

The effect of thermal requirements on microhabitat selection and activity of *Podarcis lilfordi* (Squamata: Lacertidae)

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Abstract. Selection of thermally suitable microhabitats plays an important role in the thermoregulation of ectotherms. We studied microhabitat preferences in two populations of the Balearic lizard, *Podarcis lilfordi*, that live on two coastal islets of Menorca (Balearic Islands, Spain: Aire and Colom). To assess the roles of different microclimatic traits driving lizards' decisions, we employed a case/control design. We measured microclimate variables in locations used by lizards (cases) and in paired random unused locations (controls). By comparing paired cases vs controls, we prevent spatial and temporal variation of environmental conditions. In order to test if microhabitat selection depends on thermoregulation requirements, we studied lizards in three situations: (1) 'cold', when body temperatures (T_b) of lizards were below their preferred temperature range (PTR), (2) 'optimal', when T_b were within the PTR, and (3) 'warm', when T_b exceeded the PTR. Substrate temperature was the main abiotic trait that determined microhabitat preferences of *P. lilfordi*, sometimes in conjunction with air temperature, while wind speed and humidity were not significant. 'Cold' lizards selected warmer microhabitats than the mean, but only on Colom islet. Notably, 'optimal' lizards also preferred microhabitats that were warmer than their surroundings, and 'warm' lizards did not select cold microhabitats in order to cool themselves, but rather acted randomly regarding temperature, wind and humidity. These results for 'optimal' and 'warm' lizards were consistent for both islets. We also studied the beginning and end of lizards' diel activity. We found that lizards on Aire were active for approximately one hour more per day than lizards on Colom, which might be related to differences in melanism. However, activity started at an air temperature of approximately 17–19°C and finished at approximately the same temperature on both islets.

Key words. Balearic lizard, behavioural thermoregulation, habitat choice, islands, Lacertidae, Menorca, microclimate, temperature, wind speed.

Introduction

Temperature affects all aspects of life and evolution of ectotherms (PÖRTNER 2002, ANGILLETTA 2009). One important dimension of their thermal biology is thermoregulation (e.g., HERTZ et al. 1993), that is, the ability to regulate body temperature (reviewed by ANGILLETTA 2009). Lizards mainly thermoregulate by adjusting their activity periods (HERTZ 1992, ADOLPH & PORTER 1993), shuttling between different thermal microhabitats (HEATH 1970, BAUWENS et al. 1996), or adjusting their body posture (BAUWENS et al. 1996). The combination of these strategies depends on the balance between costs and benefits (HUEY & SLATKIN 1976, BLOUIN-DEMERS & NADEAU 2005). Other abiotic factors, such as wind, can also have a significant effect on thermoregulation (SCHEERS & VAN DAMME 2002, MAIA-CARNEIRO et al. 2012, LOGAN et al. 2015, ORTEGA et al. 2017).

Lacertid lizards are heliothermic thermoregulators (ARNOLD 1987, CASTILLA et al. 1999), and the selection of suitable microhabitats is a key point of their thermoregulation (BAUWENS et al. 1996, CASTILLA et al. 1999). Microhabi-

tat selection is conditioned by a balance between the costs and the benefits of their thermal characteristics, the opportunities for reproduction and feeding, and the avoidance of predators (e.g., HUEY 1991, MARTÍN & SALVADOR 1997, DOWNES & SHINE 1998, DOWNES 2001). The study of the abiotic factors that influence habitat selection at a micro-scale helps to understand the mechanisms of thermoregulation (SCHEERS & VAN DAMME 2002, ROW & BLOUIN-DEMERS 2006). In addition, it can be important to comprehend the response of reptiles to thermal changes in their habitats, since the selection of microhabitat involves physiological consequences that can be crucial to their demography and ecology (HUEY 1991, HUEY et al. 2003).

Here we studied the influence of main abiotic variables, i.e., temperature, wind, and humidity, on the microhabitat choice of an insular lacertid lizard. Our main goal was to test how lizards selected microhabitats that allowed them to obtain body temperatures close to their optimal range. Secondly, we aimed to assess the relative importance of different abiotic traits on their microhabitat selection. We used the Balearic lizard, *Podarcis lilfordi*, as a model or-

ganism, comparing two populations that live on two islets that are situated close to each other, and differ in aspects of their thermal biology (ORTEGA et al. 2014).

Materials and methods

Study species and area

The Balearic lizard, *Podarcis lilfordi* (GÜNTHER, 1874), is an endemic lacertid of Mallorca and Menorca (Balearic Islands, Spain). We studied two subspecies, *P. l. lilfordi*, from Aire islet, and *P. l. brauni* (MÜLLER, 1927), from Colom islet. Both islets are close to the coast of Menorca.

Aire has a surface area of 35 ha, mostly covered with halophytic shrubs. The average annual temperature is 16.7°C and average annual precipitation 625 mm (JANSÀ I CLAR 1979). Food resources for lizards are limited, and predation pressure is very sporadic. *P. l. lilfordi* is a small lacertid lizard (mean snout to vent length – SVL – for males = 68.98 mm; mean weight = 9.75 g, mean SVL for females = 61.73 mm; mean weight = 6.34 g) in a melanistic population (PÉREZ-MELLADO & SALVADOR 1988). *Podarcis l. lilfordi* achieves a mean effectiveness of thermoregulation of 0.81 on Aire in spring (ORTEGA et al. 2014).

Colom has a surface area of 59 ha, and mean annual temperature and rainfall are similar to those on Aire. Its vegetation is more diverse than on the latter, with abundant and larger shrubs and even some arboreal patches. Food resources for lizards are richer on Colom than on Aire (unpubl. data). *Podarcis l. brauni* has a brownish-greenish coloration, and a significantly smaller body size than *P. l. lilfordi* (mean SVL for males = 67.96 mm; mean weight = 8.50 g, mean SVL for females = 58.68 mm; mean weight = 6.54 g). *Podarcis l. brauni* achieves a mean effectiveness of thermoregulation of 0.86 on Colom in spring (ORTEGA et al. 2014).

Daily emergence and retreat

For both islets, we recorded the occurrence of four events: (1) Emergence time: when we observed the first lizard leaving its shelter for its first basking session in the morning; (2) starting activity: when one of the first lizards basking started its activity (foraging, mating, fighting, etc.); (3) ending activity: when lizards stopped their daily activity and started their last basking session before retreating; (4) retreat time: when we observed the last lizard retreating to its shelter after its final basking session (we waited 5 minutes in order to confirm it had indeed retreated). At these four events, we measured wind speed (in ms^{-1}), relative humidity (RH, in %), and air temperature (T_a) with a Testo® 925 digital thermometer, and a Kestrel® 3000 anemometer, respectively.

Preferred temperature range (PTR)

We studied the PTR of *P. lilfordi* in spring in order to design our study of microhabitat selection. To obtain the PTR, we

measured selected body temperatures (T_{sel}) of *P. lilfordi* on 12 and 13 June 2008 in a thermal gradient laboratory experiment. Lizards captured on Aire were transported to the laboratory in Sant Lluís (Menorca) and housed in individual opaque terraria. There, lizards were fed with mealworms and crickets, and water was available to them ad libitum. The thermal gradient was built in a glass terrarium (100 × 60 × 60 cm), using a 150 W infrared lamp mounted above one of the ends, which created a gradient from 20 to 60°C. Prior to the experiment, we allowed lizards one day of acclimation to captivity, exposing them to the local natural conditions of light and temperature, which were similar to those in their habitat. Over the next two days, we measured a selected temperature of an individual lizard each hour from 08:00 to 17:00 h GMT with a Testo® 925 digital thermometer. We tested 20 adult lizards (10 males and females each), each of which was measured six times, obtaining a total of 120 (20 × 6) values of T_{sel} , of which we considered the 50% as the PTR. We released lizards in the place of their capture on Aire islet immediately after the experiment.

Microhabitat selection

We studied microhabitat selection on Aire and Colom in April and May of 2007, using a case/control design. We conducted this study during spring in order to exclude seasonal variations in thermoregulation, which is known to differ between the two islets (ORTEGA et al. 2014). We noose-captured 110 lizards on Aire and 135 on Colom during throughout their activity periods from 06:00 to 18:00 h GMT. We measured their body temperatures (T_b) immediately after capture with a digital thermometer, keeping the probe in the shade.

As we were interested in abiotic constraints and thermal influences of microhabitat choice, we sorted the lizards of both islets in three categories: (1) 'cold' lizards ($T_b < \text{PTR}$) that would need to warm up, (2) 'optimal' lizards (T_b within the PTR), and (3) 'warm' lizards ($T_b > \text{PTR}$) that would need to cool down.

For each lizard, we described the microhabitat at its point of capture (case) as to its type of substrate (rock, soil, grass or bush), degree of insolation (full sun, filtered sun, or full shade), wind speed (ms^{-1}), relative humidity (% RH), and substrate (T_s) and air (T_a) temperatures. In order to assess abiotic constraints in lizards' microhabitat preferences, we also recorded all these variables at four selected points (controls), which represent the availability of climatic conditions for a particular lizard at a certain time and place. We selected these four points at 1 m distance from the respective capture point in each compass direction (North, South, East and West). Mean values of these four points around each capture point were the control values for our microhabitat selection analysis.

Data analysis

Mean values are accompanied by standard errors (SE). Parametric statistics were performed when data followed

Table 1. Paired comparisons of the use of each microhabitat and insolation situation by lizards relative to the availability of alternatives. D.f. = 1 for all comparisons (for details, see text).

		G	p	
Colom	Substrate	Rock-soil	14.826 < 0.0001	
		Rock-grass	47.907 < 0.0001	
		Rock-bushes	62.880 < 0.0001	
		Soil-grass	2.823 0.093	
		Soil-bushes	22.594 < 0.0001	
		Grass-bushes	15.629 < 0.0001	
Insolation situation	Full sun-filtered sun	16.304 < 0.0001		
		Full sun-shade	18.227 < 0.0001	
		Filtered sun-shade	0.644 0.422	
Aire	Substrate	Rock-soil	10.914 0.001	
		Rock-grass	19.928 < 0.0001	
		Rock-bushes	20.176 < 0.0001	
		Soil-grass	5.163 0.023	
		Soil-bushes	5.900 0.015	
		Grass-bushes	0.057 0.811	
Insolation situation	Full sun-filtered sun	28.799 < 0.0001		
		Full sun-shade	49.981 < 0.0001	
		Filtered sun-shade	3.716 0.054	

the assumptions of normality and homogeneity of variances. If these assumptions were not fulfilled, even after log-transformation, non-parametric equivalents were calculated (SOKAL & ROHLF 1995, CRAWLEY 2012). Analyses were conducted in R, version 3.1.3 (R Core Team 2015).

The PTR was only used in order to establish the three categories of lizard body temperature ('cold', 'optimal' and 'warm'). First, we studied univariate microhabitat selection in the three thermoregulation situations ('cold', 'optimal', and 'warm') for both islets in order to explore the patterns of influence of the measured abiotic variables. Then, to add robustness to the repeated measuring design, we assessed microhabitat selection with a case/control procedure, using capture points of lizards as cases and the mean values of the four points surrounding each capture point as controls (COMPTON et al. 2002). This case/control design is analogous to the use/no use of MANLY et al. (2002). In order to

analyse the paired data, we applied matched-pairs logistic regression or paired logistic regression (COMPTON et al. 2002, HOSMER & LEMESHOW 2004). We selected the model that best fitted to each set of data, using the multi-model selection function of AIC_c (BURNHAM & ANDERSON 2002) with the package MuMIn (BARTON 2012). Coefficients from paired logistic regression models are interpreted in terms of odds ratios and not in absolute values (KEATING & CHERRY 2004).

Results

Body temperatures and climatic conditions

In the Aire lizards, T_b did not differ between sexes (one-way ANOVA, $F_{1,96} = 0.131$, $p = 0.718$) and age groups (one-way ANOVA, $F_{1,108} = 0.091$, $p = 0.764$), for which reason we pooled data for both sexes in subsequent analyses. In the Colom lizards, T_b were also similar between sexes (one-way ANOVA, $F_{1,118} = 0.546$, $p = 0.462$) and age groups (one-way ANOVA, $F_{1,133} = 0.019$, $p = 0.890$). Body temperatures were similar for both islets (Colom: $32.84 \pm 0.36^\circ\text{C}$; Aire: $32.85 \pm 0.24^\circ\text{C}$; Mann-Whitney U test, $U = 6814$, $p = 0.268$). Air temperatures at the points of capture were also similar on both islets (Colom: $26.29 \pm 0.33^\circ\text{C}$; Aire: $26.40 \pm 0.27^\circ\text{C}$; Mann-Whitney U test, $U = 7753$, $p = 0.860$), and substrate temperatures were marginally higher on Aire (Colom: $28.72 \pm 0.38^\circ\text{C}$; Aire: $29.71 \pm 0.39^\circ\text{C}$; one-way ANOVA, $F_{1,250} = 3.621$, $p = 0.058$). Wind speed was significantly higher on Aire (Colom: $0.29 \pm 0.05 \text{ ms}^{-1}$; Aire: $0.61 \pm 0.07 \text{ ms}^{-1}$; Mann-Whitney U test, $U = 6042.5$, $p = 0.001$), and relative humidity was also significantly higher on Aire (Colom: $61.71 \pm 1.01\%$; Aire: $69.28 \pm 0.92\%$; one-way ANOVA, $F_{1,249} = 30.178$, $p < 0.0001$, Table 1).

Regarding thermal availability, that is, the mean values of temperatures at surrounding points, available substrate temperatures were higher on Aire than on Colom (Colom: $26.24 \pm 0.41^\circ\text{C}$; Aire: $27.66 \pm 0.39^\circ\text{C}$; one-way ANOVA, $F_{1,207} = 6.210$, $p = 0.013$). Available air temperatures were also significantly higher on Aire than on Colom (Colom: $23.91 \pm 0.29^\circ\text{C}$; Aire: $25.00 \pm 0.24^\circ\text{C}$; Mann-Whitney U test, $U = 4218.00$, $p = 0.004$) and this was also the case for wind speed (Colom: $0.31 \pm 0.05 \text{ ms}^{-1}$; Aire: $0.53 \pm 0.06 \text{ ms}^{-1}$; Mann-Whitney U test, $U = 4424.50$, $p = 0.006$) and rela-

Table 2. Time (GMT), wind speed (speed), relative humidity (RH), and air temperature (T_a) of the four studied periods of the daily activity of *Podarcis lilfordi* on Aire and Colom islets (mean \pm SE).

	Islet	Time	Speed (ms^{-1})	RH (%)	T_a ($^\circ\text{C}$)
Emerging	Colom (n=4)	06:27 \pm 0:12	0.70 \pm 0.32	83.25 \pm 4.03	17.05 \pm 0.51
	Aire (n=7)	05:34 \pm 0:23	1.65 \pm 0.74	81.14 \pm 3.36	18.06 \pm 0.59
Starting activity	Colom (n=4)	06:57 \pm 0:07	1.24 \pm 0.64	79.75 \pm 4.37	19.52 \pm 0.69
	Aire (n=7)	06:11 \pm 0:16	1.45 \pm 0.74	84.00 \pm 4.81	18.96 \pm 0.38
Ending activity	Colom (n=2)	17:17 \pm 0:19	1.02 \pm 0.15	67.50 \pm 0.50	20.85 \pm 0.05
	Aire (n=7)	17:54 \pm 0:04	2.29 \pm 0.48	80.14 \pm 2.96	20.73 \pm 0.58
Retreating	Colom (n=2)	17:56 \pm 0:02	0.67 \pm 0.05	73.00 \pm 7.00	18.00 \pm 0.40
	Aire (n=7)	18:42 \pm 0:06	2.21 \pm 0.56	90.71 \pm 3.85	18.51 \pm 0.35

tive humidity (Colom: $64.53 \pm 0.89\%$; Aire: $72.70 \pm 0.67\%$; Mann-Whitney U test, $U = 2578.50$, $p < 0.0001$, Table 1).

Daily emergence and retreat

Lizards emerged from their shelters on Aire and began their activity about 30 min earlier than on Colom (Table 2). In addition, lizards on Aire spent more time on their first basking session before beginning to forage. Both humidity and wind were higher on Aire than on Colom during the four study periods. Air temperatures at which activity started and ended were similar for both islets (Table 2).

Microhabitat selection

Lizards from Colom selected rocky microhabitats significantly more commonly and avoided microhabitats of grass and bushes ($G = 89.688$, 3 d.f., $p < 0.0001$; Table 1, Fig. 1). They also preferred microhabitats in full sun and actively avoided fully shaded microhabitats ($G = 30.859$, $p < 0.0001$; Table 1). Lizards on Aire selected rocky microhabitats and avoided microhabitats of grass and bushes ($G = 38.067$, 3 d.f., $p < 0.0001$; see post-hoc comparisons in Table 1, Fig. 1). They also preferred microhabitats in full sun and actively avoided fully shaded microhabitats ($G = 66.996$, $p < 0.0001$, see post-hoc comparisons in Table 1).

The PTR of *P. lilfordi* in spring was $31.78\text{--}35.68^\circ\text{C}$. Thus, captured lizards with $T_b < 31.78^\circ\text{C}$ were assigned to the ‘cold’ thermoregulation situation, lizards with T_b within $31.78\text{--}35.68^\circ\text{C}$ were considered ‘optimal’, and lizards with $T_b > 35.68^\circ\text{C}$ were considered ‘warm’. Proportions of lizards in the three insolation situations (full sun, filtered sun, or

full shade) were similar for the three thermoregulation situations (‘cold’, ‘optimal’, and ‘warm’) on Colom ($G = 7.040$, 4 d.f., $p = 0.134$), as well as on Aire ($G = 2.690$, 4 d.f., $p = 0.611$; Fig. 2).

On Colom, a univariate test of abiotic variables demonstrated that lizards actively selected microhabitats with significantly higher substrate and air temperatures (Table 3) while wind speed was not significant (Table 3). Microhabitats with higher relative humidity were significantly more often avoided by ‘optimal’ and ‘cold’ lizards (Table 3). The paired logistic regression model that better explains the data of ‘cold’ lizards on Colom islet revealed that substrate temperature was the main abiotic trait affecting microhabitat choice, whereas the remaining abiotic traits, air temperature, wind speed and humidity, had no significant impacts (Table 4). For ‘optimal’ lizards on Colom, both air and substrate temperatures significantly affected the choice of microhabitat, whereas wind speed and humidity did not have significant effects (Table 5). An increase by 10% in air temperature (approximately 2.5°C) would increase the probability of selection of a microhabitat by 19%, and an increase by 10% (approx. 2.8°C) would increase the probability of selection by 23.7%. For ‘warm’ lizards, none of the studied

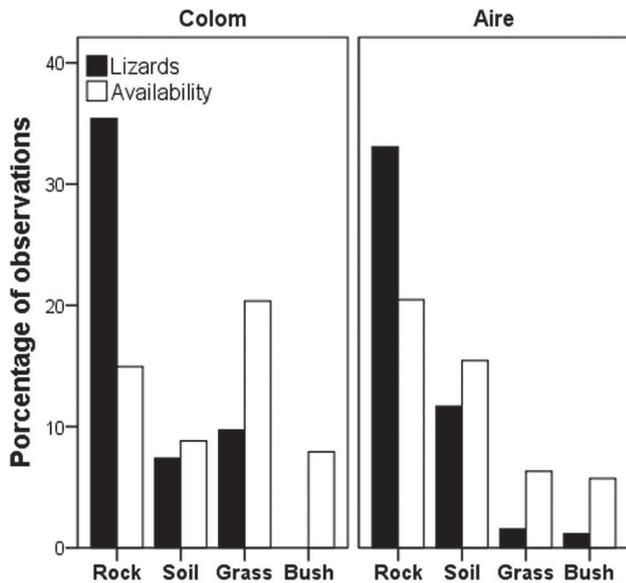


Figure 1. Proportion (%) of each microhabitat type selected by *Podarcis lilfordi* lizards and their availability on both islets.

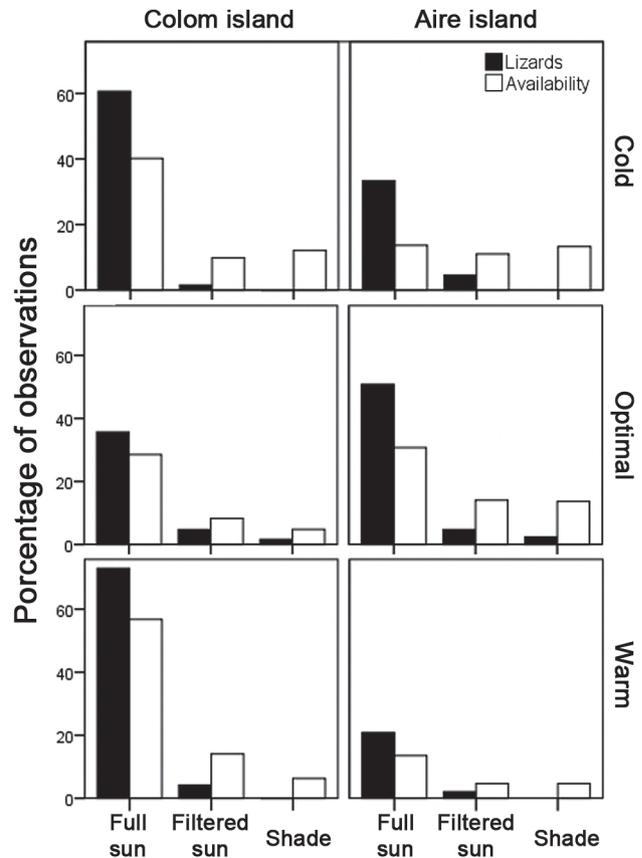


Figure 2. Proportion (%) of used (cases) and available (controls) microhabitats under each type of insolation situation (full sun, filtered sun, or shade) according to three thermal situations: (1) cold ($T_b < \text{PTR}$ [preferred temperature range]), (2) optimal (T_b within the PTR), and (3) warm ($T_b > \text{PTR}$), for both islets.

Thermal requirements affect microhabitat selection

Table 3. Mean \pm SE (n) values of four microclimatic variables on Colom, comparing the capture points of lizards (cases) to the availability of alternatives (controls) in three thermal situations: (1) cold ($T_b < PTR$), (2) optimal (T_b within PTR), and (3) warm ($T_b > PTR$).

Variable	Situation of thermoregulation	Lizards	Availability	F	p
Substrate temperature	Cold	25.55 \pm 0.61 (41)	23.55 \pm 0.30 (155)	9.245	0.003
	Optimal	29.25 \pm 0.54 (53)	27.25 \pm 0.37 (155)	8.104	0.005
	Warm	31.52 \pm 0.50 (37)	29.12 \pm 0.40 (92)	11.599	0.001
Air temperature	Cold	23.43 \pm 0.47 (41)	22.13 \pm 0.21 (155)	7.610	0.006
	Optimal	26.86 \pm 0.78 (53)	24.63 \pm 0.22 (155)	22.519	< 0.0001
	Warm	28.66 \pm 0.46 (37)	25.69 \pm 0.30 (92)	28.218	< 0.0001
Wind speed	Cold	0.24 \pm 0.05 (41)	0.33 \pm 0.03 (155)	3.351	0.069
	Optimal	0.43 \pm 0.06 (53)	0.44 \pm 0.23 (155)	0.185	0.668
	Warm	0.56 \pm 0.06 (37)	0.48 \pm 0.04 (92)	0.150	0.699
Relative humidity	Cold	70.63 \pm 1.70 (41)	70.64 \pm 0.77 (155)	0.000	0.988
	Optimal	59.19 \pm 1.19 (53)	61.75 \pm 0.63 (155)	3.994	0.047
	Warm	55.03 \pm 1.63 (37)	58.80 \pm 0.69 (92)	6.324	0.013

Table 4. Mean \pm SE (n) values of four microclimatic variables on Aire, comparing the capture points of lizards (cases) to the availability of alternatives (controls) in three thermal situations: (1) cold ($T_b < PTR$), (2) optimal (T_b within PTR), and (3) warm ($T_b > PTR$).

Variable	Situation of thermoregulation	Lizards	Availability	F	p
Substrate temperature	Cold	26.68 \pm 0.68 (22)	24.78 \pm 0.30 (99)	7.687	0.006
	Optimal	30.19 \pm 0.49 (73)	28.09 \pm 0.30 (290)	10.751	0.001
	Warm	32.69 \pm 0.99 (11)	30.76 \pm 0.61 (44)	2.154	0.148
Air temperature	Cold	24.85 \pm 0.44 (22)	23.73 \pm 0.19 (99)	6.977	0.009
	Optimal	26.86 \pm 0.37 (73)	25.27 \pm 0.16 (290)	17.469	< 0.0001
	Warm	28.58 \pm 0.55 (11)	26.47 \pm 0.28 (44)	11.204	0.002
Wind speed	Cold	0.58 \pm 0.13 (22)	0.56 \pm 0.06 (99)	0.004	0.953
	Optimal	0.62 \pm 0.72 (73)	0.55 \pm 0.04 (290)	0.664	0.416
	Warm	0.64 \pm 0.21 (11)	0.59 \pm 0.10 (44)	0.044	0.834
Relative humidity	Cold	74.23 \pm 2.23 (22)	75.06 \pm 0.68 (99)	0.572	0.451
	Optimal	70.38 \pm 1.09 (73)	72.74 \pm 0.44 (290)	5.153	0.024
	Warm	66.36 \pm 1.91 (11)	68.89 \pm 0.76 (44)	1.970	0.166

abiotic constraints had a significant effect on the microhabitat choice of *P. lilfordi brauni* lizards (Table 5).

On Aire, univariate tests demonstrated that lizards preferred microhabitats with significantly higher air temperatures, regardless of their body temperatures (Table 4). However, only 'cold' and 'optimal' lizards selected microhabitats with higher substrate temperatures (Table 4). Wind speed, again made no difference for lizard microhabitat choice, and microhabitats with high humidity were avoided only at 'optimal' body temperatures (Table 4). The paired logistic regression model that better explains data of 'cold' lizards on Aire reveals that none of the studied abiotic constraints had a significant effect on lizard microhabitat preferences (Table 6). For 'optimal' lizards, air and substrate temperatures as well as wind speed significantly affected the lizards' choice of microhabitat (Table 6). An increase by 10% in air temperature (approx. 2.5°C) would increase by 47.5% the probability of selection of a microhabitat, while an increase

by 10% in substrate temperature (approx. 2.9°C) would increase the probability of selection by 14.6%, and an increase of a 10% in wind speed (approx. 0.06 ms⁻¹) would increase the probability of selection of a microhabitat by 79.2%. Finally, the paired logistic regression model that better fits data (lowest AIC_c) of 'warm' lizards on Aire, demonstrated that none of the studied abiotic constraints had a significant effect on lizards' microhabitat choice (Table 6).

Discussion

Body temperatures of *P. lilfordi* during spring of 2007 were similar on both islets, with a mean T_b of 32.85°C. These results differ from those of a previous study in 2006, in which Balearic lizards showed a mean T_b of approximately 1°C higher on Colom during the same period (PÉREZ-MELLADO et al. 2013, ORTEGA et al. 2014). A similar situ-

Table 5. Paired logistic regression models that best predict microhabitat selection of *Podarcis lilfordi* on Colom. The model ‘cold’ analyses microhabitat selection of lizards with body temperatures (T_b) below the preferred temperature range (PTR). The model ‘optimal’ analyses microhabitat selection of lizards in which T_b fall within the PTR, and the model of ‘warm’ analyses microhabitat selection of lizards with T_b higher than the PTR.

Model	AIC _c	Variable	Coeff.	SE	p	Odds ratio (10% change)	95% CI odds ratio (10% change)
Cold	29.3	relative humidity	0.28	0.17	0.098	1.32	(0.950, 1.838)
		substrate temperature	1.43	0.50	0.004	4.18	(1.561, 11.202)
		wind speed	-3.43	2.17	0.114	0.03	(0.001, 2.291)
Optimal	27.4	relative humidity	-0.19	0.12	0.127	0.83	(0.652, 1.055)
		air temperature	0.64	0.27	0.016	1.90	(1.125, 3.202)
		substrate temperature	0.86	0.37	0.021	2.37	(1.141, 4.906)
Warm	6.6	wind speed	-3.57	1.92	0.063	0.03	(0.001, 1.210)
		air temperature	7.478e+01	4.798e+03	0.988	2.988e+32	0-∞
		substrate temperature	-1.063e+01	9.861e+02	0.991	2.422e-05	0-∞
		wind speed	6.282e+02	4.000e+04	0.987	6.406e+272	0-∞

Table 6. Paired logistic regression models that better predict microhabitat selection of *Podarcis lilfordi* on Aire. The model ‘cold’ analyses the microhabitat selection of lizards with body temperatures (T_b) below the preferred temperature range (PTR). The model ‘optimal’ analyses microhabitat selection of lizards in which T_b fall within the PTR, and the model of ‘warm’ analyses microhabitat selection of lizards with T_b higher than the PTR.

Model	AIC _c	Variable	Coeff.	SE	p	Odds ratio (10% change)	95% CI odds ratio (10% change)
Cold	18.6	air temperature	1.14	0.68	0.096	3.12	(0.817, 11.929)
		substrate temperature	0.76	0.60	0.206	2.13	(0.659, 6.884)
Optimal	44.8	air temperature	1.56	0.42	< 0.001	4.75	(2.066, 10.935)
		substrate temperature	0.38	0.16	0.020	1.46	(1.061, 2.004)
		wind speed	2.07	0.92	0.024	7.92	(1.307, 47.945)
Warm	4.6	air temperature	3.414e+01	4.368e+03	0.994	6.708e+14	0-∞
		wind speed	3.465e+01	4.601e+03	0.994	1.119e+15	0-∞

ation was observed for air and substrate temperatures at the places where lizards were captured. Although mean temperatures at the closest weather station were similar in both years (data available from the Spanish Meteorological Agency, ‘Agencia Española de Meteorología, AEMET’; <http://www.aemet.es>), it is possible that the spring of 2007 was harsher on Colom than on Aire. These results emphasize the thermal variability to which Balearic lizards are exposed from one islet to another. Wind at the capture places was twice as fast on Aire than on Colom, while the relative humidity was also significantly higher on Aire. It is possible that a higher relative humidity may be related to faster wind speeds, since the wind blows directly from the sea on these little islets. Either way, the wind speed would be the main abiotic difference between both islets during the study period. Mean abiotic conditions of the habitat, measured at the four points surrounding each lizard’s capture point, both air and substrate temperatures, as well as wind speed and relative humidity were higher on Aire than on Colom.

An interesting result is that lizards on Aire emerged from their shelters approximately half an hour before liz-

ards on Colom and took longer basking sessions before they started activity. They emerged and started their activity when the air temperature was approximately 17–19°C. They also retreated to their shelters more than half an hour later on Aire than on Colom, so that lizards on Aire have a longer diel activity than lizards on Colom. This result may be related to the melanistic coloration of Aire lizards, as has been suggested in previous studies (PÉREZ-MELLADO et al. 2013, ORTEGA et al. 2014). A tailor-made experimental study focusing on cooling and heating rates of lizard from both populations would clarify this question. Nonetheless, both populations ended their activity periods at approximately 20°C and retreated to their shelters at approximately 18°C. Differences in activity as a means of thermoregulation are common, and have been reported for other lacer-tids as a way of dealing with habitat variations, for example, in altitude (DÍAZ 1997, GVOŽDÍK 2002). A longer diel activity period could compensate for the stronger winds on Aire and also allow improving lizard physiological performance in this population (e.g., ADOLPH & PORTER 1993). Although melanistic coloration has been reported to play a role in increasing the fitness of some ectotherms living in cooler ar-

eas (CLUSELLA-TRULLAS et al. 2007), we still do not know if the melanistic coloration is related to these thermal advantages in the Aire population. It is possible that maintaining high body temperatures for longer periods of activity would allow continuous active foraging in *P. l. lilfordi*, and thus would facilitate the highly plastic omnivory of the population (PÉREZ-MELLADO 1989, PÉREZ-MELLADO & CORTI 1993, PÉREZ-CEMBRANOS & PÉREZ-MELLADO 2015, PÉREZ-CEMBRANOS et al. 2016) in a habitat that is almost free of predators (e.g., COOPER & PÉREZ-MELLADO 2004, MENCÍA et al. 2017). In fact, one of the characteristics of small isolated islets is that they have limited food resources. Consequently, foraging activity has to be extended for longer periods to satisfy the daily energetic requirements of lizards (BROWN & PÉREZ-MELLADO 1994).

Balearic lizards selected sunny microhabitats and avoided shaded places, similar to other lacertids (e.g., DÍAZ 1997, SCHEERS & VAN DAMME 2002). Shuttling between sun and shade is also a common thermoregulation mechanism (DÍAZ 1997, CASTILLA et al. 1999). We report a similar pattern of use of sun/shade patches from the Balearic lizards from both islets. This pattern could also be similar to that of other Mediterranean lacertids. For example, shuttling between sunny and shaded patches in the morning is an important mechanism in *P. liolepis* on the Columbretes Islands to avoid overheating over midday in summer (BAUWENS et al. 1996). Furthermore, Balearic lizards selected rocky microhabitats and avoided grass microhabitats, especially on Colom, where grassy areas were highly available. The selection of rocky substrates would facilitate faster heating rates (BEILLURE & CARRASCAL 2002, CARRASCAL et al. 2002). More research on the behavioural thermoregulation of Balearic lizards would help us to fully understand the mechanisms of thermoregulation on these variable little isles.

Interpreting microhabitat selection in relation to thermal requirements was confusing on Aire, because only lizards with optimal body temperatures (31.78–35.68°C) appeared to select microhabitats based on their abiotic traits. In contrast, lizards on Aire with body temperatures lower or higher than the preferred range did not choose their microhabitats based on their thermal characteristics. This result would suggest that other factors, like food availability, could influence the selection of microhabitats on Aire during spring. On Colom, *P. lilfordi* selected warmer microhabitats from those available when their body temperatures were below the optimal range. Thus, Colom lizards selected their microhabitats for warming according to their substrate temperatures, while air temperature, wind speed and humidity did not affect these choices. This is congruent with previous results from other species, since lizards prefer the substrates that facilitate faster warming rates (BEILLURE & CARRASCAL 2002). In addition, when lizards on Colom had optimal body temperatures, they also preferred the microhabitats that offered warmer substrates and higher air temperatures. Finally, lizards on Colom with body temperatures above their optimal range did not show any preferences for microhabitats according to their thermal traits.

In conclusion, wind and humidity did not affect microhabitat selection of the two Balearic lizards studied, while substrate temperature was the main factor driving the microhabitat choice of these lizards. Although a stronger wind may potentially have a cooling effect on substrates and, thus, affect thermoregulation, the wind speeds on Aire (0.61 ms⁻¹) were two times higher than on Colom (0.29 ms⁻¹) and did not affect the lizards' microhabitat selection. LOGAN et al. (2015) found that wind speed affected the activity of *Anolis lemurinus*, whereas humidity did not. We also found a detrimental effect of wind on thermoregulation effectiveness in *Iberolacerta aurelioi*, when the wind freshened up from 0.71 to 1.73 ms⁻¹ and so potentiated the cooling of substrates (ORTEGA et al. 2017). Since climate and habitat interact in shaping the thermal reaction norms of lizards (RUTSCHMANN et al. 2016), a next step could be to study the roles of the abiotic factors that affect microhabitat selection in shaping thermal reaction norms in the Balearic lizard.

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References

- ADOLPH S. C. & W. P. PORTER (1993): Temperature, activity, and lizard life histories. – *The American Naturalist*, **142**: 272–295.
- ANGILLETTA, M. J. (2009): Thermal adaptation: A theoretical and empirical synthesis. – Oxford University Press, Oxford.
- ARNOLD, E. N. (1987): Resource partition among lacertid lizards in southern Europe. – *Journal of Zoology Series B*, **1**: 739–782.
- BARTON, K. (2012): Package “MuMIn: Multi-model inference” for R, R Package Version 1.6.6. – The Comprehensive R Archive Network (CRAN), Vienna. – Available at <http://CRAN.R-project.org/package=MuMIn>, accessed 21 January, 2016.
- BAUWENS, D., P. E. HERTZ & A. M. CASTILLA (1996): Thermoregulation in a lacertid lizard: the relative contributions of distinct behavioral mechanisms. – *Ecology*, **77**: 1818–1830.
- BELLIURE, J. & L. M. CARRASCAL (2002): Influence of heat transmission mode on heating rates and on the selection of patches for heating in a Mediterranean lizard. – *Physiological and Biochemical Zoology*, **75**: 369–376.
- BLOUIN-DEMERS, G. & P. NADEAU (2005): The cost-benefit model of thermoregulation does not predict lizard thermoregulatory behaviour. – *Ecology*, **86**: 560–566.
- BROWN, R.P. & V. PÉREZ-MELLADO (1994): Ecological energetics and food acquisition in dense Menorca islet populations of the lizard *Podarcis lilfordi*. – *Functional Ecology*, **8**: 427–434.
- BURNHAM, K.-P. & D. R. ANDERSON (2002): Model selection and multimodel inference: a practical information-theoretic approach. – Springer, New York.

- CARRASCAL, L. M., P. LÓPEZ, J. MARTÍN & A. SALVADOR (1992): Basking and antipredator behaviour in a high altitude lizard: implications of heat-exchange rate. – *Ethology*, **92**: 143–154.
- CASTILLA, A. M., R. VAN DAMME & D. BAUWENS (1999): Field body temperatures, mechanisms of thermoregulation and evolution of thermal characteristics in lacertid lizards. – *Natura Croatica*, **8**: 253–274.
- CLUSELLA-TRULLAS, S. C., J. H. VAN WYK & J. R. SPOTILA (2007): Thermal melanism in ectotherms. – *Journal of Thermal Biology*, **32**: 235–245.
- COMPTON, B. W., J. M. RHYMER & M. MCCOLLOUGH (2002): Habitat selection by wood turtles (*Clemmys insculpta*): an application of paired logistic regression. – *Ecology*, **83**: 833–843.
- COOPER JR, W. E. & V. PERÉZ-MELLADO (2004): Tradeoffs between escape behavior and foraging opportunity by the Balearic lizard (*Podarcis lilfordi*). – *Herpetologica*, **60**: 321–324.
- CRAWLEY, M. J. (2012): *The R book*. – Wiley, Chichester.
- DIAZ, J. A. (1997): Ecological correlates of the thermal quality of an ectotherm's habitat: a comparison between two temperate lizard populations. – *Functional Ecology*, **11**: 79–89.
- DOWNES, S. (2001): Trading heat and food for safety: costs of predator avoidance in a lizard. – *Ecology*, **82**: 2870–2881.
- DOWNES, S. & R. SHINE (1998): Heat, safety or solitude? Using habitat selection experiments to identify a lizard's priorities. – *Animal Behaviour*, **55**: 1387–1396.
- GVOŽDÍK, L. (2002): To heat or to save time? Thermoregulation in the lizard *Zootoca vivipara* (Squamata: Lacertidae) in different thermal environments along an altitudinal gradient. – *Canadian Journal of Zoology*, **80**: 479–492.
- HEATH, J. E. (1970): Behavioral regulation of body temperature in poikilotherms. – *The Physiologist*, **13**: 399.
- HERTZ, P. E. (1992): Evaluating thermal resource partitioning by sympatric lizards *Anolis cooki* and *A. cristatellus*: a field test using null hypotheses. – *Oecologia*, **90**: 127–136.
- HERTZ, P. E., R. B. HUEY & R. D. STEVENSON (1993): Evaluating temperature regulation by field-active ectotherms: the fallacy of the inappropriate question. – *The American Naturalist*, **142**: 796–818.
- HOSMER, D. W. & S. LEMESHOW (2004): *Applied logistic regression*. – Wiley, New York.
- HUEY, R. B. (1991): Physiological consequences of habitat selection. – *The American Naturalist*, **137**: S91–S115.
- HUEY, R. B., P. E. HERTZ & B. SINERVO (2003): Behavioral drive versus behavioral inertia in evolution: a null model approach. – *The American Naturalist*, **161**: 357–366.
- HUEY, R. B. & M. SLATKIN (1976): Cost and benefits of lizard thermoregulation. – *The Quarterly Review of Biology*, **51**: 363–384.
- JANSÀ I CLAR, A. (1979): Climatología de Menorca, – pp. 89–160 in: JANSÀ I CLAR, A., X. JANSÀ I CLAR, C. LLOMPART I DÍAZ, B. MERCADAL I PONS, A. OBRADOR I TUDURÍ, J. ROSELL I SANUY, J. TRILLA I ARRUFAT & T. VIDAL I MIQUEL (eds): *Enciclopedia de Menorca I. Geografía física*. – Obra cultural de Menorca, Maó.
- KEATING, K. A. & S. CHERRY (2004): Use and interpretation of logistic regression in habitat-selection studies. – *Journal of Wildlife Management*, **68**: 774–789.
- LOGAN, M. L., S. G. FERNÁNDEZ & R. CALSBEEK (2015): Abiotic constraints on the activity of tropical lizards. – *Functional Ecology*, **29**: 694–700.
- MAIA-CARNEIRO, T., T. A. DORIGO & C. F. D. ROCHA (2012): Influences of seasonality, thermal environment and wind intensity on the thermal ecology of Brazilian sand lizards in a restinga remnant. – *South American Journal of Herpetology*, **7**: 241–251.
- MANLY, B. F. J., L. L. McDONALD, D. L. THOMAS, T. L. McDONALD & W. P. ERICKSON (2002): *Resource selection by animals: statistical analysis and design for field studies*. – Kluwer, Nordrecht.
- MARTÍN, J. & A. SALVADOR (1997): Microhabitat selection by the Iberian rock lizard *Lacerta monticola*: Effects on density and spatial distribution of individuals. – *Biological Conservation*, **79**: 303–307.
- MENCÍA, A., Z. ORTEGA & V. PÉREZ-MELLADO (2017): From tameness to wariness: chemical recognition of snake predators by lizards in a Mediterranean island. – *PeerJ*, **5**: e2828.
- ORTEGA, Z., V. PÉREZ-MELLADO, M. GARRIDO, C. GUERRA, A. VILLA-GARCÍA & T. ALONSO-FERNÁNDEZ (2014): Seasonal changes in thermal biology of *Podarcis lilfordi* (Squamata, Lacertidae) consistently depend on habitat traits. – *Journal of Thermal Biology*, **39**: 32–39.
- ORTEGA, Z., A. MENCÍA & V. PÉREZ-MELLADO (2016): Wind constraints on the thermoregulation of high mountain lizards. – *International Journal of Biometeorology*, doi:10.1007/s00484-016-1233-9.
- PÉREZ-CEMBRANOS, A. & V. PÉREZ-MELLADO (2015): The effect of plant consumption in the overall diet of an omnivorous lizard. – *Salamandra*, **51**: 63–72.
- PÉREZ-CEMBRANOS, A., A. LEÓN & V. PÉREZ-MELLADO (2016): Omnivory of an insular lizard: sources of variation in the diet of *Podarcis lilfordi* (Squamata, Lacertidae). – *PloS one*, **11**: e0148947.
- PÉREZ-MELLADO, V. (1989): Estudio ecológico de la lagartija balear *Podarcis lilfordi* (Günther, 1874) en Menorca. – *Revista de Menorca*, **80**: 455–511.
- PÉREZ-MELLADO, V. & C. CORTI (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. & A. SALVADOR (1988): The Balearic lizard *Podarcis lilfordi* (Günther, 1874) (Sauria, lacertidae) of Menorca. – *Arquivos do Museu Bocage, N.S.*, **1**: 127–195.
- PÉREZ-MELLADO, V., T. ALONSO-FERNÁNDEZ, M. GARRIDO, C. GUERRA, Z. ORTEGA & A. VILLA-GARCÍA (2013): Biología térmica de la lagartija balear, *Podarcis lilfordi* (Günther, 1874) en dos poblaciones de Menorca. – *Revista de Menorca*, **92**: 219–244.
- PÖRTNER, H. O. (2002): Climate variations and the physiological basis of temperature dependent biogeography: systemic to molecular hierarchy of thermal tolerance in animals. – *Comparative Biochemistry and Physiology – Part A*, **132**: 739–761.
- R Core Team (2015): *R: A language and environment for statistical computing*. – R Foundation for Statistical Computing, Vienna. – Available at <http://www.R-project.org/>, accessed 9 February 2016.
- ROW, J. R. & G. BLOUIN-DEMERS (2006): Thermal quality influences habitat selection at multiple spatial scales in milksnakes. – *EcoScience*, **13**: 443–450.
- RUTSCHMANN, A., D. B. MILES, L. GALLIARD, M. RICHARD, S. MOULHERAT, B. SINERVO & J. CLOBERT (2016): Climate and habitat interact to shape the thermal reaction norms of breeding phenology across lizard populations. – *Journal of Animal Ecology*, in press.
- SCHEERS, H. & R. VAN DAMME (2002): Micro-scale differences in thermal habitat quality and a possible case of flexibility in the thermal physiology of lacertid lizards. – *Oecologia*, **132**: 323–331.
- SOKAL, R. R. & F. J. ROHLF (1995): *Biometry: the principles and practice of statistics in biological research*. – State University of New York at Stony Brook, New York.