Comparing ecophysiological traits in two *Podarcis* wall lizards with overlapping ranges

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Abstract. In ectotherms, environmental factors shape the distribution of species mediated by ecophysiological constraints such as thermal requirements and water stress. Species with different distributions along an environmental gradient are expected to show contrasting responses in thermal-gradient and water-stress lab experiments. We examined basic thermal and hydric physiological traits throughout the day in two related lizard species with different, but partially overlapping, distributions in the Iberian Peninsula: *Podarcis liolepis* (abundant but mostly restricted to northeastern Iberia) and *P. muralis* (restricted in Iberia but widespread across Europe). We expected *P. liolepis* to opt for higher preferred body temperatures and have lower water loss rates as compared to *P. muralis*. Surprisingly, results revealed no differences in preferred body temperatures between species or sexes. Conversely, interspecific differences in the temporal profiles of water loss were found. Results suggest that water availability rather than thermal environment shapes the biogeographical patters of both species.

Key words. Ecophysiology, *Podarcis*, sympatry, thermal preference, water loss, Iberia.

Introduction

A species' geographic range is shaped by both biotic and abiotic factors, if the effects of geographic barriers are excluded (Díaz et al. 1996, Gvoždík 2002, Kearney & Porter 2004). Being ectotherms, reptiles are highly influenced by abiotic conditions, because they follow more closely the temporal and spatial variations of the environment, especially regarding temperature and humidity. Body temperature (Tb) has a major influence on reptile physicochemical processes (Huey 1991). When Tb comes close to the preferred temperature (Tp) which is, by definition, attained in the absence of thermoregulatory constraints (Van Damme et al. 1990, Bauwens et al. 1995, Castilla et al. 1999, Carretero et al. 2005), the performance of many biochemical processes is enhanced (Huey & Slatkin 1976, Van Damme et al. 1989, Bauwens et al. 1995, Angilletta 2002). While Tp may change within the lifespan of individuals (Van Damme et al. 1986) it tends to be conserved within species (Van Damme et al., 1990) for individuals of the same sex, reproductive state, and body condition (Carretero et al. 2005).

Although studies on thermal ecology dominate the reptilian ecophysiological literature, other environmental factors are also of relevance for lizard physiology and ecology. Several studies suggest that water constraints are as important in limiting reptile geographic ranges (Packard 1991, Packard 1999, Flatt et al. 2001, Rato et al., 2015). In particular, ecological niche models of wall lizards of the genus *Podarcis* suggest that humidity may in fact be more relevant than temperature at a geographical scale (Sá-Sousa 2000, Herkt 2007, Kaliontzopoulou et al. 2008, Sillero & Carretero 2013). On the other hand, these two thermal and hydric ecophysiological traits may trade off due to physical constraints, where one may expect lizards selecting high temperatures to suffer higher water loss (WL)

rates (Mautz 1982, Bowker 1993). Hence, restricted water availability may lead to changes in activity patterns that could in turn cause changes in body temperature, tying together both physiological traits (Andrews 1982, Adolph & Porter 1993, Lorenzon et al. 1999).

The congeneric lacertid lizards *Podarcis muralis* (Laurenti, 1768) and *P. liolepis* (Boulenger, 1905) provide a good model system for examining the potential association between biogeographical range and thermal and hydric physiology to identify possible differences in thermal and hydric physiology. These two species are closely related phylogenetically, even though not sister taxa (Harris & Arnold 1999), and very similar morphologically and ecologically. Their global distributions are for the largest part allopatric: *P. muralis* is widespread across Europe, ranging from the Netherlands to southern Italy and Greece, and from Turkey to northwestern Iberia (Pérez-Mellado et al. 2002). For its part, *P. liolepis* is restricted to northeastern Iberia and southern France (Llorente et al. 1995). Nonetheless, the ranges of both species partially overlap in the northeastern Iberian Peninsula where they are sympatric and syntopic on a regional scale (Fig. 1A; Llorente et al. 1995). In Iberia, the two species are reported to occupy habitats that are different in terms of temperature and water availability (Gosá 1985, Llorente et al. 1995, Pérez i de Lanuza et al. 2012). This suggests that both species

migth differ in their ecophysiological traits, but such a hypothesis has not been assessed yet.

Here, we use ecophysiological experiments to investigate the thermal and hydric requirements of these two locally syntopic lacertid species. While laboratory experiments may to some extent lack realism compared to field observations, they are a valuable tool for focusing only on the factors of interest (i.e., preferred body temperature and water loss rate). To put the results obtained through laboratory experiments into the real ecological and biogeographical context of the two species under examination, we also compare the thermal and hydric environments the two species are exposed to in the northeastern Iberian Peninsula, based on normalised distribution records and widescale environmental data. Specifically in this study, we aim at 1) assessing intraspecific (sex and time) and interspecific variation in Tp; 2) identifying WL rates and their daily variation for both species and sexes; and 3) testing for the existence of a trade-off between Tp and WL.

Materials and methods
Study area and sample size

Twenty-one *P. liolepis* (9 males and 12 females) were collected in Palau Reial (Barcelona city; 41°23'N, 2°07'E; 76 m
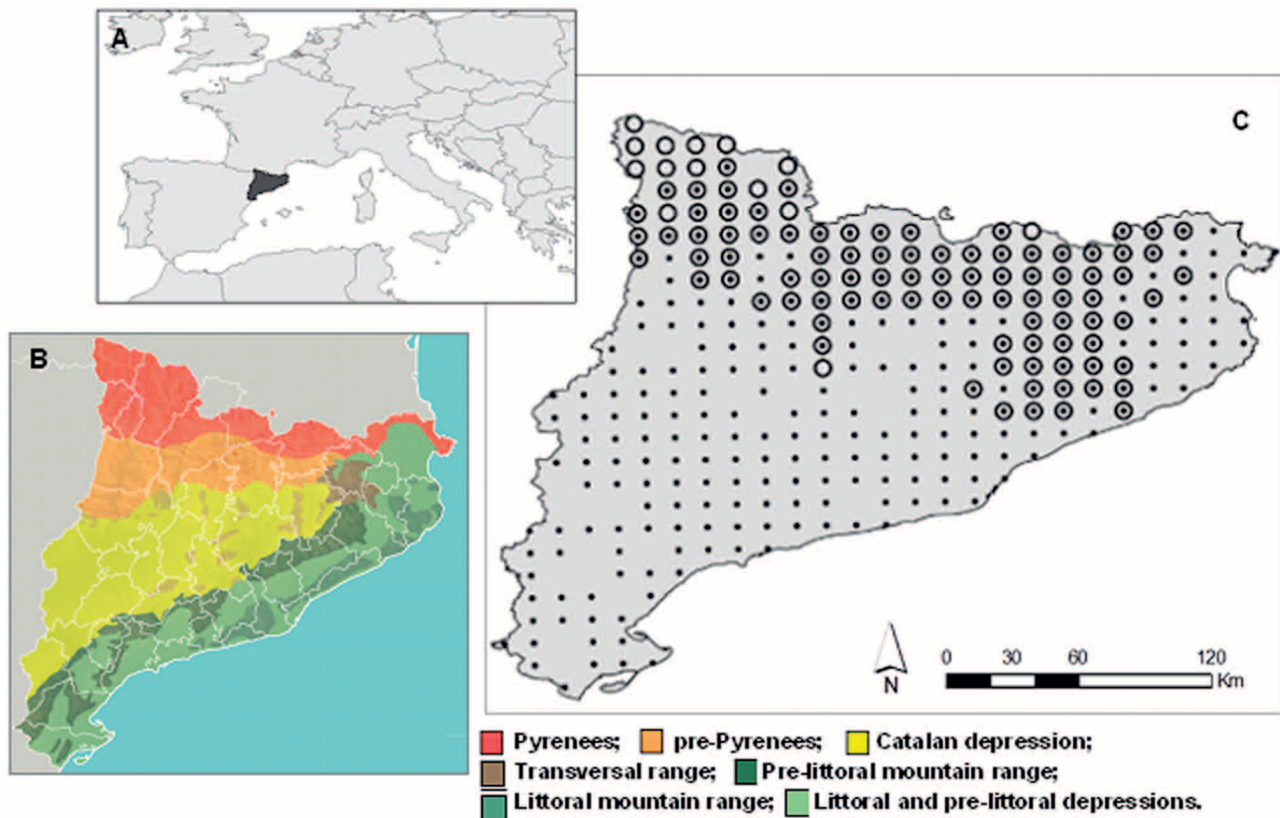

Figure 1. Location (A) and geography (B) of Catalonia; presence records (in 10 × 10 km resolution) of *Podarcis muralis* (open circles) and *P. liolepis* (closed circles) (C). Sympatry areas are marked with both circles.

altitude; datum = WGS84) dominated by *Pinus pinea*, *P. halepensis*, *Cedrus deodara*, and *Cupressus sempervirens* vegetation. Fifteen *P. muralis* (7 males and 8 females) were collected from Santa Fé del Montseny (Montseny Natural Park, 41°46' N, 2°27' E; 1136 m; datum = WGS84) dominated by *Quercus ilex* and *Fagus sylvatica* forests. All lizards were captured by noosing (García-Muñoz & Sillero 2010) in May 2011 and were of adult size (minimum adult snout–vent length [SVL] 38 mm for *P. liolepis*, Carretero & Llorente 1993; Kaliontzopoulou et al., 2006; and 46 mm for *P. muralis*, Diego-Rasilla 2009).

All specimens were transported to the facilities of the University of Barcelona, where they were kept individually in 20 × 10 × 15 cm terraria under natural-light conditions. Food (*Achaeta domestica* and larval *Tenebrio molitor*) and water were provided ad libitum on days during which the lizards were not involved in experiments. In accordance with the phenology of both species in the region (Rivera et al. 2011), all females were diagnosed as gravid based on belly circumference, the presence of copulation marks, and egg palpation.

For each lizard, we measured the SVL to the nearest 0.01 mm using digital callipers. All lizards were first subjected to an experiment designed to identify temperature preferences, followed by an experiment to quantify water loss in the subsequent day. No food or water were provided during and between these experiments. Only lizards with unbroken or fully regenerated tails were used. When accidental autotomy occurred during the experiments, subsequent Tp and WL measurements were excluded from the analyses since tail loss may interfere with thermoregulation and rate of water loss, as it changes the shape and exposed surface area (Chapple & Swain 2004).

Thermal gradient experiment

Lizards of both species were individually exposed to a thermal gradient (ranging from 25 to 45°C) produced by a 150-W infra-red reflector bulb fixed 25 cm above the substrate on one side of a 100 × 40 × 30 cm terrarium with a thin layer of soil. The range of temperatures within the thermal gradient was measured by recording the temperature at either end of the terrarium before each Tp measurement. The Tp within the gradient (Licht et al. 1966, Bauwens et al. 1995) was recorded during a single day at ten consecutive hourly intervals distributed throughout the period of daily activity observed in the field (from 8 through 17 h, UTC + 1:00 Madrid). The bulb was switched on one hour in advance (at 7 h, UTC + 1:00 Madrid) in order to avoid outliers created by the early-morning warm-up (Bauwens et al. 1995). The natural photoperiod was maintained by exposing the terraria to external light. Body temperature was recorded using a type-k thermocouple HIBOK® 18 (precision 0.1°C) by inserting a probe of 1.5 mm diameter into the cloaca (Carretero et al. 2006, Veríssimo & Carretero 2009). No more than 10 seconds elapsed between the capture of the animal from the terrarium and the measurement of body temperature, to minimize lizard stress and manipulation time. This procedure represents a compromise between invasiveness and accuracy: these species were too small to properly insert permanent cloacal probes or implant internal transmitters (Clusella-Trullas et al. 2007) and too slender for obtaining accurate infrared readings (see Hare et al. 2007, Carretero 2012). No interspecific differences in activity that could constrain their thermoregulatory behaviour (Dillon et al. 2012) were obvious within the gradient.

Water loss experiment

This experiment was conducted in sealed chambers (40 × 30 × 20 cm), which kept the animals in the dark and at a relative humidity of ~35% attained by affixing 100g of silica gel on the bottom side of the chamber lid (Osojnik et al. 2013) and at an air temperature of ~24°C, which is a realistic emulation of the thermal situation the animals face in the wild during spring (see http://weatherspark.com/). Temperature and humidity inside this chamber were monitored to the nearest 0.1°C and 0.1%, respectively, using a Fluke®-971 hygrothermometer. Each individual was introduced to a sealed chamber with a false bottom containing five grams of silica gel. WL was quantified by weighing the individuals (inside their individual plastic boxes in order to avoid stress from handling) using a digital scale (precision 0.0001 g). Weights were measured every hour for 12 consecutive hours that covered the normal activity period of the lizards (7–19 h, solar time). The weight difference observed between measurements and water loss rates directly reflect the amount of cutaneous, pulmonary, ocular, and excreta water loss. Although defecation and urination make a relatively low contribution to total water loss (Munsey 1972), these products were not removed from the individual plastic boxes during the experimental process, and as such, water loss due to these physiological functions was also included in the calculation of water-loss rates. Defecation was scarce and randomly distributed along time and species (our observations). Since manipulation was minimized and conditions were dark (opaque chamber), the lizards remained inactive from the beginning of the experiment with no external signs of stress.

Environmental characterization at a geographic scale

To describe differences in the thermal and hydric environments experienced by the two species in nature, and considering the area where the study was conducted, we examined environmental variation in the distribution area of the two species in Catalonia, northeastern Iberian Peninsula (Fig. 1A). This region is large enough to include areas of allopatry and sympatry for both species while providing a reasonable representation of the different environments occupied by them. Moreover, within this territory, there are no potential conflicts due to misidentifica-

tion or ecological interaction between the two species under study and members of the *P. hispanica* species complex (Carretero 2008). A total of 377 records of *Podarcis* (273 *P. liolepis* and 104 *P. muralis*) in Catalonia were obtained at a 10 × 10 km resolution from the Spanish Atlas of Amphibians and Reptiles (Montori et al. 2005). To describe the thermal environment experienced by the two species, we considered eight variables describing temperature mean values, extremes, and variation that were obtained from the Worldclim database (http://www.worldclim.org/bioclim; Hijmans et al. 2005). Similarly, we explored the hydric environment experienced by the two species in Catalonia through eight variables describing annual precipitation and variation that were obtained from the same source.

Statistical analyses

All data were log-transformed to meet the assumptions of normality, homoscedasticity, and sphericity as confirmed through Shapiro-Wilk's tests (P > 0.05 in all cases), multivariate Box M and univariate Levene's tests (P > 0.05 in most cases), and Mauchley's tests (P > 0.05 in all cases), respectively. To test whether significant variation in selected temperatures existed between the studied species and sexes, while also examining temporal variation throughout the day, we performed Repeated Measures ANOVAs (RM-ANOVAs) with sex and species as between-subject factors and time interval as a within-subject factor.

We examined both the instantaneous WL (relative to initial weight, W_o; [WL = $(W_n-W_{n+1})/W_o$]) and the cumulative WL (WL = [W_o-W_n]/W_o) in each time interval between species and sexes. Instantaneous WL captures the amount of WL in each moment whereas cumulative WL provides a quantitative measurement of the water already lost by lizards throughout the experiment. RM-ANOVAs were performed for instantaneous WL using sex and species as between-subject factors and time interval as a within-subject factor. ANOVAs for each time interval of cumulative WL were performed to identify putative differences between species and sexes (between-subject factors).

The possible trade-off between Tp and WL was investigated through Pearson correlation coefficients between mean Tp and total WL (calculated as WL = [W_o-W_{12}]/W_o) for each sex-by-species group separately. ANCOVAs using SVL, initial weight (W_o) and SVL and W_o as covariates were also employed for the two experiments to test whether size, shape or both had an influence on the two ecophysiological characteristics. Duncan post-hoc tests were used for pairwise comparisons between groups for each experiment.

To test whether thermal and hydric conditions differed between the distribution areas of the two species in Catalonia, we performed MANOVA comparisons on the multivariate temperature and precipitation datasets separately, as well as ANOVA comparisons on single variables. Statistica 7.1 (StatSoft 2005) was used to perform all analyses. Significance was evaluated at an α-value of 0.05.

Results

ANOVA comparisons revealed a significant sexual dimorphism in SVL, with inverse patterns between species: *P. liolepis* males were larger than females, whereas the opposite was true for *P. muralis*. Males and females of *P. muralis* also differed in W_o, with females being heavier (Tab. S1). Males of both species only differed in SVL whereas females also differed in W_o (Duncan post-hoc test P < 0.05 for all significant differences). ANCOVA performed on W_o with sex and species as within-subject factor and SVL as covariate revealed that *P. muralis* was relatively heavier than *P. liolepis* ($F_{1,29}$ = 32.54; P < 10^{-6}).

Environmental differences on a geographic scale

Regarding the thermal and hydric environments experienced by *P. liolepis* and *P. muralis* throughout their respective distribution areas in Catalonia, we found significant differences both in temperature (MANOVA: F = 15.274; df = 1,375; P = 2.14^*10^{-19}) and precipitation variable sets (MANOVA: F = 16.0374; df = 1,375; P = 2.44^*10^{-20}). This result is also corroborated by the examination of individual variables (results not presented here; available from the authors upon request). Specifically, the area occupied by *P. muralis* is generally characterized by lower temperatures and higher precipitation levels when compared to that of *P. liolepis* (Fig. 2).

Thermal gradient experiment

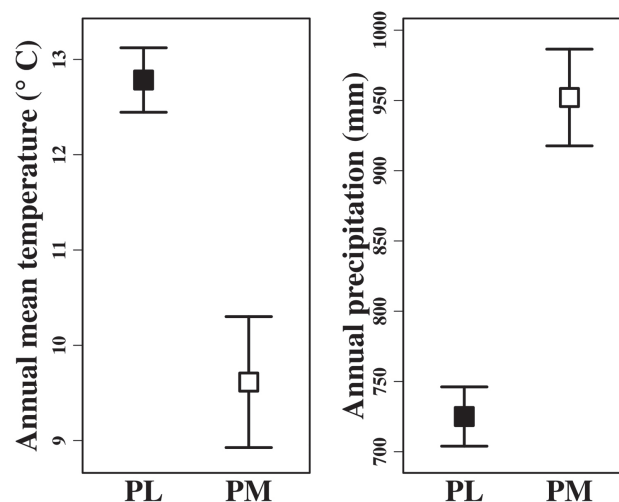Overall Tp of *P. liolepis* females was (mean ± SE) 31.22 ± 0.32°C while *P. liolepis* males selected 31.97 ± 0.51°C. The

Figure 2. Annual mean temperature (°C) and annual precipitation (mm) experienced by *Podarcis liolepis* and *P. muralis* in natural conditions in Catalonia. Whiskers represent ± 0.95 confidence intervals.

mean Tp of *P. muralis* females was 31.28 ± 0.26°C and that of *P. muralis* males was 31.76 ± 0.17°C (Fig. 3). RM-ANO-VA revealed statistical differences along time intervals, but not between sexes or species (Tab. 1). Subsequent RM-AN-COVA using W_o and SVL as covariates did not reveal any statistical difference between species or sexes (Tab. 1). No significant interactions were detected.

Water loss experiment

RM-ANOVA showed a statistical significance for time and time*species, indicating that species have different WL patterns throughout the day, even when variation due to SVL is taken into account (Fig. 4). Using W_o as the covariate rendered the time*species effect non-significant, but species, sex and species*sex presented a statistically significant effect on WL, indicating that the sexes of each species lose water at different rates (Tab. 1). When using both SVL and W_o as covariates, sex and species were the only significant effects, indicating differences in the patterns of WL only between species and sexes. Duncan post-hoc tests between species and sexes using W_o as the covariate only revealed significant differences between *P. muralis* females and *P. liolepis* males (P < 0.05). When no covariates were considered, no statistical differences were found.

Examination of the daily patterns of WL (Fig. 4A) suggested that *P. liolepis* males lost more water after 3–4 hours in the experimental setting whereas *P. muralis* only started losing more during the second half of the experiment (after 6–7 hours). Differences in accumulative WL between species were detected in the last three hours of the experiment once corrected for SVL and W_o (Tab. S2).

Tp vs. water loss

No significant correlations between mean Tp and total WL were detected for any of the sexes or species, indicating a lack of support for a trade-off between both variables (*P. liolepis* males: r^2 = 0.04; P = 0.62; *P. liolepis* females: r^2 = 0.02; P = 0.70; *P. muralis* males: r^2 = 0.06; P = 0.59; *P. muralis* females: r^2 = 0.001; P = 0.94).

Discussion

Our results reveal that environmental humidity may be more relevant for lacertid ecology than temperature, which is usually assumed to be the main factor influencing ectothermic species. The patterns of water loss differ between the two investigated species with regard to the time from the beginning of the experiment and body size. In fact, *P. liolepis* and *P. muralis* exhibit divergent trends in daily WL patterns, although both select similar Tps. Several other lacertid species are known to diverge in terms of preferred hydric environment when occurring in sympatry, either by selecting microhabitats with different humidity characteristics (even though structurally similar), or by differing in their distance to water bodies (Arnold 1987).
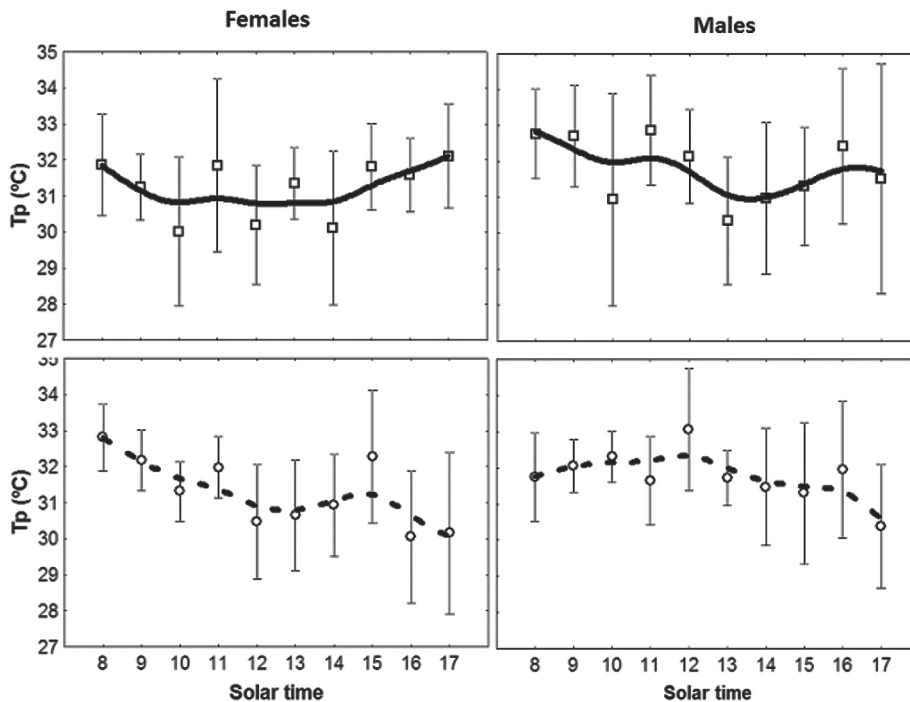

Figure 3. Daily Tp variation pattern of females and males of *Podarcis liolepis* (top, continuous line) and *P. muralis* (bottom, dashed line). Whiskers represent ± 0.95 confidence intervals.

This also seems to be the case in NE Iberia, where *P. muralis* occurs in more humid places compared to *P. liolepis* (Rivera et al. 2001, Fig. 2).

In terms of proximate causation, since experimental conditions allow discarding differential stress between species during the experiments, the trends observed in WL are likely to arise from intraspecific differences in physiological compensatory mechanisms. In fact, this is indicated by the reduction of WL in the first time interval exhibited by *P. liolepis* males (1–2 in Fig. 4A) whereas, if WL rates were uniform across time intervals, a linear cumulative WL profile should be expected. The observed deviation from such a pattern (Fig. 4B) suggests that the quantity of water already lost at the beginning of the experiment had a negative impact on the subsequent water loss rate. After this initial period, *P. liolepis* males were not capable of main-
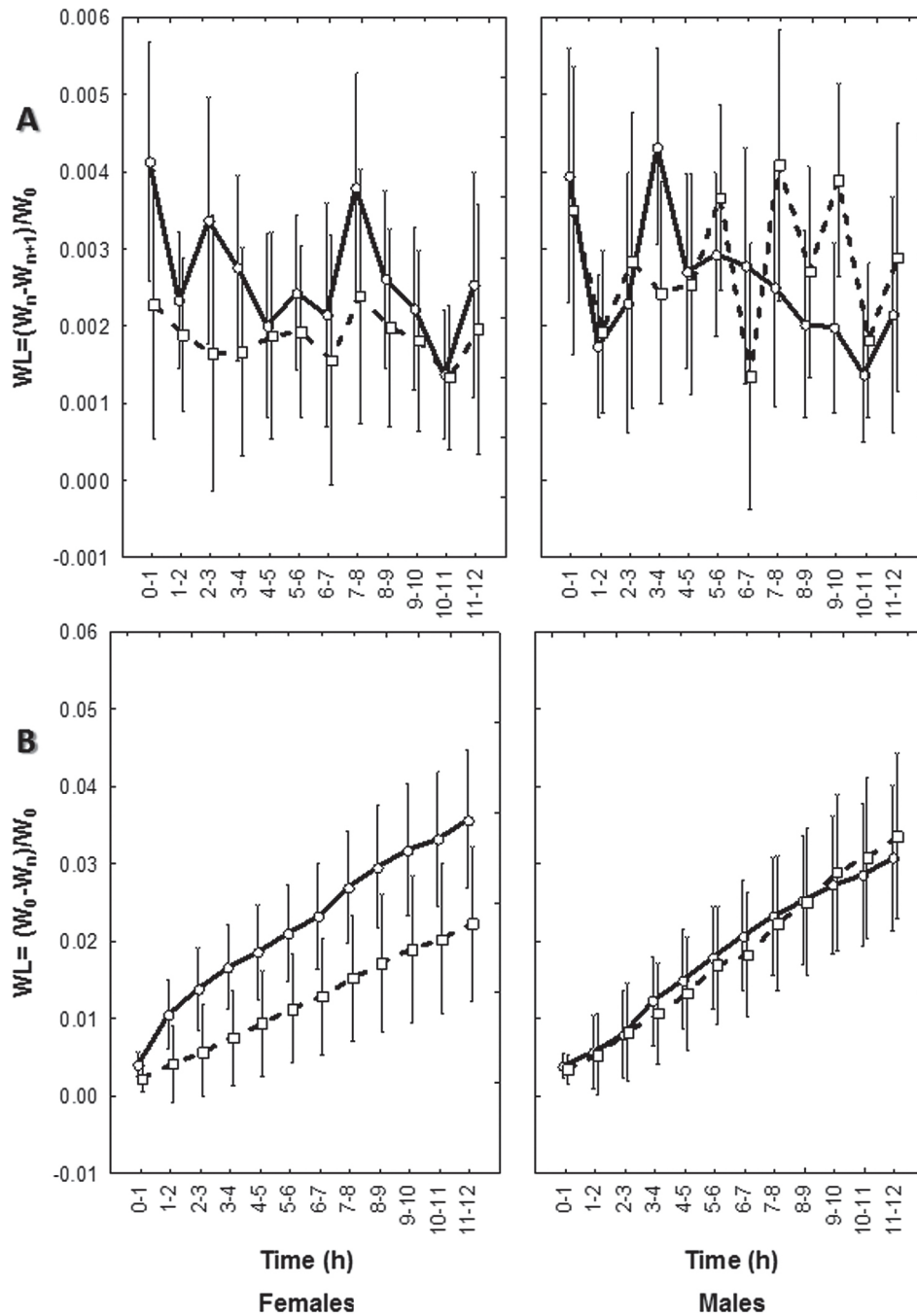

Figure 4. Variation patterns of instantaneous (A) and cumulative (B) water loss of females and males of *Podarcis liolepis* (full line) and *P. muralis* (dashed line) during 12 h in sealed chambers. Whiskers represent ± 0.95 confidence intervals.

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Table 1. RM-ANOVA and RM-ANCOVAs results of Tp and instantaneous WL data using SVL, W_0 or both W_0 and SVL as covariates. Significant effects are in bold. Data are log-transformed.

	Tp experiment results			WL experiment results		
RM-ANOVA	df	F	p	df	F	p
Species	1,30	0.0	0.89	1,21	1.82	0.19
Sex	1,30	2.5	0.12	1,21	1.41	0.25
Species*Sex	1,30	0.0	0.90	1,21	0.32	0.58
Time	9,270	2.3	**0.02**	11,231	2.54	**0.01**
Time*Species	9,270	1.1	0.33	11,231	1.89	**0.04**
Time*Sex	9,270	1.6	0.12	11,231	0.89	0.55
Time*Species*Sex	9,270	1.0	0.42	11,231	1.36	0.19
RM-ANCOVAs	df	F	p	df	F	p
Covar. (SVL)	1,29	0.22	0.64	1,20	10^{-4}	0.99
Species	1,29	0.01	0.91	1,20	1.69	0.21
Sex	1,29	2.43	0.13	1,20	1.33	0.26
Species*Sex	1,29	0.03	0.87	1,20	0.21	0.65
Time	9,261	0.33	0.96	11,220	0.38	0.96
Time*(SVL)	9,261	0.35	0.96	11,220	0.38	0.96
Time*Species	9,261	1.13	0.34	11,220	1.94	**0.04**
Time*Sex	9,261	1.55	0.13	11,220	0.87	0.58
Time*Species*Sex	9,261	0.55	0.84	11,220	1.00	0.45
Covar. (W_0)	1,29	0.18	0.68	1,20	32.48	**<0.01**
Species	1,29	0.04	0.84	1,20	6.49	**0.02**
Sex	1,29	2.19	0.15	1,20	6.76	**0.02**
Species*Sex	1,29	0.02	0.90	1,20	4.80	0.04
Time	9,261	0.81	0.60	11,220	0.48	0.92
Time*(W_0)	9,261	1.00	0.43	11,220	0.66	0.78
Time*Species	9,261	1.43	0.18	11,220	1.26	0.25
Time*Sex	9,261	1.57	0.12	11,220	0.93	0.51
Time*Species*Sex	9,261	1.10	0.36	11,220	1.26	0.25
Covar. (SVL)	1,28	0.11	0.74	1,19	3.99	0.06
Covar. (W_0)	1,28	0.07	0.80	1,19	41.32	**<10^{-6}**
Species	1,28	0.01	0.91	1,19	8.56	**0.01**
Sex	1,28	2.17	0.15	1,19	6.99	**0.02**
Species*Sex	1,28	0.06	0.81	1,19	1.61	0.22
Time	9,252	0.41	0.93	11,209	0.49	0.91
Time*(SVL)	9,252	0.47	0.89	11,209	0.54	0.87
Time*(W_0)	9,252	1.11	0.36	11,209	0.81	0.63
Time*Species	9,252	1.44	0.17	11,209	1.20	0.29
Time*Sex	9,252	1.52	0.14	11,209	0.90	0.54
Time*Species*Sex	9,252	0.71	0.70	11,209	0.96	0.49

taining any kind of initial compensatory mechanism, and as such they started losing water at a more constant rate. Conversely, *P. muralis* males showed a higher WL rate during the second half of the experiment, suggesting that longer-term compensatory mechanisms may operate in this species. Confirming that such proximate compensatory mechanisms are in action would require a study of differences in several relevant physiological properties (pul-

monary respiration rate, ocular evaporation, skin permeability; e.g., Bentley & Schmidt-Nielsen 1966, Roberts 1968, Dmi'el 1972, Eynan & Dmi'el 1993). Regarding thermal physiology, both *P. liolepis* and *P. muralis* select similar preferred temperatures (Tp). Given that these two species are not sister taxa but belong to different clades within the genus *Podarcis* (Harris & Arnold 1999, Harris et al. 2005), and since phylogenetically intermediate *Podarcis* forms display different Tps (Veríssimo & Carretero 2009), the lack of differences reported here may lend support to the hypothesis that both species have converged in terms of thermal physiology. A phylogenetically informed comparative analysis including more species of the genus is, however, needed in order to confirm this hypothesis, as other factors such as habitat use and historical biogeography of both species in question may have shaped the observed patterns.

Furthermore, Tp may also vary within the lifespan of individuals (Braña 1993, Castilla et al. 1999, Carretero et al. 2005), as our results seem to suggest in terms of the Tp of females (gravid). In fact, the females analysed here selected lower Tps than males, which has previously been reported for other populations of the same species (Braña 1993) and for other lacertid lizards (Van Damme et al. 1987, Castilla et al. 1999, Carretero et al. 2005, 2006). Such a trend may reflect the physiological requirements of the embryos rather than those of the female herself (Van Damme et al. 1986, Castilla et al. 1999, Gvoždík & Castilla 2001, Carretero et al. 2005, 2006, Veríssimo & Carretero 2008). Therefore, extrapolating these differences between sexes over time is risky since lizards were caught during the beginning of the breeding season and seasonal variation is expected (Huey 1976, Van Damme et al. 1987, Harris et al. 1998).

Some studies suggest that Tp and WL may trade off intra- and interspecifically between closely related species (Warburg 1965, Tracy & Christian 2005, Tracy et al. 2008), a prediction that is also reasonable from a biophysical point of view. Yet, this is not the case here, probably due to two factors. Firstly, thermal rigidity at intraspecific level has been reported for many lacertids (Van Damme et al. 1989, Gvoždík & Castilla 2001, Carretero et al. 2005, Díaz et al. 2006), including *P. muralis* (Tosini & Avery 1993), so that it is likely to also occur in *P. liolepis*. In such a scenario, Tp may not vary even if the WL rates are altered. Again, a phylogenetically informed analysis of evolutionary rates in both traits would aid in deciphering whether WL is more prone to change than Tp. In fact, such a thermal "rigidity" would also explain why the two species are differentiated in WL patterns but not in TP in spite of the evident differences in the thermal environments they experience, at least in this part of their distribution range (Fig. 2). Secondly, variation in adult body size, as represented by SVL, is certainly lower within a given population than across populations of the same species (Kaliontzopoulou et al. 2012), which could explain the differences in the results obtained here when compared to previous studies.

Further comparative studies against a phylogenetic background are necessary in order to identify to which extent the physiologies of sympatric lizard species may vary and interact across taxa and geographic regions. However, the results obtained here are highly concurrent with those recently reported by Osojnik et al. (2013) and García-Muñoz & Carretero (2013) for other lacertid species, highlighting the importance of incorporating water ecology experiments (in combination with the classic thermal ones) in the framework of lizard ecophysiological studies. This evidence also contributes to future biogeographical analyses and predictions resulting from climate change by emphasizing that humidity-related factors and not only a raise in global mean temperatures may have substantial effects on species distributions and extinction risks.

Acknowledgements

References

Adolph, S. C. & W. P. Porter (1993): Temperature, activity, and lizard life histories. – American Naturalist, **142**: 273–295.

Andrews, R. M. (1982): Patterns of growth in reptiles. – pp. 273–319 in: Gans C. & F. H. Pough (eds): Biology of the Reptilia. Vol. 13. – Academic Press. New York.

Arnold, E. N. (1987): Resource partition among lacertid lizards in southern Europe. – Journal of Zoology, **4**: 739–782.

Avery, R. A. (1982): Field studies of body temperatures and thermoregulation. – pp. 93–146 in: Gans C. & F. H. Pough (eds): Biology of the Reptilia. Vol. 12. – Academic Press. New York.

Bauwens, D., T. Garland Jr., A. M. Castilla & R. Van Damme (1995): Sprint speed in lacertid lizards: morhological, physiological and behavioral covariation. – Evolutionary Ecology, **49**: 848–863.

Bentley, P. & K. Schmidt-Nielsen (1966): Cutaneous water loss in reptiles. – Science, **151**: 1547–1549.

Bowker, R. G. (1993): The thermoregulation of the lizards *Cnemidophorus exanguis* and *C. velox*: some consequences of high body temperature. – pp. 117–132 in: Wright, J. W. & L. J. Vitt (eds): Biology of Whiptail Lizards (genus *Cnemidophorus*). – Norman, Oklahoma Museum of Natural History.

Braña, F. (1991): Summer activity patterns and thermoregulation in the wall lizard, *Podarcis muralis*. – Herpetological Journal, **1**: 544–549.

Braña, F. (1993): Shifts in body temperature and escape behaviour of female *Podarcis muralis* during pregnancy. – Oikos, **66**: 216–222.

Carretero, M. A. (2008): An integrated assessment of a group with complex systematics: the Iberomaghrebian lizard genus *Podarcis* (Squamata, Lacertidae). – Integrative Zoology, **3**: 247–266.

Carretero, M. A. (2012): Measuring body temperatures in small lacertids: Infrared vs. contact thermometers. – Basic and Applied Herpetology, **26**: 99–105.

Carretero, M. A. & G.A. Llorente (1993): Morfometría en una comunidad de lacértidos mediterráneos, y su relación con la ecología. – Historia Animalium, **2**: 77–79.

Carretero, M. A., J. M. Roig & G. A. Llorente (2005): Variation in preferred body temperature in an oviparous population of *Lacerta* (*Zootoca*) *vivipara*. – Herpetological Journal, **15**: 51–55.

Carretero, M. A., E. Marcos & P. de Prado (2006): Intraspecific variation of preferred temperatures in the NE form of *Podarcis hispanica**. – pp. 55–64 in: Corti, C., P. Lo Cascio & M. Biaggini (eds): Mainland and insular lacertid lizards: a Mediterranean perspective. – Firenze University Press. Florence.

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.

Chapple, D. G. & R. Swain. (2004): Caudal autotomy does not influence thermoregulatory characteristics in the metallic skink, *Niveoscincus metallicus*. – Amphibia-Reptilia, **25**: 326–333.

Costa, G. C., C. Wolfe, D. B. Shepard, J. P. Caldwell & L. J. Vitt (2008): Detecting the influence of climatic variables on species distributions: a test using GIS niche-based models along a steep longitudinal environmental gradient. – Journal of Biogeography, **35**: 637–646.

Diego-Rasilla, F. J. (2001): Effects of density on the population dynamics and autoecology of the Iberian wall lizard (*Podarcis hispanica*) (Squamata, Lacertidae). – Revista Española de Herpetología, **15**: 1–140.

Diego-Rasilla, F. J. & V. Pérez-Mellado (2000): The effects of population density on time budgets of the Iberian Wall lizard (*Podarcis hispanica*). – Israel Journal of Zoology, **46**: 215–229.

Díaz, J. A., R. Díaz-Uriarte & A. Rodriguez (1996): Influence of behavioral thermoregulation on the use of vertical surfaces by Iberian wall lizards *Podarcis hispanica*. – Journal of Herpetology, **30**: 548–552.

Díaz. J. A., P. Iraeta & C. Monasterio (2006): Seasonality provokes a shift of thermal preferences in a temperate lizard, but altitude does not. – Journal of Thermal Biology, **31**: 237–242.

Dillon M. E., R. Liu, G. Wang & R. B. Huey (2012): Disentangling thermal preference and the thermal dependence of movement in ectotherms. – Journal of Thermal Biology, **37**: 631–639.

Dmi'el, R. (1972): Effect of activity and water and temperature on metabolism loss in snakes. – American Journal of Physiology, **223**: 510–516.

Eynan, M. & R. Dmi'el (1993): Skin resistance to water loss in agamid lizards. – Oecologia, **95**: 290–294.

Flatt, T., R. Shine, P. A. Borges-Landaez & S. J. Downes (2001): Phenotypic variation in an oviparous montane lizard (*Bassiana duperreyi*): the effects of thermal and hydric incubation environments. – Biological Journal of the Linnean Society, **74**: 339–350.

Galán, P. (1986): Morfología y distribución del género *Podarcis* Wagler, 1830 (Sauria: Lacertidae) en el noroeste de la Península Ibérica. – Revista Española de Herpetología, **1**: 85–142.

Galán, P. (1995): Ciclos de actividad de *Podarcis bocagei* en el noroeste ibérico. – Revista Española de Herpetología, **9**: 37–47.

García-Muñoz, E. & M. A. Carretero (2013): Comparative ecophysiology of two sympatric lizards. Laying the groundwork for mechanistic distribution models. – Acta Herpetologica, **8**: 123–128.

García-Muñoz, E. & N. Sillero (2010): Two new types of noose for capturing herps. Acta Herpetologica, **5**: 259–263.

Gosá, A. (1985): Taxonomía de las lagartijas del genero *Podarcis* en el País Vasco. Estudio Biométrico. Eusko Ikaskuntza Ciencias Naturales, **2**: 23–46.

Grbac, I. & D. Bauwens (2001): Constraints on Temperature Regulation in Two Sympatric *Podarcis* Lizards during Autumn. – Copeia, **2001**: 178–186.

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.

Gvoždík. L. & A. M. Castilla (2001): A Comparative Study of Preferred Body Temperatures and Critical Thermal Tolerance Limits among Populations of *Zootoca vivipara* (Squamata: Lacertidae) along an Altitudinal Gradient. – Journal of Herpetology, **35**: 486–492.

Harris, D. J. & E. N. Arnold (1999): Relationships of Wall Lizards, *Podarcis* (Reptilia: Lacertidae) based on mitochondrial DNA sequences. – Copeia, **1999**: 749–754.

Harris, D. J., Arnold, E. N. & R. H. Thomas (1998): Relationships of lacertid lizards (Reptilia, Lacertidae) estimated from mitochondrial DNA sequences and morphology. – Procedings of the Royal Society of London B, **265**: 1939–1948.

Harris, D. J., C. Pinho, M. A. Carretero, C. Corti & W. Böhme (2005): Determination of genetic diversity within the insular lizard *Podarcis tiliguerta* using mtDNA sequence data, with a reassessment of the phylogeny of *Podarcis*. – Amphibia-Reptilia, **26**: 401–407.

Herkt, M. (2007): Modelling habitat suitability to predict the potential distribution of Erhard's wall lizard *Podarcis erhardii* on Crete. – MSc thesis. International Institute for Geo-Information Science and Earth Observation. Enschede.

Hijmans, R. J., S. E. Cameron, J. L. Parra, P. G. Jones & A. Jarvis (2005): Very high resolution interpolated climate surfaces for global land areas. – International Journal of Climatology, **25**: 1965–1978.

Huey, R. B. (1976): Temperature, Physiology, and the Ecology of Reptiles. – pp. 25–91 in: Gans, C. & F. H. Pough (eds): Biology of the Reptilia. Vol. 12. – Academic Press, New York.

Huey, R. B. (1991): Physiological Consequences of Habitat Selection. – American Naturalist, **137**: 91–115.

Huey, R. B. & M. Slatkin (1976): Cost and Benefits of Lizard Thermoregulation. – The Quarterly Review of Biology, **51**: 363–384.

Kaliontzopoulou, A., J. C. Brito, M. A. Carretero, S. Larbes & D. J. Harris (2008): Modelling the partially unknown distribution of wall lizards (*Podarcis*) in North Africa: ecological affinities, potential areas of occurrence, and methodological constraints. – Canadian Journal of Zoology, **86**: 992–1001.

Kaliontzopoulou, A., M. A. Carretero & G. A. Llorente (2012): Morphology of the *Podarcis* wall lizards (Squamata: Lacertidae) from the Iberian Peninsula and North Africa: patterns of variation in a putative cryptic species complex. – Zoological Journal of the Linnean Society, **164**: 173–193.

Kearney, M. R. & W. P. Porter (2004): Mapping the fundamental niche: physiology, climate, and the distribution of a nocturnal lizard. – Ecology, **85**: 3119–3131.

Llorente, G. A., A. Montori, X. Santos & M. A. Carretero (1995): Atlas dels Anfibis y Rèptils de Catalunya i Andorra. – Edicions El Brau. Figueres.

Lorenzon, P., J. Clobert, A. Oppliger & H. John-Alder (1999): Effect of water constraint on growth rate, activity and body temperature of yearling common lizard (*Lacerta vivipara*). – Oecologia, **118**: 423–430.

Martín-Vallejo, J., J. García-Fernández, V. Pérez-Mellado & J. L. Vicente-Villardón (1995): Habitat selection and thermal ecology of the sympatric lizards *Podarcis muralis* and *Podarcis hispanica* in a mountain region of Central Spain. – Herpetological Journal, **5**: 181–188.

Mautz, W. J. (1982): Patterns of evaporative water loss. – pp. 443–481 in: Gans C. & F. H. Pough (eds): Biology of the Reptilia. Vol. 12. – Academic Press. New York.

Munsey, L. D. (1972): Water loss in five species of lizards. – Comparative Biochemistry and Physiology A, **43**: 781–794.

Osojnik, N., A. Žagar, M. A. Carretero, E. García-Muñoz & A. Vrezec (2013): Ecophysiological dissimilarities of two sympatric lizards. – Herpetologica, **69**: 445–454.

Packard, G. C. (1991): Physiological and ecological importance of water to embryos of oviparous reptiles. – pp. 213– 228 in: Deeming, D. C. & M. W. J. Ferguson (eds): Egg incubation: its effects on embryonic development in birds and reptiles. – Cambridge University Press. Cambridge.

Packard, G. C. (1999): Water Relations of Chelonian Eggs and Embryos: Is Wetter Better? – American Zoologist, **39**: 289–303.

Pérez i de Lanuza, G., S. Luna & J. Lozano (2012): Actualización de la distribución de *Podarcis muralis* en el Penyagolosa (País Valenciano). – Boletín de la Asociación Herpetológica Española, 23: 73–79.

Pérez-Mellado, V. (2002): *Podarcis muralis*. – pp. 250–252 in: Pleguezuelos, J. M., R. Márquez & M. Lizana (eds): Atlas y Libro Rojo de los Anfibios y Reptiles de España. – Asociación herpetológica Española – Dirección General de Conservación de la Naturaleza. Madrid.

Rato, C. & Carretero, M. A. (2015): Ecophysiology tracks phylogeny and meets ecological models in an Iberian gecko. – Physiological and Biochemical Zoology (in press).

Rismiller, P. D. & G. Heldmaier (1982): The Effect of Photoperiod on Temperature Selection in the European Green Lizard, *Lacerta viridis*. – Oecologia, **53**: 222–226.

Rivera, X., D. Escoriza, J. Maluquer-Margalef, O. Arribas & S. Carranza (2011): Amfibis i rèptils de Catalunya, País Valencià i Balears. – Lynx Edicions. Bellaterra.

Roberts, L. (1968): Water loss in the desert lizard *Uta stansburiana*. – Comparative Biochemistry and Physiology A, **27**: 583–589.

StatSoft, Inc. (2007): Program STATISTICA (data analysis software system), version 8.0. – www.statsoft.com.

Sá-Sousa, P. (2000): A predictive distribution model for the Iberian Wall lizard (*Podarcis hispanicus*) in Portugal. – Herpetological Journal, **10**: 1–11.

Sillero, N. & M. A. Carretero (2013): Modelling the past and future distribution of contracting species. The Iberian lizard *Podarcis carbonelli* as a case study. – Zoologischer Anzeiger, 252: 289–298.

Tosini, G. & R. Avery (1993): Intraspecific variation in lizard thermoregulatory set points: a thermographic study in *Podarcis muralis*. – Journal of Thermal Biology, **18**: 19–23.

Tosini, G., S. Jones & R. Avery (1994): Effects of feeding on set point temperatures and thermoregulatory behaviour in the lizards *Podarcis muralis* and *Lacerta vivipara*. – Amphibia-Reptilia, **15**: 257–265.

Tracy, C. R. & K. A. Christian (2005): Preferred Temperature Correlates with Evaporative Water Loss in Hylid Frogs from Northern Australia. – Physiological and Biochemical Zoology, **78**: 839–846.

Tracy, C. R., K. A. Christian & G. Betts (2008): Body temperature and resistance to evaporative water loss in tropical Australian frogs. – Comparative Biochemistry and Physiology A, **150**: 102–108.

Van Damme, R., D. Bauwens & R. F. Verheyen (1986): Selected body temperatures in the lizard *Lacerta vivipara*: variation within and between populations. – Journal of Thermal Biology, **11**: 219–222.

Van Damme, R., D. Bauwens & R. F. Verheyen (1987): Thermoregulation responses to environmental seasonality by the lizard *Lacerta vivipara*. – Herpetologica, **43**: 405–415.

Van Damme, R., D. Bauwens, A. M. Castilla & R. F. Verheyen (1989): Altitudinal variation of the thermal biology and running performance in the lizard *Podarcis tiliguerta*. – Oecologia, **80**: 516–524.

Van Damme, R., D. Bauwens & R. F. Verheyen (1990): Evolutionary rigidity of thermal physiology: the case of the temperate lizard *Lacerta vivipara*. – Oikos, **57**: 61–67.

Veríssimo, C. V. & M .A. Carretero (2008): Preferred temperatures of *Podarcis vaucheri* from Morocco: intraspecific variation and interspecific comparisons. – Amphibia-Reptilia, **30**: 17–23.

Warburg, M. R. (1965): The influence of ambient temperature and humidity on the body temperature and water loss from two Australian lizards, *Tiliqua rugosa* Gray (Scincidae) and *Amphibolurus barbatus* Cuvier (Agamidae). – Australian Journal of Zoology, **13**: 331–350.

Supplementary material

Additional information is available in the online version of this article at http://www.salamandra-journal.com

2 Supplementary tables

Table 1. Descriptive statistics of SVL, W_0, Tp, and instantaneous WL.

Table 2. ANOVA accumulated WL.

Online Supplementary data

2 Supplementary tables

Supplementary table S1. Descriptive statistics of SVL, W_0, Tp, and instantaneous WL (relative to initial weight, W_0; [WL = $(W_n - W_{n+1})/W_0$]) at each time interval for each species and sex.

P. liolepis males	N	Mean	Min.	Max.	SD	SE	P. liolepis females	N	Mean	Min.	Max.	SD	SE
SVL (mm)	9	60.60	56.87	63.65	2.21	0.74	SVL (mm)	10	55.17	47.94	63.47	4.63	1.46
W_0 (g)	9	4.72	4.23	5.57	0.41	0.14	W_0 (g)	10	3.08	1.95	4.05	0.67	0.21
Tp (°C)							Tp (°C)						
Tp 9	9	32.77	30.60	36.00	1.61	0.53	Tp 9	10	31.87	29.10	35.20	1.96	0.62
Tp 10	9	32.71	30.10	35.80	1.83	0.61	Tp 10	10	31.25	30.00	34.10	1.28	0.41
Tp 11	9	30.94	24.00	35.50	3.84	1.28	Tp 11	10	30.01	24.70	34.40	2.89	0.91
Tp 12	8	32.88	30.90	35.40	1.83	0.65	Tp 12	10	31.85	25.40	35.70	3.34	1.06
Tp 13	8	32.15	29.60	34.50	1.56	0.55	Tp 13	10	30.19	24.90	33.40	2.31	0.73
Tp 14	8	30.35	26.10	33.60	2.13	0.75	Tp 14	10	31.35	28.20	33.10	1.40	0.44
Tp 15	8	30.98	26.90	34.20	2.52	0.89	Tp 15	10	30.11	26.20	34.60	2.97	0.94
Tp 16	8	31.31	29.20	35.50	1.97	0.70	Tp 16	10	31.82	29.70	34.70	1.68	0.53
Tp 17	8	32.43	29.10	37.30	2.57	0.91	Tp 17	10	31.59	28.60	33.70	1.42	0.45
Tp 18	8	31.51	25.50	37.00	3.82	1.35	Tp 18	10	32.11	29.50	36.40	2.03	0.64
WL (g)							WL (g)						
$(W_0-W_1)/W_0$	9	0.004	0.002	0.01	0.001	0.0005	$(W_0-W_1)/W_0$	10	0.004	0.001	0.013	0.004	0.0010
$(W_0-W_2)/W_0$	9	0.002	0.0004	0.004	0.001	0.0004	$(W_0-W_2)/W_0$	10	0.002	0.001	0.004	0.001	0.0004
$(W_0-W_3)/W_0$	9	0.002	0.0001	0.01	0.002	0.0006	$(W_0-W_3)/W_0$	10	0.003	-0.004	0.010	0.004	0.0010
$(W_0-W_4)/W_0$	9	0.004	0.002	0.01	0.003	0.0008	$(W_0-W_4)/W_0$	10	0.003	0.0001	0.010	0.002	0.0006
$(W_0-W_5)/W_0$	9	0.003	0.0001	0.01	0.002	0.0008	$(W_0-W_5)/W_0$	10	0.002	0.0002	0.004	0.001	0.0004
$(W_0-W_6)/W_0$	9	0.003	0.001	0.01	0.002	0.0005	$(W_0-W_6)/W_0$	10	0.002	0.001	0.005	0.001	0.0005
$(W_0-W_7)/W_0$	9	0.003	-0.001	0.01	0.002	0.0007	$(W_0-W_7)/W_0$	10	0.002	-0.005	0.005	0.003	0.0009
$(W_0-W_8)/W_0$	9	0.003	0.001	0.01	0.001	0.0004	$(W_0-W_8)/W_0$	10	0.004	0.002	0.010	0.002	0.0006
$(W_0-W_9)/W_0$	9	0.002	0.0002	0.004	0.001	0.0004	$(W_0-W_9)/W_0$	10	0.003	0.001	0.010	0.002	0.0007
$(W_0-W_{10})/W_0$	9	0.002	-0.0001	0.004	0.001	0.0005	$(W_0-W_{10})/W_0$	10	0.002	0.0003	0.004	0.001	0.0004
$(W_0-W_{11})/W_0$	9	0.001	-0.0003	0.003	0.001	0.0003	$(W_0-W_{11})/W_0$	10	0.001	0.0002	0.003	0.001	0.0003
$(W_0-W_{12})/W_0$	9	0.002	-0.0005	0.005	0.001	0.0005	$(W_0-W_{12})/W_0$	10	0.003	-0.0004	0.009	0.003	0.0009

P. muralis males	N	Mean	Min.	Max.	SD	SE
SVL (mm)	7	55.64	46.07	66.45	6.20	2.34
W_0 (g)	7	6.09	3.55	9.43	2.31	0.87
Tp (°C)						
Tp 9	7	31.74	29.50	33.40	1.32	0.50
Tp 10	7	32.06	30.80	33.30	0.80	0.30
Tp 11	7	32.31	30.70	32.90	0.77	0.29
Tp 12	7	31.64	30.50	34.40	1.32	0.50
Tp 13	7	33.06	30.00	35.20	1.82	0.69
Tp 14	7	31.71	30.90	33.20	0.82	0.31
Tp 15	7	31.47	29.20	34.40	1.76	0.66
Tp 16	7	31.30	28.60	34.70	2.12	0.80
Tp 17	7	31.94	29.20	35.40	2.04	0.77
Tp 18	7	30.39	26.60	32.10	1.85	0.70
WL (g)						
$(W_0-W_1)/W_0$	7	0.004	0.001	0.006	0.002	0.0007
$(W_0-W_2)/W_0$	7	0.002	-0.0004	0.005	0.002	0.0007
$(W_0-W_3)/W_0$	7	0.003	0.001	0.006	0.002	0.0006
$(W_0-W_4)/W_0$	7	0.002	0.0005	0.005	0.002	0.0006
$(W_0-W_5)/W_0$	7	0.003	0.001	0.006	0.002	0.0008
$(W_0-W_6)/W_0$	7	0.004	0.001	0.006	0.002	0.0008
$(W_0-W_7)/W_0$	7	0.001	-0.002	0.004	0.003	0.0010
$(W_0-W_8)/W_0$	7	0.004	0.001	0.012	0.004	0.0015
$(W_0-W_9)/W_0$	7	0.003	0.0003	0.006	0.002	0.0008
$(W_0-W_{10})/W_0$	7	0.004	0.001	0.008	0.003	0.0010
$(W_0-W_{11})/W_0$	7	0.002	-0.002	0.005	0.003	0.0008
$(W_0-W_{12})/W_0$	7	0.003	0.0003	0.009	0.003	0.0012

P. muralis females	N	Mean	Min.	Max.	SD	SE
SVL (mm)	8	61.06	57.42	64.82	3.19	1.13
W_0 (g)	8	8.12	3.76	11.15	2.92	1.03
Tp (°C)						
Tp 9	8	32.81	31.2	34.60	1.12	0.40
Tp 10	8	32.19	30.70	33.80	1.003	0.35
Tp 11	8	31.31	29.90	32.60	0.99	0.35
Tp 12	8	31.98	30.90	34.00	1.03	0.36
Tp 13	8	30.48	27.50	32.50	1.91	0.67
Tp 14	8	30.65	27.80	33.40	1.85	0.65
Tp 15	8	30.93	28.70	32.90	1.70	0.60
Tp 16	8	32.28	29.80	36.00	2.20	0.78
Tp 17	8	30.05	25.40	32.60	2.19	0.78
Tp 18	8	30.15	23.60	31.80	2.70	0.95
WL (g)						
$(W_0-W_1)/W_0$	8	0.002	0.0008	0.004	0.001	0.0004
$(W_0-W_2)/W_0$	8	0.002	0.0005	0.004	0.001	0.0004
$(W_0-W_3)/W_0$	8	0.002	0.0008	0.003	0.001	0.0002
$(W_0-W_4)/W_0$	8	0.002	0.0003	0.003	0.001	0.0003
$(W_0-W_5)/W_0$	8	0.002	0.0001	0.003	0.001	0.0004
$(W_0-W_6)/W_0$	8	0.002	0.0010	0.004	0.001	0.0004
$(W_0-W_7)/W_0$	8	0.002	0.0003	0.003	0.001	0.0004
$(W_0-W_8)/W_0$	8	0.002	0.0002	0.005	0.002	0.0006
$(W_0-W_9)/W_0$	8	0.002	0.0002	0.004	0.001	0.0005
$(W_0-W_{10})/W_0$	8	0.002	0.0009	0.003	0.001	0.0003
$(W_0-W_{11})/W_0$	8	0.001	0.0007	0.003	0.001	0.0003
$(W_0-W_{12})/W_0$	8	0.002	0.0008	0.003	0.001	0.0003

Supplementary table S2. ANOVA accumulated WL of each time intervals between species and sexes using the covariates SVL and W_0.

| | df | $(W_0-W_1)/W_0$ | | $(W_0-W_2)/W_0$ | | $(W_0-W_3)/W_0$ | | $(W_0-W_4)/W_0$ | | $(W_0-W_5)/W_0$ | | $(W_0-W_6)/W_0$ | |
		F	p	F	p	F	p	F	p	F	p	F	p
Species	1, 30	1.54	0.22	3.16	0.09	0.36	0.55	3.38	0.08	2.29	0.14	3.00	0.09
Sex	1, 30	1.9	0.18	0.09	0.77	0.3	0.59	0.49	0.49	0.57	0.46	1.02	0.32
Species*Sex	1, 30	0.1	0.75	0.75	0.39	0.19	0.67	0.70	0.41	0.43	0.52	1.12	0.30
SVL (covar.)	1, 29	0.07	0.79	0.04	0.85	0.11	0.76	0.10	0.75	0.08	0.78	0.05	0.83
Species	1, 29	1.52	0.23	3.08	0.09	0.37	0.55	3.33	0.08	2.26	0.14	2.94	0.10
Sex	1, 29	1.85	0.18	0.09	0.77	0.29	0.59	0.47	0.50	0.55	0.46	0.99	0.33
Species*Sex	1, 29	0.17	0.69	0.66	0.42	0.28	0.60	0.73	0.40	0.48	0.49	0.97	0.33
W_0 (covar.)	1, 29	5.99	0.02*	7.70	0.01	2.36	0.14	6.47	0.02	7.30	0.01*	11.7	$<10^{-3}$*
Species	1, 29	0.61	0.44	0.33	0.57	0.42	0.52	0.15	0.70	0.54	0.47	0.97	0.33
Sex	1, 29	3.35	0.08	0.01	0.94	0.61	0.44	1.26	0.27	1.47	0.23	2.75	0.11
Species*Sex	1, 29	1.10	0.30	0.51	0.48	0.22	0.65	0.40	0.53	0.76	0.39	0.70	0.41
SVL (covar.)	1, 28	1.77	0.19	1.93	0.18	0.95	0.34	2.08	0.16	2.16	0.15	2.99	0.09
W_0 (covar.)	1, 28	7.83	0.01*	9.83	$<10^{-3}$*	3.20	0.08	8.66	0.01	9.65	$<10^{-3}$*	15.4	$<10^{-3}$*
Species	1, 28	1.2	0.28	0.81	0.37	0.75	0.39	0.54	0.47	1.18	0.29	1.99	0.17
Sex	1, 28	3.74	0.06	0.03	0.87	0.70	0.41	1.51	0.23	1.76	0.20	3.31	0.08
Species*Sex	1, 28	0.25	0.62	0.03	0.87	0.01	0.94	$<10^{-3}$*	0.95	0.08	0.78	0.03	0.87

| | df | $(W_0-W_7)/W_0$ | | $(W_0-W_8)/W_0$ | | $(W_0-W_9)/W_0$ | | $(W_0-W_{10})/W_0$ | | $(W_0-W_{11})/W_0$ | | $(W_0-W_{12})/W_0$ | |
		F	p	F	p	F	p	F	p	F	p	F	p
Species	1, 30	3.79	0.06	3.84	0.06	3.31	0.08	2.69	0.11	2.32	0.14	2.52	0.12
Sex	1, 30	0.60	0.44	0.52	0.48	0.39	0.54	0.65	0.43	0.69	0.41	0.63	0.43
Species*Sex	1, 30	0.84	0.37	1.53	0.23	1.6	0.22	1.97	0.17	2.05	0.16	2.29	0.14
SVL (covar.)	1, 29	0.15	0.70	0.10	0.75	0.14	0.71	0.29	0.60	0.32	0.57	0.06	0.80
Species	1, 29	3.75	0.06	3.77	0.06	3.27	0.08	2.70	0.11	2.35	0.14	2.47	0.13
Sex	1, 29	0.59	0.45	0.50	0.49	0.38	0.54	0.63	0.43	0.68	0.42	0.61	0.44
Species*Sex	1, 29	0.94	0.34	1.41	0.24	1.55	0.22	2.09	0.19	2.22	0.15	1.89	0.18
W_0 (covar.)	1, 29	11.6	$<10^{-3}$*	17.2	$<10^{-4}$*	18	$<10^{-4}$*	18.1	$<10^{-4}$*	16.9	$<10^{-4}$*	24.4	$<10^{-5}$*
Species	1, 29	0.65	0.43	1.48	0.23	1.93	0.18	2.42	0.13	2.47	0.13	3.99	0.06
Sex	1, 29	1.94	0.17	2.21	0.15	1.93	0.18	2.61	0.12	2.61	0.12	3.12	0.09
Species*Sex	1, 29	0.93	0.34	0.96	0.33	0.98	0.33	0.73	0.40	0.58	0.45	1.01	0.32
SVL (covar.)	1, 28	3.93	0.06	5.21	0.03*	5.93	0.02 *	7.48	0.01*	7.28	0.01*	6.86	0.01 *
W_0 (covar.)	1, 28	16.4	$<10^{-4}$*	24.8	$<10^{-5}$*	26.7	$<10^{-5}$*	29.1	$<10^{-5}$*	27.20	$<10^{-5}$*	36.10	$<10^{-6}$*
Species	1, 28	1.70	0.20	3.31	0.08	4.21	0.05	5.47	0.03*	5.49	0.03 *	7.64	0.01 *
Sex	1, 28	2.50	0.13	2.98	0.10	2.72	0.11	3.81	0.06	3.78	0.06	4.39	0.05
Species*Sex	1, 28	0.05	0.83	0.02	0.89	0.01	0.92	0.02	0.90	0.04	0.83	0	0.95