Habitat shapes the thermoregulation of Mediterranean lizards introduced to replicate experimental islets

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ABSTRACT

Both environmental temperatures and spatial heterogeneity can profoundly affect the biology of ectotherms. In lizards, thermoregulation may show high plasticity and may respond to environmental shifts. In the context of global climate change, lizards showing plastic thermoregulatory responses may be favored. In this study, we designed an experiment to evaluate the extent to which lizard thermoregulation responds to introduction to a new environment in a snapshot of time. In 2014, we captured individuals of the Aegean Wall lizard (*Podarcis erhardii*) from Naxos Island (429.8 km^2) and released them onto two small, lizard-free islets, Galiatsos (0.0073 km^2) and Kampana (0.004 km^2) (Aegean Sea, Greece). In 2017, we returned to the islets and estimated the effectiveness (*E*), accuracy and precision of thermoregulation measuring operative, preferred (*T$_{pref}$*) and body temperatures. We hypothesized that the three habitats would differ in thermal quality and investigated the extent to which lizards from Naxos demonstrate plasticity when introduced to the novel, islet habitats. Thermal parameters did not differ between Galiatsos and Naxos and this was reflected in the similar *E* and *T$_{pref}$*. However, lizards from Kampana deviated in all focal traits from Naxos, resulting in higher *E* and a preference for higher *T$_{pref}$*. In sum, Naxos lizards shifted their thermoregulatory profile due to the idiosyncratic features of their new islet habitat. Our results advocate a high plasticity in lizard thermoregulation and suggest that there is room for effective responses to environmental changes, at least for *Podarcis* lizards in insular habitats.

1. Introduction

The effective and precise regulation of body temperature affects every aspect of ectothermic function, from intracellular biochemical reactions to an organism's performance (Pörtner, 2002; Angilletta, 2009). Among reptiles in particular, thermoregulation underlies all life history strategies and physiological patterns. As a result, thermoregulation attracted early research interest that has produced an impressive body of literature over the years (Weese, 1917; Ortega and Martín-Vallejo, 2018). The effectiveness, accuracy, and precision with which lizards thermoregulate defines their overall performance and, ultimately, represents an absolute criterion for survival (Hertz et al.,

1993). As all the abovementioned parameters depend on thermal availability and preferences, possible shifts in the latter would have a direct impact on thermoregulation. Of course, not all reptiles thermoregulate effectively, precisely and accurately (Shine and Madsen, 1996).

Lizards have been suggested to be particularly threatened by climate change (Sinervo et al., 2010); average global warming means that lizards now have to deal with higher and more extreme environmental temperatures that last for longer periods (Huey et al., 2012; Pontes da Silva et al., 2018 but see Lara-Reséndiz et al., 2015; Valenzuela-Ceballos et al., 2015). Accordingly, lizards may be pushed to the limit of their physiological tolerance to overheating, and thus need to adjust
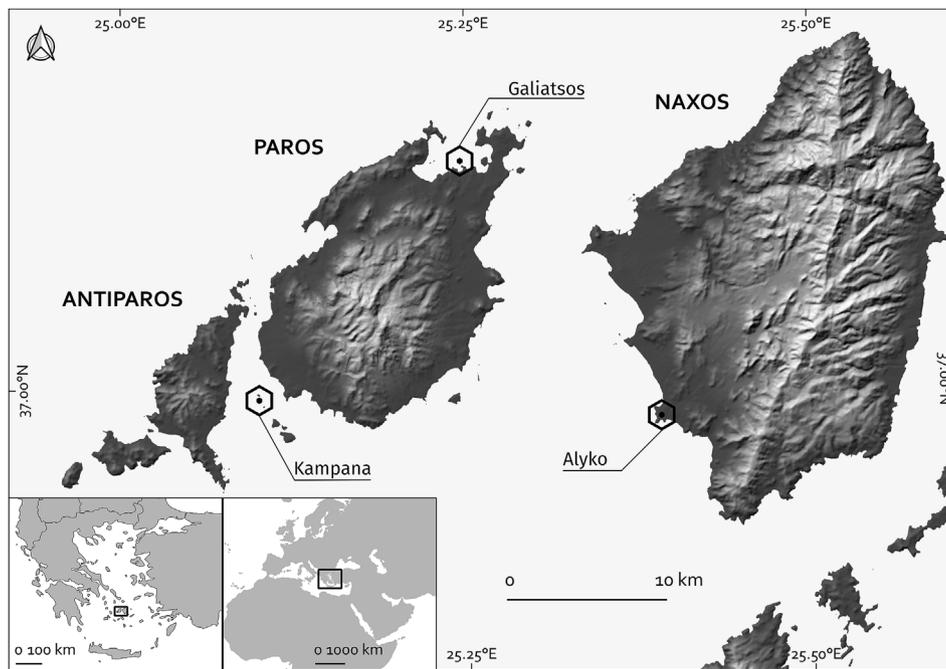
Fig. 1. Map of the study system in the Aegean Sea (East Mediterranean Sea). Hexagons denote the focal sites.

aspects of their thermoregulation and/or physiological parameters (e.g. thermal maxima and minima) to accommodate the environmental changes (Deutsch et al., 2008; Medina et al., 2016). Those species that are able to adapt their thermal preferences have better chances to survive (Logan et al., 2014). However, is saurian thermoregulation flexible enough to compensate for the higher and more prolonged thermal loads that are pushing physiological limits?

Lizards, and particularly island lizards, are considered Krogh's models (Krebs, 1975) for investigating the plasticity of ecophysiological traits. Habitat alterations, natural disasters or invasive species exert particularly strong pressure on insular populations. Numerous studies have shown that, within short periods, insular lizards are capable of rapidly responding to external stimuli and thereby undergo substantial adaptive changes. These adaptations have included shifts in thermal physiology (Salazar et al., 2019), digestive structures and efficiency (Herrel et al., 2008; Vervust et al., 2010), toe pad morphology and clinging capacity (Stuart et al., 2014; Donihue et al., 2018), body size and mass (Marnocha et al., 2011), and head size and diet (Amorim et al., 2017). In this study we aimed to determine whether lizards could adjust their thermoregulatory behavior in narrow time-periods through plasticity.

Typically, thermoregulation studies are limited in scope to a single, relatively short, time period. However, there is a general scarcity of longitudinal research on the plasticity of thermoregulatory patterns through time. Here, we designed an experiment to evaluate the extent to which lizard thermoregulation responds to introduction to a new environment in a snapshot in time (Heath, 1965). We collected Aegean wall lizards (*Podarcis erhardii*) from Naxos Island (Aegean Sea, Greece) and introduced them to two small, lizard-free islets nearby. Three years later we returned to all three islands to take thermal measurements.

To assess thermoregulation, three temperature parameters are used: body (T_b), operative (T_e, the temperature a non-thermoregulating model achieves in the field), and preferred (T_{pref}, the temperature animals achieve in the lab under no ecological restrictions; Bakken, 1992; Hertz et al., 1993). Taken together, these parameters can be used to define the effectiveness of thermoregulation (E). In thermally demanding habitats, animals are expected to reach high E values in their effort to achieve T_b within the T_{pref} spectrum (Hertz et al., 1993; Zamora-Camacho et al., 2016). Conversely, in benign habitats, animals

display low E values, as the difference between T_b and T_{pref} is smaller or even negligible (Hertz et al., 1993).

We hypothesized that the thermal quality of the focal study sites would differ. Islands tend to have milder thermal environments compared to the mainland due to the buffering sea effect (Schwaner, 1989; Whittaker and Fernández-Palacios, 2007). That said, islands may also be subject to stronger winds (Ortega et al., 2016). As a result, island lizards typically exhibit lower E values than their mainland peers (Grbac and Bauwens, 2001; Sagonas et al., 2013a). However, very small islets depart from this pattern because of their low altitude and relative homogeneity. Thus, lizards on very small islets often experience harsh thermal conditions, and exhibit high E values (Sartorius et al., 2002; Ortega et al., 2014; Pafilis et al., 2016; Belasen et al., 2017). Interestingly, despite decades of research on island biology, detailed data on insular microclimatic conditions are relatively scarce and consequently the thermal profile of different island habitats is not well known. We investigated the extent to which lizards from a large island demonstrate plasticity when introduced to a novel, small-island habitat. We presume that the (alleged) thermal homogeneity of the two islets, in contrast with the higher heterogeneity of Naxos, would affect the main thermal parameters and ultimately thermoregulation.

2. Materials and methods

2.1. Study system

Podarcis erhardii is a medium-sized (average snout to vent length, SVL: 60 mm) heliothermic lacertid lizard that feeds on arthropods, occasionally including other food sources (Adamopoulou et al., 1999; Brock et al., 2014). The species range includes the southern Balkans, with a wider distribution in the Aegean Sea where it is highly differentiated into 18 of the 21 recognized subspecies (Lymberakis et al., 2018). The Aegean wall lizard occurs on almost every Cycladic Island (save the Milos Archipelago where it is replaced by the endemic *Podarcis milensis*), even on tiny islets with a surface area of a few dozen square meters (Valakos et al., 2008).

In 2014, we collected lizards from Naxos (the largest island of the Cyclades group, area: 429.7 km², highest point: 1003 m). The initial sampling took place at Alyko, a dune ecosystem at sea level in

Fig. 2. The three sampling habitats: (A) Alyko on Naxos Island, (B) Galiatsos islet, (C) Kampana islet.

southwestern Naxos, the vegetation of which is dominated by the prickly juniper (*Juniperus oxycedrus macrocarpa*) and lentisk (*Pistacia lentiscus*). Eight males and 12 females were released to each of two *Podarcis*-free small islets, Galiatsos (area: $0.0073 \, km^2$, highest point: 2 m) and Kampana (area: $0.004 \, km^2$, highest point: 4 m) (Fig. 1). The islets differ from Naxos not only in the thermal environment but also in substrate and microhabitat. Both islets are rocky with a very thin soil layer. The dominant plants on Galiatsos are *Suaeda vera, Convolvulus oleifolius* and *Mandragora officinarum*, and there are several dense mats of junipers around the periphery of the island. On Kampana, besides *C. oleifolius*, there is also *Eryngium campestre, Thymus capitatus, Capparis spinosa* and 10 medium-sized lentisks. We estimated vegetation cover on each islet in QGIS 2.18 using satellite images from 2016 and hi-res drone (DJI Mavic Pro) images collected during our fieldwork (e.g. Fig. 2). Predation regime also differs on the islets compared to Naxos: the two islets experience minimal predation with no terrestrial predators, and saurophagus birds have never been sighted on either islet. In contrast, Naxos hosts numerous lizard-eating predators, including domestic cats and snakes (Li et al., 2014; Brock et al., 2015). In this place, we have to point out an innate limitation in the approach of the thermal environment. As in most thermal studies, we assessed only one population from Naxos. Presumably, islands at Naxos' size are expected to show more variation.

2.2. Field body temperatures (T_b)

Body temperatures of the three populations were measured on different days within the same week (13–21 May 2017), during which the weather was consistent (Table 1). In 2017 we worked with lizards that were born on the islets and excluded the initially introduced individuals. Lizards were caught by noose and their temperatures were recorded within 10 s of capture (Veríssimo and Carretero, 2009; Osojnik et al., 2013) using a quick reading cloacal thermometer (Miller

& Weber Inc., Queens, NY, accurate to 0.1 °C). SVL (in mm) and mass (in g) were measured with digital calipers (Silverline 380244, accurate to 0.01 mm) and a digital scale (i500 Backlit Display, My Weight, accurate to 0.1 g), respectively. Measurements were taken during the peak of the reproductive period of the species (Valakos, 1990), and thus we excluded females since gravidity is known to affect thermal parameters (Carretero et al., 2005). All body temperatures were taken between 09:00 and 17:00, when the animals are most active.

2.3. Preferred temperatures (T_{pref} and T_{set})

Preferred temperatures (T_{pref}) were measured in the laboratory for 15 adult males from each population. Measurements of T_{pref} were taken immediately after the arrival of the lizards in the lab. A specially designed terrarium ($100 \times 15 \times 25$ cm) – including a thin layer of sand as substrate, one heat source (a 100 W lamp suspended 20 cm above the substrate) at one end and two icepacks at the other – was used to simulate a thermal gradient of 15–55 °C (Van Damme et al., 1986). Within this setting, lizards were able to achieve their T_{pref} without constraints. Measurements took place between 08:00 and 14:30. An hour prior to the experiment the icepacks were placed in position and the lamp was turned on so as to obtain the thermal gradient. Afterwards, lizards were individually placed inside the gradient and left for 60 min to acclimate (Carretero, 2012; Carneiro et al., 2015). Subsequently, body temperature measurements were recorded every 30 min from 10:00 until 14:30 (10 measurements per individual). Body temperature was measured using a quick reading cloacal thermometer.

Preferred temperature for each individual lizard was estimated as the mean of all body temperatures selected by that individual while in the thermal gradient. The mean T_{pref} for each population was subsequently calculated as the mean of all individual T_{pref} from that population. Set point range (T_{set}) for each individual lizard was estimated as the central 50% of all body temperatures selected by that individual

Table 1
The thermal variables and the thermoregulation index (*E*) measured in the three populations. Field body temperatures (T_b), deviation of T_b from the set point-range (d_b), preferred temperatures (T_{pref}), operative temperatures (T_e) and deviation of T_e from the set point-range (d_e). Means ± SD, (minimum – maximum), N = sample size. Differences present the significance of statistical tests (ANOVA or Kruskal-Wallis). Post-hoc presents significant (Tukey HSD or Dunn) pairwise comparisons (K: Kampana, G: Galiatsos, N: Naxos).

Population	T_b	T_e	T_{pref}	d_b	d_e	E
Naxos	33.14 ± 1.91 (29.00–36.80) N = 22	35.53 ± 8.02 (19.40–54.10) N = 578; 34	35.20 ± 1.14 (33.31–36.87) N = 15	1.39 ± 1.46 (0.00–5.17) N = 22	5.65 ± 4.12 (0.00–17.44) N = 578; 34	0.75 ± 0.06 (0.57–0.91) N = 1000
Galiatsos	33.60 ± 1.57 (29.00–36.20) N = 56	36.52 ± 7.18 (23.30–55.10) N = 578; 34	35.68 ± 1.09 (32.75–37.03) N = 15	1.41 ± 1.45 (0.00–5.91) N = 56	4.93 ± 3.92 (0.00–17.96) N = 578; 34	0.71 ± 0.04 (0.58–0.83) N = 1000
Kampana	34.85 ± 1.39 (32.50–37.20) N = 22	36.49 ± 6.04 (22.80–51.60) N = 578; 34	34.50 ± 1.28 (32.47–36.71) N = 15	0.36 ± 0.53 (0.00–1.51) N = 22	4.13 ± 3.57 (0.00–15.91) N = 578; 34	0.91 ± 0.03 (0.80–0.98) N = 1000
Differences	P = 0.0016	P = 0.0362	P = 0.0296	P = 0.0044	P < 0.0001	P < 0.05
Post hoc	K - G K–N	K–N	K - G	K - G	K - G K–N G - N	K - G K–N

while in the thermal gradient (Hertz et al., 1993). The T_{set} for each population was subsequently calculated as the mean of lower and upper limits of individual Tsets. We note that the distribution of T_{pref} is not exactly symmetrical but tends to be biased.

2.4. Operative temperatures (T_e)

Operative temperatures were measured using 34 copper tubes as models at each field site. Measurements were taken from 09:00 to 17:00 (at 15 min intervals) on the same days that T_b was measured. The models were similar in size to *P. erhardii* and were painted brownish-green to resemble typical coloring and reflectance (Bakken, 1992; Bakken and Angilletta, 2014). The models were arrayed to encompass as many of the available thermal microhabitats as possible. Both ends of the copper models were sealed with plasticine and 2.5–3 ml of water was added inside so that the model would resemble the heat storage capacity of lizards (Grbac and Bauwens, 2001; Lutterschmidt and Reinert, 2012). Operative temperatures were measured with the use of data loggers (Onset HOBO U12-008 4-Channel External Data Logger), the sensor probe of which was inserted through a small opening in the plasticine at one end (Díaz, 1997). The thermal heterogeneity of the habitat was quantified as the standard deviation of the mean T_e (Logan et al., 2015).

In order to ensure the similarity between the thermal responses of the copper models and the lizards, we performed a pilot experiment in the laboratory examining cooling and heating rates (Hertz, 1992; Lutterschmidt and Reinert, 2012). We placed a lizard and a model side-by-side under a 150 W lamp and then measured their temperatures at 5-min intervals for 1 h with a quick-reading cloacal thermometer. At the end of this period, we turned off the heat lamp and started recording temperatures during the cooling phase that lasted for another 90 min. Regression analysis of the thermal values of the lizard and the model suggested comparable body and model temperatures (regressions statistics ± SE; slope = 0.981 ± 0.032, intercept = −1.145 ± 0.954; $r^2 = 0.978$, $N = 28$, $P < 0.001$).

2.5. Effectiveness of thermoregulation (E)

Thermoregulation effectiveness (*E*) was estimated with the classic method proposed by Hertz et al. (1993) that, despite some innate flaws (e.g., the excessive importance of d_b and d_e, the problematic use of a ratio), is still widely used. We applied the frequently used formula:

$$E = 1 - (d_b/d_e),$$

where d_b represents the mean deviation of T_b from T_{set}, and d_e the mean deviation of T_e from T_{set}. Mean d_b is a measure of the thermoregulation accuracy. Similarly, mean d_e is a measure of the habitat thermal quality. Thus, a low d_e value shows a habitat of higher thermal quality, where the majority of recorded T_e values fall within the T_{set} limits.

In order to compare *E* between the three populations, we performed bootstrap resampling with replacement (Hertz et al., 1993) and 1000 values of E were computed using the observed distributions of d_b and d_e. According to Hertz et al. (1993), differences between two populations are considered significant if one population has higher E value than the other in more than 950 comparisons; since we pairwise compared all three populations, we adjusted this limit using the Bonferroni correction for three tests ($\alpha = 0.05/3$) and thus differences were considered significant at the 0.05 level if one population had higher E value in more than 983 comparisons.

2.6. Statistical analysis

We examined normality with the Shapiro-Wilk test and homogeneity of variances with the Brown-Forsythe test. When our samples did not deviate significantly from normality, we used the Student's t-test to compare two means (or Welch's *t*-test if variances were not

homogenous). When both assumptions were violated, we compared two variables using the non-parametric Mann–Whitney U test. Likewise, we used ANOVA to compare multiple means, unless parametric assumptions were violated, in which case the non-parametric Kruskal–Wallis rank sum test was used instead. For post-hoc comparisons we used Tukey's HSD after significant parametric tests, and Dunn's test after significant nonparametric tests. Data analysis was performed in R 3.5.1 (R Core Team, 2018).

3. Results

3.1. Comparison of SVL and mass among populations

We detected significant differences in SVL (ANOVA $F_{2,97} = 6.158$, $P = 0.003$) and mass (ANOVA $F_{2,97} = 4.411$, $P = 0.015$) among the three populations. Lizards from Galiatsos (62.6 ± 4.4 mm) were larger than lizards from Naxos (59.1 ± 6.7 mm, Tukey HSD $P = 0.013$) and Kampana (58.9 ± 5.3 mm, Tukey HSD $P = 0.021$). Additionally, Galiatsos lizards (5.83 ± 1.14gr) were heavier than their counterparts from Kampana (5.0 ± 1.23gr, Tukey HSD $P = 0.034$) and tended to be heavier than those from Naxos (5.11 ± 1.71gr, Tukey HSD $P = 0.076$).

3.2. Thermal variables (T_b, T_{pref}, T_e)

All thermal parameters examined in this study showed differences among populations. Analyses yielded statistically significant differences among the body temperatures of the three populations (ANOVA, $F_{2, 97} = 6.906$, $P = 0.0016$). This difference remained after controlling for the effect of SVL on T_b (ANCOVA, $F_{2, 94} = 7.207$, $P = 0.0012$) or both the effects of both SVL and mass (ANCOVA, $F_{2, 93} = 7.368$, $P = 0.0011$). Post-hoc pairwise comparisons showed that Kampana lizards had higher mean T_b compared to lizards on Naxos (Tukey HSD, $P = 0.0019$) or Galiatsos (Tukey HSD, $P = 0.0077$) (Table 1), while T_b on Naxos and Galiatsos did not statistically differ from one another (Tukey HSD, $P = 0.49$).

The three populations also differed in T_{pref} (ANOVA, $F_{2, 42} = 3.831$, $P = 0.0296$). The difference did not change after controlling for the effect of SVL on T_{pref} (ANCOVA, $F_{2,39} = 4.199$, $P = 0.0223$) or the effects of both SVL and mass (ANCOVA, $F_{2, 38} = 4.227$, $P = 0.0220$). Post-hoc pairwise comparisons showed that lizards from Galiatsos preferred significantly higher temperatures than lizards from Kampana (Tukey HSD, $P = 0.0231$, Table 1).

Finally, the differences in T_e were statistically significant as well (Kruskal-Wallis rank sum test, $\chi^2_2 = 6.64$, $P = 0.0362$): Dunn's post hoc test showed that lizards on Galiatsos had similar T_e to both Kampana and Naxos, but T_e on Kampana was significantly higher than on Naxos. Operative temperatures showed high fluctuations during the day for all populations, ranging from 23.3 °C to 55.1 °C for lizards from Galiatsos, 22.8 °C–51.6 °C for Kampana lizards and 19.4 °C–54.1 °C for Naxos lizards (Table 1). The thermal heterogeneity was calculated for each island separately (Naxos: 8.02 °C, Galiatsos: 7.18 °C, Kampana: 6.04 °C, $N = 34$ in all cases) (Table 1).

3.3. Effectiveness of thermoregulation (E)

The accuracy of thermoregulation (d_b) was significantly different among the three populations (Kruskal-Wallis rank sum test, $\chi^2_2 = 10.84$, $P = 0.0044$) (Table 1). Dunn's post hoc test showed that while d_b was similar between Galiatsos and Naxos, the d_b of Kampana was lower than that of both Galiatsos and Naxos. The thermal quality (d_e) of the focal habitats differed as well (Kruskal-Wallis rank sum test, $\chi^2_2 = 38.71$, $P < 0.0001$) (Table 1). In this case, Dunn's post hoc test showed all pairwise comparisons were significant.

Thermoregulation effectiveness, as calculated through the index *E* (Hertz et al., 1993), was higher on Kampana (0.91) compared to Naxos (0.75) and Galiatsos (0.71). Bootstrap resampling with replacement

showed that these differences hold at the 0.05 level, with Kampana achieving higher E in 997 and 1000 of the random pairwise comparisons against Naxos and Galiatsos, respectively. The difference in E values between Naxos and Galiatsos was not significant.

3.4. Vegetation cover on the islets

The two islets differ in the percentage of vegetation cover. On Galiatsos, plants with dense canopy, such as junipers or *S. vera*, are considerably more abundant and cover around 29% of the total islet area (3711 m^2), providing numerous and extensive well-shaded thermal refuges where lizards can take shelter during the warmer hours of the day (Fig. 2). In contrast, Kampana's very few dense-canopy plants occupy only 7.4% of the total islet area (599 m^2), which results in a limited number of high-quality thermal shelters. The majority of Kampana is either nearly bare (57.9%) or covered by small plants that provide limited shade (34.7%) (Fig. 2).

4. Discussion

Traditionally, small islands are considered to be relatively homogenous (Triantis et al., 2006; Sfenthourakis and Triantis, 2009), thereby presenting limited thermal heterogeneity (Pafilis et al., 2016). However, our results demonstrate that small, offshore islets may be more thermally heterogeneous than previously appreciated, resembling larger islands in thermal profile. Indeed, one of the two experimental populations (Galiatsos) differed from the source population (Naxos) in only one thermal parameter. On the other hand, the other introduced population (Kampana) differed from Naxos in all thermal parameters examined. This contrasting result is not paradoxical but instead can be attributed to the particularities of each habitat. On a highly localized scale, shifts in thermal environmental parameters affected lizard thermoregulation, which shows substantial plasticity in response to the lizards' environmental conditions. At this point, we have to state that limited sample sizes and the fact that Naxos thermal environment was represented by a single population/habitat, preclude us from making generalized statements on the relation between island size and microclimate.

The experimental islets in this study differed in thermal quality from Naxos (mean d_e), but not in the manner we predicted. We initially hypothesized that the islets, due to low altitude and poor spatial heterogeneity, would have lower thermal quality than the source population. To the contrary, the Naxos population had the highest mean d_e (5.65), indicating the lowest thermal quality in this study (Table 1). Moreover, the two islets differed from each other, with Galiatsos having a lower thermal quality (Table 1). Mean d_e is a useful index that permits a quick assessment of the overall thermal quality (Hertz et al., 1993). However, in the effort to accurately evaluate the thermal profile of a given habitat, one should not neglect the importance of additional features, such as operative temperature fluctuations and their distribution.

The two experimental islets share an almost identical mean operative temperature (Table 1) but differed both in the fluctuation thereof and their thermal heterogeneity. Kampana T_e showed little fluctuation and ranged within a narrow thermal window of only 28.8 °C (varying from 22.8 °C to 51.6 °C), whereas the range for Galiatsos was 31.8 °C (Table 1, Fig. 3). Moreover, Kampana's thermal heterogeneity (the standard deviation of the mean T_e) was lower than that of Galiatsos and Naxos (6.04 vs 7.18 and 8.02, respectively; Table 1). Furthermore, the T_e distribution on Kampana was skewed towards the upper thermal limit: T_e readings were higher than T_{set} 54.3% of the time, compared to 46% on Galiatsos and 48% on Naxos (Fig. 3). The hours during which T_e exceed the upper bound of T_{pref} are known as hours of restriction (Sinervo et al., 2010). During these hours, lizards have to resort to thermal shelters to avoid overheating, thus limiting time for foraging and reproduction (Sinervo et al., 2010; Kubisch et al., 2016). Kampana
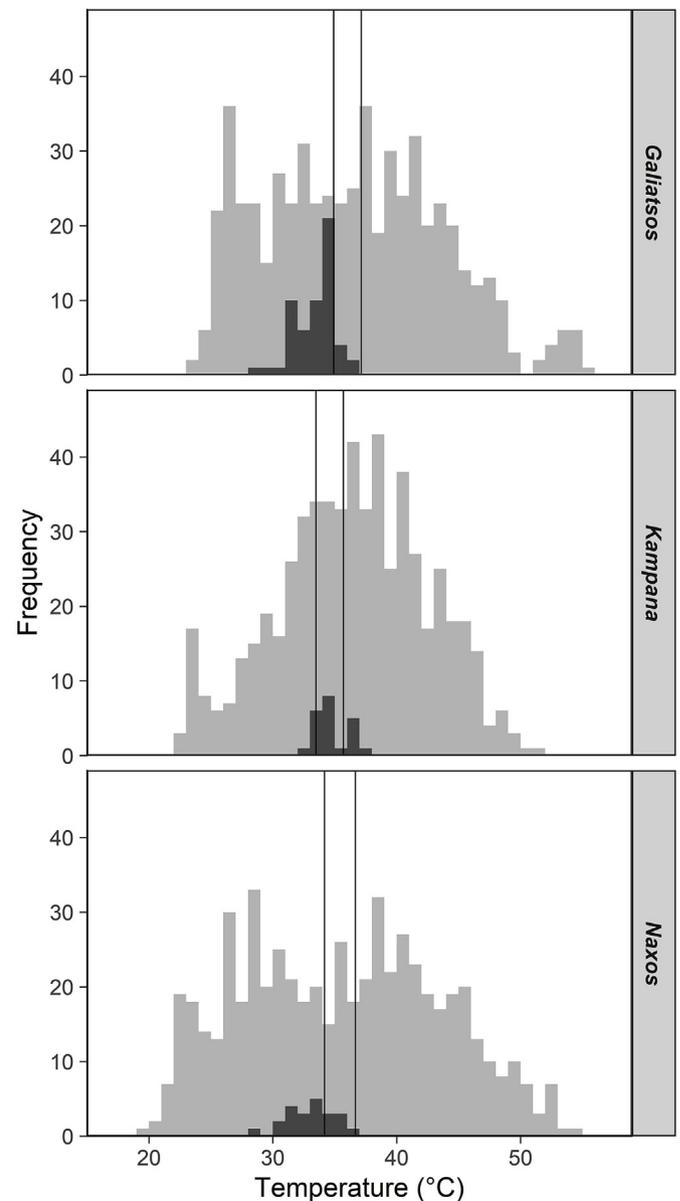

Fig. 3. Thermal parameters measured at each of the three study sites. Frequency of field body temperatures (T_b, dark gray) and operative temperatures (T_e, light gray). Vertical black solid lines indicate the set-point range temperatures (T_{set}).

lizards displayed the higher value for hours of restriction. Finally, the lack of extreme values combined with the low standard deviation of the mean T_e (Table 1), dictated the low thermal heterogeneity on Kampana. In other words, to sketch out the thermal profile of a given habitat it is important to take into account not only operative temperatures, but also parameters such as T_e distribution and fluctuation, thermal heterogeneity and hours of restriction (Huey, 1991).

Contrary to our predictions, Galiatsos' thermal parameters did not differ from those of the Naxos population. In fact, the only statistically significant difference we detected was in mean d_e (Table 1). For the remaining parameters, Galiatsos lizards achieved analogous T_b in the field and selected similar T_{pref} in the lab compared to their Naxos peers (Table 1). Also, in both cases, a similarly small percentage of T_b values fell within the T_{set} (23.21% for Galiatsos and 27.27% for Naxos), indicating comparable values in thermoregulation accuracy (Table 1, Fig. 3). Ultimately, the two populations attained very similar values of thermoregulation effectiveness (Galiatsos: 0.71, Naxos: 0.75), despite

their different mean d_e values.

Solely referencing mean d_e may mask important ecological information (Camacho et al., 2015). The higher d_e (5.65) at the sandy Naxos site indicates a lower thermal quality compared to Galiatsos (4.93). Sand may be a demanding substrate that induces high E values (Sagonas et al., 2013b; Kapsalas et al., 2016), but lizards dwelling in sandy habitats have developed strategies to overcome such challenges. They avoid basking in bare sand and preferred semi-shaded microhabitats (Adamopoulou and Valakos, 2005) or warm up inside burrows and come out on the sand surface only for short periods on the sand surface (Pérez-Mellado, 1992; Carretero and Llorente, 1995). Consequently, Naxos lizards achieved T_b within T_{set} without devoting too much effort, as is reflected in the moderately high E value, which is similar to that of Galiatsos. A similar finding for *P. erhardii* (identical E values for habitats with different d_e values) has been reported before (Belasen et al., 2017). That is, the Galiatsos habitat did not differ in essence from Naxos, and thus the lizards born there retained their parental thermoregulatory phenotype derived from the source population.

Preferred temperature is the most decisive parameter in thermal studies as it is comprised by and therefore defines all thermoregulation indices (d_e, d_b and E). Thermal preferences express the innate ability for accurate thermoregulation, an intrinsic choice on the part of lizards (Corn, 1971; Dzialowski, 2005). In our study system, the Galiatsos population maintained the same thermal preference as the source Naxos population, in contrast to the Kampana population. We believe that the underlying reason can be explained by the differences among habitats. Galiatsos, with its rich availability of high-quality thermal shelters, "permits" lizards that were imported from Naxos to preserve their "ancestral" T_{pref}. Lizards are known to thermoregulate more accurately in places where thermal resources are distributed throughout the habitat (Žagar et al., 2015; Sears and Angilletta, 2015; Sears et al., 2016). In contrast, the challenging Kampana habitat, with a small number of thermal shelters concentrated in a relatively few spots, appears to impose distinct shifts in thermal preferences and thermoregulatory patterns. Lizards living in low-quality landscapes thermoregulate effectively in order to survive (Hertz et al., 1993; Basson et al., 2017). Kampana lizards not only achieved high E values, but T_b experienced limited diel variation (a yardstick of thermoregulatory precision) and fell within T_{set} resulting in a very low d_b (an index for high thermoregulatory accuracy). In short, Kampana lizards are precise, accurate and effective thermoregulators. A common garden experiment and genomic analyses would shed further light into these findings and determine the extent to which these observed patterns are heritable. At the same line, the considerable divergence in T_{pref} in our study system could be considered an indication of natural selection. However, lacking solid analyses as mention above, we cannot rule out the effect of plasticity. Differences in T_{pref} could simply represent the result of plastic responses to the new habitats that subsequently would shape the thermal profile of the new populations. Further experimental work to this direction would unravel the role of plasticity.

Our results highlight the importance of idiosyncratic habitat characteristics in thermoregulation. Islets that would typically be considered interchangeable and homogenous because of their small size may actually differ considerably due to particular features such as exposure to high winds, altitude, shelter availability, marine subsidies or the presence of introduced domestic animals or pests (Polis and Hurd, 1996; Triantis et al., 2006; Sfenthourakis and Triantis, 2009; Pafilis et al., 2013). Despite the intrinsic limitations of large-scale field studies and introduction experiments (e.g., limited island number, genetic bottlenecks and founder effects), our experimental findings shed light on the thermoregulation of lizards and reveal a complicated scenario. Thermoregulation is not necessarily intrinsic and can flexibly respond to novel thermal conditions if selection is strong.

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