



Sexual differences in behavioral thermoregulation of the lizard *Scelarcis perspicillata*



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ABSTRACT

Temperature determines all aspects of the biology of ectotherms. Although sexual differences in thermal ecology are not the rule in lizards, some species exhibit such differences. We studied the effect of sex and reproductive condition on the thermoregulation of an introduced population of *Scelarcis perspicillata* during the summer in Menorca (Balearic Islands, Spain). These lizards live in the wall surfaces of a limestone quarry, where the sun is scarce because of the narrowness of the quarry walls. The population is sexually dimorphic, with larger males than females. We measured body temperature (T_b) of adult males and females in the field, and air (T_a) and substrate temperature (T_s) at the capture sites, and recorded exposure to sunlight, height of the perch, and type of substrate. We also recorded operative temperatures (T_e) as a null hypothesis of thermoregulation. Finally, we studied the thermal preferences of adult males and females in a laboratory thermal gradient. Thermal preferences were similar for pregnant and non-pregnant females, and sex did not affect the thermal preferences of lizards, even after controlling for the effect of body size. However, in the field, females achieved higher T_b than males, and occupied microhabitats with higher T_a and T_s and lower perch heights than males. Furthermore, females selected perches in full sun at a higher frequency than males. As a consequence, females achieved a higher accuracy and effectiveness of thermoregulation (0.89) than males (0.84). Thus, all else being equal, females would achieve a higher performance than males. The observed results are attributable to sexual differences in behaviour, probably in relation with the reproductive season.

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1. Introduction

Although sex differences in thermal ecology are not the rule in lizards (Angilletta, 2009; Huey and Pianka, 2007), there are examples of differences in thermal preferences, use of microhabitats, activity times, or thermoregulation behaviour between males and females (Bull et al., 1991; Butler et al., 2000; Kerr and Bull, 2006; Schoener, 1967; Stamps et al., 1997). Gender differences on thermal biology could relax ecological competition between males and females. Male-biased sexual size dimorphism could relate to different selection pressures in males and females, with increasing fitness conferred on larger males (Beal et al., 2014; Blanckenhorn, 2005; Bonneaud et al., 2015; Cox et al., 2007; Zamudio, 1998). Sex differences in thermal ecology could be more common for species showing sexual size dimorphism (Huey and Pianka, 2007; Lailvaux, 2007; Perez-Mellado and De la Riva, 1993), since body size is positively correlated with thermal inertia (Bell, 1980; Stevenson, 1985; Zamora-Camacho et al., 2014a, 2014b). Thus, the study of the effect of sex in thermal biology of sexually dimorphic lizards

should also explore the effects of body size (e.g. Beal et al., 2014).

We examine the thermal ecology of *Scelarcis perspicillata*, a sexually dimorphic lacertid lizard, living at a limestone quarry in Menorca (Spain). The high limestone walls shade the habitat for much of the day. The scarcity of sunny patches might lead to intra-specific differences in the spatial distribution of individuals, or even competition between lizards in order to occupy the limited sunny microhabitats. Our goal is to compare behavioral thermoregulation of males and females and to determine if the thermal quality of the habitats, accuracy and effectiveness of thermoregulation, and the selection of sun-shade patches differ between males and females of *S. perspicillata*. Furthermore, we also compare the thermal ecology of pregnant vs non pregnant females.

2. Material and methods

2.1. Studied species and studied area

The Moroccan rock lizard, *Scelarcis perspicillata* Duméril and Bibron (1839), is a small insectivorous lacertid lizard living in mountain areas of Morocco and Algeria (Bons and Geniez, 1996;

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Perera et al., 2006, 2007; Schleich et al., 1996). This lizard has introduced populations in the limestone quarry in Pedreres de S' Hostal or Lithica and in other localities of Menorca (Balearic Islands, Spain; Perera, 2002). Limestone quarrying ceased in Lithica in 1994 and is now a tourist spot. The quarry consists of limestone walls of more than 5 m tall with a maze-like path of sand at the bottom of the walls (Vitt et al., 2002). Little is known about the reproduction of *S. perspicillata* in Menorca, but gravid females carrying from 1 to 5 eggs have been observed in July (Barbadillo et al., 1999; pers. obs.).

2.2. Field sampling

Between the 18th and 26th of July of 2013 we noosed active adult lizards, during their daily activity period, between 07:00 and 17:00 GMT. Immediately after capture, we measured body temperature (T_b) with a Testo[®] 925 digital thermometer, shadowing the probe, as well as air temperature (T_a) 1 cm above the capture point, and substrate temperature (T_s) of the capture point. We also recorded type of substrate (rock, soil, or grass), orientation of the substrate (flat, North, South, East, or West), perch height (in cm), exposure to sunlight (full sun, filtered sun, or full shade), snout-vent length (SVL) of lizards, measured with a ruler (precision 0.1 mm), and body weight, measured with a dynamometer (precision 0.1 g). Finally, we measured wind speed with a Kestrel[®] 3000 anemometer, but it was almost insignificant (a mean of 0.04 ms^{-1}), so we discarded it as a possible variable affecting thermal behaviour of lizards.

We used 15 hollow copper models as null T_e models, mimicking the size, shape and colour of adult *S. perspicillata* (Bakken and Angilletta, 2014). They were not calibrated to a *S. perspicillata* individual lizard, but were previously calibrated with another species of similar size and shape (Ortega et al., 2014). We placed one thermocouple probe into each hollow model and connected it to a data logger HOBO[®] H8 (Onset Computer Corporation), programmed to take a temperature record every five minutes, concurrently with T_b studies. We placed the copper models in different microhabitats for periods of 48 h, obtaining a total record of 4226 T_e . Because the habitat in the quarry is mainly made of big walls of rock, we also considered different rock orientations.

2.3. Preferred temperature range (PTR)

We measured selected body temperatures (T_{sel}) of *S. perspicillata* from the 27th to the 30th of July of 2013 in a laboratory thermal gradient experiment. Lizards captured from the same location of field sampling were transported to the laboratory in Es Castell (Menorca, Spain), housed in opaque individual terraria and fed with mealworms and crickets. Water was provided ad libitum. We built a thermal gradient in a glass terrarium ($100 \times 60 \times 60 \text{ cm}$) inside an air conditioned room, using a 150 W infrared lamp over one of the ends, obtaining a gradient of 20–60 °C. Prior to the experiment, we allowed lizards one day of acclimation to captivity, maintaining the natural conditions of light and temperature, which were similar to the conditions of their habitat. Over the next two days, we measured a selected temperature of an individual lizard each hour from 08:00 to 17:00 GMT with a Testo[®] 925 digital thermometer. We tested 24 *S. perspicillata* adult lizards: 11 males and 13 females, of which 8 were pregnant. We measured each individual 6 times, obtaining a total of 144 (24×6) values of selected temperatures. We considered the 50% of the central values of selected body temperatures as the preferred temperatures range (PTR) in all analysis, as it is the more common measure, although we also reported the 80% PTR since it is a preference for some authors (Hertz et al., 1993; Blouin-Demers and Nadeau, 2005). We released lizards in the place of capture immediately after the experiment.

2.4. Data analysis

To test the null hypothesis of thermoregulation (that is, if lizards use microhabitats randomly regarding temperature) we followed the protocol developed by Hertz et al. (1993), and calculated the three indexes of thermoregulation. The first is the index of accuracy of thermoregulation (mean d_b) that is the mean of absolute values of the deviations between each T_b from the preferred temperature range. Thus, the values of the index of accuracy of thermoregulation are opposite to their meaning: higher values of d_b indicate lower accuracy of thermoregulation, and vice-versa. The second is the index of thermal quality of the habitat (mean d_e), calculated as the mean of absolute values of the deviations of each T_e from the preferred temperature range. Accordingly, the values of the index of thermal quality of the habitat are also opposite to their meaning: higher values of d_e indicate a lower thermal quality of the habitat, and vice-versa. The third is the index of effectiveness of thermoregulation (E), that is calculated as $E = 1 - (d_b/d_e)$. Hence, values of E range from 0 to 1, where a higher effectiveness of thermoregulation translates into a higher value of E (see Hertz et al., 1993). Effectiveness of thermoregulation was calculated with THERMO, a Minitab module written by Richard Brown. THERMO has been used in previous studies of thermal biology (Ortega et al., 2014, 2016a) and uses three kinds of input data: T_b , T_e and T_{sel} of the preferred temperature range, and was programmed to perform bootstraps of 100 iterations, building pseudo-distributions of three kinds of output values: the arithmetic mean of the index of accuracy of thermoregulation (d_b), the arithmetic mean of the index of thermal quality of the habitat (d_e), and the arithmetic mean of the index of effectiveness of thermoregulation (E).

We performed parametric statistics when data followed the assumptions of normality and variance homogeneity. When data did not meet these assumptions, even after log-transformations, we carried out equivalent non-parametric tests (Crawley, 2012; Sokal and Rohlf, 1995). We conducted all analyses on R, version 3.1.3 (R Core Team, 2015), and we computed post-hoc comparisons of Kruskal-Wallis tests with Nemenyi test with the package PMCMR (Pohlert, 2014). We compared selected body temperatures (T_{sel}) and activity body temperatures (T_b) between genders with ANCOVA, including body size (SVL) as the covariate. All assumptions of ANCOVA were tested before analysis. We reported mean values of variables accompanied by standard errors. Significance level was $\alpha = 0.05$.

3. Results

The population exhibited sexual size dimorphism: mean SVL was $48.89 \pm 2.27 \text{ mm}$ (mean \pm SE; $N = 23$) for males and $37.68 \pm 3.54 \text{ mm}$ ($N = 30$) for females (Mann-Whitney U test, $U = 114.00$, $p < 0.0001$), and mean weight was $3.46 \pm 0.20 \text{ g}$ ($N = 23$) for males and $1.99 \pm 0.20 \text{ g}$ ($N = 30$) for females (one-way ANOVA, $F_{1, 51} = 26.501$, $p < 0.0001$; Fig. 1).

The interaction between sex and body size (SVL, as a covariate) in the ANCOVA was not significant (interaction $SVL \times \text{sex}$: $F_{1, 21} = 0.099$, $p = 0.756$). In addition, there was also no significant effect of SVL on T_{sel} (main effect of SVL: $F_{1, 21} = 1.016$, $p = 0.325$). Selected body temperatures (T_{sel}) of females were similar regardless reproductive condition (mean T_{sel} : pregnant: $34.45 \pm 0.26 \text{ °C}$; non-pregnant: $34.77 \pm 0.27 \text{ °C}$; Mann-Whitney U test, $U = 15.00$, $p = 0.524$). Thus, we pooled data of females together. T_{sel} were also similar for males and females (mean T_{sel} : males = $35.11 \pm 0.22 \text{ °C}$; females = $34.56 \pm 0.19 \text{ °C}$; Mann-Whitney U test, $U = 41.00$, $p = 0.082$). Thus, we pooled the data of T_{sel} of females and males in a single preferred temperature range (PTR) for *S. perspicillata*: $33.90\text{--}36.10 \text{ °C}$ for the 50% of the central values

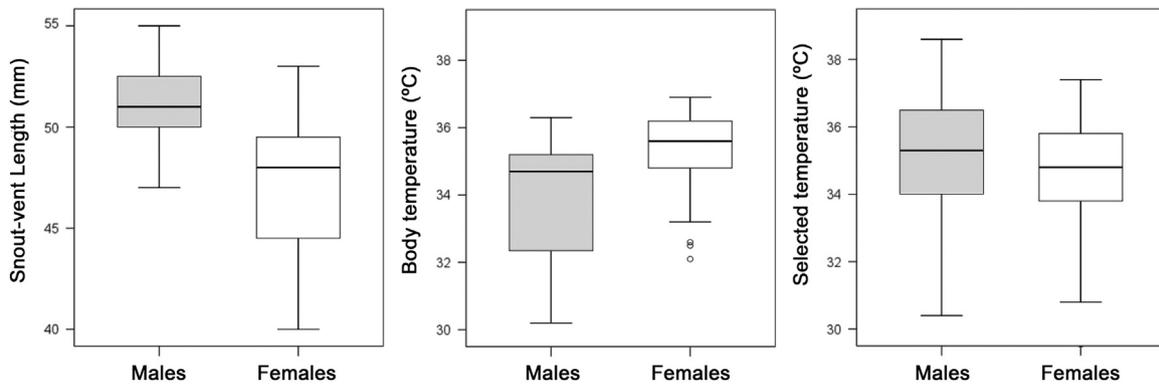


Fig. 1. Mean body size (Snout-vent length, in mm) and mean body temperatures for males and females of the Moroccan rock lizard, *Scelarcis perspicillata*.

of the T_{sel} (50% PTR), and 32.60–36.90 °C for the 80% of the central values of the T_{sel} (80% PTR).

Regarding body temperature (T_b), the interaction between sex and SVL (covariate) in the ANCOVA was not significant (interaction SVL*sex: $F_{1, 46}=0.109$, $p=0.743$). There was also no significant effect of SVL on T_b of lizards ($F_{1, 46}=0.001$, $p=0.970$). Among females, T_b was similar for pregnant and for non-pregnant lizards (one-way ANOVA, $F_{1, 28}=0.020$, $p=0.889$). However, T_b was significantly higher in females than in males (one-way ANOVA, $F_{1, 51}=5.744$, $p=0.020$; Table 1). Air temperatures (T_a) at female capture sites were significantly higher than those of males (Mann-Whitney U test, $U=220.50$, $p=0.025$; Table 1), as well as the substrate temperatures (T_s ; Mann-Whitney U test, $U=163.00$, $p=0.001$; Table 1).

Slopes of linear regression between T_b and T_a were similar between males and females (interaction term sex* T_a of ANCOVA: $F_{1, 46}=0.868$; $p=0.356$). There was a significant correlation between T_b and T_a ($r=0.729$, $p<0.0001$, $N=50$). The linear regression slope of T_a on T_b was also significant ($\beta=0.813$, $p<0.0001$, $N=50$; $R^2=0.531$). Slopes of linear regression between T_b and T_s were similar between sexes (interaction term sex* T_a of ANCOVA: $F_{1, 46}=0.108$; $p=0.744$). There was also a significant correlation between T_b and T_s ($r=0.532$, $p<0.0001$, $N=50$). The linear regression slope of T_a on T_b was also significant ($\beta=0.462$, $p<0.0001$, $N=50$; $R^2=0.283$).

There were differences between the operative temperatures (T_e) at the microhabitats under study (Kruskal-Wallis test, $H=2638.302$, $p<0.0001$, $N=4228$, d.f.=12; Fig. 2). There was suitable T_e (that is, T_e matching the PTR of the species) during the hourly periods of the daily activity of Moroccan rock lizards in Lithica (Fig. 2). Nonetheless, the microhabitats in full shade offered suboptimal T_e during the day, while the microhabitats of grass and soil in full sun offered T_e that exceeded the PTR during almost the entire day. Finally, for rocky substrates in full sun and soil and grass microhabitats in filtered sun, T_e fell within the PTR, but only for certain periods of the day (Fig. 2). Thus, lizards should select between microhabitats in order to achieve body temperatures that would be close to the PTR.

As females showed significantly higher T_b , we calculated the indexes of thermoregulation separately for males and females. Although T_{sel} were similar between sexes, we calculated the indexes of thermoregulation using the specific 50% PTR of each sex: 33.90–36.50 °C for males and 33.65–35.85 °C for females, in order to avoid potential artifacts from pooling data of T_{sel} of sexes. The index of thermal quality of the habitat (d_e) was significantly higher for females (males: mean $d_e=5.03 \pm 0.021$ °C, $N=100$; females: mean $d_e=5.25 \pm 0.019$ °C; Mann-Whitney U test, $U=2189.0$, $p<0.0001$). The index of accuracy of thermoregulation (d_b) was significantly lower for females of *S. perspicillata* than for males (males: mean $d_b=0.79 \pm 0.018$ °C, $N=100$; females: mean

Table 1

Mean (\pm SE) body temperatures (T_b), air temperatures (T_a) and substrate temperatures (T_s) of *Scelarcis perspicillata* and results of the paired comparisons among genders. Temperatures are in °C.

	Males (N=23)	Females (N=30)
T_b	33.93 \pm 0.38	35.09 \pm 1.13
T_a	28.84 \pm 1.92	31.34 \pm 1.13
T_s	29.44 \pm 1.96	32.93 \pm 1.20

$d_b=0.56 \pm 0.018$ °C, $N=100$; Mann-Whitney U test, $U=1816.5$, $p<0.0001$), which means that thermoregulation was more accurate in females than in males. Finally, females achieved a significantly higher value of the index of effectiveness of thermoregulation (E) than males (males: mean $E=0.84 \pm 0.004$, $N=100$; females: mean $E=0.89 \pm 0.003$, $N=100$; Mann-Whitney U test, $U=1587.0$, $p<0.0001$). N of the indexes of thermoregulation reports the number of iterations in the bootstraps, while number of lizards is 53. The operative temperatures and the PTR is the same for both sexes, so the differences in d_b and E were due to differences in T_b , and, thus, to thermoregulation behaviour. Among the 53 individuals of *S. perspicillata*, 26 were found in shaded microhabitats ($\approx 49\%$ of the sample). However, the use of sun-shade patches varied among sexes (G-test, $G=10.446$, $p=0.005$; Fig. 3 and Table 2). In addition, females of *S. perspicillata* selected perches at lower altitudes than males (males: 103.16 \pm 18.26 cm, $N=19$; females: 59.17 \pm 11.64 cm; $N=24$, one-way ANOVA, $F_{1, 41}=4.458$, $p=0.041$).

4. Discussion

Thermal preferences of females of *S. perspicillata* were similar regardless of reproductive condition, similar to the findings of Braña (1993) in *Podarcis muralis*. However, there are contradictory examples, as happens in *Sceloporus jarrovi*, where females prefer lower temperatures during pregnancy (Mathies and Andrews, 1997). Pregnant and non-pregnant females of *S. perspicillata* also achieved similar body temperatures in the field. Zamora-Camacho et al. (2014a, 2014b) found that females of *Psammmodromus algirus* reached similar sprint speed independently of their reproductive status. Furthermore, pregnant females of *Sceloporus adleri* have been reported to reach similar body temperatures under different conditions, because they adjust their thermoregulatory behaviour to maintain stable body temperatures within their thermal preferences for development of the offspring (López-Alcaide et al., 2014).

In addition, thermal preferences of *S. perspicillata* were similar for females and males, even accounting for body size. Similar thermal preferences of genders are the most common

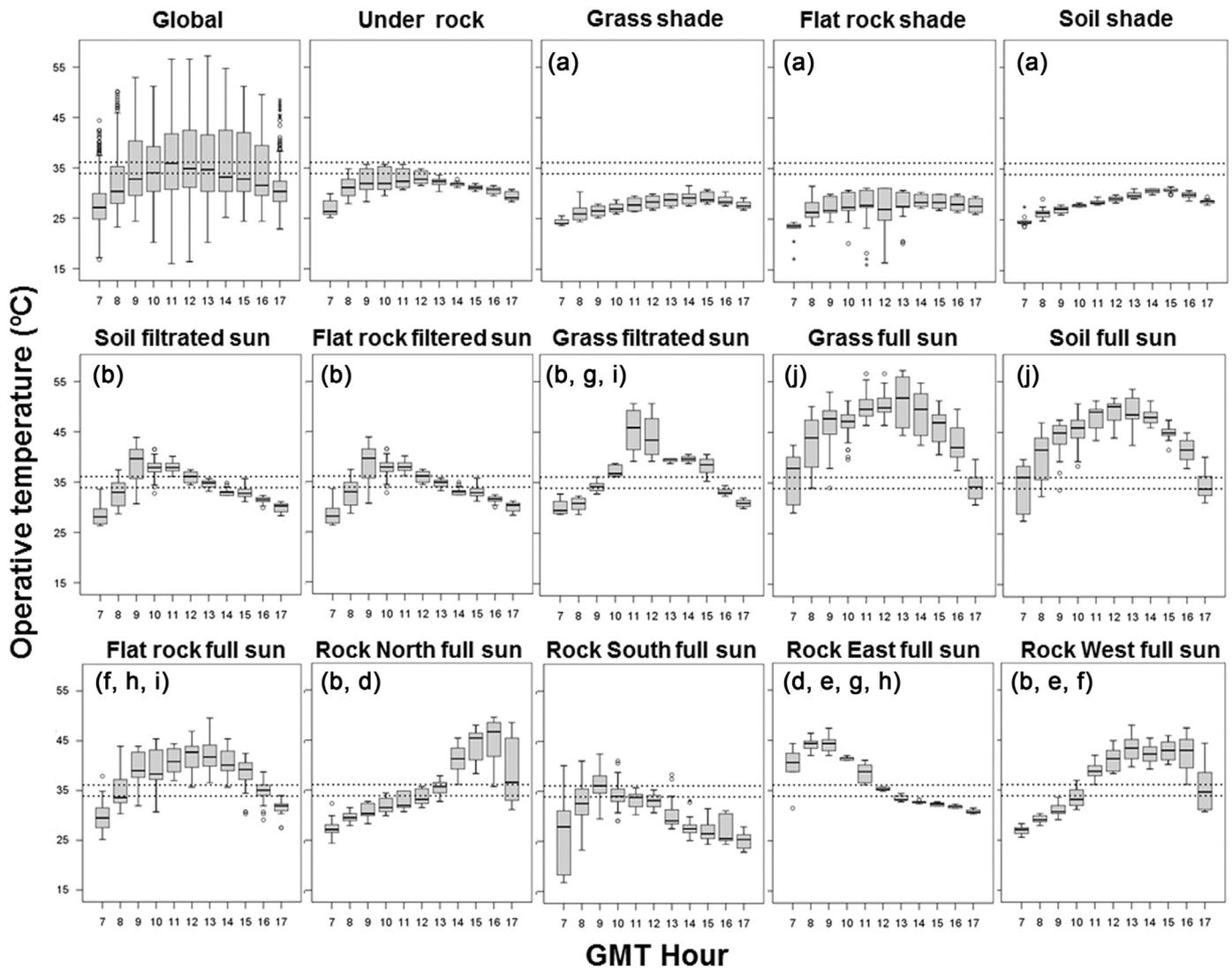


Fig. 2. Operative temperatures offered by the different microhabitats available for the thermoregulation of *Scelarcis perspicillata* in the quarry of Lithica among all the daily activity period of lizards. The dotted lines comprise the preferred temperature range of the species. The letters between brackets match the non-significant pairs of the Nemenyi post-hoc comparisons of the Kruskal-Wallis test ($p > 0.05$).

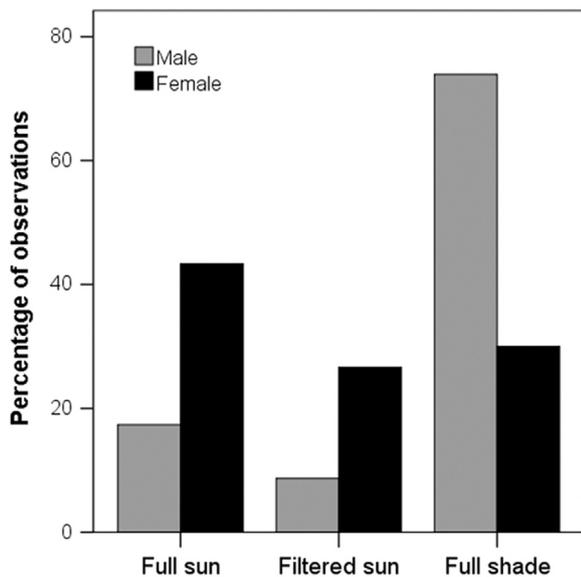


Fig. 3. Frequencies (%) of observations of males and females of *Scelarcis perspicillata* regarding the exposure to sunlight.

Table 2

Paired comparisons of the frequencies of use of each category of exposure to sunlight by males and females of *Scelarcis perspicillata*.

	G	p	d.f.
Full sun - Filtered sun	0.046	0.830	1
Full sun - Full shade	7.495	0.006	1
Filtered sun - Full shade	6.246	0.012	1

circumstance in reptiles (Huey and Pianka, 2007), even for sexually dimorphic species (Cecchetto and Naretto, 2015; Ortega et al., 2014, 2016b; Tang et al., 2013). However, although sexual differences in thermal biology are not the rule in lizards, when there are sexual differences, they most often consist of differences with the thermal preferences (Huey and Pianka, 2007). This is the case of *Zootoca vivipara*, where females are larger and select higher temperatures than males (Patterson and Davies, 1978; Van Damme et al., 1986). In *Podarcis hispanicus*, females are smaller than males but select higher temperatures (Carretero et al., 2006). In *Podarcis vaucheri*, females are also smaller than males and also select higher temperatures, and their thermal preferences also depend on the reproductive condition (Verissimo and Carretero, 2009).

Females of *S. perspicillata* exhibited significantly higher body temperatures than males, independent of their body size. Similar results have been reported in other species, as *Diporiphora winneckei*, where females showed body temperatures 2 °C higher than males (Huey and Pianka, 2007). Furthermore, substrate and air temperatures of the microhabitats occupied by females were significantly higher than those of the microhabitats occupied by males. Females were occupying mostly sunny patches whereas the majority of males were found in shaded patches. Sunny microhabitats would allow females to heat faster than males in shaded areas (e.g., Díaz et al., 1996; Schwarzkopf and Shine, 1991). Our study reveals that behavioral thermoregulation is different for males and females of *S. perspicillata* from Menorca, where females occupied the microhabitats with higher thermal quality (i.e. with operative temperatures closer to the thermal preferences of lizards), while males were found in thermally suboptimal microhabitats. In addition, males were observed at significantly higher height on walls than females. It is conceivable that higher perches had other advantages, perhaps in relation with territorial defense, feeding opportunities, or escape from terrestrial predators, which could counteract the thermal drawback. For example, males of *Anolis conspersus* occupied higher perches than females allowing them to capture bigger preys (Schoener, 1967). Lailvaux et al. (2003) found an opposite result in *Platysaurus intermedius*, where both sexes selected the same thermal optimum in the laboratory, but males achieved higher body temperatures in the wild. In this case, thermal differences in body temperatures were apparently related to a higher locomotor performance in males, while females would rely more on crypsis than in fleeing in order to avoid predators (Lailvaux et al., 2003).

Either way, it is interesting that the sexual differences in thermal ecology of *S. perspicillata*, contrary to the majority of studies reporting sexual differences in lizards, is not based on different thermal preferences between males and females, but rather in different behavioral thermoregulation through microhabitat selection. It is also noticeable that females show similar thermal preferences and similar behavioral thermoregulation regardless of their reproductive status. These results highlight the variability of the patterns with the effect of sex in thermal ecology of lizards, and invites further research in order to identify the main factors that would drive these patterns.

5. Conclusions

Overall, we have shown that male and female *S. perspicillata* differ on behavioral thermoregulation during the summer, while thermal preferences are similar among them. Body size was independent of thermal preferences and body temperatures of lizards, which could discard a direct effect of sexual size dimorphism as a cause of the observed sexual differences in thermoregulation. The different thermoregulatory behaviour of females, using sunny patches more frequently, led them to achieve a significantly higher accuracy and effectiveness of thermoregulation than males. Finally, this could entail a higher physiological performance for females during this period of annual activity, probably in relation with reproduction, although no effect of reproductive status was found within females of this species.

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