

## Size-dependent heating rates determine the spatial and temporal distribution of small-bodied lizards

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**Abstract.** The rate of heat exchange with the environment is of obvious importance in determining the time budget of behavioural thermoregulation in ectotherms. In small reptiles, heating rate depends mainly on their physical characteristics. We analysed the effect of body size, and the possible joint effects originating from shape and colour differences on heating rate in three small-bodied (0.15-20 g) sympatric lizard species. Heating rate was strongly influenced by body size, while no joint effects with the two other factors were detected. We found that the increase in heating rate with decreasing body size accelerated dramatically below a body weight of 2-3 g. We also analysed associations between body size, seasonal activity patterns and thermal characteristics of the sites where lizards were encountered in the field. Differently sized lizards occurred in thermally different sites and differed in their seasonal activity patterns, both within and among species. Smaller (<2-3 g) lizards occurred in cooler sites and exhibited very low activity during summer. Our results suggest that body size has a considerable influence on the spatial and temporal distribution of extremely small lizards in environments subject to a danger of overheating.

### Introduction

The importance of the thermal environment for ectotherms has been recognized for some time (e.g., Cowles and Bogert, 1944; Bartlett and Gates, 1967). Keeping body temperature ( $T_b$ ) in the thermally optimal range is necessary for maintaining the efficiency of physiological processes (e.g., Stevenson, 1985a; Angilletta et al., 2002). Furthermore, a variety of traits are affected by  $T_b$  in lizards, such as prey handling time (Avery and Mynott, 1990), foraging and prey capture (Avery et al., 1982; Belliure et al., 1996), consumption and gut-passage time (Van Damme et al., 1991), locomotory performance (Avery and Bond, 1989; Van Damme et al., 1990; Du et al., 2000), escape behaviour (Smith, 1997; Cooper, 2000) and reproduction (Shine and Harlow, 1993; Rock et al., 2002).

Ectotherms use a number of ways to control  $T_b$ . Physiological adjustments, and different behavioural mechanisms such as shuttling between different patches of the thermal environment, postural adjustments and the times of seasonal and daily activity should occur together (Stevenson, 1985a), but behavioural thermoregulation seems to be predominant if solar radiation is available (Stevenson, 1985a; Adolph, 1990; Bauwens et al., 1996).

Although behavioural thermoregulation by microhabitat selection is beneficial, it is also costly. The cost is higher in more thermally challenging environments, simply because more time is devoted to this behaviour (Huey and Slatkin, 1976). The higher the proportion of patches with disadvantageous or lethal temperatures in a microhabitat, the more costly the individual activity (movements, foraging, etc.) becomes (Grant and Dunham, 1988). Heating rates determined by the physical properties of small lizards (e.g., size, shape, colour/absorbance) should predict their opportunities to be active under extreme temperatures. The heat exchange rate with the environment increases with decreasing size (Grigg et al., 1979; Carrascal et al., 1992; Martín and López, 2003), thus, selecting an inappropriate thermal microclimate

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for even a few minutes can be fatal for small lizards (Stevenson, 1985b; Grant and Dunham, 1988). However, previous studies suggest that differences in absorptance are not important in heat exchange in small-bodied species. Even extreme colour differences due to melanism only caused negligible effects on the thermoregulation of small lacertid lizards such as *Lacerta dugesii* (Crisp et al., 1979), *Podarcis muralis* (Tosini et al., 1992) or *Zootoca vivipara* (Gvoždik, 1999), while Shine and Kearney (2001) found only minor colour effects beside size with physical models, and only for those in the large size category.

Overheating is a more serious danger than cooling when lizards change their microhabitats. This is because heating rates are usually higher than cooling rates (Grigg et al., 1979; O'Connor, 1999), and  $T_{bs}$  temporarily lower than the preferred range have less harmful effects on the individuals. In the temperate zone, where the activity season includes both relatively cold and hot periods, individuals with large differences in heating rates may differ in their activity times and microhabitat use, irrespective of differences in their thermoregulation strategy and the efficacy of that strategy.

The upper and lower quartiles of the critical thermal maxima (see Brattstrom, 1965) of 32 lizard species (data from: Brattstrom, 1965; Brown, 1996; Witz, 2000; Gvoždik and Castilla, 2001) were 45.5 and 41.7°C respectively. At our study site the near-ground air temperature ( $T_g$ ; measured <0.5 cm above the ground) in summer exceeds 50°C from 10:00 h to 16:00 h in a large proportion of the open habitats where most of the lizards are encountered, and during this period  $T_g$  even in the shade is routinely above 30°C (Herczeg et al., unpubl. data). Although  $T_g$  might differ from the operative temperature ( $T_e$ ;  $T_e$  actually gives an estimate of  $T_b$  for an object that does not behaviourally or physiologically thermoregulate and is at equilibrium; Bakken et al., 1985; Hertz et al., 1993), we assumed that high  $T_g$  is a good predictor of high  $T_e$ , as Vitt and Sartorius (1999) found that

even external probes of data-loggers provide a good estimate of  $T_e$  for small ectotherms. Even though critical thermal maxima may co-adapt with optimal temperatures that evolve with the level of field  $T_{bs}$  (Huey and Kingsolver, 1993),  $T_{gs}$  around 50°C presumably represent harmful or lethal temperatures for most reptile species.

The aim of this study was to demonstrate that body size is the predominant factor in determining the heating rate and in shaping the temporal and spatial distribution of extremely small lizards in environments subject to a danger of overheating. We examined (1) if there is a joint effect besides size originating from shape and colour differences on the heating rate of three sympatric small-bodied lizard species; (2) if there is a link between the size of the lizards, their thermal microhabitat use and seasonal activity patterns in the field.

## Materials and methods

### *Study species and study site*

The Snake-eyed Skink (*Ablepharus kitaibelii* Bibron and Bory, 1833) is one of the smallest lizards of Europe, with snout to vent length (SVL) of 20-55 mm and body weight (BW) of 0.15-1.5 g. It is a ground-dwelling, insectivorous heliotherm. It has a shiny brown dorsal colour pattern and an elongated body shape with reduced legs and small head. The Common Wall Lizard (*Podarcis muralis* Laurenti, 1768) is a rock-dwelling, insectivorous heliotherm and has SVL between 30 to 65 mm and BW of 0.7-6.5 g. Its dorsal colour is flat greyish brown. It has a flattened body shape and relatively long legs as compared to *A. kitaibelii*. The Green Lizard (*Lacerta viridis* Laurenti, 1768) is one of the largest lizards in Europe, but still relatively small in a worldwide scale with its SVL ranging from 30 to 115 mm and BW of 0.9-20 g. It is a ground-dwelling, insectivorous heliotherm. *L. viridis* is a robust lacertid lizard with strong legs. Dorsal colour is flat greenish brown in adult females but intense green in adult males. Juveniles are greyish brown.

Fieldwork was carried out in the Sas Hill Nature Reserve (N19°51'; E47°30'), a dolomite hill (maximum elevation is 259 m a.s.l.) within the area of Budapest, Hungary. The local vegetation was composed of dolomite grasslands with single or aggregated scrubs, trees and rock outcrops.

### *Measurements of heating rate*

The heating rate of *A. kitaibelii* ( $N = 9$ ), *L. viridis* ( $N = 8$ ), and *P. muralis* ( $N = 9$ ) individuals with intact tails, covering all size categories were measured in the laboratory.

**Table 1.** Body weight (BW; g) range of the lizard groups ( $N$  = number of the measured individuals) used in the analysis of the field data. The samples were taken from our field study site.

	BW range	N
<i>Ablepharus kitaibelii</i>	0.15-1.5	31
Adult <i>Ablepharus kitaibelii</i>	0.7-1.5	18
Juvenile <i>Lacerta viridis</i>	0.9-2.5	13
Adult <i>Podarcis muralis</i>	2.5-5.1	11
Large <i>Lacerta viridis</i>	6.3-17.5	10

The lack of *L. viridis* individuals with BW between 2.5 and 6.3 g (table 1) represents the size gap between age groups in autumn, when the experiments were carried out. Experimental lizards were anaesthetized with Halothane (Újvári et al., 1999), SVL measured to the nearest 1 mm, mid-body width (MW; measured in the widest part of the body with a digital calliper) measured to the nearest 0.01 mm, and BW measured with a METTLER PM 4800 (Mettler-Toledo AG, Greifensee, Switzerland) balance to the nearest 0.01 g before the trial. Lizards were placed on a white plastic board (25 × 45 cm) on stands (15 cm high) to reduce conductance with the substrate. A K-type thermocouple connected to a digital thermometer (TESTO 925, TESTO GmbH, Lenzkirch, Germany) was inserted to about 5 mm depth into the lizard cloaca. A 100 W reflector bulb was suspended above the centre of the board, placed at the height required to produce permanent 50°C  $T_e$ , to mimic the harmful natural conditions of the study area in summer. Lizards were cooled to 15°C before they were placed under the bulb.  $T_b$  between 20 and 35°C (to keep  $T_b$  in a tolerable range) was recorded at 15 s intervals. Note that this procedure did not allow lizards to use postural adjustments during the experiment, as we were not interested in measuring behavioural interspecific differences.

Operative temperature of the experimental area was measured with a physical lizard model (Hertz et al., 1993). A hollow copper pipe (65 mm long, 12 mm in external diameter, 1 mm wall thickness) sealed with plastic caps, painted brown was used and the thermocouple used to measure  $T_b$  of the lizards was inserted. The same physical model was used for all studied individuals, as the differences originating from model properties are probably small (Shine and Kearney, 2001; but see Dzialowski, 2005). However, we measured  $T_e$  only to assure that the thermal conditions were constant, and in the harmful range.

Heating rates (C°/min) were determined as the slopes of the linear regressions relating  $T_b$  and time elapsed (e.g., Díaz, 1991; Belliure et al., 1996). This was an appropriate procedure, as  $T_b$  increased linearly with time in each case (mean  $R^2$  = 0.98; SE = 0.002; range: 0.96-0.99; all  $P$  < 0.001) and lizards had not attained an equilibrium temperature. Thus, we did not use analytical procedures that assume a non-linear relation between  $T_b$  and time (Spotila et al., 1973).

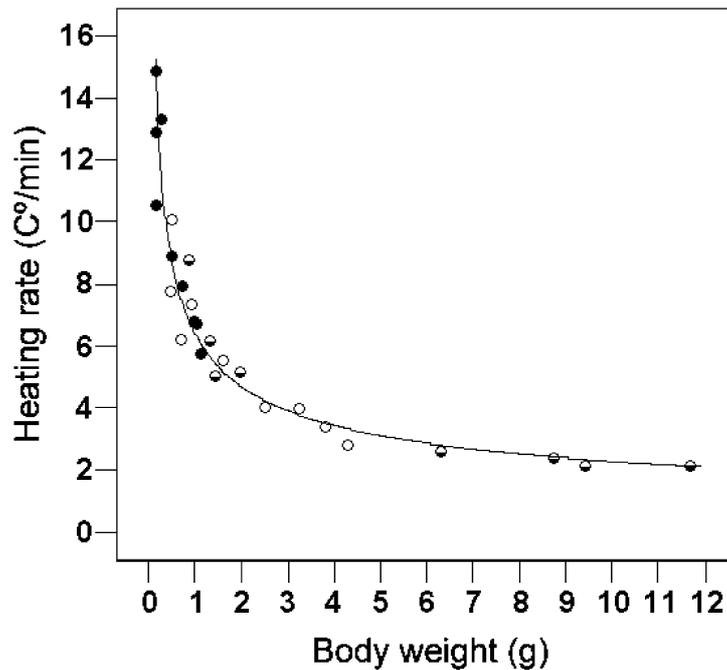
#### Field methods

Sampling was undertaken during the spring of 2002, from 12 March to 25 May (on 6 days), in summer from 20 June to 17 August (on 5 days), and in autumn from 2 September to 12 November (on 6 days). Sampling was conducted every second week during days with mostly or totally clear sky and low or no wind conditions. Samples were always taken by the first author (GH) from 07:00 h to 19:00 h on each day. A constant effort was made to ensure observations were evenly distributed over the daily activity period and between the different microhabitats. GH walked slowly through the study area, searching for field-active lizards. If a lizard was detected, species, size group (hatchlings or yearlings; subadults; adults) and  $T_g$  of the exact site (<0.5 cm above the ground) where the individual had been first seen were all recorded. For the temperature measurements the external probe (covered with white plastic; diameter ca. 3 mm) of a digital thermometer (ETHG913R, Oregon Scientific, Maidenhead, UK) was used. Constructing and validating sufficient  $T_e$  models for the studied lizards (with respect to differences in size, shape and reflectance) would have been complicated, thus we measured  $T_g$  instead of  $T_e$ . However, this variable described the actual thermal environment irrespective of the individual, assuring that significant differences in the measured temperature type between lizards meant different spatial and/or temporal occurrence. Hence, this variable fit well to our purposes. We note that this approach is not adequate to evaluate the thermal resource partitioning patterns, but we focused on the exact spatial and temporal distribution of the individuals.

#### Data analyses

BW was used as a proxy of body size to examine the relationship between size and heating rate. BW was  $\log_{10}(\text{lg})$  transformed to achieve normality. We used the residuals from the  $\text{lgMW} - \text{lgSVL}$  (both transformed for normality) regression as a variable describing shape (slimness) to examine the relationship between shape and heating rate. We did not quantify absorptance, but the differences between the studied species, at least in the human-visible colour range, are evident (Gruber, 1981; Netmann and Rykena, 1984; Gruschwitz and Böhme, 1986). We assumed that the differences in heating rate after body size and shape were controlled for reflect the effect of reflectance differences. Heating rate values were also  $\text{lg}$  transformed, to avoid the effect of the relative dominance of smaller individuals in the data set (fig. 1). The relationships between size, shape, species and heating rate were analysed with MANOVA and ANCOVA models.

In the analyses of field data, only data from *A. kitaibelii*, *L. viridis* and adult *P. muralis* were incorporated, as the amount of data from juvenile and subadult *P. muralis* was insufficient for statistical analysis. *A. kitaibelii*, juvenile *L. viridis* (small body size, high heating rate;  $N$  = 47; 50, respectively), adult *P. muralis* (average body size and heating rate;  $N$  = 65) and subadult and adult *L. viridis* (large body size, low heating rate; hereafter large *L. viridis*;  $N$  = 72) groups were compared with each other (fig. 1; table 1). Intraspecific differences between size groups in the case of



**Figure 1.** The relationship between body weight and heating rate in *Ablepharus kitaibelii* (filled circles;  $N = 9$ ), *Lacerta viridis* (half-filled circles;  $N = 8$ ) and *Podarcis muralis* (open circles;  $N = 9$ ). Although both body weight (to achieve normality and linearity), and heating rate (to avoid the effect of the relative dominance of smaller individuals in the data) were  $\log_{10}$  transformed for the statistical analyses, we provide the original data here. Note that adult *L. viridis* can grow even larger (ca. 20 g).

*L. viridis*, interspecific differences in the same size group (*A. kitaibelii* and juvenile *L. viridis*), and interspecific differences between size groups were also investigated. In this way size effects were separated from the potential effects of age and species. Although BW and heating rate ranges of *A. kitaibelii* and juvenile *L. viridis* were not exactly similar (fig. 1; table 1), similar thermal constraints were hypothesized for these lizard groups due to the considerable overlap in their heating rates and the similar position in the scale of our study species' size range (BW from ~0.15 to ~20 g). However, to justify handling *A. kitaibelii* and juvenile *L. viridis* as similarly sized, all analyses were also performed including only adult *A. kitaibelii* ( $N = 32$ ) in which case the size ranges of the two groups were even more similar (fig. 1; table 1). As the results did not change qualitatively, only results from the original dataset are reported here.

Three sets of analyses were performed to explore the differences between lizard groups in their thermal microhabitats. First, the four groups were compared using data only from spring and autumn, as *A. kitaibelii* and juvenile *L. viridis* were almost completely absent in summer (figs 2, 3) using a two-way ANOVA (to compare the  $T_{gs}$  they experienced during their common activity period). Second, differences in the recorded  $T_{gs}$  between the lizard groups during the whole activity period irrespective of their seasonal activity patterns were analysed with an ANOVA (to compare the  $T_{gs}$  they experienced during their whole activity period).

Third, adult *P. muralis* and large *L. viridis* were compared using data only from summer with a Student *t*-test. To compare the seasonal activity patterns, the percentage of distribution of the lizards encountered among seasons weighted with the number of sampling days within season was used in the log-linear analysis. All statistical analyses were carried out using the SPSS 12.0 for Windows (SPSS Inc. Chicago, Illinois) and the STATISTICA 7.0 for Windows (StatSoft. Inc. Tulsa, Oklahoma) softwares.

## Results

### *Heating rate in relation to body size, shape and species*

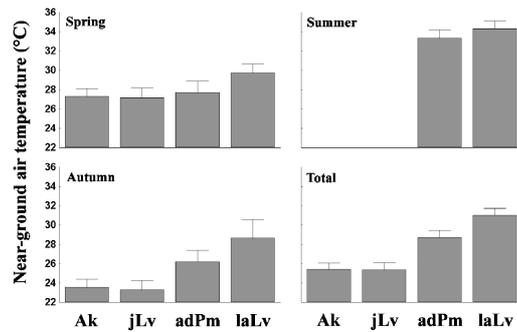
Both body size and shape differed among species (MANOVA: Wilks'  $\lambda = 0.18$ ;  $F_{4,44} = 14.71$ ;  $P < 0.001$ ). Post-hoc tests (LSD tests) revealed that the skink *A. kitaibelii* differed in body size from both lacertids ( $P < 0.01$ ), whereas lacertids differed only marginally ( $P = 0.065$ ) from each other. The non-significant *P*-value is probably due to the small sample

size, but the size difference between adult *L. viridis* and *P. muralis* is evident (e.g., Netmann and Rykena, 1984; Gruschwitz and Böhme, 1986). *A. kitaibelii* was significantly “slimmer” than the lacertids (LSD-tests:  $P < 0.001$ ), while the lacertids were of similar body shape to each other (LSD-test:  $P = 0.96$ ).

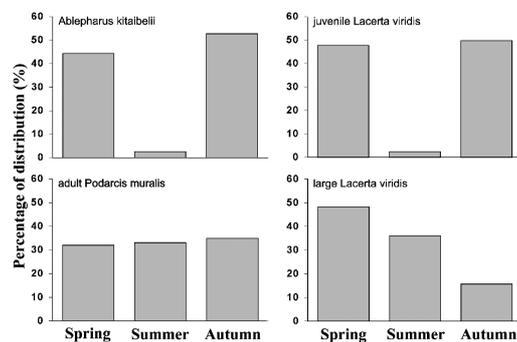
An ANCOVA revealed a significant positive relationship between body size and heating rate (fig. 1;  $F_{1,17} = 128.46$ ,  $P < 0.001$ ), while no relationship between shape and heating rate was found ( $F_{1,17} = 0.58$ ,  $P = 0.45$ ). The size – heating rate and shape – heating rate relationships did not differ between the species (species\**size*:  $F_{2,17} = 1.73$ ,  $P = 0.21$ ; species\**shape*:  $F_{2,17} = 0.38$ ,  $P = 0.69$ ). Heating rate corrected for body size and shape did not differ between the species either ( $F_{2,17} = 1.35$ ,  $P = 0.29$ ). Thus, our data did not indicate the presence of any effects of colour or other characteristics besides size and shape. In addition, we plotted heating rate against BW (fig. 1), using the untransformed data, and found that the equation of the best-fit curve is:  $Y = 6.391 * X^{-0.447}$  (power regression model:  $R^2 = 0.96$ ;  $F_{1,24} = 553.28$ ;  $P < 0.001$ ). The critical weight where the increase in heating rate with decreasing BW accelerates seemed to be around 2-3 g (fig. 1).

*Relationships of heating rate with field T<sub>g</sub>s and seasonal activity*

A two-way ANOVA, using T<sub>g</sub> as the dependent variable, and lizard group (*A. kitaibelii*, juvenile *L. viridis*, adult *P. muralis* and large *L. viridis*) and season (spring and autumn) as factors, revealed significant effects of both factors (lizard group:  $F_{3,180} = 5.09$ ;  $P < 0.002$ ; season:  $F_{1,180} = 10.90$ ;  $P < 0.001$ ) while their interaction was nonsignificant ( $F_{3,180} = 0.86$ ;  $P = 0.46$ ). In the post hoc comparisons *A. kitaibelii*, juvenile *L. viridis* and adult *P. muralis* did not differ significantly (LSD tests; all  $P > 0.1$ ), while all of them differed from large *L. viridis* (LSD tests; all  $P < 0.05$ ; fig. 2).



**Figure 2.** Mean (±S.E.) near-ground air temperatures of the sites selected by *Ablepharus kitaibelii* (Ak), juvenile *Lacerta viridis* (jLv), adult *Podarcis muralis* (adPm) and large *L. viridis* (laLv) in the different seasons and in total, irrespective of seasons. Note that *A. kitaibelii* and juvenile *L. viridis* were almost completely missing in summer (see fig. 3).



**Figure 3.** Seasonal activities of *Ablepharus kitaibelii*, juvenile *Lacerta viridis*, adult *Podarcis muralis* and large *L. viridis*. The percentage of distribution among seasons was weighted with the number of sampling days within season.

An ANOVA testing for differences in T<sub>g</sub>s experienced among the lizard groups during the whole activity period, irrespective of season, showed significant differences among the lizard groups ( $F_{3,228} = 15.29$ ;  $P < 0.001$ ). In the post hoc comparisons, T<sub>g</sub>s of *A. kitaibelii* and juvenile *L. viridis* did not differ (LSD test:  $P = 0.94$ ), but both of them differed from adult *P. muralis* and large *L. viridis* (LSD tests; all  $P < 0.01$ ; fig. 2). Adult *P. muralis* and large *L. viridis* also differed from each other (LSD test:  $P = 0.01$ ; fig. 2). Near-ground air temperatures of the sites of adult *P. muralis* and large *L. viridis* did not differ significantly from each other in summer ( $t_{39} = 0.8$ ;  $P = 0.43$ ; fig. 2).

Activity patterns showed a highly significant interaction between season and lizard group ( $\chi^2 = 93.32$ ;  $df = 6$ ;  $P < 0.001$ ) in the log-linear analysis. The pairwise  $\chi^2$  tests (with Bonferroni adjustment) revealed that apart from the *A. kitaibelii* – juvenile *L. viridis* pair ( $\chi^2 = 0.44$ ;  $df = 2$ ;  $P = 0.8$ ) all other pairs differed significantly in their seasonal activity patterns ( $\chi^2 > 29.32$ ;  $df = 2$ ;  $P < 0.001$ ; fig. 3).

### Discussion

We found a strong relationship between body size and heating rate without any joint effect despite the considerable differences in body shape and human-visible colour of the studied species, which implies that body size is the dominant determinant of this variable and the effects of other factors (e.g., absorptance of solar radiation, shape, structure of skin surface) are negligible. Theoretically, the other factors could nullify each other or counteract in such a way that their summed effect is exactly equal in the three species. It is noteworthy that the ability to physiologically control heat exchange by altering blood flow shows a decreasing tendency in reptiles weighing less than 1 kg (Dzialowski and O'Connor, 1999), thus it might be irrelevant in our study species, especially for *A. kitaibelii* or juvenile *L. viridis* (<2-3 g). In our laboratory experiment, we measured heating rate providing radiant heat source. In the field, size-dependent and absorptance-independent conductance with the substrate and mainly convection with the near-ground air layer – heated by the substrate (Bakken, 1989) – could also be important in the heat exchange of small, ground-dwelling lizards, as a consequence of the thin boundary layers of their small bodies (Porter et al., 1973; Porter and James, 1979; Belliure and Carrascal, 2002); and should further strengthen the importance of body size. Hence, we conclude that the influence of the joint effect of the other factors is negligible in the small size category, or in other words, ectotherms as small as our study species warm up so rapidly that slight differ-

ences in the energy input due to colour or shape differences do not cause appreciable differences in the rate of heating (Tosini et al., 1992). In fact, earlier studies using living animals or physical models in the size category of our study species confirm this phenomenon (Crisp et al., 1979; Hertz, 1992; Tosini et al., 1992; Gvoždik, 1999; Shine and Kearney, 2001). However, experimental studies have shown a thermoregulatory advantage of melanism for larger amphibians and snakes as well as for much smaller insects (Gibson and Falls, 1979; Forsman, 1995, 1997; de Jong et al., 1996; Vences et al., 2002). To translate heating rate:  $T_b$  of an average individual of *A. kitaibelii* or juvenile *L. viridis* increased from 20°C to 35°C (on  $T_e = 50^\circ\text{C}$ ) in 2-3 minutes (only 1-1.5 minutes for a juvenile *A. kitaibelii*) while it takes 7 or even more minutes for an adult *L. viridis* (fig. 1; note that *L. viridis* can grow up to ca. 20 g). If one inspects fig. 1, it is obvious that heating rate changes very fast with body size in the size range of *A. kitaibelii* and juvenile *L. viridis*, while this rate of change slows down in the size range of adult *P. muralis* and large *L. viridis*. Thus, inclusion of species/individuals weigh less than 2-3 g seems to be of crucial importance for interpreting the ecological consequences of heating rates in small bodied lizards.

Carrascal et al. (1992) showed that in the small lacertid lizard *Lacerta monticola*, juvenile individuals with small body mass and thus high heating rate basked more frequently but for shorter periods, and devoted more time to locomotion than adults. In the same species, Martín and López (2003) found that ontogenetic changes in size-dependent heating rates result in size-dependent use of thermally unfavourable refuges. In the studies mentioned above (Carrascal et al., 1992; Martín and López, 2003), lizards were faced with the challenge of thermoregulating in a cool environment, while in our study site the danger of overheating was relevant in summer. In the medium sized (up to 90 g) *Agama agama*, body size predicted seasonal and daily activity, and distribution of

the individuals in an extremely hot environment (Porter and James, 1979).

We found bimodal seasonal activity patterns (i.e. a lack of activity in summer) in juvenile *L. viridis* and in *A. kitaibelii*, but not in adult *P. muralis* or in the large size group of *L. viridis*. This bimodality could be a bias originating from a seasonal shift in microhabitat use (in summer smaller individuals are expected to move into more sheltered sites), but during the fieldwork, all microhabitat types were equally sampled. Furthermore, for other reasons, we searched for temporarily inactive lizards under rocks (an area often used by *A. kitaibelii*) over the whole activity season, and in summer these places were empty. We did not observe nocturnal activity in the studied species. Since fieldwork in summer was carried out on “typical” summer days (mostly or totally clear sky conditions), on clouded (therefore cooler) days the activity patterns could be different. However, the high  $T_g$ s experienced in summer by adult *P. muralis* and large *L. viridis* groups demonstrate the thermal challenge for the small bodied *A. kitaibelii* and juvenile *L. viridis* that could result in the bimodal activity pattern seen in these groups. Our results show that the constraint of high temperatures determines not only daily (Grant, 1990; Melville and Swain, 1997) but also seasonal activity patterns of lizards with a high heating rate (i.e. small individuals). The constraint of lower temperatures on lizards with a lower heating rate (i.e. larger individuals) seems to be less important as adult *P. muralis* and large *L. viridis* occurred in both relatively cold and hot places. Taking into account the type of our comparisons (age independence), the effect of behavioural differences among juvenile and adult individuals can be excluded. Some additional factors we did not control for could have strengthened the effect of the high environmental temperature in summer. Water availability and humidity is known to influence lizard physiology and behaviour, and according to physical laws, evaporation increases when temperature increases (Lorenzon et al., 1999). Hence, there

is a high risk of overheating, coupled with the danger of desiccation during summer for small-bodied lizards. Moreover, both thermal and water constraints could be similar for their prey. In summary, the body size of small diurnal lizards seems to determine their seasonal activity in the temperate zone where there is a seasonal danger of overheating.

We found differences between size groups in  $T_g$  of the sites that were selected by lizards irrespective of consideration of all seasons or only the common activity periods of the species. Larger lizards preferred/tolerated higher  $T_g$ , while both *A. kitaibelii* and juvenile *L. viridis* were found equally at cooler sites. There was no difference found between adult *P. muralis* and large *L. viridis* in summer, probably because heating rate does not change so dramatically with size in their size category, as in the size range of *A. kitaibelii* or juvenile *L. viridis*. We note that  $T_g$  is only one of many variables (e.g., solar radiation, wind speed) that potentially affects heating rate and  $T_b$ , but the difference among size groups irrespective of species and age indicates a temperature or temperature-time related size-dependent difference in microhabitat selection.

According to theoretical models of ectotherms in environments where solar radiation is available, behavioural mechanisms provide many times greater ranges of available  $T_b$  than physiological adjustments, and the timing of seasonal and daily activities seems to be the most critical factor determining  $T_b$  (Stevenson, 1985a). During activity, thermal microhabitat selection is the predominant thermoregulatory behaviour (Stevenson, 1985a). Our data suggests that lizards weighting less than 2-3 g – according to their extremely high heating rates – cannot cope with the danger of overheating in summer by shuttling between thermally different patches, thus the only available behavioural option for them is to cease activity. Within their activity period, smaller lizards are restricted spatially and/or in time to use only cooler sites. Unfortunately, we do not have sta-

tistically sufficient amount of data on small *P. muralis*, although we observed some active juveniles of the species in summer. This rock-dwelling species is probably constrained differently by the thermal environment, as deep crevices should provide efficient cooling sites even in the hottest period of the year, while such cooling sites are not available for the ground-dwelling *A. kitaibelii* and juvenile *L. viridis*.

In conclusion, heating rate seems only to be body size dependent with a lack of any “species effect” in the size range of our study species. We found age- and species-independent differences between differently sized lizards – using intra- and interspecific comparisons – in their seasonal activity and the thermal characteristics of the sites where they were recorded. Based on this, we suggest that body size, the main predictor of heating rate, is a fundamental factor in determining temporal and spatial distribution of small bodied lizards (BW less than 2-3 g) with extremely low thermal inertia in environments subject to a danger of overheating.

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