ECOPHYSIOLOGY

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Micro-scale differences in thermal habitat quality and a possible case of evolutionary flexibility in the thermal physiology of lacertid lizards

Abstract We studied the thermal ecology of the lacertid lizards *Lacerta oxycephala* and *Podarcis melisellensis* on the Adriatic island of Vis (Croatia) during summer. These species obviously differ in microhabitat use: *L. oxycephala* climbs on rocks and stone walls, whereas *P. melisellensis* is mainly ground-dwelling in vegetation. Since theoretical considerations predict a difference in thermal quality between the species' microhabitats, this system seems to present a good opportunity to test the influence of thermal microhabitat quality on body temperature, thermoregulatory behaviour and evolution of thermal characteristics. Data on thermoregulatory behaviour, body temperatures (T_b) and habitat quality were collected in the field and selected temperatures (T_{sel}) were estimated in a laboratory thermogradient. Accuracy and effectiveness of thermoregulation were quantified. Thermoregulatory behaviour consisted of timing of activity, selection of places in full sun and near sun-shade transitions, and basking. As predicted, *L. oxycephala* occupied the microhabitat with the lower thermal quality and had on average a lower T_b. However, *L. oxycephala* also selected lower temperatures in the experimental thermogradient. Thus, if T_{sel} can be regarded as the thermoregulatory target, both species proved to be accurate and effective thermoregulators. These results corroborate the "labile view" on the evolution of thermal physiology: both *L. oxcephala* and *P. melisellensis* appear to be adapted to their respective thermal microhabitat. This is a surprising conclusion, since earlier studies have found the thermal characteristics of Lacertidae to be evolutionarily rigid.

Keywords Adaptation · Habitat partitioning · *Lacerta oxycephala* · *Podarcis melisellensis* · Thermal ecology

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Introduction

Habitat partitioning between species is usually assumed to result from past or present competitive interaction, with the dominant species forcing the subordinate species into less favourable microhabitats (Gause 1934; Hardin 1960; McArthur 1968). Especially in spatially limited or structurally poor environments (e.g. islands), the survival chances of the latter species will depend on its behavioural, physiological or evolutionary flexibility. For ectotherms, thermal suitability constitutes an important element of (micro)habitat quality, since thermal conditions determine the degree to which an ectotherm can perform near physiologically optimal levels. Unfortunately, past studies of thermal biology have primarily concentrated on among-habitat variation in thermal characteristics (e.g. along altitudinal or latitudinal gradients) (e.g. Tauber and Tauber 1987; Wilson and Echternacht 1987; Christian et al. 1988; Van Berkum 1988; John-Alder et al. 1989; Van Damme et al. 1989, 1990; Smith and Ballinger 1994; Beaupre 1995; Qualls and Shine 2000; Wilson 2001; review in Spicer and Gaston 1999). Differences on a smaller spatial scale (among microhabitats within a habitat) have received far less attention. As a consequence, it is difficult to judge potential effects of a shift in structural microhabitat in terms of thermal quality. Furthermore, if thermal quality differs, it is unclear how, and how fast, ectotherms can respond.

Lacertid lizards are typical heliothermic ectotherms that thermoregulate behaviourally to keep body temperatures near physiologically optimal levels. Where species of lacertid lizards co-occur on Mediterranean islands, the "dominant" species typically occupies the terrestrial, vegetated ("horizontal") microhabitats, while the "subordinate" species is mostly confined to rocks and walls (the "vertical" microhabitats) (Arnold 1987). We use this study system to evaluate whether thermal conditions can vary on a microgeographic scale between microhabitats within one habitat, how this may affect ectotherm performance abilities and how the animals may respond to overcome the potential problem of a thermally variable or unfavourable microhabitat.

Some theoretical arguments suggest that the microhabitat of a climbing species on stony substrates might be thermally different from, and perhaps inferior to that of a ground-dwelling species in vegetation. First, the sun's altitude varies throughout the course of the day and as a consequence, solar radiation is higher on vertical substrates in the morning and in the late afternoon and higher on horizontal substrates around midday. Second, a climbing lizard has to take the orientation of the walls into account in order to receive sufficient insolation, whereas this problem is almost non-existent for a ground-dwelling species. For example, insolation of an eastward oriented wall is restricted to the early morning, but a moderately vegetated area at ground level provides sunny and shaded patches during the entire day. Third, wind speed above a soil surface depends on vegetation height: the taller the vegetation crop, the lower the wind speed (Campbell and Norman 1998). Consequently, convection (an important source of heat loss in small lizards) will be higher in species occurring on stony substrates than in species occurring in vegetation.

Ectotherms can compensate for changes in their thermal environment in different ways. Behavioural adjustments (e.g. changes in the frequency and/or duration of basking bouts, adoption of special postures, selection of particular substrates, etc.) – as demonstrated repeatedly in lacertid (e.g. Van Damme et al. 1987; Castilla and Bauwens 1991; Díaz 1994; Bauwens et al. 1996), agamid (e.g. Schäuble and Grigg 1998) and iguanid (e.g. Cowles and Bogert 1944; DeWitt 1967) lizards and in many other reptiles (review in Avery 1982) and insects (review in Heinrich 1981, 1993) – constitute a first, short-term possibility. However, this behavioural thermoregulation may be insufficient to counteract long-term changes in the thermal environment, and a directional selection pressure on thermal physiological characteristics will be created. The question if and how fast these characteristics evolve has frequently been debated among investigators and two competing views can be distinguished (Hertz et al. 1983).

The "static" view that thermal physiology is evolutionarily conservative and relatively insensitive to directional selection is supported by studies indicating that closely related lizard species or conspecific populations, even when they occur in climatically distinctive habitats, show little differentiation in activity temperatures (e.g. Cowles and Bogert 1944; Hertz and Nevo 1981), selected temperatures (e.g. Bennett and John-Alder 1986; Van Damme et al. 1989, 1990) or optimal temperatures of sprint speed (e.g. Hertz et al. 1983; Crowley 1985). Furthermore, this view is supported by studies on other ectotherms, such as insects (e.g. Chown 2001) and bacteria (e.g. Bronikowski et al. 2001)

In contrast, the "labile" view holds that thermal physiology responds readily to directional selection. This view is mainly based on research on the tropical iguanid genus *Anolis*. In this genus, interspecific and interpopulation variation in activity temperatures (Rand 1964; Huey and Webster 1975), selected temperatures (Ruibal

1960; Huey and Webster 1976) and optimal temperatures (Van Berkum 1986) represents ecological variation, rather than phylogenetic relationships. Illustrating the existing controversy in this research domain, the labile view is supported by studies on other ectotherms as well, such as amphibians (e.g. Chen et al. 2001; Wilson 2001), insects (e.g. Marden 1995; Forsman 1999, 2000) and bacteria (e.g. Bennett et al. 1992; Mongold et al. 1996).

In this paper, we compare microhabitat use, thermal quality of the environment, thermoregulation and thermal physiology of two lacertids occurring syntopically on the island of Vis in the Adriatic Sea. *Lacerta oxycephala* is a climbing species, whereas *Podarcis melisellensis* is mainly ground-dwelling. We apply the protocol of Hertz et al. (1993) to answer the following questions:

1. Is the thermal quality of the microhabitat used by *L. oxycephala* inferior to that of the microhabitat used by *P. melisellensis*, as expected?
2. Do *L. oxycephala* and *P. melisellensis* thermoregulate behaviourally and how accurate and effective is their thermoregulation?
3. Which of the two contrasting views on evolution of thermal characteristics, the static or the labile one, is supported by the thermal ecology of *L. oxycephala* and *P. melisellensis* on the island of Vis?
4. To what extent do our results permit us to reconstruct the historical pathways of habitat partitioning by these two species?

Materials and methods

Study species and area

Both *Lacerta oxycephala* and *Podarcis melisellensis* are small (adult snout–vent length 55–65 mm), diurnal lacertid lizards whose geographic distributional range is limited to the former Yugoslavia and its islands in the Adriatic Sea. *L. oxycephala* occurs primarily on vertical substrates, such as walls and rocks, whereas *P. melisellensis* is mainly ground-dwelling, in more or less dense vegetation (Arnold et al. 1978; Bischoff 1984; Tiedemann and Henle 1986; Arnold 1987; Gasc et al. 1997).

Both species occur on the island of Vis (43°03′N, 16°10′E) in the Adriatic Sea, ca. 45 km off the coast of Split (Croatia). *L. oxycephala* as well as *P. melisellensis* are very abundant in the surroundings of the ruins of Fort King George, in the north of the island. *L. oxycephala* is seen on the stone walls of the fort and *P. melisellensis* occupies the herbaceous vegetation surrounding the fort. The climate on the island is Mediterranean, with warm, dry summers (mean air temperature in June, 25.6°C; mean rainfall May–October, 117 mm) and temperate, wet winters (mean air temperature in January, 6.8°C; mean rainfall November–December, 407 mm).

Field body temperatures and lizard behaviour

Field work was carried out between 31 August and 12 September 2000. Both measurements of field body temperatures (T_b) and observations of behaviour were conducted throughout the lizard's daily activity period at that time of the year [0800–1800 hours, Central European time (CET), daylight saving time; corresponding to solar noon around 13.00 h at this degree of longitude].

During random walks throughout the study area, we captured lizards by noose and measured cloacal temperature (T_b) to the

nearest 0.1°C with a thermocouple connected to a digital thermometer. We also noted species, age/sex class (subadult, adult male or adult female), date, time of day, weather conditions (sunny, variable, cloudy), exposure to sun (full sun, filtered sun, shade), distance to nearest sun or shadow, substrate (vegetation, stone, other), slope (horizontal, vertical, oblique) and posture/movement (moving, perching, basking – as defined in Hertz and Nevo 1981). All these characteristics were recorded upon first sighting of a lizard.

Additional behavioural observations were conducted using the instantaneous sampling method, as described in Martin and Bateson (1986). Lizards were observed during 10-min recording sessions, divided into 10-s sample intervals. Every tenth second, we recorded slope (horizontal, vertical, oblique), posture/movement (moving, perching, basking) and exposure to sun (full sun, filtered sun, shade). We also noted date, time of day, species, age/sex and the substrate occupied during the session. Because there were too few recording sessions to analyse behaviour from hour to hour, we divided the day into four intervals: morning (0800–1100 hours), midday (1100–1400 hours), early afternoon (1400–1600 hours) and late afternoon (1600–1800 hours). Two-way ANOVA on arcsin-transformed data and Tukey's a posteriori tests were used to test differences between species and time intervals.

Operative temperatures

Operative temperatures (T_e) were measured using hollow copper models of lizards (Bakken 1992; Hertz et al. 1993). All models were painted dark green to match the lizards' absorptivity for solar radiation. To compare the models' responses to changing heat loads with those of living *P. melisellensis* and *L. oxycephala*, we restrained one model and two live lizards (one of each species) side by side on a cardboard sheet. The model and the lizards were irradiated from above by a SOL 500 (Dr Hönle) light source, with a spectral distribution similar to that of the sun. A constant flow of air from a room fan provided convective cooling. Temperatures of the lizards and the model were measured at 10-s intervals with thermocouples connected to digital thermometers. We recorded temperatures from the moment the light source was switched on, until the lizards had reached their equilibrium temperature. We repeated this procedure, varying the distance between the cardboard sheet and the light source, changing the speed of the fan, and using different lizard specimens and models. The models heated much faster than the live lizards, but the differences in equilibrium temperatures between the model and the lizards were always <0.5°C.

T_es were measured from 31 August to 8 September (from 0800 until 1800 hours). Forty models were distributed randomly throughout the study area and were relocated daily. At 30-min intervals, we measured internal temperatures of the models (i.e. T_e) to the nearest 0.1°C and recorded the following additional data: date, time of day, substrate/inclination (vegetation, stone horizontal, stone vertical), weather conditions (sunny, variable, cloudy), exposure to sun (full sun, filtered sun, shade) and distance to nearest sun or shadow. Since both species occupy a limited part of the available microhabitats, not all randomly placed copper models are relevant to each species. Therefore, T_es were divided into a *L. oxycephala* category (with T_es measured on vertical and horizontal stony substrates) and a *P. melisellensis* category (with T_es measured on horizontal substrates, in vegetation as well as on stone).

Six additional models were used to estimate maximum and minimum available temperatures (T_{max} and T_{min}, respectively). Three of these models were placed in full sun (one in vegetation, one on a flat stone and one hanging on a wall) and three in deep shadow (same distribution).

Selected body temperatures

On 13 September 2000 we transported 28 adult lizards (17 *P. melisellensis* and 11 *L. oxycephala*) to the laboratory. Lizards were kept in terraria (five animals in each cage, species separated), where two 100-W light bulbs, suspended above one end, created a thermogradient ranging from 20°C to 50°C. Food (crickets) and water were provided ad libidum. We recorded body temperatures of active (moving, perching or basking) lizards, using the same thermometer as that in the field. Eighty T_bs were collected for each species, spread equally among all individuals. We defined the selected temperature range (T_{sel}) as the central 50% of all temperature recordings around the median value (or, in other words, the interval enclosing the second and third quartile of the sample) (Hertz et al. 1993) and assume that these T_bs represent the temperatures that lizards would achieve in the field in the absence of physical and biotic restrictions (Licht et al. 1966; Castilla and Bauwens 1991).

Indices of thermal habitat quality and thermoregulation

We followed the procedure of Hertz et al. (1993) to evaluate accuracy and effectiveness of thermoregulation and thermal suitability of the habitat, and therefore calculated the following indices:

1. δ_b, which is the mean value of all absolute deviations (d_b) of T_bs from the nearest limit of T_{sel}. When T_b falls within T_{sel}, d_b=0. δ_b is a measure of the accuracy of thermoregulation: the lower δ_b, the higher the accuracy.
2. δ_e, which is computed analogously to δ_b, but for T_es. In this regard, δ_e measures the quality of the thermal environment from the organism's perspective. The lower δ_e, the higher the habitat quality.
3. E, the effectiveness of temperature regulation, computed as $1-\delta_b/\delta_e$. When animals thermoregulate carefully and successfully, $\delta_b<\delta_e$ and E will approach one. Conversely, when animals do not thermoregulate, δ_b and δ_e will be similar and E will approach zero. Active avoidance of suitable microclimates ($\delta_b>\delta_e$) results in a negative value of E.

We used bootstrap resampling to define the 95% confidence intervals for E and to compare effectiveness of thermoregulation between species (Hertz et al. 1993). We repeated the procedure 1,000 times and judged species to be significantly different if one species had the greater E value in 95% or more of the paired comparisons.

Results

Activity and thermoregulatory behaviour

Lizards were active between 0800 and 1800 hours (CET, daylight saving time). The number of lizards captured per hour varied throughout the course of the day in both species (χ^2 test: *L. oxycephala*, χ^2=21.95, df=9, P=0.009; *P. melisellensis*, χ^2=38.60, df=9, P<0.001). However, when data were corrected for capture intensity (number of person-hours per hour), no significant diurnal variation was found (*L. oxycephala*, χ^2=16.45, df=9, P=0.06; *P. melisellensis*, χ^2=13.90, df=9, P=0.13).

As expected, species clearly differed in substrate use. *L. oxycephala* was mainly observed on stone, whereas *P. melisellensis* was seen on stone as well as in vegetation (RxC test: Pearson χ^2=60.44, df=2, P<0.001; Fig. 1A, B) Additionally, *L. oxycephala* generally used vertical substrates, whereas the vast majority of *P. melisellensis* individuals were seen on horizontal substrates (χ^2=86.22, df=2, P<0.001; Fig. 1C, D). No diurnal variation was found in these patterns (all P>0.05).

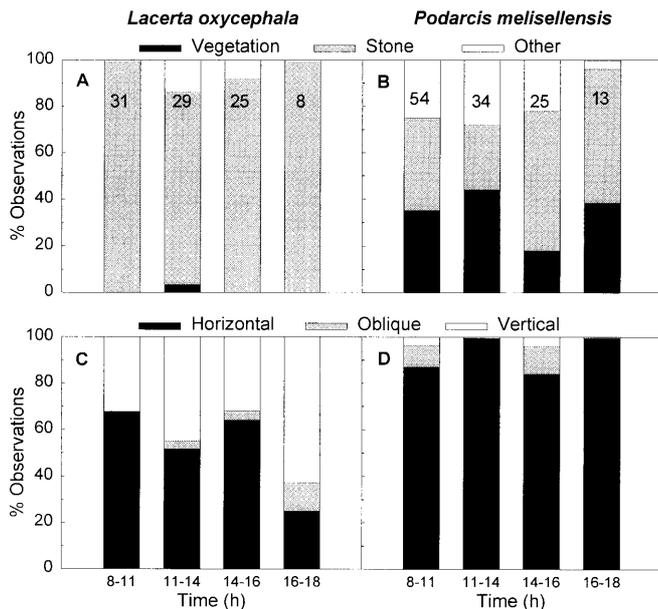*P. melisellensis* was scored significantly more as "moving" than *L. oxycephala* (χ^2=13.14, df=2, P=0.001).

Fig. 1 Diel variation in relative substrate use, concerning type of substrate (**A**, **B**) and inclination (**C**, **D**), in *Lacerta oxycephala* (**A**, **C**) and *Podarcis melisellensis* (**B**, **D**), recorded upon first sighting of lizards. **A**, **B** *Numbers on bars* indicate sample sizes
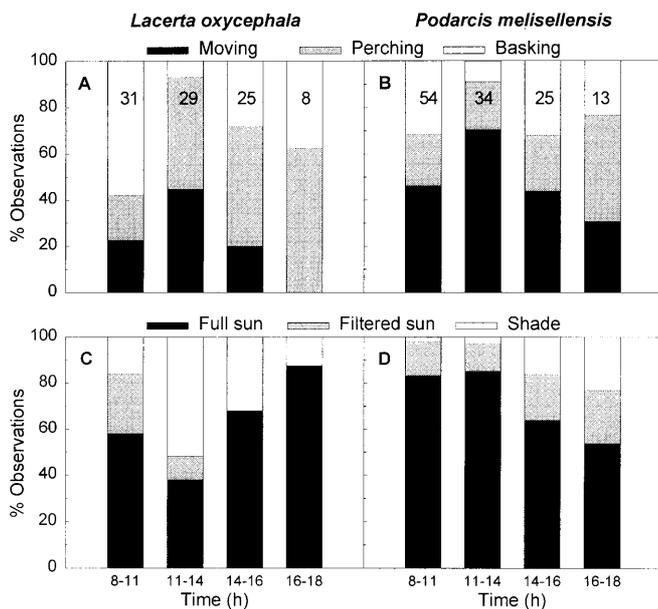

Fig. 2 Diel variation in the relative activity (**A**, **B**) and use of solar microclimates (**C**, **D**) in *Lacerta oxycephala* (**A**, **C**) and *Podarcis melisellensis* (**B**, **D**), recorded upon first sighting of lizards. **A**, **B** *Numbers on bars* indicate sample sizes

The proportion of lizards seen basking was highest in the morning (0800–1100 hours) and the late afternoon (1600–1800 hours) and lowest at midday (1100–1400 hours) ($\chi2=29.58$, $df=6$, $P<0.001$; Fig. 2A, B).

Overall, most lizards were seen in full sun, but the proportion of lizards observed in full sun declined significantly at midday in *L. oxycephala* ($\chi2=21.22$, $df=6$, $P=0.002$). No significant diurnal variation was found in *P. melisel-*
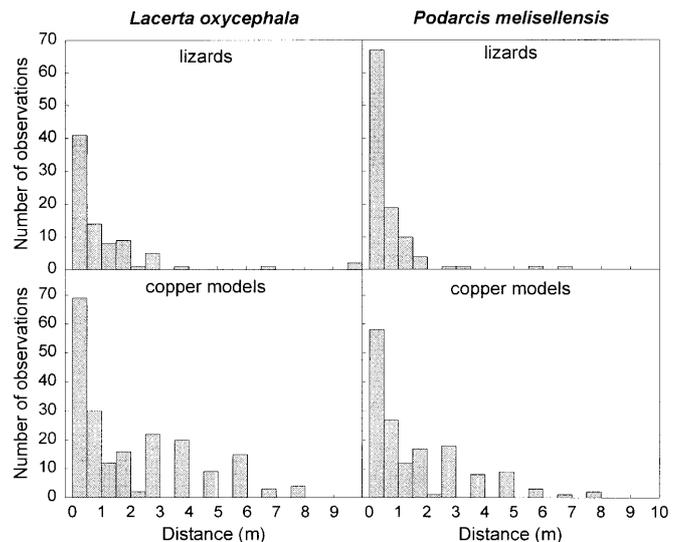

Fig. 3 Distribution of distances to nearest sun or shadow by real lizards and copper models in *Lacerta oxycephala* and *Podarcis melisellensis*

lensis ($\chi2=8.61$, $df=6$, $P=0.07$) (Fig. 2C, D). Considering copper models, distributed randomly throughout the study area, as a measure for available sunlight and shade, we found that *L. oxycephala* ($\chi2=25.68$, $df=2$, $P<0.001$), as well as *P. melisellensis* ($\chi2=69.59$, $df=2$, $P<0.001$), were observed much more in full sun than expected when lizards would use patches of sun and shade randomly. Additionally, estimated distances to nearest sun or shade were lower than expected in *L. oxycephala* (one-way ANOVA on $\log_{10}$: $F_{1,280}=23.07$, $P<0.001$) and in *P. melisellensis* ($F_{1,255}=42.77$, $P<0.001$), but did not differ between species ($F_{1,181}=1.65$, $P=0.20$) (Fig. 3).

T_{e}s and T_{b}s

T_{e}s and T_{b}s in both species were significantly higher during sunny or moderately cloudy ("mosaic") weather than under cloudy conditions (one-way ANOVA, all $P<0.001$). Therefore, data collected under cloudy conditions were excluded from further analyses.

A two-way ANOVA shows a difference in T_{e} between the *L. oxycephala* and *P. melisellensis* category ($F_{1,385}=6.75$, $P=0.01$) and a highly significant diurnal variation in T_{e} ($F_{9,385}=14.57$, $P<0.001$). Diurnal fluctuations were similar in both categories, as indicated by the non-significant interaction ($F_{9,385}=1.37$, $P=0.20$) (Fig. 4).

T_{b}s differed significantly between species (two-way ANOVA: $F_{1,211}=45.83$, $P<0.001$), but not among age/sex classes (subadult, adult male or adult female) ($F_{2,211}=1.67$, $P=0.19$). No interaction was found ($F_{2,211}=0.20$, $P=0.82$). We therefore lumped data for age/sex classes in both species (Table 1). Another two-way ANOVA revealed a significant difference between species ($F_{1,193}=45.70$, $P<0.001$), but no diurnal variation in T_{b}s ($F_{8,193}=1.13$, $P=0.35$). The significant interaction effect
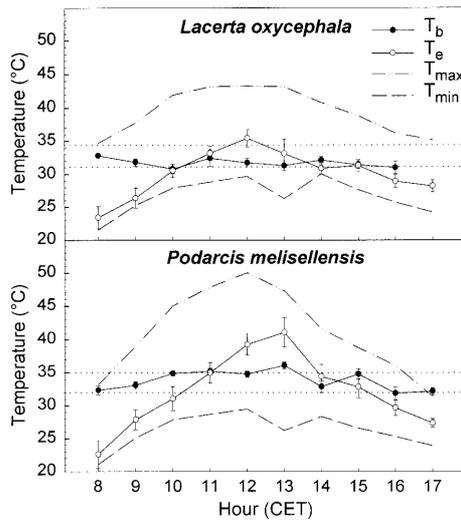
Fig. 4 Body temperature (T_b) (mean±SE), average operative temperature (T_e) (mean±SE), minimum and maximum T_e in *L. oxycephala* and *P. melisellensis*. The *area marked out by the dotted horizontal lines* denotes the setpoint range of the species considered. *CET* Central European time

Table 1 Statistics of body (T_b) and operative (T_e) temperatures, recorded during the field study, and selected temperatures (T_{sel}) in a laboratory thermogradient. *Med* Median, *Q1–Q3* central 50% around median, *Min–Max* minimum–maximum

		Lacerta oxycephala	*Podarcis melisellensis*	ANOVA
T_b	0±SE	31.6±0.2	34.1±0.2	$P<0.001$
	Med	32.3	34.5	
	Q_1–Q_3	30.4–33.3	32.6–35.8	
	Min–Max	24.3–36.1	23.6–38.7	
	n	93	124	
T_e	0±SE	31.2±0.4	33.3±0.6	$P<0.01$
	Med	29.3	29.7	
	Q_1–Q_3	27.1–33.6	26.7–38.5	
	Min–Max	20.9–54.9	18.7–54.9	
	n	217	188	
T_{sel}	0±SE	32.6±0.3	33.9±0.2	$P<0.01$
	Med	33.0	34.2	
	Q_1–Q_3	31.1–34.4	32.9–35.2	
	Min–Max	23.3–37.3	27.8–38.1	
	n	80	80	

($F_{8,193}$=2.34, P=0.02) indicates that the difference between species was not constant throughout the course of the day. Before 1000 and after 1600 hours, *L. oxycephala* and *P. melisellensis* had nearly similar T_bs, but between these hours, *P. melisellensis* obviously maintained higher T_bs than *L. oxycephala* did (Fig. 4).

Behavioural observations by the instantaneous sampling method

Again, we found a difference between species in substrate use (Fig. 5A, B). All *L. oxycephala* individuals
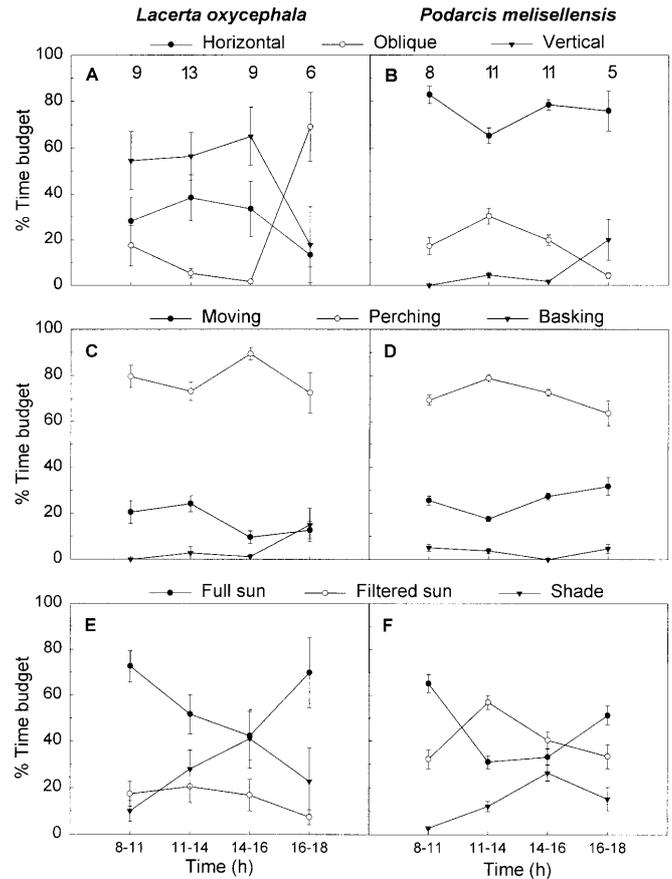

Fig. 5 Diurnal variation in substrate use (**A**, **B**), activity (**C**, **D**) and use of solar microclimates (**E**, **F**) in *Lacerta oxycephala* (**A**, **C**, **E**) and *Podarcis melisellensis* (**B**, **D**, **F**), as revealed by the instantaneous sampling method. All values are mean±SE. **A**, **B** *Numbers on bars* indicate sample size

were observed on stony substrates (walls and rocks), whereas most *P. melisellensis* individuals were seen in vegetation or on flat stones at ground level. *P. melisellensis* was more often seen on horizontal substrates than *L. oxycephala* (two-way ANOVA: $F_{1,64}$=34.43, $P<0.001$). There was no diurnal variation in this pattern ($F_{3,64}$=0.22, P=0.88) and no species×time interaction ($F_{3,64}$=0.88, P=0.46). Vertical substrates were significantly more occupied by *L. oxycephala* than by *P. melisellensis* ($F_{1,64}$=39.95, $P<0.001$). Again, we found no diurnal variation ($F_{3,64}$=0.84, P=0.48), but there was a significant interaction ($F_{3,64}$=3.49, P=0.02), due to a shift from strictly vertical substrates (walls) to more oblique substrates (rocks and boulders) by *L. oxycephala* in the late afternoon. Species did not differ in the use of oblique substrates ($F_{1,64}$=0.35, P=0.56) and no diurnal variation was found ($F_{3,64}$=1.92, P=0.14). The significant interaction ($F_{3,64}$=8.29, $P<0.001$) can be explained by the shift in substrate use by *L. oxycephala*, as described above.

Activity did not fluctuate throughout the course of the day ($F_{3,64}$=0.57, P=0.63). *P. melisellensis* was observed moving more than *L. oxycephala* ($F_{1,64}$=5.03, P=0.03). The

difference between species was more pronounced during the afternoon (1400–1800 hours), which explains the significant interaction ($F_{3,64}=3.57$, $P=0.02$) (Fig. 5C, D). In the category "perching", we found no difference between species ($F_{1,64}=2.49$, $P=0.12$), no hour effect ($F_{3,64}=1.42$, $P=0.24$) and no interaction ($F_{3,64}=1.92$, $P=0.14$). The same result was obtained in the category "basking" (species, $F_{1,64}=0.34$, $P=0.56$; hour, $F_{3,64}=2.42$, $P=0.07$; interaction, $F_{3,64}=1.55$, $P=0.21$).

L. oxycephala tended to use sunny places more frequently than *P. melisellensis*, but this difference was marginally non-significant ($F_{1,64}=3.53$, $P=0.06$). Lizards were more often seen in full sun during the first and last time interval than at midday and in the early afternoon ($F_{3,64}=4.18$, $P=0.009$). There was no species×time interaction ($F_{3,64}=0.31$, $P=0.83$) (Fig. 5E, F). The opposite tendency was found in the use of shaded places: lizards found themselves more in shade at midday and in the early afternoon than in the morning and the late afternoon ($F_{3,64}=3.75$, $P=0.02$). *L. oxycephala* tended to be more often in shade, but again, the difference between species was non-significant ($F_{1,64}=3.33$, $P=0.07$) and no interaction effect was found ($F_{3,64}=0.20$, $P=0.90$). Time spent in filtered sun did not vary throughout the day ($F_{3,64}=1.25$, $P=0.30$), but differed between species ($F_{1,64}=12.08$, $P<0.001$): *P. melisellensis* was observed more in filtered sun than *L. oxycephala*. No interaction was found ($F_{3,64}=0.31$, $P=0.65$).

Selected temperatures

L. oxycephala and *P. melisellensis* selected different temperatures in the laboratory thermogradient (one-way ANOVA: $F_{1,158}=9.73$, $P=0.002$) (Table 1, Fig. 4).

Thermoregulation

The mean deviation of the T_bs from T_{sel} (i.e. δ_b) did not differ significantly between *L. oxycephala* (0.84 ± 0.16°C) and *P. melisellensis* (1.04 ± 0.13°C) (one-way ANOVA: $F_{1,217}=1.08$, $P=0.30$), which indicates an equal rate of accuracy of thermoregulation in both species. The mean deviation of the T_es from T_{sel} (i.e. δ_e), as a measure for habitat quality, was 3.78 and 6.27 for *L. oxycephala* and *P. melisellensis*, respectively. Consequently, *E*, computed as $1-\delta_b/\delta_e$, was 0.78 for *L. oxycephala* and 0.83 for *P. melisellensis*. Bootstrap resampling revealed no significant difference in *E*: *P. melisellensis* had the higher value of *E* in 854 of 1,000 simulations ($P>0.05$).

During the whole period of activity, T_{min} and T_{max} in the microhabitat of *L. oxycephala* were respectively lower and higher than this species' setpoint range, suggesting that it was possible to keep T_b within this range (Fig. 4). Indeed, *L. oxycephala* maintained a highly constant T_b throughout the course of the day, well within the selected temperature interval. However, mean T_e exceeded the lower or upper limit of the setpoint range several times. This implicates an accurate thermoregulation during these hours, in order to keep T_b within the setpoint range. The same pattern was found in *P. melisellensis* (Fig. 4). T_{max} and T_{min} were always above and under the setpoint range respectively (except T_{max} in the intervals 0800–0900 hours and 1700–1800 hours), allowing the maintenance of T_b within this range. Indeed, T_bs were kept within the setpoint range, but T_e fell outside this range during considerable parts of the day, forcing *P. melisellensis* individuals towards an accurate thermoregulatory behaviour.

Discussion

Body temperatures and thermoregulatory behaviour

Body temperatures of both *Lacerta oxycephala* and *Podarcis melisellensis* exhibited little diurnal variation and fell within each species' setpoint range during the period of activity. As a consequence, accuracy of thermoregulation was high in both species. This high accuracy does not necessarily imply active thermoregulation, since it may also be caused by a favourable thermal environment (Hertz et al. 1993). However, the following results strongly suggest effective behavioural thermoregulation in both species. First, lizards were observed more frequently in full sun than randomly distributed copper models. Moreover, diurnal variation in the lizard's use of sun and shadow was opposite to the variation in the availability of sun and shadow. Second, lizards were significantly closer to sun-shade transitions than were copper models, suggesting that they tried to reduce the time or energy costs associated with shuttling between sun and shadow (Huey and Slatkin 1976; Huey and Pianka 1981). Third, basking behaviour, a mechanism that increases the rate of heat gain (Avery 1976; Bauwens et al. 1996) was observed in both species. Finally, T_bs were on average closer to T_{sel} than were T_es and, as a consequence, the calculated value of *E* was close to one in both species, indicating a high effectiveness of thermoregulation (Hertz et al. 1993).

These results coincide with those of earlier studies on thermal ecology in lacertid lizards (Pérez-Mellado 1983; Van Damme et al. 1987, 1989, 1990; Bauwens et al. 1990, 1996; Braña 1991; Castilla and Bauwens 1991; Díaz 1994; Grbac and Bauwens 2001), all suggesting a high degree of behavioural thermoregulation in species belonging to this family.

Two distinct methods were used to quantify microhabitat use and thermoregulatory behaviour (see Materials and methods). In general, results obtained by the instantaneous sampling method agreed with those gathered by recording the behaviour of a lizard captured afterwards, but there was one striking exception. The instantaneous sampling method yielded much lower estimates of basking frequency than the capture data did. Although the result obtained by analysis of capture data (relatively high basking frequency, especially in the morning and late after-

noon) is consistent with several other studies on thermoregulation in lacertid lizards (e.g. Van Damme et al. 1987; Castilla and Bauwens 1991; Grbac and Bauwens 2001), we judge the results obtained by the instantaneous sampling method to be more reliable. Since basking or moving lizards are probably more easily detectable than perching lizards (Huey 1982), data could be biased (i.e. basking time could be overestimated) when behaviour is only recorded upon first sighting of a lizard. This problem is circumvented by monitoring an undisturbed individual during a recording session that lasts for several minutes. Clearly, continuous monitoring of body temperatures using telemetry would provide superior information on the thermoregulation of these animals. However, even the smallest transmitters available today still weigh 10–20% of the body mass of adult *P. melisellensis* and *L. oxycephala*, so telemetry was not an option in this study.

Thermal habitat quality and evolution of thermal characteristics

Our field data on the microhabitat use of both species conform to the descriptions found in reference works. *L. oxycephala* individuals were most often seen on walls and boulders and proved to be excellent climbers, whereas *P. melisellensis* individuals occurred mostly in vegetation or on flat stones and were only occasionally seen climbing (cf. Arnold et al. 1978; Bischoff 1984; Tiedemann and Henle 1986; Arnold 1987; Gasc et al. 1997).

Thermal quality differed between these microhabitats in the expected way. In the early morning and late afternoon, available temperatures (T_e) were a little higher on the vertical walls than on horizontal substrates, due to the low solar altitude at those times of the day. For most of the day, however, T_es were significantly higher in the *P. melisellensis* microhabitat, which can be explained by the higher solar altitude and differences in convection between vegetation-covered and bare substrates (Campbell and Norman 1998). Therefore, overall absolute thermal quality appeared to be higher in the *P. melisellensis* microhabitat.

Theoretically, *L. oxycephala* may respond to the cooler conditions in its microhabitat in three different ways: (1) by increasing thermoregulatory efforts (relative to *P. melisellensis*) in order to attain a T_b comparable to that of *P. melisellensis*, (2) by maintaining a "normal" level of thermoregulation and being active at suboptimal T_bs, or (3) in an adaptive way by lowering selected (or optimal) temperatures. The first possibility can be rejected on the basis of our field data: we found no difference in thermoregulatory behaviour between species and T_bs of *L. oxycephala* were significantly lower than those of *P. melisellensis*. Furthermore, our results indicate that most *L. oxycephala* individuals are active at T_bs well within the range of selected temperatures, which allows us to reject the second possibility as well (considering T_{sel} as a compromise to the thermal optima of different performance functions, Van Damme 1989).

Thus, T_{sel} corresponds remarkably well to T_b and T_e in both species, indicating an adaptive response to the thermal conditions in their respective microhabitat. This conclusion is consistent with the labile view on the evolution of thermal physiology. This is rather unexpected, since earlier studies supported the static view on the evolution of thermal characteristics in the Lacertidae (Van Damme et al. 1989, 1990). However, in both papers mentioned, an intraspecific comparison was made between a lowland and a mountain population (in *Podarcis tiliguerta* and *Lacerta vivipara*, respectively), whereas our study focused on interspecific microclimatological differences within a habitat. Possibly, *L. oxycephala* and *P. melisellensis* may have had more time to adapt to their respective thermal microhabitat on Vis.

Clearly, further work is necessary to elucidate general trends in the thermal quality of different microhabitat types and in the evolution of thermal physiology in lacertids. This study has provided a research protocol that can be applied to several existing systems of two lacertid lizard species living in the same macrohabitat, but differing in microhabitat use (review in Arnold et al. 1978, Arnold 1987).

Historical pathways in microhabitat use

Although both species appear to be adapted to their respective microclimate, the hypothesis that *P. melisellensis* forced *L. oxycephala* into a thermally inferior microhabitat cannot be rejected, since thermal quality of the "vertical" microhabitat was lower than that of the "horizontal" microhabitat. Two possible historical pathways can be distinguished. The microhabitat, occupied by *L. oxycephala* on Vis, may represent the species' preferred microhabitat, irrespective of the presence or absence of a ground-dwelling species. On the other hand, it is possible that *L. oxycephala* is actually more catholic in its microhabitat preference and has been forced into a rather narrow and thermally inferior microhabitat by *P. melisellensis*.

In order to investigate these possibilities, other islands where populations of *L. oxycephala* and *P. melisellensis* occur syntopically should be investigated, and compared to those where one of these species lives in isolation. Measurement and comparison of microhabitat use, T_e, T_b, T_{sel} and T_{opt} of ecologically relevant performance functions (e.g. sprint speed) may reveal the possible competitive impact of *P. melisellensis* and *L. oxycephala* on each other's microhabitat use, thermal ecology and performance.

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