

# Broad seasonal changes in thermoregulation of *Podarcis lilfordi* (Squamata, Lacertidae) at Binicodrell islet (Menorca, Spain)

Zaida Ortega<sup>1</sup>, Abraham Mencía<sup>2</sup>, Aline Giroux<sup>1</sup>, Valentín Pérez-Mellado<sup>3</sup>

<sup>1</sup> Programa de Pós-Graduação em Ecologia e Conservação, Instituto de Biociências, Universidade Federal do Mato Grosso do Sul, ZIP 79070-900, Campo Grande, Mato Grosso do Sul, Brazil.

<sup>2</sup> Programa de Pós-Graduação em Biologia Animal, Instituto de Biociências, Universidade Federal do Mato Grosso do Sul, ZIP 79070-900, Campo Grande, Mato Grosso do Sul, Brazil.

<sup>3</sup> Department of Animal Biology, University of Salamanca, Campus Miguel de Unamuno, 37007, Salamanca, Spain.

<http://zoobank.org/0A90CC23-1A5F-4598-A39A-3010BFB39570>

Corresponding author: Zaida Ortega (zaidaortega@usal.es)

Academic editor: Günter Gollmann ♦ Received 31 October 2018 ♦ Accepted 20 March 2019 ♦ Published 13 May 2019

## Abstract

Most lizards maintain quite constant body temperatures by behavioural means. Seasonal variations of environmental factors, such as temperature, sunlight exposure and wind intensity, influence lizard thermoregulatory abilities. Understanding how seasonal environmental shifts influence lizards' thermoregulation helps us to know how they deal behaviourally with environmental changes, in general. We examined seasonal shifts (spring vs. summer) in behavioural thermoregulation in *Podarcis lilfordi* from Binicodrell islet (Menorca, Spain). Operative temperatures varied between microhabitats and seasons, being lower in spring than in summer, regardless of sunlight exposure. Lizard body temperatures were also lower in spring than in summer. Lizards used sunny microhabitats more frequently in spring and shaded areas in summer. Habitat thermal quality was similar during both seasons, but lizards thermoregulated less accurately in spring than in summer. Thermoregulatory effectiveness was low in spring (0.28) and moderate in summer (0.76). In comparison with previously published results, our findings showed the marked seasonal variation in the effectiveness of thermoregulation amongst island populations, which should be considered in future comparative studies.

## Key Words

temperature, behavioural thermoregulation, seasonality, lacertids, islands, Balearic lizard, environmental changes

## Introduction

As ectotherms, lizards' performance and fitness depend on their body temperatures (Angilletta 2009). Lizards often maintain their body temperatures within a relatively narrow range using behavioural thermoregulation, which involves various mechanisms, e.g. adjusting activity periods, changing body posture to maximise heat gain or loss or moving between hot and cool microhabitats (Carrascal et al. 1992; Adolph and Porter 1993; Bauwens et al. 1996;

Sears et al. 2016). The extent of behavioural thermoregulation depends on its costs and benefits (Huey and Slatkin 1976; Sears and Angilletta 2015). Costs of thermoregulation mainly entail wasted energy and time, predation risk and losing opportunities for other activities. Meanwhile, benefits are clear: maximising physiological performance and, accordingly, individual fitness. The balance between these costs and benefits will determine the extent to which a lizard thermoregulates in a given habitat (Huey and Slatkin 1976; Sears and Angilletta 2015).

Energetic costs of thermoregulation increase as environmental temperatures depart from the thermal optima for the lizard's physiological functions (Huey and Slatkin 1976; Sears and Angilletta 2015). Accordingly, spatio-temporal variation in biotic and abiotic environmental factors influences the degree of lizard thermoregulation. In temperate lizards, their microhabitat selection and thermoregulatory effectiveness is greatly influenced by the seasonal variation in environmental conditions (Van Damme et al. 1987; Díaz et al. 2006; Ortega and Pérez-Mellado 2016). For example, Mediterranean laceritids usually thermoregulate more effectively in the summer, when environmental temperatures are higher, than in the spring (Ortega and Martín-Vallejo 2018).

This is also the case in the Balearic lizard, *Podarcis lilfordi*. A previous study, examining the seasonal shift in thermal ecology of two populations, showed different seasonal effects on thermoregulation (Ortega et al. 2014). The magnitude of seasonal changes in thermoregulatory effort was higher in the population from the smaller islet. Probably its lower plant cover, smaller heterogeneity of microhabitats and smaller size (higher exposure to sea winds) offered fewer options for lizards to thermoregulate than on the larger islet. However, studying only two populations precluded the testing of this hypothesis.

To test the hypothesis that seasonal changes in thermal ecology depend on islet size and traits, studies of several insular populations of the same species are needed. Here, we examine the thermal ecology of a third *P. lilfordi* population, living on Binicodrell, an islet located south of Menorca (Spain). This population occupies the small islet (0.5 ha), which is located less than 30 km away from larger islets with previously studied populations (Fig. 1). The smaller the islet, the more it is subjected to sea winds (Nitis et al. 2005) and the lower habitat and, consequently, climatic heterogeneity (Algar and Mahler 2016). This would entail a negative relationship between island size and the seasonal variation of the climatic niche available for lizards (Algar and Mahler 2016; Pafilis et al. 2016). Thus, other factors being equal, within the same lizard species, we would expect a negative relationship between the area of the islet and the magnitude of seasonal thermoregulatory variation. We predicted that (i) lizards from Binicodrell thermoregulate accurately and effectively and (ii) the magnitude of seasonal variation in the accuracy and effectiveness of thermoregulation will be higher than in lizards from the previously studied populations.

## Materials and methods

### Study species and area

The Balearic lizard, *Podarcis lilfordi* (Günther, 1874), is endemic in the Balearic Islands (Spain), where it lives in the coastal islets of Mallorca and Menorca and the Cabrera Archipelago. Amongst its 23 subspecies, we

study here *P. lilfordi codrellensis*, which only inhabits two small islets of the south of Menorca: Binicodrell Gran and Binicodrell Petit. We studied the population of Binicodrell Gran (Fig. 1). Lizards from this population are not melanic, but rather show a brownish dorsal colouration (Garrido and Pérez-Mellado 2014). As is common in the Balearic lizard, this subspecies shows sexual size dimorphism, with larger males (mean snout-vent length [SVL] = 64.5 mm) than females (mean SVL = 57.3 mm).

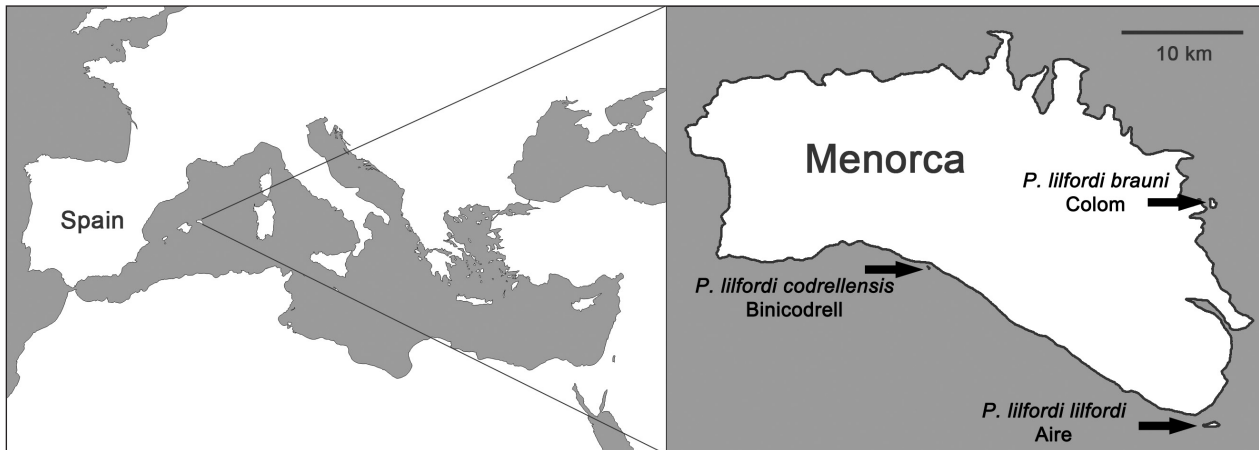
There are three common traits of Balearic islets that highly influence the ecology and evolution of *P. lilfordi*: food resources are scant, predation pressure is low and microclimatic conditions are highly variable. Hence, Balearic lizards tend to have high population densities, low clutch sizes and extended reproductive periods. In addition, they are highly opportunistic feeders with relaxed anti-predatory responses (Perera and Pérez-Mellado 2002; Pérez-Mellado et al. 2008; Pérez-Cembranos et al. 2016; Mencía et al. 2017).

### Thermal ecology of *P. lilfordi*

Thermal ecology has been studied for two subspecies that inhabit nearby islets: *P. lilfordi lilfordi* from Aire and *P. lilfordi brauni* from Colom (Fig. 1). The 50% preferred temperature range (PTR), which approximates to the target temperatures an ectotherm aims to achieve, varied from 32–36 °C in spring (Aire islet; Ortega and Pérez-Mellado 2017) to 34–36 °C in summer (Aire and Colom islets; Bauwens et al. 1996; Ortega et al. 2014). Lizards from Aire showed body temperatures ( $T_b$ ) of  $\approx 33$  °C in spring and  $\approx 36$  °C in summer, whereas those from Colom showed less seasonal variation in  $T_b$  ( $\approx 34$  °C in spring and  $\approx 35$  °C in summer). Although they thermoregulated accurately and effectively in both islets, lizards from Aire, however, showed higher seasonal variations relative to thermoregulation than those from Colom (Ortega et al. 2014). In spring, lizards from Aire began their activity before and ended it after those from Colom, at temperatures between 17 and 19 °C. In addition, wind speed is higher in Aire than Colom ( $\approx 0.7$  vs. 0.3 m/s), while relative humidity is lower in Aire than Colom ( $\approx 65$  vs. 73%). Microhabitat selection was somehow different regarding the influence of environmental temperatures; however, the lizards similarly selected insulated (or partially insulated) microhabitats, avoiding shaded areas and acting independently of wind speed and humidity (Ortega and Pérez-Mellado 2017).

### Body temperatures

We captured active lizards in May (spring) and July (summer) of 2013 by noosing during the daily activity period of lizards (08:00 – 17:00 h GMT). We measured their cloacal body temperature ( $T_b$ ) within 10 s



**Figure 1.** Map of the three studied populations of the Balearic lizard: *Podarcis lilfordi codrellensis* from Binicodrell islet, assessed in the present study and *P. lilfordi lilfordi* from Aire islet and *P. lilfordi brauni* from Colom islet, studied in Ortega et al. (2014).

after capture, shadowing the lizard and the probe, with a Testo® 925 digital thermometer and a thermopar probe (precision 0.1 °C).

## Environmental variables

In order to characterise the lizards' habitat use and thermoregulatory behaviour, we also measured environmental variables that are usually important for thermoregulation (Angilletta 2009; Ortega et al. 2014). Thus, we measured the air temperature ( $T_a$ ), 1 cm above the capture point and substrate temperature ( $T_s$ ) of the capture point and recorded the type of substrate (rock, soil, grass), the perch height (in cm) and the sunlight exposure (full sun, filtered sun, shade). Finally, we measured wind speed with a Kestrel® 3000 anemometer. All temperatures were measured with a Testo® 925 digital thermometer and a thermopar probe (precision 0.1 °C).

## Operative temperatures

Operative temperatures ( $T_o$ ) provide a null hypothesis for thermoregulation, as they represent the  $T_b$  that lizards would achieve if they were not thermoregulating (i.e. behaving randomly regarding environmental temperatures; Dzialowski 2005). We registered the  $T_e$  and  $T_b$  simultaneously to avoid possible variations in weather conditions. We used 15 hollow copper models as null  $T_e$  models (Bakken and Angilletta 2014), that mimicked the colour, size and shape of lizards, similar to adults of *P. lilfordi*. 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 record every five minutes. We haphazardly placed the copper models in different microhabitats for periods of 48 hours, obtaining a total record of 3714  $T_e$ s. Data loggers were placed at the same microsites in spring and

summer to obtain comparable information about lizard's thermal environment.

## Quantification of behavioural thermoregulation

To assess the seasonal shift in lizards' thermoregulatory effort, we calculated three thermoregulatory indices (Hertz et al. 1993). The first is the index of thermoregulatory accuracy (mean  $d_b$ ), which is the mean absolute deviation of  $T_b$  from the PTR. As it measures the departure of  $T_b$  from the thermal preferences, this index is counter-intuitive: higher values of  $d_b$  indicate a lower accuracy of thermoregulation and vice versa. The second is the index of thermal quality of habitat (mean  $d_e$ ), which is the mean absolute deviation of  $T_e$  from the PTR. It is also counter-intuitive: higher values of  $d_e$  indicate a lower thermal quality of the habitat and vice versa. The third is the index of thermoregulation effectiveness ( $E$ ), calculated as  $E = 1 - (\text{mean } d_b / \text{mean } d_e)$ . Values of  $E$  can range from 0 to 1, with larger  $E$  meaning higher thermoregulation effectiveness (see Hertz et al. 1993). We also provided the values of the alternative index of thermoregulation effectiveness proposed by Blouin-Demers and Weatherhead (2001) as  $(d_e - d_b)$ . Indices were calculated with THERMO, a Minitab module that has been used in previous studies (e.g. Ortega et al. 2014, 2016a, 2016b). It uses three kinds of input data:  $T_b$ ,  $T_e$  and the PTR and was programmed to perform bootstraps of 500 iterations, building pseudo-distributions of three kinds of output values: mean  $d_b$ , mean  $d_e$  and mean  $E$ . We performed statistical analyses of the bootstrapped values of the indices.

## Statistical analysis

Means are reported with standard deviations (SD). We studied the effect of different variables in lizard's  $T_b$  us-

ing a general linear model. As  $T_a$  and  $T_s$  were strongly correlated ( $r = 0.882$ ), we decided to only include  $T_a$  in this analysis. We used ANCOVA to compare  $T_b$  between spring and summer, with  $T_a$  as the covariate. We assessed if the linear relationships between  $T_b$  and  $T_s$  and  $T_b$  and  $T_a$  varied seasonally, calculating the interaction term with the season of the respective ANCOVAs. We compared the frequencies of use of different sunlight exposures with the G-test of independence. Data on  $T_e$  and indices of thermoregulation did not fulfil the assumptions of parametric tests. Hence, we tested the effect of season and sunlight situations on these variables using the Mann-Whitney's U tests (Crawley 2012). We conducted the analyses on R, version 3.1.3 (R Development Team 2017).

## Results

Males and females maintained similar  $T_b$  (Table 2). In addition, the sunlight situation and the wind speed had a significant effect on  $T_b$ , but not the substrate. The only studied factors affecting  $T_b$  were the season, with higher temperatures in summer and the  $T_a$ , with a positive relationship (Table 1, Table 2). Body temperatures varied seasonally when correcting by  $T_a$  variation ( $F_{1,80} = 63.663$ ,  $p < 0.0001$ ). Linear regression slopes between  $T_b$  and environmental temperatures were similar for both seasons ( $T_b - T_a$ :  $F_{1,75} = 0.010$ ,  $p = 0.919$ ;  $T_b - T_s$ :  $F_{1,75} = 1.599$ ,  $p = 0.210$ ; Fig. 2).

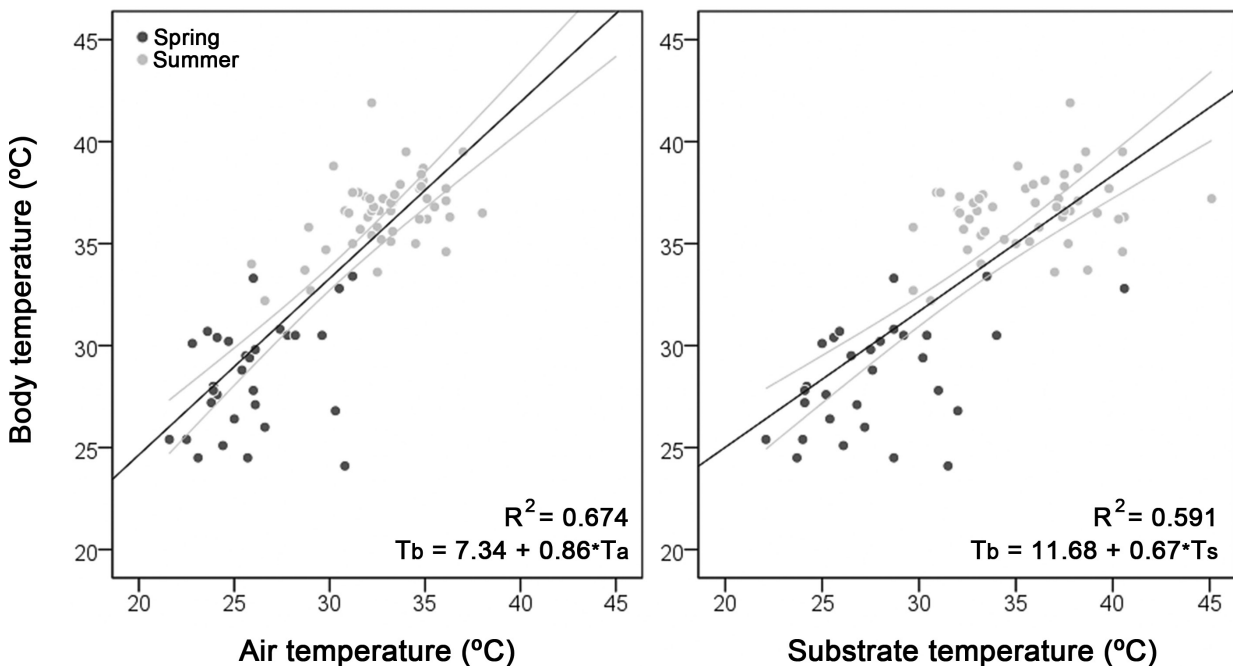
Operative temperatures were lower in spring than in summer for all sunlight exposures (Table 3). Lizards' microhabitat use varied amongst different sunlight exposures

in each season. In spring, they used places under the full sun more frequently ( $G = 6.930$ ;  $p = 0.008$ ), whereas in summer, they used shaded areas more frequently ( $G = 3.865$ ;  $p = 0.049$ ). The use of microhabitats under filtered sun was similar for both seasons ( $G = 0.452$ ;  $p = 0.501$ ; Fig. 3).

In spring, 90% of  $T_b$ s were below the PTR and only 10% fell within the PTR. In summer, 28.3% of  $T_b$ s were within the PTR and 71.7% were above it. The index of accuracy of thermoregulation was significantly higher in the spring than in the summer ( $U = 0.00$ ,  $p < 0.0001$ ; Table 1). The index of habitat thermal quality was similar within seasons ( $U = 4427.00$ ,  $p = 0.161$ ; Table 1). *Podarcis lilfordi codrellensis* showed a poor thermoregulatory effectiveness in spring, significantly lower than in summer ( $U = 0.00$ ,  $p < 0.0001$ ; Table 1).

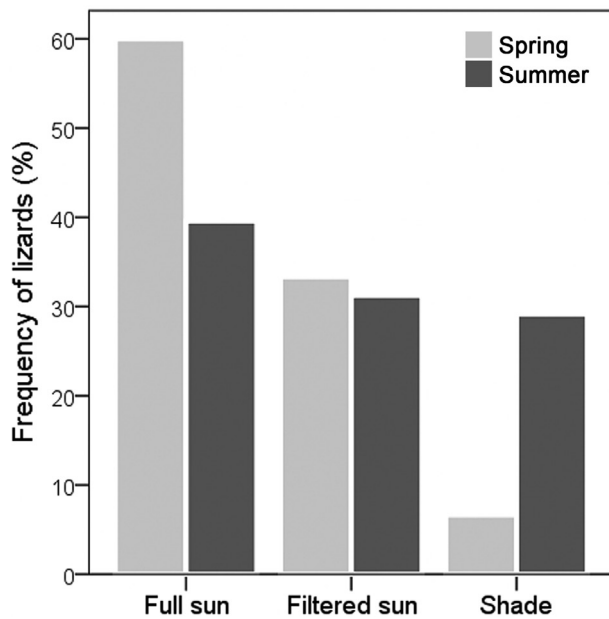
**Table 1.** Descriptive characteristics (mean  $\pm$  SD) of measured environmental variables, lizard body temperatures and thermoregulatory indices in *Podarcis lilfordi codrellensis* from Binicodrell islet (Menorca, Spain).

Variable	Spring (N = 30)	Summer (N = 49)
Body temperature ( $^{\circ}\text{C}$ )	28.48 $\pm$ 2.64	36.54 $\pm$ 1.77
Air temperature ( $^{\circ}\text{C}$ )	25.89 $\pm$ 2.59	32.86 $\pm$ 2.52
Substrate temperature ( $^{\circ}\text{C}$ )	27.92 $\pm$ 3.86	35.63 $\pm$ 3.34
Wind speed (m/s)	0.04 $\pm$ 0.13	0.33 $\pm$ 0.10
Accuracy of thermoregulation ( $^{\circ}\text{C}$ )	3.67 $\pm$ 0.45	1.23 $\pm$ 0.18
Thermal quality of the habitat ( $^{\circ}\text{C}$ )	5.11 $\pm$ 0.25	5.21 $\pm$ 0.59
Effectiveness of thermoregulation (E)	0.28 $\pm$ 0.10	0.76 $\pm$ 0.04
Effectiveness of thermoregulation ( $d_e - d_b$ ) ( $^{\circ}\text{C}$ )	1.44	3.98



**Figure 2.** Left: linear regressions between body temperature ( $T_b$ ) and air temperature ( $T_a$ ). Right: linear regressions between  $T_b$  and substrate temperature ( $T_s$ ) of the studied population of *Podarcis lilfordi codrellensis* at Binicodrell island (Menorca, Spain). Slopes of both regressions are similar for spring and summer. 95% CI are depicted by grey lines.





**Figure 3.** Frequency of observations (%) of *Podarcis lilfordi codrellensis* lizards under different sunlight exposures for spring and summer. Frequency of use of sunny microhabitats was significantly higher in spring than in summer and the opposite took place for shaded microhabitats, while the use of filtered microhabitats was similar in both seasons.

**Table 2.** Linear model showing the effect of biotic and abiotic factors on body temperatures ( $T_b$ ) in *Podarcis lilfordi codrellensis* at Binicodrell island, Menorca (Spain). Factors and their categories: season: spring, summer; sex: female, male; substrate: grass, log, rock, soil; sun: filtered, full, shade; wind speed (m/s), air temperature ( $^{\circ}\text{C}$ ). Significant results are marked in bold.

	Coefficient	SE	t	P
Intercept	19.039	2.775	6.861	<b>&lt;0.001</b>
Season: summer	5.585	0.878	6.363	<b>&lt;0.001</b>
Sex: male	0.630	0.459	1.373	0.174
Substrate: log	-0.967	2.145	-0.451	0.653
Substrate: rock	-0.224	0.609	-0.368	0.714
Substrate: soil	-0.490	0.695	-0.706	0.483
Sun: full	0.313	0.525	0.596	0.553
Sun: shade	-0.049	0.647	-0.077	0.939
Wind	-0.049	0.260	-0.189	0.851
Air temperature	0.356	0.101	3.513	<b>&lt;0.001</b>

Residual standard error: 2.004 on 73 degrees of freedom  
 Multiple R-squared: 0.8164, Adjusted R-squared: 0.7938  
 F-statistic: 36.07 on 9 and 73 DF, p-value: < 2.2e-16

**Table 3.** Mean operative temperatures ( $^{\circ}\text{C}$ ), provided by microhabitats in full sun, filtered sun or full shade, on the islet of Binicodrell, are compared between seasons. Significant results are marked in bold. Values are means  $\pm$  SD.

	Spring	N	Summer	N	U	p
Full sun	34.43 $\pm$ 8.27	1502	45.05 $\pm$ 6.14	246	57029.5	<b>&lt; 0.0001</b>
Filtered sun	27.50 $\pm$ 5.08	367	39.97 $\pm$ 9.21	615	21100.0	<b>&lt; 0.0001</b>
Shade	25.91 $\pm$ 3.77	377	30.26 $\pm$ 2.74	486	23813.0	<b>&lt; 0.0001</b>
Total	21.86 $\pm$ 8.10	2246	38.53 $\pm$ 9.74	1468	1016032.0	<b>&lt; 0.0001</b>

## Discussion

Seasonal shifts in the extent of behavioural thermoregulation of *P. lilfordi codrellensis* at Binicodrell islet were notably broad. In the nearby islets of Aire and Colom, body temperatures of *P. lilfordi lilfordi* and *P. lilfordi brauni*, respectively, show a much lower degree of seasonal variation. Body temperatures found in Binicodrell were lower in spring than those from Aire and Colom and were similar in summer (Ortega et al. 2014). Linear relationships between body and air temperatures varied seasonally in lizards of Aire and Colom islets (Ortega et al. 2014), whereas we found similar slopes for lizards of Binicodrell.

Microhabitat use also changed seasonally. In spring, lizards behaved similarly regarding the use of sun patches at Binicodrell when compared to the other two studied islets (Ortega and Pérez-Mellado 2017), preferring sunny areas, that offered temperatures closer to the optimum of sprint speed ( $\approx 35^{\circ}\text{C}$ ; Bauwens et al. 1995). In summer, Binicodrell lizards used shaded places ( $\approx 30^{\circ}\text{C}$ ) significantly more than in spring, while they used sunny patches ( $\approx 45^{\circ}\text{C}$ ) less. The use of microhabitats under filtered sun was similar in spring and summer. By using microhabitats differently, lizards can achieve different thermoregulation accuracy and effectiveness and seasonal changes are a key factor in conditioning lacertid’s thermoregulatory effort (Ortega and Martín-Vallejo 2018).

Thermoregulatory accuracy of this population is different from those previously studied. In spring, it ranged from  $1.9^{\circ}\text{C}$  in Aire to  $1.1^{\circ}\text{C}$  in Colom (Ortega et al. 2014), whereas the studied lizards from Binicodrell showed a mean of  $3.7^{\circ}\text{C}$  of deviations of body temperatures from the PTR. Additionally, during summer they deviated more from the PTR:  $0.4^{\circ}\text{C}$  in Aire,  $0.6^{\circ}\text{C}$  in Colom (Ortega et al. 2014) and  $1.2^{\circ}\text{C}$  in Binicodrell. Thus, assuming the PTR and its seasonal acclimatisation are similar in all populations (Gvoždík 2012), the body temperatures of the studied lizards deviated by more than double from their thermal preferences vs. those of the nearby isles.

There are two ways for lizards to cope with seasonal environmental variation: (1) behavioural thermoregulation and (2) physiological thermal acclimatisation of preferred body temperatures (Little and Seebacher 2016) and a mix of both strategies would also be possible. Some lacertids change their preferred temperature range to adapt to seasonal thermal requirements, as is the case for *Iberolacerta galani* (Ortega et al. 2016c). Nevertheless, it seems not to be the case for *P. lilfordi*, whose preferred temperature range is similar during spring and summer. Hence, *P. lilfordi* seems to rely on behavioural strategies to adapt their thermoregulation to seasonal shifts.

Our present and past results (Ortega et al. 2014) illustrate the strong intraspecific variability in the thermoregulatory abilities of the Balearic lizard. In addition, the interaction between the seasonal changes in thermoregulation effectiveness and the population (Ortega et al. 2014) is reinforced with the results of *P. lilfordi* from Binicodrell. Lizards are predicted to increase thermoreg-

ulation accuracy with habitat heterogeneity (Sears et al. 2016). Heterogeneity of vegetation and substrates is greater in Colom islet (*P. lilfordi brauni*), intermediate in Aire islet (*P. lilfordi lilfordi*) and lower in Binicodrell (*P. lilfordi codrellensis*; see data in niche breadth and biotic capacity of the three islets in Garrido and Pérez-Mellado (2014)). Although thermal heterogeneity is probably closely related to the heterogeneity of substrates and vegetation, we do not have the empirical evidence that relates both variables. Nonetheless, lizards thermoregulate less effectively (and suffer from a greater seasonal shift in thermoregulation abilities) in the less heterogeneous habitat (Binicodrell). Previous studies in other Mediterranean lacertids found a lack of general thermoregulation patterns at small islets (Pafilis et al. 2016). In any case, applying new thermoregulation metrics can lead us to a better understanding of the influence of habitat thermal quality in thermoregulation effort of this and other lizard species and its flexibility between seasons and islets (Vickers and Schwarzkopf 2016).

Furthermore, thermoregulation differences found on the different populations of *P. lilfordi* might be connected with biological differences amongst the three subspecies. They differ in many biological traits (e.g. size, colour, diets and foraging behaviour) which could influence their thermal biology. Lizards from Aire (*P. lilfordi lilfordi*) are melanistic and larger than the others, lizards from Colom (*P. lilfordi brauni*) are non-melanistic (brownish-greenish colouration) and of intermediate size and lizards from Binicodrell (*P. lilfordi codrellensis*) are also non-melanistic (brownish) and smaller than the others (Salvador 2014; Mencía et al. 2017). Their foraging behaviour and predation pressure are also highly variable (Pérez-Mellado and Corti 1993; Pérez-Cembranos and Pérez-Mellado 2016; Mencía et al. 2017). Small behavioural differences, even in morphotypes of the same species sharing the same habitat, can lead to different body temperatures, as found in *Podarcis melisellensis* (Huyghe et al. 2007).

A reciprocal transplant experiment showed that *Phrynosoma hernandesi* lizards living at different elevations immediately adjusted to the use of light environment by means of phenotypic plasticity (Refsneider et al. 2018). Phenotypic plasticity can have an important role in the thermoregulation variability found in the Balearic lizard. This would provide lizards with the potential to behaviourally buffer the impacts of climate change, whenever cool microsites are available within their habitats (Refsneider et al. 2018). The fact that lizards adapt to seasonal changes in thermal conditions suggests, at least, some degree of phenotypic plasticity. We still do not know whether the high thermoregulation flexibility found in the Balearic lizard is due to habitat differences, local adaptation or phenotypic plasticity. It is probable that all three causes contribute to the observed flexibility in behavioural thermoregulation and disentangling their relative contributions will be necessary to understand how insular populations of lizards modulate their thermoregulation responses to environmental changes.

## Acknowledgements

Lizards were captured under permit CEP 35/2013 of the Balearic Islands' Government. We thank M. Garrido and A. Pérez-Cembranos for support during fieldwork. We thank Mary Trini Mencía and Joe McIntyre for linguistic revision. During fieldwork, funding was provided to Z. O. and A. M. by predoctoral grants from the University of Salamanca (FPI program) and partially supported by the research project CGL2012-39850-CO2-02 (Spanish Ministry of Science and Innovation). We also thank the financial support of Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES, Brazil) and the Programa de Pós-graduação em Ecologia e Conservação (PPGEC) and Programa de Pós-graduação em Biologia Animal (PPGBA) of the UFMS. During analysis and writing, A. G. was funded by a CNPq Master's Scholarship and Z. O. and A. M. were funded by PNDP/CAPES post-doctoral fellowships. All research was conducted in compliance with ethical standards and procedures of the University of Salamanca.

## References

- Adolph SC, Porter WP (1993) Temperature, activity, and lizard life histories. *The American Naturalist* 142: 273–295. <http://doi.org/10.1086/285538>
- Angilletta MJ (2009) Thermal adaptation: a theoretical and empirical synthesis. Oxford University Press, Oxford.
- Algar AC, Mahler DL (2016) Area, climate heterogeneity, and the response of climate niches to ecological opportunity in island radiations of *Anolis* lizards. *Global Ecology and Biogeography* 25: 781–791. <https://doi.org/10.1111/geb.12327>
- Bakken GS, Angilletta MJ (2014) How to avoid errors when quantifying thermal environments. *Functional Ecology* 28: 96–107. <https://doi.org/10.1111/1365-2435.12149>
- Basson CH, Levy O, Angilletta MJ, Clusella-Trullas S (2016) Lizards paid a greater opportunity cost to thermoregulate in a less heterogeneous environment. *Functional Ecology* 31: 856–865. <https://doi.org/10.1111/1365-2435.12795>
- Blouin-Demers G, Weatherhead PJ (2001) Thermal ecology of black rat snakes (*Elaphe obsoleta*) in a thermally challenging environment. *Ecology* 82: 3025–3043. [https://doi.org/10.1890/0012-9658\(2001\)082\[3025:TEOBRS\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2001)082[3025:TEOBRS]2.0.CO;2)
- Bauwens D, Garland JrT, Castilla AM, Van Damme R (1995) Evolution of sprint speed in lacertid lizards: morphological, physiological, and behavioral covariation. *Evolution* 49: 848–863. <https://doi.org/10.1111/j.1558-5646.1995.tb02321.x>
- Bauwens D, Hertz PE, Castilla AM (1996) Thermoregulation in a lacertid lizard: the relative contributions of distinct behavioral mechanisms. *Ecology* 77: 1818–1830. <https://doi.org/10.2307/2265786>
- Carrascal LM, López P, Martín J, Salvador A (1992) Basking and antipredator behaviour in a high altitude lizard: implications of heat-exchange rate. *Ethology* 92: 143–154. <https://doi.org/10.1111/j.1439-0310.1992.tb00955.x>
- Crawley MJ (2012) *The R book*. Wiley, Chichester. <https://doi.org/10.1002/9781118448908>

- Díaz JA, Iraeta P, Monasterio C (2006) Seasonality provokes a shift of thermal preferences in a temperate lizard, but altitude does not. *Journal of Thermal Biology* 31: 237–242. <https://doi.org/10.1016/j.jtherbio.2005.10.001>
- Dzialowski EM (2005) Use of operative temperature and standard operative temperature models in thermal biology. *Journal of Thermal Biology* 30: 317–334. <https://doi.org/10.1016/j.jtherbio.2005.01.005>
- Garrido M, Pérez-Mellado V (2014) Assessing factors involved in determining fluctuating asymmetry in four insular populations of the Balearic lizard *Podarcis lilfordi*. *Salamandra* 50: 147–154.
- Gvoždík L (2012) Plasticity of preferred body temperatures as means of coping with climate change? *Biology Letters* 8: 262–265. <https://doi.org/10.1098/rsbl.2011.0960>
- Hertz PE, Huey RB, Stevenson RD (1993) Evaluating temperature regulation by field-active ectotherms: the fallacy of the inappropriate question. *The American Naturalist* 142: 796–818. <https://doi.org/10.1086/285573>
- Huey RB, Slatkin M (1976) Cost and benefits of lizard thermoregulation. *The Quarterly Review of Biology* 51: 363–384. <https://doi.org/10.1086/409470>
- Huyghe K, Vanhooydonck B, Herrel A, Tadić Z, Van Damme R (2007) Morphology, performance, behavior and ecology of three color morphs in males of the lizard *Podarcis melisellensis*. *Integrative and Comparative Biology* 47: 211–220. <https://doi.org/10.1093/icb/pcm043>
- Little AG, Seebacher F (2016) Acclimation, acclimatization, and seasonal variation in amphibians and reptiles. In: Vieira de Andrade D, Bevier CR and Carvalho JE (Eds) *Amphibian and reptile adaptations to the environment: interplay between physiology and behaviour*. Taylor and Francis Group, Florida, 41–62. <https://doi.org/10.1201/b20420-3>
- Mencia A, Ortega Z, Pérez-Mellado V (2017) From tameness to wariness: chemical recognition of snake predators by lizards in a Mediterranean island. *PeerJ* 5: e2828. <https://doi.org/10.7717/peerj.2828>
- Nitis T, Kitsiou D, Klaić ZB, Prtenjak MT, Moussiopoulos N (2005) The effects of basic flow and topography on the development of the sea breeze over a complex coastal environment. *Quarterly Journal of the Royal Meteorological Society* 131: 305–327. <https://doi.org/10.1256/qj.04.42>
- Ortega Z, Martín-Vallejo FJ (2018) Main factors affecting lacertid lizard thermal ecology. *Integrative Zoology*. <https://doi.org/10.1111/1749-4877.12363>
- Ortega Z, Pérez-Mellado V (2016) Seasonal patterns of body temperature and microhabitat selection in a lacertid lizard. *Acta Oecologica* 77: 201–206. <https://doi.org/10.1016/j.actao.2016.08.006>
- Ortega Z, Pérez-Mellado V (2017) The effect of thermal requirements on microhabitat selection and activity of *Podarcis lilfordi* (Squamata: Lacertidae). *Salamandra* 53: 351–358.
- Ortega Z, Mencia A, Pérez-Mellado V (2016a): Sexual differences in behavioral thermoregulation of the lizard *Scelarcis perspicillata*. *Journal of Thermal Biology* 61: 44–49. <https://doi.org/10.1016/j.jtherbio.2016.08.006>
- Ortega Z, Mencia A, Pérez-Mellado V (2016b) The peak of thermoregulation effectiveness: thermal biology of the Pyrenean rock lizard, *Iberolacerta bonnali* (Squamata, Lacertidae). *Journal of Thermal Biology* 56: 77–83. <https://doi.org/10.1016/j.jtherbio.2016.01.005>
- Ortega Z, Mencia A, Pérez-Mellado V (2016c) Adaptive seasonal shifts in the thermal preferences of the lizard *Iberolacerta galani* (Squamata, Lacertidae). *Journal of Thermal Biology* 62: 1–6. <https://doi.org/10.1016/j.jtherbio.2016.10.005>
- Ortega Z, Pérez-Mellado V, Garrido M, Guerra C, Villa-García A, Alonso-Fernández T (2014) Seasonal changes in thermal biology of *Podarcis lilfordi* (Squamata, Lacertidae) consistently depend on habitat traits. *Journal of Thermal Biology* 39: 32–39. <https://doi.org/10.1016/j.jtherbio.2013.11.006>
- Pafilis P, Lymberakis P, Sagonas K, Valakos E (2016) The particularities of a remote islet shape the thermoregulatory profile of an endemic Mediterranean lizard. *Journal of Thermal Biology* 61: 55–60. <https://doi.org/10.1016/j.jtherbio.2016.08.007>
- Perera A, Pérez-Mellado V (2002) Ausencia de plasticidad fenotípica en las estrategias reproductoras de la lagartija balear, *Podarcis lilfordi* (Squamata, lacertidae). *Revista de Menorca* 86: 159–171. <https://www.raco.cat/index.php/RdM/article/view/340935>
- Pérez-Cembranos A, León A, Pérez-Mellado V (2016) Omnivory of an insular lizard: sources of variation in the diet of *Podarcis lilfordi* (Squamata, Lacertidae). *PLoS one* 11: e0148947. <https://doi.org/10.1371/journal.pone.0148947>
- Pérez-Mellado V, Corti C (1993) Dietary adaptations and herbivory in lacertid lizards of the genus *Podarcis* from western Mediterranean islands (Reptilia, Sauria). *Bonner Zoologische Beiträge* 44: 193–220.
- Pérez-Mellado V, Martín-Vallejo J, Brown R, Picornell A, Castro J, Ramón MM, Terrassa B, García-Díez T, Hernández-Estévez JA (2008) Population density in *Podarcis lilfordi* (Squamata, Lacertidae), a lizard species endemic to small islets in the Balearic Islands (Spain). *Amphibia-Reptilia* 29: 49–60. <https://doi.org/10.1163/156853808783431587>
- R Development Core Team (2017) R: A language and environment for statistical computing.
- Refsnider JM, Qian SS, Streby HM, Carter SE, Clifton IT, Siefker AD, Vazquez TK (2018) Reciprocally transplanted lizards along an elevational gradient match light environment use of local lizards via phenotypic plasticity. *Functional Ecology* 32: 1227–1236. <https://doi.org/10.1111/1365-2435.13071>
- Salvador A (2014) *Podarcis lilfordi* (Günther, 1874). In: Salvador A (Eds) *Reptiles Fauna Ibérica edición revisada y aumentada*. Museo Nacional de Ciencias Naturales, Madrid, 556–576.
- Sears MW, Angilletta MJ (2015) Costs and benefits of thermoregulation revisited: both the heterogeneity and spatial structure of temperature drive energetic costs. *The American Naturalist* 185: E94–E102. <https://doi.org/10.1086/680008>
- Sears MW, Jr. Angilletta MJ, Schuler MS, Borchert J, Dilliplane KF, Stegman M, Rusch TW, Mitchell WA (2016) Configuration of the thermal landscape determines thermoregulatory performance of ectotherms. *Proceedings of the National Academy of Sciences* 113: 10595–10600. <https://doi.org/10.1073/pnas.1604824113>
- Van Damme R, Bauwens D, Verheyen RF (1987) Thermoregulatory responses to environmental seasonality by the lizard *Lacerta vivipara*. *Herpetologica* 43: 405–415.
- Vickers M, Schwarzkopf L (2016) A random walk in the park: an individual-based null model for behavioral thermoregulation. *The American Naturalist* 187: 481–490. <https://doi.org/10.1086/685433>