Thermal ecology of *Podarcis siculus* (Rafinesque-Schmalz, 1810) in Menorca (Balearic Islands, Spain)

Zaida Ortega*, Abraham Mencía, Valentín Pérez-Mellado

*Department of Animal Biology, University of Salamanca, Campus Miguel de Unamuno, 37007, Salamanca, Spain .*Corresponding author.* E-mail: zaidaortega@usal.es

Abstract. We studied the thermal ecology of an introduced population of the Italian wall lizard, *Podarcis siculus*, in Menorca (Balearic Islands, Spain). We measured field body temperatures of adult lizards, as well as air and substrate temperatures at their capture places, during spring and summer. We assessed the relations between body and air temperatures, and between body and substrate temperatures, for both seasons. We studied the preferred temperature range of *P. siculus* in a laboratory thermal gradient. In addition, we recorded the operative temperatures of the habitat of the Italian wall lizard during summer. Then, we calculated the three indexes of behavioural thermoregulation for summer: thermal quality of the habitat, accuracy of thermoregulation, and effectiveness of thermoregulation. As expected, our results show that Italian wall lizards achieved significantly higher body temperatures during summer than during spring. Body temperatures were not significantly related to air temperatures in spring, but the correlation was significant in summer. In addition, body temperatures were not significantly related to substrate temperatures for any season. The preferred temperature range of the species was similar for males and females: 28.40-31.57 °C. Introduced Italian wall lizards of Menorca are effective thermoregulators, with an effectiveness of 0.82 during summer.

Keywords. Thermal biology, behavioural thermoregulation, temperature, heliothermy, Lacertidae, Italian wall lizard, *Podarcis siculus*.

INTRODUCTION

Thermal ecology is a central point in the biology of squamate vertebrates. Their ability to exploit any resource is closely related to an effective control of their body temperature (Cowles and Bogert, 1974; Huey, 1974; Adolph and Porter, 1993). Themal ecology would cover two important traits: thermal sensitivity and thermoregulation (Angilletta, 2009). Thermal sensitivity is the dependence of physiological performance on temperature, which ranges from thermal specialists to generalists (Angilletta et al., 2002; Angilletta, 2009). Thermoregulation is the capacity to regulate body temperatures, which ranges from thermoconformers, whose body temperatures would totally depend on ambient temperatures, to perfect thermoregulators, whose body temperatures would be constant, regardless of ambient temperatures (Huey, 1974; Hertz et al., 1993; Sears and Angilletta, 2015).

Lizards mainly use three mechanisms to regulate their body temperature: adjusting activity periods (Hertz, 1992; Adolph and Porter, 1993), shuttling between different microhabitats (Heath, 1970; Bauwens et al., 1996), and adjusting their body posture (Bauwens et al., 1996). The combination of these strategies depends on the balance between costs and benefits, which in turn depends on different biotic and abiotic factors (Huey and Slatkin, 1976; Sears and Angilletta, 2015). Within lizards, Lacertids generally are effective thermoregulators and mostly

heliothermic, which use to move between sunny and shade microhabitats for thermoregulation (Avery, 1976; Van Damme et al., 1990; Castilla et al., 1999; Ortega et al., 2016a).

Our aim is to study the thermal ecology of an introduced population of the Italian wall lizard, *Podarcis siculus*, in Menorca (Balearic Islands, Spain). We measured body temperatures of active lizards, as well as air and substrate temperatures of the microhabitats occupied by lizards. In order to search for seasonal effects in the thermoregulation, we compared these measures for spring and summer. We hypothesized that lizards would achieve higher body temperatures in summer than in spring, as it is usual in lacertid lizards (e.g. Díaz and Cabezas-Díaz, 2004; Ortega et al., 2014). We also measured the thermal preferences of lizards in a thermal gradient. In addition, we recorded the operative temperatures of the habitat during summer. Finally, we studied the thermal quality of the habitat, the accuracy of thermoregulation, and the effectiveness of thermoregulation (Hertz et al., 1993) of the Italian wall lizard during summer.

MATERIAL AND METHODS

Study species and area

The Italian wall lizard *Podarcis siculus* (Rafinesque-Schmalz, 1810) is a robust ground-dwelling lacertid lizard. The original distribution covers Italy (continental Italy, Sardinia, Sicily and several coastal islets), Corsica (France) and the east coast of the Adriatic Sea, from Slovenia to Montenegro (Henle and Klaver, 1986). However, *P. siculus* has been introduced in many Mediterranean countries and in the United States (Corti et al., 2004). Here we studied the population of Menorca (Balearic Islands, Spain), which inhabits all kinds of habitats, from coastal dunes to forests and anthropogenic walls (Pérez-Mellado, 1998; Pérez-Mellado, 2002), and would be introduced from Sicily and/or Sardinia (Silva-Rocha et al., 2012). The Italian wall lizard is a heliothermic lizard, which previously reported mean temperatures range between 29 °C in spring and approximately 33 °C in summer (Avery, 1978; Van Damme et al., 1990; Foà et al., 1992; Tosini et al., 1992).

We studied the population of Es Canutells, in Southern Menorca (Spain), an almost undisturbed Mediterranean habitat of mixed woodland and scrubland (patches of pines and holm oaks, and patches of large shrubs, mainly *Pistacia lentiscus*), spotted with large rocks. The studied population exhibited a clear sexual size dimorphism, with larger (mean SVL males: 73.35 ± 1.22 mm, n = 20; mean SVL females: 64.97 ± 1.00 mm, n = 9; one-way ANOVA, $F_{1, 27} = 18.417$, P < 0.0001) and heavier (mean weight males: 10.28 ± 0.41 g, n = 20; mean weight females: 7.09 ± 0.41 g, n = 9; one-way ANOVA, $F_{1, 27} = 22.061$, P < 0.0001) males.

Field sampling

We recorded field temperatures of *Podarcis siculus* between 27 May and 30 July 2013, in 12 sunny days of fieldwork (7 in spring and 5 in summer). We considered the natural seasons: the data obtained before the 21st of June have been considered as spring data, and those obtained after that date as summer data. We captured active adult lizards by noosing, during their daily activity period, from 07:00 to 17:00 h (GMT), 16 in spring (11 males and 5 females) and 15 in summer (11 males and 4 females). Immediately after capture (within 30 s), we measured cloacal body temperature (T_b) with a Testo° 925 digital thermometer, shadowing the probe, as well as air temperature (T_a) 1 cm above the capture point, and substrate temperature (T_s) of the capture point. We also recorded the type of substrate, the height of the perch (in cm), and the sunlight situation (full sun, filtered sun, or full shade). Finally, we measured wind speed with a Kestrel° 3000 anemometer, but during field work, its variation was almost insignificant (a mean of 0.15 ms^{-1}). So, for this study, we discarded the wind as a possible variable affecting thermal behaviour of lizards.

As a null hypothesis for thermoregulation, we recorded operative temperatures (T_e). We recorded T_e during the same days of the field sampling of summer (between 16 July 2013 and 30 July 2013) in the same area of study (Es Canutells), in order to control for potential variations in weather conditions. We used copper models as null T_e models (Bakken and Angilletta, 2014). These models achieve similar temperatures to those of non-thermoregulating lizards. We placed one thermocouple probe into each hollow model and connected it to a data logger HOBO° H8 (Onset Computer Corporation), programmed to take a temperature record every five minutes. We randomly placed the copper models in different microhabitats and used the T_e hourly mean of each microhabitat for analysis, since raw T_e data could be autocorrelated. Based in observations of the behaviour of lizards, we selected four types of microhabitats: rock, soil, grass, and logs of *Pistacia lentiscus*; each of them was considered in the three sunlight situations (see above).

Preferred temperature range (PTR)

We measured selected body temperatures (T_{sel}) of *P. siculus* between 12 June 2013 and 14 June 2013 in a laboratory thermal gradient. We captured lizards from the same location of field sampling and immediately transported them to the laboratory in Es Castell (Menorca, Spain). There, we housed lizards on individual terraria and fed them with mealworms and crickets. Water was provided *ad libitum* during the length of the experiment. We built the thermal gradient in a glass terrarium (100 x 60 x 60 cm) with a 150 W infrared lamp over one of the sides, obtaining a gradient between 20 to 60 °C. Then, we measured the selected temperature of a lizard each hour from 08:00 to 17:00 h (GMT) with a digital thermometer. We used 24 *P. siculus* adult lizards, 14 males and 10 females. We considered the 50% of the central values of selected body temperatures as the preferred temperatures range (PTR) in all analyses, as it is the more common procedure, although we also report the 80%

PTR, since some authors employ this range (Hertz et al., 1993; Blouin-Demers and Nadeau, 2005). We released lizards at their capture places immediately after the experiment.

Data analysis

To test the null hypothesis of thermoregulation, that is, if lizards use microhabitats randomly regarding temperature, we followed the protocol developed by Hertz et al. (1993), and calculated their three indexes of thermoregulation. The first is the index of accuracy of thermoregulation ($\overline{d}_b$), that is the mean of absolute values of the deviations between each T_b from the preferred temperature range. Thus, the values of the index of accuracy of thermoregulation are counterintuitive: higher values of $\overline{d}_b$ indicate lower accuracy of thermoregulation, and vice-versa. The second is the index of thermal quality of habitat ($\overline{d}_e$), calculated as the mean of absolute values of the deviations of each T_e from the preferred temperature range. Accordingly, the values of the index of thermal quality of the habitat are also counterintuitive: higher values of $\overline{d}_e$ indicate a lower thermal quality of the habitat, and vice-versa. The third is the index of effectiveness of thermoregulation (E), that is calculated as E = 1 - ($\overline{d}_b$/ $\overline{d}_e$). Hence, values of E range from 0 to 1, meaning the higher effectiveness of thermoregulation the higher the value of E (see Hertz et al., 1993). Effectiveness of thermoregulation was calculated with THERMO, a Minitab module written by Richard Brown. THERMO uses three kinds of input data: T_b, T_e and T_{sel} of the preferred temperature range, and was programed to perform bootstraps of 100 iterations, building pseudo-distributions of three kinds of output values: the arithmetic mean of the index of accuracy of thermoregulation ($\overline{d}_b$), the arithmetic mean of the index of thermal quality of the habitat ($\overline{d}_e$), and the arithmetic mean of the index of effectiveness of thermoregulation (E). As we measured T_e in summer, we only computed this protocol of study for the body temperatures of summer.

We performed parametric statistics when data followed the assumptions of normality and variance homogeneity. When data did not fulfill these assumptions, even after log-transformations, we carried out non-parametric equivalent tests (Sokal and Rohlf, 1995; Crawley, 2012). We conducted all analyses on R, version 3.1.3 (R Core Team, 2015), and we computed *post-hoc* comparisons of Kruskal-Wallis tests with Nemenyi test with the package PMCMR (Pohlert, 2014). We reported mean values of variables accompanied by standard errors. Significance level was α = 0.05.

RESULTS

Selected body temperatures (T_{sel}) were similar regarding sex (mean T_{sel} of males: 29.84 ± 0.41 °C, n = 14; mean T_{sel} of females: 30.15 ± 0.31 °C, n = 10; one-way ANOVA, $F_{1, 22}$ = 0.301, P = 0.589). Thus, we pooled them in subsequent analyses, and considered a preferred temperature range (PTR) for this population. The 50% PTR is 28.40 - 31.57 °C, and the 80% PTR is 26.85-32.54 °C.

Body temperatures (T_b) were also similar regarding sex (mean T_b of males = 30.99 ± 0.53 °C, n = 22; mean T_b of females = 30.23 ± 1.09 °C, n = 9; one-way ANOVA, $F_{1, 29}$ = 0.494, P = 0.488). Thus, also in this case, we pooled data from males and females for subsequent analyses. Body temperatures (T_b) of lizards (one-way ANOVA, $F_{1, 29}$ = 7.996, P = 0.008), as well as air temperatures (one-way ANOVA, $F_{1, 29}$ = 18,704, P < 0.0001) and substrate temperatures (T_s; one-way ANOVA, $F_{1, 29}$ = 8.244, P = 0.008) were significantly higher in summer than in spring (Table 1). Although sample size for subsets of each sex within each season is small, we checked for potential differences in T_b between sexes, in order to confirm if males and females should be pooled together within each season. Results show similar T_b of males and females both in spring (one-way ANOVA, $F_{1, 15}$ = 0.136, P = 0.718) and in summer (one-way ANOVA, $F_{1, 14}$ = 0.267, P = 0.614).

An ANCOVA test reveals that the linear relation between T_b and T_a significantly changed between spring and summer (T_a as a covariate; interaction season*T_a: $F_{1, 27}$ = 5.590, P = 0.026). Thus, linear regressions must be studied separately regarding season. Correlation between T_b and T_a was not significant in spring (r = 0.209, P = 0.438, n = 16), but was significant in summer (r = 0.756, P = 0.001, n = 15). The linear regression slope of T_a on T_b was also not significant (β = 0.21, P = 0.438, n = 16; R^2 = 0.044; Fig. 1) in spring, and was statistically significant in summer (β = -0.61, P = 0.001, n = 15; R^2 = 0.571; Fig. 1). However, the slope of the linear regression of T_s on T_b was similar for both seasons (ANCOVA, T_s as covariate; interaction season*T_s: $F_{1, 27}$ = 0.042, P = 0.839). The correlation coefficient was significant (r = 0.481, P = 0.003), as well as the regression coefficient (β = 0.38, P = 0.006, n = 31; R^2 = 0.231; Fig. 1).

The available microhabitats at the study site provided different operative temperatures (Kruskal-Wallis test, H = 222.525, P < 0.0001, n = 528, df = 12; see Table 2 and Fig. 2). Only grass and rock in full shade provided optimal temperatures for the thermoregulation of *P. siculus* (i.e., within the PTR) during all hourly periods of the day (Fig. 2).

The index of thermal quality of the habitat (d_e) showed a mean of 8.07 ± 0.05, the index of thermal accu-

Table 1. Mean ± SE (sample size) body temperatures (T_b), air temperatures (T_a) and substrate temperatures (T_s) of *Podarcis siculus* at Menorca (Balearic Islands, Spain). Temperatures are in °C.

	Spring	Summer
T_b	29.57 ± 0.56 (16)	32.05 ± 0.68 (15)
T_a	25.77 ± 0.56 (16)	28.92 ± 0.45 (15)
T_s	27.11 ± 0.76 (16)	30.27 ± 0.80 (15)
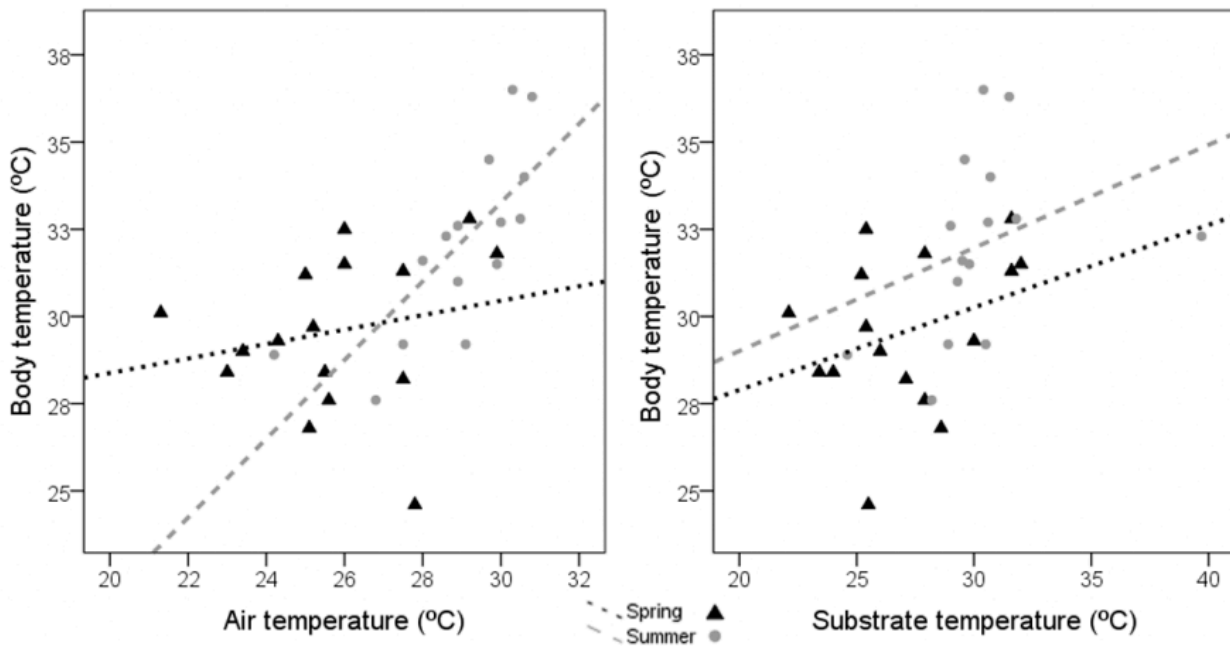
Fig. 1. Slopes of the simple linear regressions models of body temperatures of *Podarcis siculus* lizards (T_b; left plot) and of the simple linear regressions of T_b against substrate temperatures (T_s; right plot) in spring and summer. The regression T_b-T_a was not significant in spring, but was is significant in summer, and the regression T_b-T_s was significant and had a similar slope for both seasons (see results in the text).

Table 2. Mean values of the operative temperatures (T_e) of the different microhabitats studied for *Podarcis siculus* at Menorca (Balearic Islands, Spain). Temperatures are in °C. The letters between brackets match the non-significant pairs of the Nemenyi post-hoc comparisons of the Kruskal-Wallis test (P > 0.05 in the paired comparisons). To avoid pseudoreplication, calculations are based in the hourly means of T_e so sample size coincides with the hours of monitoring of each microhabitat at the study site.

	n	T_e	SE
Under rock (b, d)	44	37.55	0.88
Rock Full sun (a)	33	45.40	1.08
Rock Filtered sun (h, i)	44	40.64	1.12
Rock Full shade	44	30.78	0.28
Soil Full sun (a)	11	47.57	3.84
Soil Filtered sun (f, g, h)	44	39.98	1.19
Soil Full shade	44	29.30	0.33
Grass Full sun (a)	44	51.56	1.75
Grass Filtered sun (e, f, i)	44	40.59	1.38
Grass Full shade	44	30.37	0.29
Pistacia Full sun (b, c)	44	36.86	0.94
Pistacia Filtered sun (c, d, e, g)	44	38.48	1.20
Pistacia Full shade (b)	44	36.43	0.92

racy (d_b) was 1.41 ± 0.04, and the index of effectiveness of thermoregulation (E) of *P. siculus* in summer was 0.820 ± 0.005.

DISCUSSION

The preferred temperature range of *P. siculus*, obtained in the late spring, ranges from 28.40 to 31.70 °C. This is lower than the preferred temperature range of the endemic lacertid lizard from Menorca, *P. lilfordi*, which showed a range between 31.78 and 35.68 °C during spring (unpublished data), and 32-36 °C during summer (Pérez-Mellado et al., 2013; Ortega et al., 2014). This is also lower than the preferred temperature range of the third lacertid lizard present in Menorca, *Scelarcis perspicillata*, which showed a range from 33.90 to 36.10 °C during summer (Ortega et al., 2016b). Thus, the precision of thermoregulation obtained for the Italian wall lizard was 3.3 °C, while the Balearic lizard exhibited 3.9 °C, and the Moroccan rock lizard 2.2 °C. The thermal preferences in a laboratory thermal gradient represent the optimal temperatures that lizards would intend to achieve in their habitats if there were no other ecological constraints than temperature (e.g., Dawson, 1975; Huey and Bennett,
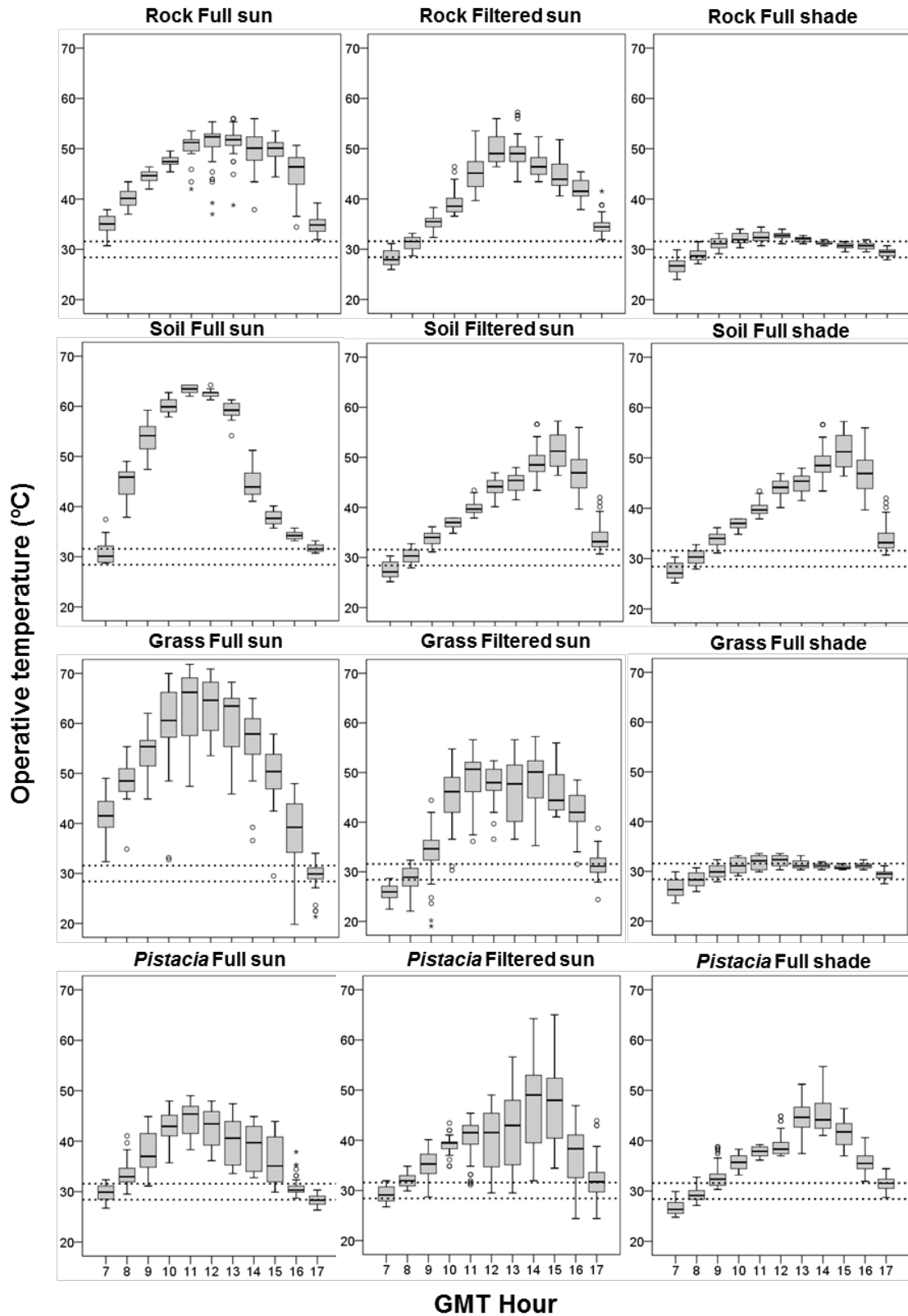
Fig. 2. Operative temperatures (T_e) provided by the different microhabitats studied in Es Canutells (Menorca, Spain) for the Italian lizard, *Podarcis siculus*. The dotted lines comprise the preferred temperature range (PTR) of the species.

1987). The thermal preferences are closely related with thermal sensitivity of performance (Angilletta et al., 2002; Martin and Huey, 2008). Our results suggest that *P. siculus* would perform better at lower temperatures than the other two diurnal lacertid lizards inhabiting Menorca.

Our results were coherent with previous studies about body temperatures of *P. siculus*. Italian wall lizards showed mean body temperatures approximately 2 °C lower in June and July at Menorca than those recorded near Florence, in Italy (Avery, 1978). However, mean body temperatures found in summer in Menorca are similar to those found in summer near Pisa, (Tosini et al., 1992). Regarding spring thermoregulation, our data were similar to those found in Corsica (France) in May: mean T_b are ≈ 2 °C lower, mean T_a are ≈ 2 °C higher, and mean T_s are similar (Van Damme et al., 1990). In addition, the regression slope between body and air temperatures was very similar to the slope reported by Van Damme et al. (1990) for *P. siculus* of Corsica during spring, and was also not significantly different from zero. Our results also confirmed the conclusion of Van Damme et al. (1990) and Tosini et al. (1992) about the lack of a sexual effect on body temperatures of *P. siculus*.

Mean body temperatures of the Italian wall lizard were significantly higher in summer than in spring, but approximately 3 °C lower, for each season, than the body temperatures of the Balearic lizard in the close islets of Aire and Colom (Ortega et al., 2014). Mean body temperatures were also approximately 2 °C lower than those of the Moroccan rock lizard in Menorca (Ortega et al., 2016b). During summer, the Italian wall lizard achieved a lower accuracy and effectiveness of thermoregulation ($\bar{d}_b$ ≈ 1.41 °C; E ≈ 0.82) than the Balearic lizard ($\bar{d}_b$ ≈ 0.50 °C; E ≈ 0.91; Ortega et al., 2014) and the Moroccan rock lizard ($\bar{d}_b$ ≈ 0.62 °C; E ≈ 0.88; Ortega et al., 2016b). However, our data shows that the Italian wall lizard is an effective thermoregulator lacertid, which seems well adapted to inhabit a wide range of microhabitats. A comparative study on the flexibility of thermal physiology and behavioural thermoregulation of *P. siculus* lizards and the species with which they coexist worldwide would help explain the possible causes of the remarkable ability of this species to adapt to different environments.

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