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## Journal of Thermal Biology

journal homepage: [www.elsevier.com/locate/jtherbio](http://www.elsevier.com/locate/jtherbio)

## Seasonal changes in thermal biology of *Podarcis lilfordi* (Squamata, Lacertidae) consistently depend on habitat traits

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## ARTICLE INFO

## Article history:

Received 17 February 2013

Accepted 7 November 2013

Available online 15 November 2013

## Keywords:

Behavioral thermoregulation

Thermal effectiveness

Daily activity

Islands

*Podarcis lilfordi*

Seasonal variation

## ABSTRACT

During spring and summer, we studied the thermal ecology of two populations of the Balearic lizard, *Podarcis lilfordi*, from two coastal islets of Menorca (Balearic Islands, Spain): Aire and Colom. We calculated the accuracy of thermoregulation, that is, the extent to which body temperatures are close to species' thermal optima, the thermal quality of the habitat as the proximity of operative temperatures to thermal optima and effectiveness of thermoregulation, as the extent to which accuracy is higher than thermal quality of the habitat. We found that seasonality affects thermoregulation differently, depending on the lizard population. Those effects are consistent for all thermal parameters under study. The effects of seasonality were significantly stronger in Aire than in Colom islet. Many factors may be responsible for this different effect of seasonality, from differences on physiological traits to differences in the environmental conditions of the two islets, as their resource availability, predator pressure or habitat structure. Identifying the factors that boost or inhibit those seasonal changes would be important to understand thermoregulation in lizards. Slight changes on two similar populations can lead to great differences in thermal ecology of conspecific ectotherms.

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## 1. Introduction

Accuracy in the maintenance of a nearly constant body temperature is a central point in the biology of squamate vertebrates. The ability of ectotherms to exploit resources is closely related to an effective control of their body temperature (Adolph and Porter, 1993; Cowles and Bogert, 1974; Huey, 1974). Lizards use three main mechanisms to regulate their body temperature adjusting activity periods (Adolph and Porter, 1993; Hertz, 1992), shuttling between different microhabitats (Bauwens et al., 1996; Heath, 1970) or adjusting their body posture (Bauwens et al., 1996). The combination of these strategies depends on the balance between their costs and benefits (Huey and Slatkin, 1976). In addition, feeding, reproduction or risk of predation can also affect the thermoregulatory balance (Herczeg et al., 2008).

From an evolutionary viewpoint, two different types of thermoregulatory adjustments are considered (1) fast adjustments to daily and seasonal changes of thermal environment, and (2) fixed thermal adjustments (Angilletta, 2009; Castilla et al., 1999). Fast adjustments include behavioral and physiological adjustments as a result of short-term changes in environmental temperatures. Fixed adjustments would cover changes in thermal sensitivity of

biological functions, changes in optimal temperatures selected in a thermal gradient ( $T_{set}$ , see Pough and Gans, 1982) and long term modifications of fast adjustments, physiological or behavioral, between populations or species, as a response to local selective pressures (Angilletta, 2009). This evolutionary perspective will give us a starting point to study the effects of environmental factors and biological constraints on thermal strategies of the same species in different habitats (Angilletta, 2009).

Lacertids are heliothermic lizards that maintain their body temperatures ( $T_b$ ) near their physiological optima (Avery, 1976; Van Damme et al., 1990). Since the set-point range of  $T_{set}$  (Hertz et al., 1993) is considered a conservative phenotypic trait (Huey et al., 2003), we could expect small variations within lacertid lizards, due to their common phylogenetic history (Kapli et al., 2011; Mayer and Pavlicev, 2007). Nonetheless, substantial differences have been detected between species of Lacertidae (Pérez-Mellado, 1983; Scheers and Van Damme, 2002), between different populations of the same species (Gvozdić, 2002; Van Damme et al., 1986) and, within the same population, among seasons (Díaz et al., 2006), or even among certain groups of individuals (Martín and Salvador, 1993).

The aim of this work is to study the effect of seasonality in the thermal biology of two populations of an insular lizard that inhabits two close coastal islets. That is, we want to check how lizards cope with environmental changes between seasons and in two different populations that show subtle differences in habitat structure and environmental conditions. We measured, during

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spring and summer, three parameters: body temperatures of active lizards ( $T_b$ ), operative temperatures of random microhabitat offer ( $T_e$ ) and air temperatures at the capture point ( $T_a$ ). We evaluated the thermal quality of the habitats from both populations, based on operative temperatures. Finally, we compared accuracy and effectiveness of thermoregulation in both populations (see Hertz et al., 1993). We expected that lizards inhabiting the most suitable thermal habitat would exhibit higher values of accuracy and effectiveness during both seasons.

## 2. Materials and methods

### 2.1. Studied species and habitat

*Podarcis lilfordi* (Günther, 1874) is a medium-sized lizard of Lacertidae (Squamata), endemic to the Balearic Islands (Spain). There are currently 23 subspecies of *P. lilfordi* living in Cabrera Archipelago and coastal islets of Mallorca and Menorca. Several coastal islets of the Balearic Islands share some features as their scarce food availability, low predation pressure and unpredictable weather conditions. As a result, lizards tend to share some features, as high population densities (Pérez-Mellado, 1989; Pérez-Mellado et al., 2008), low clutch sizes and extended reproductive periods (Perera and Pérez-Mellado, 2002). On these islets it is also common an extremely opportunistic omnivorism, and some unique interactions with plants (Brown et al., 1992; Pérez-Mellado et al., 2000; Pérez-Mellado and Corti, 1993). We studied two subspecies of *P. lilfordi* that occupy two coastal islets of Menorca Island: *P. lilfordi lilfordi* from the Aire islet and *P. lilfordi brauni* from the Colom islet.

#### 2.1.1. *Podarcis lilfordi lilfordi* and Aire islet

Aire islet in one nautical mile apart from SE coast of Menorca, it has a surface of 35 Ha, mostly occupied by shrub halophyte vegetation. Mean annual temperature is 16.7 °C and mean annual precipitation 625 mm. Food resources for lizards are limited, and predation pressure very sporadic. The few potential predators are some birds: kestrels, *Falco tinnunculus*, and other bird species that visit Aire sporadically during spring and autumn migrations. *P. lilfordi lilfordi* is a melanistic lizard, with males (average SVL=68.98 mm and average weight=9.75 g) larger than females (average SVL=61.73 and average weight=6.34 g).

#### 2.1.2. *Podarcis lilfordi brauni* and Colom islet

Colom islet is 200 m from NE coast of Menorca, with a surface of 59 Ha. Mean annual temperature and precipitation are similar to Aire islet. Vegetation is more diverse in Colom, with abundant and bigger shrubs and some arboreal patches. Food resources for lizards are higher in Colom than in Aire (unpub. data), due to its higher diversity of plants species. Predation pressure is slightly higher in Colom, with terrestrial predators as the Ladder Snake (*Rhinechis scalaris*) and some kestrels breeding in the island. *P. lilfordi brauni* has a non-melanistic coloration, with brownish and greenish back, and a significantly smaller body size than *P. lilfordi lilfordi* (Pérez-Mellado and Salvador, 1988).

## 2.2. Temperature sampling

### 2.2.1. Body temperatures

Both populations were simultaneously studied between March and July 2006, alternating the days of visits to each islet. Active adult lizards were captured covering their daily activity period, from 0800 to 1700 GMT, with an equal sampling effort for each hourly interval. We measured cloacal body temperatures ( $T_b$ ) with a Testo® digital thermometer (accuracy 0.1 °C). Immediately after

capture, we measured air temperature ( $T_a$ ) 1 cm above the capture point, and substrate temperature ( $T_s$ ) at the capture point. SVL, weight and sex were obtained from each individual, as well as its location in relation with sun (in open sun, in the shade or in an area of filtered sun) and behavior (active, basking or still).

### 2.2.2. Operative temperatures

Operative temperatures ( $T_e$ ) are the temperatures that lizards would exhibit if they do not thermoregulate (Bakken et al., 1981; Hertz et al., 1993), so they can be used as a null hypothesis for thermoregulation. We employed 15 hollow copper models (Bakken and Angilletta, 2013) with the shape and size of an adult *P. lilfordi* as null  $T_e$  models. Models were black painted, but it is well known that color has a negligible influence in the thermal balance of the model with the environment (Shine and Kearney, 2001). Even if shape and color do not have an important impact in the values of  $T_e$ , it is recommended to simulate the aspect of the lizard as realistic as possible, in order to avoid even small deviations of  $T_e$  (Bakken and Angilletta, 2013). The same models employed in this study were previously tested with another lizard species (Vitt et al., 2005). One thermocouple probe was placed into each hollow model and independently connected to a data logger HOBO H8® (Onset Computer Corporation) programmed to take a temperature record every 5 min.

Each model was randomly placed in a given microhabitat during 48 h, and then moved to a different location. We used 15 data loggers during 50 working days in both islets, 31 days during spring and 6 days during summer in Aire and 8 days during spring and 7 days during summer in Colom, obtaining 44,981 measures of  $T_e$ . Sampling of operative temperatures was large enough to guarantee reliable measurements of all available microhabitats (Bakken and Angilletta, 2013). In order to record thermal parameters under similar conditions, sampling was simultaneous for  $T_e$  and  $T_b$  (Hertz et al., 1993). We defined a microhabitat as a combination of a given substrate and an insolation condition (see above). Regarding substrates, we considered substrates that are common in both islets and some specific substrates that only occur on Aire or in Colom. General substrates are rock, soil, grass, *Suaeda vera* shrubs, *Crithmum maritimum* shrubs, and *Pistacia lentiscus* shrubs.

### 2.2.3. Set-point temperatures

Set-point temperatures ( $T_{set}$ ) of *P. lilfordi* were measured in a laboratory thermal gradient in 1989. Lizards were captured from Aire and Colom islets in spring of 1989 and transported to the University of Salamanca. The thermal gradient was built in a glass terrarium (1 m long) with a 150 W lamp above, obtaining a gradient between 20 °C and 60 °C. Ad libitum water was provided to lizards during all the experiment (Licht et al., 1966). A sample of a selected temperature for a lizard was measured with a digital thermometer each hour. Eleven adult lizards from Colom and ten from Aire were employed, obtaining, respectively, 121 and 99 selected temperatures. The 50% of central values of all body temperatures were considered as the set-point range of the species (Hertz et al., 1993). The same set-point range was employed in a previous study that included *P. lilfordi* (Bauwens et al., 1995). Furthermore, thermal gradient experiments were replicated in 2007 for both populations of *P. lilfordi*, finding similar results (unpublished data).

## 2.3. Data analysis

We considered spring data those from March, April and May, and only July data for summer analyses. Activity of lizards was assessed for each season and population, exploring daily evolution of  $T_b$  and relations between  $T_b$  and  $T_a$  on each situation. To test the null hypothesis of thermoregulation, we calculated accuracy of thermoregulation ( $d_b$ ), thermal quality of habitats ( $d_e$ ) and effectiveness of

thermoregulation ( $E$ ) for each population and season, following the protocol developed by Hertz et al. (1993). Effectiveness of thermoregulation was obtained with THERMO, a Minitab module written by Richard Brown. THERMO uses three kind of input data:  $T_b$ ,  $T_e$  and  $T_{set}$ , performing bootstraps of 500 iterations and then building pseudo-distributions of three kinds of output values: the arithmetic mean of  $d_b$ , the arithmetic mean of  $d_e$  and the arithmetic mean of  $E$ . Arithmetic means of temperatures are reported with standard errors (SE). Parametric statistics were performed when data follow the assumptions of normality and variance homogeneity. If these

assumptions were not fulfilled, even after log-transformations, non-parametric equivalent tests were carried out.

### 3. Results

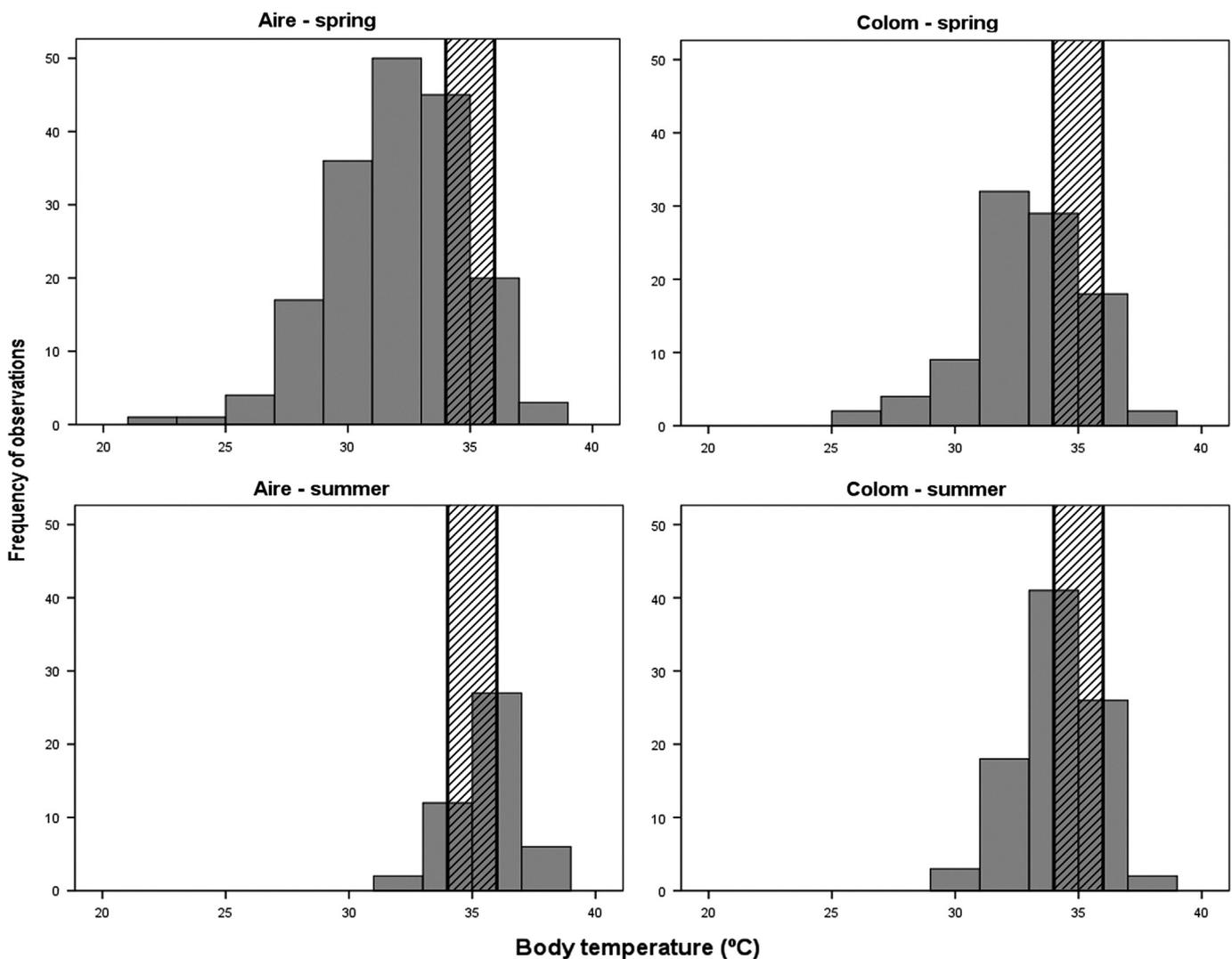
#### 3.1. Body temperatures

Regarding body temperatures, mean  $T_b$  of different age and sex categories were statistically similar ( $p > 0.05$  in one-way ANOVAs for all group comparisons; see Table 1 for average values of  $T_b$ ).

**Table 1**

Body temperatures of age and sex categories of *P. lilfordi* lizards. Mean body temperatures ( $T_b$ ) of active juveniles and adult males and females of *P. lilfordi* lizards sampled in spring and summer at Aire and Colom islets of Menorca, Spain.  $T_b$  values are provided in °C, with sample errors and sample sizes.

Islet	Season	$T_b$ of juveniles	$T_b$ of adult males	$T_b$ of adult females
Aire	Spring	32.35 ± 0.96 (N=8)	33.17 ± 0.22 (N=138)	32.99 ± 0.48 (N=47)
	Summer	35.38 ± 0.66 (N=6)	36.20 ± 0.22 (N=40)	35.85 ± 0.33 (N=13)
Colom	Spring	35.36 ± 0.48 (N=13)	34.46 ± 0.26 (N=66)	33.93 ± 0.48 (N=37)
	Summer	35.30 ± 0.27 (N=21)	35.37 ± 0.18 (N=72)	35.02 ± 0.22 (N=41)

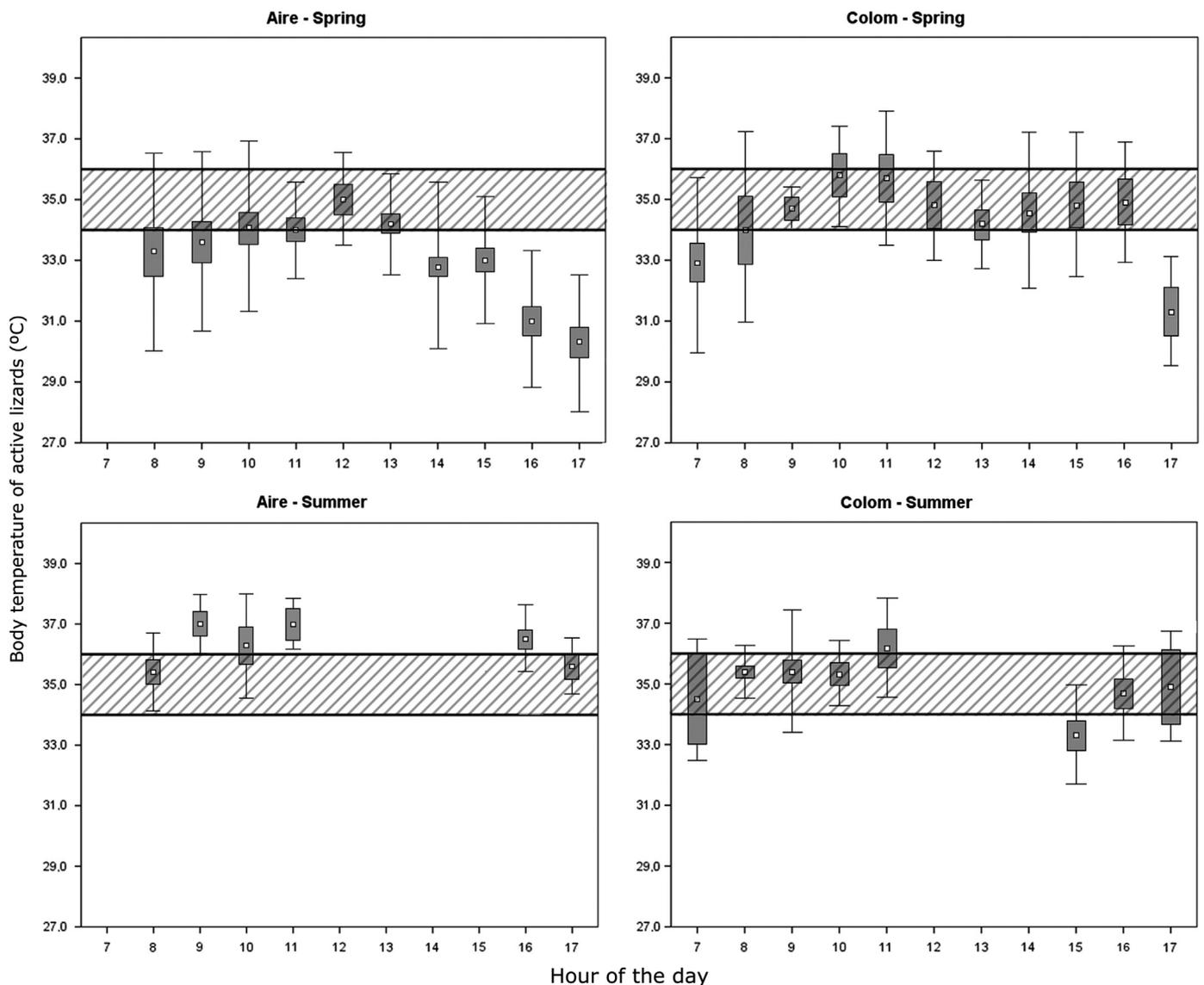


**Fig. 1.** Frequency distributions of body temperature of active *P. lilfordi* lizards. Frequency distribution of body temperature ( $T_b$ ) of active lizards for both islets and seasons included in the study. Note that distributions are narrower during summer for both populations, and that the population from Aire islet experiences a more abrupt seasonal change for this variable.

Hence, we merged  $T_b$  of different sex and age classes for further analysis of both islets and seasons. In addition, we compared thermoregulation at spring and summer employing  $T_b$  data of active individuals. Variances were heterogeneous in Aire, for both rough (Levene test,  $F_{1,236}=23.34$ ,  $p < 0.001$ ) and log-transformed data ( $F_{1,236}=26.46$ ,  $p < 0.001$ ). Thus, we used the non-parametric Mann–Whitney  $U$ -test. We detected significant differences between  $T_b$  of active individuals during spring and summer. That is, active lizards showed higher  $T_b$  during summer in Aire (average  $T_b$  of spring= $33.12 \pm 0.19$  °C,  $n=185$ , average  $T_b$  of summer= $36.12 \pm 0.18$  °C,  $n=53$ ; Mann–Whitney  $U$ -test:  $U=1496$ ,  $Z=-7.71$ ,  $p < 0.001$ ). We found the same situation in Colom, with heterogeneous variances both in rough (Levene test,  $F_{1,216}=16.47$ ,  $p < 0.001$ ) and log-transformed data ( $F_{1,216}=17.44$ ,  $p < 0.001$ ).  $T_b$  of active lizards were also significantly higher during summer than during spring in Colom (average  $T_b$  during spring= $34.31 \pm 0.23$  °C,  $n=108$ ;  $T_b$  during summer= $35.24 \pm 0.14$  °C,  $n=113$ ; Mann–Whitney  $U$ -test,  $U=4582.5$ ,  $Z=-3.20$ ,  $p=0.001$ , Fig. 1)

Daily patterns of  $T_b$  of lizards from Aire and Colom were assessed for both seasons. During spring, lizards from Aire only

matched the set-point range of  $T_{set}$  from 1100 GMT to 1300 GMT, while they maintained suboptimal  $T_b$  during the rest of the day. Hourly  $T_b$  were significantly different (one-way ANOVA,  $F_{9,167}=5.17$ ,  $p < 0.001$ ), particularly due to significantly lower  $T_b$  from 1600 GMT to 1800 GMT, comparing with  $T_b$  from 1000 GMT to 1400 GMT and to significantly different  $T_b$  for 0900–1000 GMT and 1700–1800 GMT hourly segments (Tukey test for unequal sample sizes,  $p < 0.05$  for all *post hoc* comparisons, Fig. 2). The situation is different in Colom during spring, with  $T_b$  of lizards matching set-point range from 0800 GMT to 1700 GMT. Significant differences between hourly  $T_b$  (one-way ANOVA,  $F_{10,85}=2.60$ ,  $p=0.008$ ) were due to different  $T_b$  in 1000–1200 GMT and 1700–1800 GMT hourly segments (Tukey test,  $p < 0.05$ ). In Aire and during summer, lizards showed  $T_b$  within the set-point range, almost during the whole daily activity period, even with higher values than  $T_{set}$  during the central hourly segments, but without significant differences between average  $T_b$  of hourly periods (one-way ANOVA,  $F_{8,38}=1.74$ ,  $p=0.12$ , Fig. 2). Finally, hourly  $T_b$  showed a similar pattern in Colom during summer (one-way ANOVA,  $F_{7,80}=0.87$ ,  $p=0.53$ ), mainly within the set-point range of  $T_{set}$ . It is important to notice



**Fig. 2.** Daily evolution of body temperature of *P. lilfordi* lizards. Evolution of body temperature ( $T_b$ ) of active *P. lilfordi* lizards along the day, for each islet and season. The center of the diagram (the white square) is the median value of  $T_b$ , the box comprises from first to third quartiles and the whiskers cover the range spread. Set-point temperatures ( $T_{set}$ ) are marked in all graphics with a striped band. Notice that lizards are inactive during central hours of the day in summer.

the lack of observations of lizards during summer in both islets during the period from 1200 GMT to 1600 GMT in the case of Aire and from 1200 to 1500 GMT in Colom (see Fig. 2).

### 3.2. Air temperatures

As expected, there were significant differences between air temperatures ( $T_a$ ), recorded at the same time as  $T_b$ , both in Aire (average  $T_a$  in spring =  $21.34 \pm 0.19$  °C,  $n = 184$ ; average  $T_a$  in summer =  $31.99 \pm 0.38$  °C,  $n = 53$ ; one-way ANOVA,  $F_{1,235} = 657.9$ ,  $p < 0.001$ ) and Colom (average  $T_a$  in spring =  $27.14 \pm 0.36$  °C,  $n = 108$ ; average  $T_a$  in summer =  $32.38 \pm 0.68$  °C,  $n = 113$ ; one-way ANOVA,  $F_{1,219} = 45.53$ ,  $p < 0.001$ ). A similar pattern was observed in substrate temperatures of Aire in both seasons (average  $T_s$  of spring =  $23.85 \pm 0.26$  °C,  $n = 184$ ; average  $T_s$  of summer =  $34.71 \pm 0.50$  °C,  $n = 53$ ; one-way ANOVA,  $F_{1,235} = 389.38$ ,  $p < 0.001$ ), as well as in Colom (average  $T_s$  of spring =  $30.06 \pm 0.40$  °C,  $n = 108$ , average  $T_s$  of summer =  $33.49 \pm 0.36$  °C,  $n = 113$ ; one-way ANOVA,  $F_{1,219} = 40.87$ ,  $p < 0.001$ ).

### 3.3. Relation between $T_b$ and $T_a$ among islets and seasons

An ANCOVA analysis in Aire, taking  $T_a$  as the covariate and season as the factor, shows that there are significant differences between adjusted means of  $T_b$  for spring and summer ( $F_{1,233} = 7.38$ ,  $p = 0.007$ ). Besides,  $T_a$  affected  $T_b$  differently during summer than during spring ( $F_{1,233} = 19.46$ ,  $p < 0.001$ ), being  $T_b$  more independent of  $T_a$  values during summer. The situation in Colom was different: the effect of  $T_a$  on  $T_b$  is also significantly different in spring and summer (one-way ANCOVA,  $F_{2,217} = 18.16$ ,  $p < 0.001$ ), but we do not detected differences among adjusted means of both seasons ( $p > 0.05$  for the ANCOVA analysis, Fig. 3). Thus, we can conclude that although in Colom and Aire lizards showed higher  $T_b$  during summer, differences were minimized in Colom, if we consider higher  $T_a$ . In other words, although  $T_a$  values were higher

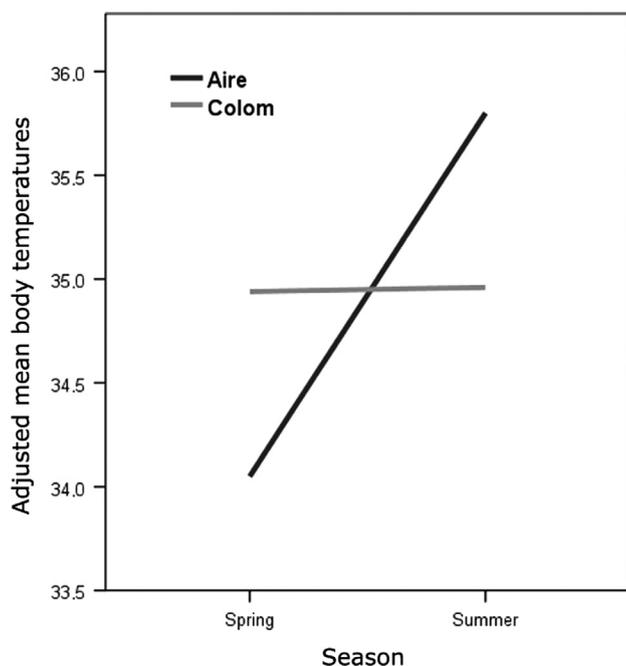


Fig. 3. Seasonal differences in the effect of air temperature in body temperature of *P. lilfordi* lizards. For body temperature ( $T_b$ ) data of lizards of both islets, a one-way ANCOVA analysis was performed, considering season as factor and adjusting  $T_b$  means regarding air temperature ( $T_a$ ). Significant results show that  $T_a$  affects  $T_b$  of lizards differently during summer than during spring. Furthermore, the effect of air temperature ( $T_a$ ) on body temperature ( $T_b$ ) decreases more drastically from spring to summer in Aire than in Colom.

in summer than in spring in Colom, it did not result in significant differences of  $T_b$  between seasons.

Finally, we performed a two-way ANOVA, with islet and period as factors. We found a significant interaction between islet and season ( $F = 19.75$ ,  $p < 0.001$ ). Consequently, the main effects of islet and season depend on each other, and should not be interpreted in isolation. Specifically, variation in  $T_b$  between seasons is much larger for Aire than for Colom.

### 3.4. Operative temperatures

In Aire islet and during spring, operative temperatures ( $T_e$ ) of different substrates fell below set-point range (average =  $25.52 \pm 0.05$  °C, range: 6.62–52.95,  $n = 21,383$ ). However, highest values of  $T_e$  clearly ranged within the thermal optimum during almost all the day, with the exception of the last daily period, 1700–1800 GMT (see Fig. 4). There were significant differences between  $T_e$  of different hourly periods (Kruskal–Wallis test,  $H = 7006.06$ ,  $p < 0.001$ ). Also we found significant differences among  $T_e$  of different substrates (Kruskal–Wallis test,  $H = 1888.99$ ,  $p < 0.001$ ). Thus, habitat structure showed a high thermal heterogeneity. During spring, open sun substrates (herbaceous substrate, rock and open ground) were the most suitable microhabitats for lizard thermoregulation, with  $T_e$  higher and closer to the set-point range. During summer,  $T_e$  were significantly higher than those of spring (Mann–Whitney  $U$ -test,  $Z = -107.37$ ,  $p < 0.001$ , see Fig. 4). Moreover,  $T_e$  of open sun substrates were only suitable during early morning, reaching  $T_e$  far above  $T_{set}$  during the rest of the day (Fig. 4). In Colom and during spring,  $T_e$  showed values closer to  $T_{set}$  almost during the whole daily period of activity. We also found significant differences between  $T_e$  of different hourly periods (Kruskal–Wallis test,  $H = 2884.78$ ,  $p < 0.001$ , Fig. 4), and between different thermoregulation substrates (Kruskal–Wallis test,  $H = 2418.53$ ,  $p < 0.001$ ). Open sun substrates were the closest to  $T_{set}$  in spring, followed by sun-filtered-by-vegetation substrates, which also fell within  $T_{set}$  during the central hours of the day. There were also significant differences between  $T_e$  of hourly periods of Colom during summer (Kruskal–Wallis test,  $H = 1702.13$ ,  $p < 0.001$ , Fig. 4), as well as between substrates (Kruskal–Wallis test,  $H = 792.17$ ,  $p < 0.001$ ).

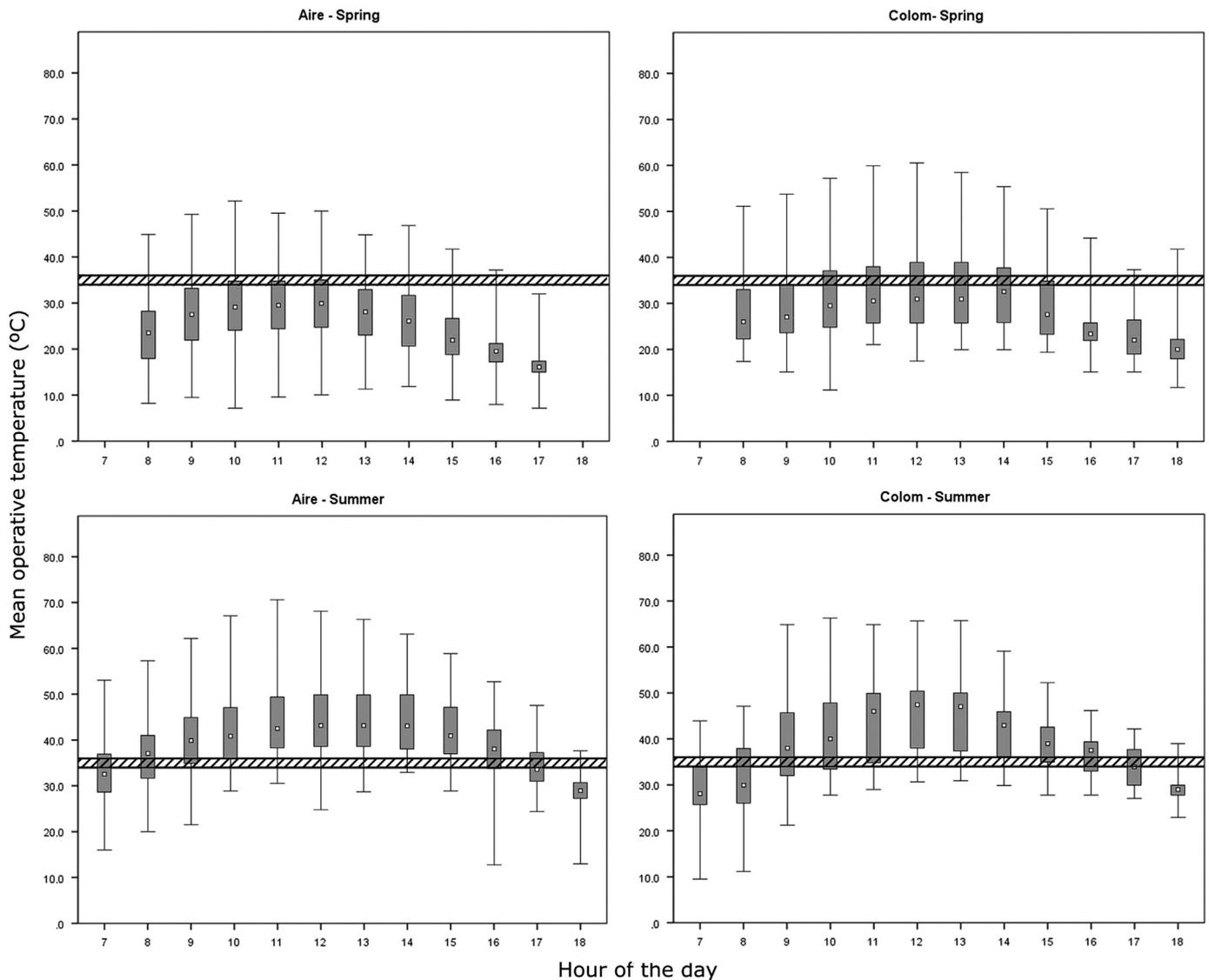
### 3.5. Thermoregulation assessment

#### 3.5.1. Accuracy of thermoregulation

Data of accuracy of thermoregulation (Table 2) were analyzed with a bifactorial ANOVA, with islet and season as factors and  $d_b$  as the response variable. We found a significant interaction between islet and season ( $F_{1,1996} = 9837.2$ ,  $p < 0.001$ ). Consequently, main effects should not be interpreted separately and the interaction can be interpreted. In our case, the highest thermoregulatory accuracy was obtained for lizards in Aire and during summer. While lizards from Colom showed a higher thermoregulatory accuracy than lizards from Aire during spring.

#### 3.5.2. Thermal quality of habitats

Analysis of thermal quality of the habitat was first performed separately for both seasons. In Aire, thermal quality was significantly lower during summer than during spring (Mann–Whitney  $U$ -test,  $Z = 31.61$ ,  $p < 0.001$ ). The opposite situation was true in Colom, with a better thermal quality, during summer than during spring (Mann–Whitney  $U$ -test,  $Z = 27.37$ ,  $p < 0.001$ ). Consequently, in a separated comparison of islets for each season, thermal quality was significantly lower in Colom than in Aire during spring (Mann–Whitney  $U$ -test,  $Z = 31.61$ ,  $p < 0.001$ ). The opposite happened during summer, with a lower thermal quality in Aire (Mann–Whitney  $U$ -test,  $Z = -22.41$ ,  $p < 0.001$ ).



**Fig. 4.** Daily evolution of operative temperatures. Mean operative temperatures ( $T_e$ ) of all available substrates at each hourly period are provided for Aire and Colom islets during each season. These values give us an idea of the thermal environment available for lizard thermoregulation. Set-point temperatures ( $T_{set}$ ) are marked in all graphics with a striped band, so one can visualize the general thermal quality of the habitat of each situation. Notice that Aire microhabitats are clearly suboptimal during spring and both Aire and Colom islets are too warm during central periods of the day in summer.

### 3.5.3. Effectiveness of thermoregulation

Effectiveness of thermoregulation ( $E$ ) was substantially high for both populations of *P. lilfordi* during both seasons, with average value of  $0.88 \pm 0.001$  (Table 2). A bifactorial ANOVA of thermoregulation effectiveness, with islet and season as factors, revealed a significant interaction between islet and season ( $F_{1, 1996} = 4099.0$ ,  $p < 0.001$ , Fig. 5).

## 4. Discussion

The Balearic lizard has an excellent capacity of thermoregulation under different, even suboptimal, conditions. Effectiveness of thermoregulation of the species ranges from 0.81 to 0.93, with a mean 0.88. Other species of the genus, as *Podarcis atrata* (Bauwens et al., 1996), *Podarcis tiliguerta* and *Podarcis sicula* (Van Damme et al., 1990) showed also a great ability for thermoregulation. During spring, lizards from Aire islet were even able to accurately thermoregulate in a suboptimal thermal environment.

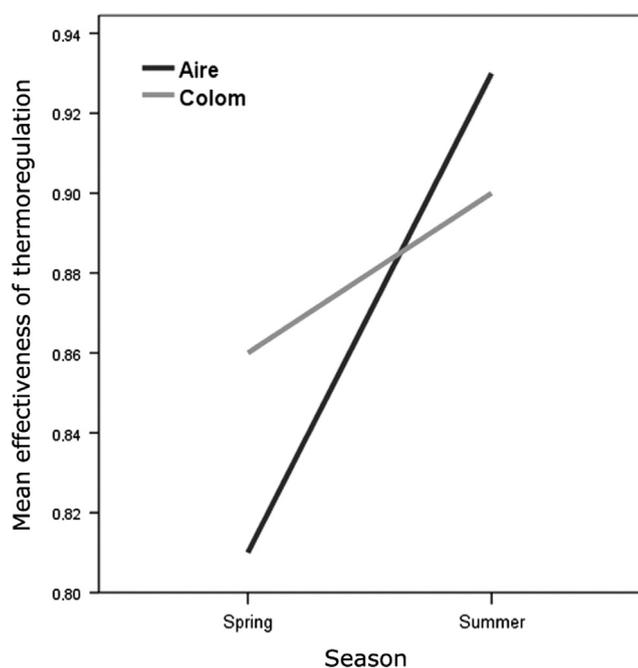
The ability of the Balearic lizard to maintain body temperatures close to the thermal optima would be essential to perform an intense foraging activity in habitats with poor food resources. Lizards remain active during long daily periods in both islets and seasons, and retreat to burrows only under extreme hot conditions during summer at midday (unpublished data). Such intense activity allows a continuous search for food (Pérez-Mellado, 1989; Pérez-Mellado and Corti, 1993). Furthermore, this kind of thermoregulation and feeding strategy, demanding an intense daily activity, can only be possible with a low predation pressure, as it is characteristic of several insular environments (Vitt et al., 2005).

Aire and Colom are only a few kilometers apart and both populations, even if described as different subspecies, shared most of their evolutionary history (Terrasa et al., 2008). The season has a greater effect in thermal biology of the population of Aire than those of Colom. One explanation is that the higher heterogeneity of habitats in Colom islet would allow lizards to buffer the effects of air temperatures. Thus, lizards from Colom can perch in wind-protected microhabitats during spring, while lizards from Aire

**Table 2**

Accuracy and effectiveness of thermoregulation of *P. lilfordi* lizards. Mean values and standard errors of accuracy ( $d_b$ ) and effectiveness of thermoregulation ( $E$ ) of *P. lilfordi* are provided for both studied seasons and islets.

Islet	Season	$d_b$	$E$
Aire	Spring	1.89 ± 0.007	0.81 ± 0.0007
	Summer	0.39 ± 0.004	0.93 ± 0.0006
	Total	1.14 ± 0.020	0.87 ± 0.0020
Colom	Spring	1.08 ± 0.006	0.86 ± 0.0007
	Summer	0.61 ± 0.003	0.90 ± 0.0005
	Total	0.84 ± 0.008	0.88 ± 0.0007
Total	Spring	1.48 ± 0.010	0.84 ± 0.0010
	Summer	0.49 ± 0.004	0.92 ± 0.0006
	Total	0.99 ± 0.010	0.88 ± 0.0010



**Fig. 5.** Interaction between the effect of seasonality and habitat on the effectiveness of thermoregulation of *P. lilfordi* lizards. As for accuracy, interaction between season and islet is significant for the effectiveness of thermoregulation ( $E$ ) of *P. lilfordi* lizards. Effectiveness of thermoregulation increases from spring to summer in the studied populations, being this growth higher for lizards of Aire than for those of Colom islet.

would be more exposed to the cooling effect of wind. Conversely, opportunities for wind cooling during summer would be more advantageous for lizard thermoregulation in Aire than in Colom. This hypothesis can be tested in the future measuring wind speeds and other environmental conditions on capture sites of lizards and on randomly placed null models (work in progress). Another hypothesis would be that physiological differences on thermal characteristics of the two populations are due to color differences, since lizards from Aire are melanistic and those from Colom are non-melanistic. But, apparently, our results are against this hypothesis, because selected temperatures showed no differences between populations and detected differences in thermoregulation accuracy and effectiveness were always accompanied with differences in the thermal quality of the habitat. Hence, we do not have supporting evidences that melanism would offer physiological advantages to individuals of *P. lilfordi*. Nevertheless, we need to extend the present study to other melanistic and non-melanistic population of the species, in order to

disentangle the potential role of melanism in this species. In addition, we would need information about heating and cooling rates as well as other physiological parameters, to eventually discard a role of melanism in thermal biology of the Balearic lizard, as it was shown in other lizard species (Clusella-Trullas et al., 2008; Crisp et al., 1979; Tosini et al., 1992). In conclusion, the thermoregulation of the Balearic lizard depends on several ecological and environmental factors and can subtly vary among close populations of the same species. Seasonality greatly affects thermal biology of ectotherms, but its effects can be quite different according to habitat characteristics.

## Acknowledgments

Financial support was provided to Zaida Ortega by predoctoral grant of the University of Salamanca (FPI program). This work was supported at their final steps by the research projects CGL2009-12926-C02-02 and CGL2012-39850-CO2-02 from the Spanish Ministry of Science and Innovation.

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