukey *HSD* post hoc test), with the first demonstrating higher accuracy of thermoregulation than the latter (Table 1). The mean deviation of T_e from T_{set} ($\overline{d_e}$) also differed among species (ANOVA; $F_{2,2733}$=44.18, $P < 0.001$). Pairwise comparison (Tukey *HSD* post hoc test) indicated that microhabitats (based on sunlight exposure) used by *P. muralis* had high thermal quality, whereas the microhabitats of *P. peloponnesiacus* and *P. tauricus* were of low thermal quality (Tables 1 and 2).

The effectiveness of thermoregulation differed among the three species (Table 1). Bootstrap resampling revealed significant differences between species, with *P. tauricus* demonstrating higher effectiveness than *P. peloponnesiacus* and *P. muralis* (in both cases we found higher values of *E* in 1000 of 1000 simulations, $P < 0.05$ after Tukey correction). The index $\overline{d_e}$-$\overline{d_b}$ (Blouin-Demers and Weatherhead, 2001) corroborate the above results: *P. tauricus* received the higher value ($\overline{d_e}$-$\overline{d_b}$=6.32), followed by *P. peloponnesiacus* and *P. muralis* (Table 1). Bootstrap resampling also revealed significant differences. *Podarcis tauricus* and *P. peloponnesiacus* demonstrated higher thermoregulatory effectiveness than *P. muralis* (higher values of $\overline{d_e}$-$\overline{d_b}$ in more than 984 of 1000 simulations in both pairwised comparisons, all $P < 0.05$ after Tukey correction). No differences were found between *P. peloponnesiacus* and *P. tauricus*.

4. Discussion

Sympatrically coexisting lizards tend to differentiate their niche and, consequently, their thermoregulatory behavior (Cádiz et al., 2013; Scheers and Van Damme, 2002; Martín-Vallejo et al., 1995). In line with our initial hypotheses, the thermal quality of the habitats used by the three species differed considerably. Moreover, all three species thermoregulated effectively and kept their body temperatures close to their preferred temperatures, indicating high thermoregulation accuracy. Furthermore, the three species had similar thermal preferences (T_{set}), despite the differences in the thermal quality of their habitats, a finding that might advocate the "static" view on the evolution of thermal physiology (Losos et al., 2003).

The study species partition their habitat in order to coexist in the

Table 2
Values for Te of the three different microclimates (in terms of exposure to sunlight). Mean ± standard deviation, range (in parenthesis) and sample size (*N*) (in parenthesis the number of copper models). Results of one-way ANOVA and pairwise comparison (Tukey HSD test) for the available thermal microhabitats. *Pt* referes to *P. tauricus*, *Pp* to *P. peloponnesiacus* and *Pm* to *P. muralis*.

Species	Shade (S) (°C)		Semi-light (SL) (°C)		Full-light (FL) (°C)		F-statistics
	T_e	d_e	T_e	d_e	T_e	d_e	
P. peloponnesiacus	33.59 ± 6.84 (19.0–54.0) *N*=304 (*8*)	4.49 ± 4.34	39.90 ± 5.98 (26.5–54.5) *N*=380 (*10*)	7.22 ± 4.51	43.59 ± 7.31 (25.0–66.2) *N*=380 (*10*)	10.38 ± 6.53	$F_{2,1061}$=189.5 $P < 0.001$ {S}{SL}{FL}
P. tauricus	33.58 ± 6.71 (19.0–52.2) *N*=304 (*8*)	4.39 ± 3.96	39.85 ± 5.86 (26.5–54.8) *N*=380 (*10*)	6.64 ± 4.21	43.60 ± 7.19 (25.0–67.5) *N*=380 (*10*)	9.78 ± 6.17	$F_{2,1061}$=196.1 $P < 0.001$ {S}{SL}{FL}
P. muralis	30.34 ± 3.73 (23.6–38.7) *N*=152 (*4*)	2.41 ± 2.33	36.23 ± 5.54 (26.3–53.3) *N*=228 (*6*)	3.62 ± 4.36	41.36 ± 8.28 (28.0–60.0) *N*=228 (*6*)	7.96 ± 7.58	$F_{2,605}$=137.4 $P < 0.001$ {S}{SL}{FL}
Statistics	$F_{2,757}$=16.24 $P < 0.001$		$F_{2,985}$=34.33 $P < 0.001$		$F_{2,9851}$=7.85 $P < 0.001$		
GROUPS	{*Pm*}{*Pp,Pt*}		{*Pm*}{*Pp,Pt*}		{*Pm*}{*Pp,Pt*}		

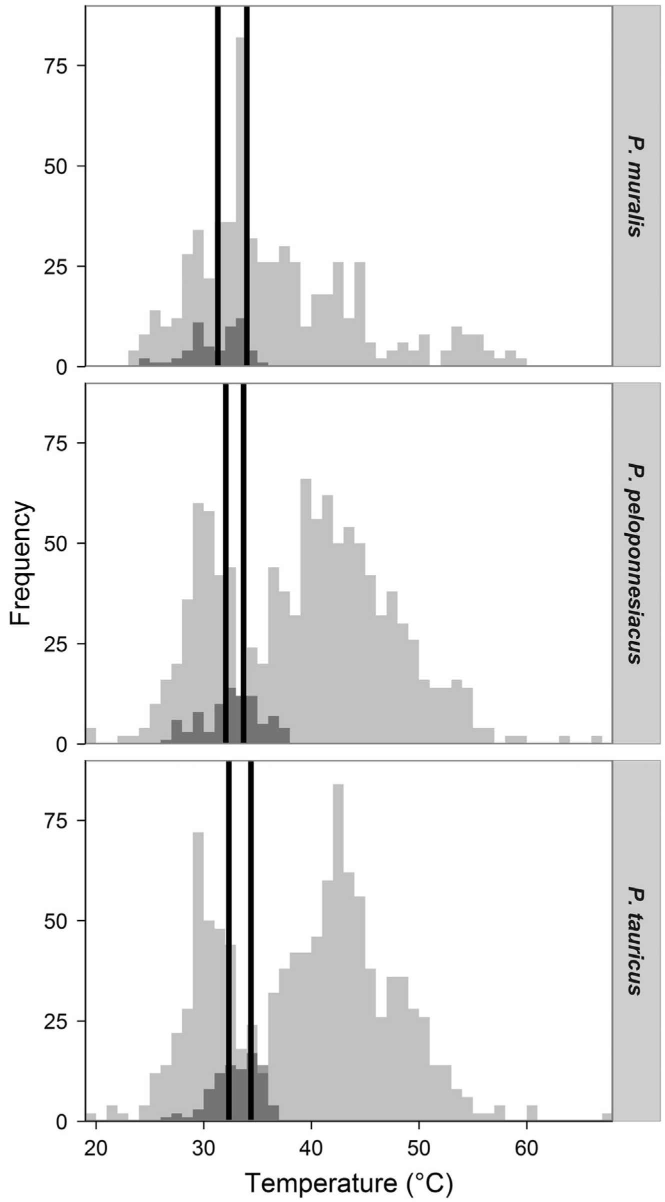

Fig. 3. Frequency of field body temperatures (T_b, dark gray) and operative temperatures (T_e, light gray). Vertical black solid lines indicate the set-point range temperatures (T_{set}).

quite restricted focal site (Mayer and Beyerlein, 1999), similar to other sympatric lizard species (Cádiz et al., 2013; Corbalán et al., 2013; Dias and Rocha, 2007; Harmon et al., 2007). This spatial variation led, as expected, to substantial differences in the thermal quality ($\overline{d_e}$) of the habitats used by each species and the available operative temperatures (Tables 1 and 2). *Podarcis muralis* experienced a more benign thermal environment, though cooler compared to the habitats of the other two species (mean T_e=36.68 °C, mean d_e=4.94 °C), with lower fluctuations and fewer extreme values than *P. peloponnesiacus* and *P. tauricus* (mean T_e ~39.5 °C, mean d_e ~6.1). Field data indicated that for most of the time (approximately 72%) T_es records were higher than T_{set} for *P. peloponnesiacus* and *P. tauricus* (Fig. 3). On the other hand, the equivalent period for *P. muralis* dropped to 45%. When the exposure to sunlight (define the different microhabitats) was taken into account, an interesting finding arose: though *P. peloponnesiacus* and *P. tauricus* models achieve low d_es (high thermal quality) only in shady microhabitats, *P. muralis* models demonstrated low d_es in both shade and semi-light microhabitats (Table 2). All the above emphasize the higher thermal quality of the habitat used by *P. muralis* and also indicate the great thermal variation between the microhabitats used by *P. peloponnesiacus* and *P. tauricus,* which makes them constantly move between different microhabitats in order to thermoregulate effectively.

Body temperatures that lizards achieved in the field were within the same range as other Mediterranean lacertids that live in mountain habitats (Monasterio et al., 2009; Ortega et al., 2016a, 2016c; Zamora-Camacho et al., 2015). Nonetheless, T_bs differed among the three species: *P. muralis* achieved lower T_bs than *P. tauricus* and *P. peloponnesiacus* (Table 1). This finding has been reported before: *P. muralis* achieved T_bs varying from 30.4 °C, (Grbac and Bauwens, 2001) to 32.2 °C (Martín-Vallejo et al., 1995) and *P. peloponnesiacus* from 33.43°C to 34.52 °C (Maragou, 1997; Pafilis, 2003); no data exist for *P. tauricus*. As stated above, *P. muralis* used cooler (than the other two species) and more shady microhabitats and achieved T_b almost 1.5 °C lower than its T_{set} (Table 1). An interesting finding was that 50% of *P. muralis* T_bs records were lower than T_{set} (30% for the other two species). The fact that *P. muralis* is so active at suboptimal body temperatures might permit the species to exploit thermally cooler habitats that are probably avoided by the other two species, reducing competitive interactions (Murray et al., 2016; Schoener, 1974a). This eurythermy might also explain its wide range expansion (Huey and Webster, 1975; Ruibal and Philibosian, 1970).

Despite the different thermal quality of the habitats used and the different body temperatures in the field, the preferred body temperature did not differ among the species (Table 1) and reached values similar to other *Podarcis*, including the Greek species (see Tables in Kapsalas et al., 2016 and Pafilis et al., 2016). Thermal inertia is common among lizards (Corbalán et al., 2013; Grover, 1996; Hertz et al., 1983) as the evolution of thermal biology often requires adjustments in the performance of other complex physiological traits such as sprint and locomotion (Crowley, 1985; Zhang and Ji, 2004), metabolism and digestion (Angilletta, 2001; McConnachie and Alexander, 2004) and reproduction (Shine and Harlow, 1993; Van Damme et al., 1992). Our results deviate from the few studies that support the evolutionary flexible aspect of lacertid thermoregulation (Sagonas et al., 2013b; Scheers and Van Damme, 2002) and comply with the 'static' view according to which the thermal physiology is evolutionarily conservative and does not respond to directional selection (Hertz et al., 1983; Losos et al., 2003). However, the lack of T_{set} and T_b values from allopatric populations of the three species does not permit us to make solid arguments on the evolution of thermoregulation.

Thermoregulation was effective for all species, in accordance with our second hypothesis. Both indices of thermoregulation yielded the same results: in descending order, *P. tauricus* achieved the higher *E* value, followed by *P. peloponnesiacus* and *P.muralis* (Table 1). The complementary approach proposed by Blouin-Demers and Weatherhead (2001) highlighted the less effective thermoregulation of *P. muralis* in a more striking way: the respective values for *P. tauricus* and *P. peloponnesiacus* were almost twofold higher over that of *P. muralis*. The higher the magnitude of the difference between $\overline{d_b}$ and $\overline{d_e}$ is, the more effective thermoregulation appears (Blouin-Demers and Weatherhead, 2001). The lower thermoregulation effectiveness of *P. muralis* should be sought to its distribution and ecological requirements. Although *P. tauricus* and *P. peloponnesiacus* in Greece occur always in sites with high sun exposure and from sea level up to 2000 m, *P. muralis* is a predominantly mountain species that prefers humid, semi-shady places (Arnold and Ovenden, 2002; Valakos et al., 2008). Ergo, the very same mountain climate that is hard and of low thermal quality for *P. peloponnesiacus* ($\overline{d_e}$=7.57) and *P. tauricus* ($\overline{d_e}$=7.15), appears to be benign and of high thermal quality for *P. muralis* ($\overline{d_e}$=4.94), which, thus can afford a lower thermoregulatory effectiveness. On the other hand, the different *E* value could also be attributed to the type of microhabitats the species frequent. Indeed, *P. muralis* were mostly captured in shady and semi-light microhabitats where the amplitude of T_es is more restricted and close to T_{set}. On the contrary, *P.*

peloponnesiacus and *P. tauricus* were caught in all different types of microhabitat, experiencing a great variation of T_es, and thus have to thermoregulate within T_{set} by shuttling between sun and shade. Nevertheless, we should point out that though *E* and thermal preferences may vary within the year, or with habitat, altitude and latitude (Díaz and Cabezas-Díaz, 2004; Díaz et al., 2006; Monasterio et al., 2009; Sears and Angilletta, 2015).

To summarise, the three focal species, in order to coexist in the same, narrow site, used different microhabitats and adjusted accordingly their thermal physiology. All of them are active and effective thermoregulators and share similar thermal preferences. However, they differ in the extent of thermoregulation depending on the thermal quality of the microhabitat used. Interestingly, the common wall lizard is frequently active at temperatures lower to their T_{set} and exploits thermally cooler microhabitats that are not occupied and/or are avoided from *P. tauricus* and *P. peloponnesiacus*. Overall our findings depict the differentiation of habitat thermal quality, even in a very small scale, and pave the way for better understanding the adjustments to which ectotherms resort to live in syntopy.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.jtherbio.2017.02.014.

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