

## Constraints on Temperature Regulation in Two Sympatric *Podarcis* Lizards during Autumn

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We studied the impact of restrictions by the thermal environments on body temperatures ( $T_b$ s) and microhabitat use of the lacertid lizards *Podarcis melisellensis* and *Podarcis muralis* in a Mediterranean area (Croatia) during autumn. The thermal conditions at available microhabitats were assessed with copper models that measured the operative temperatures ( $T_e$ ) at different sites. We estimated the thermal suitability of microhabitats by quantifying the extent of similarity between the  $T_e$ s and the range of selected temperatures (i.e., the  $T_b$ s that lizards maintain in zero-cost conditions in a laboratory thermogradient;  $T_{sel}$ ). Both species maintained, throughout most of day,  $T_b$ s that were on average 2–4 C below both  $T_{sel}$  and the  $T_b$ s recorded in the field during summer. Nevertheless, the  $T_b$ s measured during autumn were in the upper range of available  $T_e$ s and were much closer to the  $T_{sel}$  than were the  $T_e$ s. In addition, lizards were most often observed in the warmest microhabitats and were often seen basking. These results indicate that lizards were actively thermoregulating. The  $T_e$  measurements show that lizards encounter suitable thermal conditions (i.e., where  $T_e$ s is within  $T_{sel}$ ) in only a restricted subset of the available microhabitats and during only a relatively short period of the day. Thus, lizards are constrained to maintain relatively low  $T_b$ s during autumn by the generally low available  $T_e$ s. Although lizards were clearly thermoregulating, they appeared to accept lower  $T_b$ s during activity in autumn than in summer. A possible reason for this seasonal shift in activity  $T_b$ s is that achievement of higher  $T_b$ s during autumn is only feasible by confining activities to some specific microhabitats, which may severely constrain other behaviors, such as foraging.

MANY small diurnal lizards, especially species that inhabit climates characterized by wide fluctuations of ambient temperatures, maintain high and relatively constant body temperatures ( $T_b$ s) during periods of activity (Avery, 1982; Huey, 1982). They achieve this by behavioral adjustments (Huey, 1982; Stevenson, 1985), in particular selection of activity times and thermal microclimates, shuttling between hot and cool microhabitats, and postural modifications that alter the rates of heating and cooling (Huey et al., 1977; Hertz and Huey, 1981; Bauwens et al., 1996). The abilities to maintain  $T_b$ s at or near the selected level (the range of  $T_b$ s maintained in the absence of physical restrictions; Licht et al., 1966), depend critically on environmental conditions, which determine the availability of thermally acceptable microhabitats. Thus, the spatial and temporal distributions of thermal microclimates act as constraints on the  $T_b$ s that lizards can achieve (e.g., Christian et al., 1983; Grant and Dunham, 1988; Huey, 1991).

Several detailed studies have examined the extent to which the thermal environment constrains opportunities for thermoregulation in lizards and snakes. Most of this research was conducted in hot environments and during

summer months, when animals are forced to restrict activity to the coolest times of day and/or available microclimates (e.g., Grant, 1990; Beaupre, 1995; Bashey and Dunham, 1997). However, because these studies focused on conditions wherein ectotherms run a substantial risk of overheating, they provide a one-sided view of the type and extent of thermal constraints. Indeed, most temperate-zone and subtropical areas are subject to important seasonal variation in ambient factors, and thermal conditions during the cooler months may actually impede or hamper ectotherms to attain  $T_b$ s within their selected range (e.g., Van Damme et al., 1987; Firth and Belan, 1998; Schauble and Grigg, 1998). Lizards may respond to cool thermal conditions by thermoregulating at the highest possible level (Van Damme et al., 1987), by shifting regulatory set-points (Christian and Bedford, 1995) or by diminishing thermoregulatory efforts (Schauble and Grigg, 1998).

Here we report on a short-term study of the thermal biology during autumn of two species of the lacertid genus *Podarcis* in a Mediterranean climate area. The two species (*Podarcis melisellensis* and *Podarcis muralis*) are phylogenetically close, share many aspects of their general morphology and biology (Arnold, 1987), and

coexist in the same macrohabitat. The number of active lizards peaks during the warm and dry spring and summer. However, relatively large numbers can also be seen on sunny days in autumn, when ambient temperatures and radiation intensity are much lower. To explore responses of lizards to the thermal conditions in autumn, we gathered data on their  $T_b$ s and aspects of thermoregulatory behavior and estimated thermal constraints by measuring the operative temperatures ( $T_e$ s) in a range of available microhabitats. Our objectives are to (1) estimate the "accuracy" and "effectiveness" of thermoregulation (sensu Hertz et al., 1993) and document behavioral aspects of temperature regulation (i.e., microclimate use and basking behavior); (2) compare  $T_b$ s maintained in autumn to those achieved in summer; (3) examine to what extent autumn  $T_b$ s are limited by environmental temperatures; and (4) estimate the relative levels of an whole-animal performance characteristic (sprinting speed) at the observed  $T_b$ s.

#### MATERIALS AND METHODS

*Study area and species.*—The study area is located approximately 2 km west of the village of Beli (45°06'N, 14°21'E) on the island Cres (Northern Adriatic, Croatia). The site is an open meadow bordered by a piled stone wall and surrounded by deciduous woodland. The meadow is dominated by short-grazed grasses, with scattered rocks, dried tree-logs and branches, and isolated bushes and trees (dominant species: *Quercus pubescens*, *Juniperus oxycedrus*, *Prunus spinosa*, *Acer monspessulanum*). We caught lizards in the meadow and on the surrounding stone wall.

The study species (*P. melisellensis* and *P. muralis*) are small lacertids (adult snout-vent length: 55–66 mm). Both species forage actively for a wide range of invertebrate prey and are basking heliotherms. They occur syntopically at the study site but exhibit subtle differences in microhabitat choice: *P. melisellensis* is mainly ground-dwelling, whereas *P. muralis* is a primarily climbing species, but it is not exceptional to encounter both species in the same microhabitat.

*Body temperatures and lizard behavior.*—Fieldwork was carried out on 30 and 31 October 1998, two days with highly similar weather conditions (sunny throughout, no wind). We made walks in random directions through the study area and used a constant sampling effort throughout the lizards' period of activity (0900–1500 h). We collected data for adult lizards (snout-vent

length > 55 mm) only. Upon sighting a lizard, we recorded species, sex (judged on color pattern and relative head size), time of day, solar microclimate (= exposure to sunshine: full sun, partial shade, shade), structural microhabitat (stone wall or rock, log or tree-trunk, bush, grass), and its posture and movement [basking (dorsoventrally flattened, body perpendicular to sun), perching, walking]. Note that our definition of basking includes a postural component, unlike the definition used in some other studies (i.e., perching in sun; e.g., Diaz, 1991; Hertz, 1992). We subsequently attempted to capture the lizard with a noose. If the lizard was caught within 30 sec, we measured its body temperature (cloacal =  $T_b$ ) to the nearest 0.1 C with a quick-reading Miller-Weber thermometer. The lizard was then released at the place of initial sighting. Because we did not mark the lizards, we cannot rule out the possibility that some individuals were caught more than once. However, any sampling bias is likely to be very small, given the high estimated density of both species at the study site (approximately 400–500 individuals/ha; unpubl. data).

*Operative temperatures.*—We measured operative temperatures ( $T_e$ ) using physical models of lizards. Models were 13.5 cm long sections of copper tubes (diameter: 12.2 mm, wall thickness: 1.3 mm) that were painted brown. Hollow models are known to have considerably faster heating and cooling rates than real lizards (Bakken, 1992; Hertz, 1992; Bauwens et al., 1996). To increase the heat storage capacity of the models, we filled them with water (Bakken, 1992). One end of the models was sealed with silicon, the other end with a tight-fitting rubber stopper. We checked the accuracy of the models by exposing pairs of models and anaesthetized lizards (*P. muralis*) to a range of ambient temperatures and radiation conditions in the field and laboratory. Differences between the equilibrium  $T_e$ s and  $T_b$ s (range: 20–38 C) were always  $\leq 1$  C. The regression equation relating  $T_b$  to  $T_e$  had a slope not different from 1 and intercept not different from 0 ( $b = 1.026 \pm 0.036$ ,  $P > 0.40$ ;  $a = -0.671 \pm 1.127$ ,  $P > 0.50$ ;  $R^2 = 0.965$ ,  $n = 31$ ).

Operative temperatures were measured on 31 October 1998 from 0900 h (approximately 15 min after local sunrise) until 1510 h (approximately 20 min after the sunset behind a hill located west of the study area). Temperatures of the models were recorded by inserting the probe of a temperature-datalogger (HOBO type H08-002-01) through a slit in the rubber stopper. The temperature-loggers of the different

models were programmed to simultaneously sample the temperature at 2-min intervals. From these data, we subsequently calculated, for each model, the mean  $T_c$  recorded over 30-min intervals; these values were used for all further calculations.

We used 19 models to measure  $T_c$ s at three solar microclimates (full sun, partial shade, shade) and different microhabitats used by lizards in the field. Sunlit patches were sampled with seven models; four models were placed on rocks at the base of the stone wall (two models perpendicular to sun, two models at 45° angle to sun), one on grass, one on a tree-log and one at the base of a shrub (all three perpendicular to the sun). The  $T_c$ s of partially shaded microclimates were estimated with eight models; four models were located on rocks, one on grass, one on a tree-log and two at the edge of shrubs. We sampled the shaded microclimates with four models; two were placed in crevices in the staple wall and another two in the center of bushes. All models were checked at 30-min intervals and, if necessary, relocated to maintain their original position with respect to solar microclimate and orientation to sun.

*Indices of microclimate suitability and thermoregulation.*—We follow the procedures of Hertz et al. (1993) to evaluate the accuracy and effectiveness of temperature regulation, and the thermal suitability of solar microclimates. Briefly, this methodology consists of quantifying the extent of similarity between the  $T_b$ s or  $T_c$ s and the target  $T_b$ s that thermoregulating lizards attempt to achieve. We estimated the target temperature range for thermoregulation by the selected temperature range ( $T_{sel}$ ), which is defined as the central 80% of the  $T_b$ s maintained by surface-active lizards in a laboratory photo-thermogradient, where the costs of thermoregulation are negligible (Bauwens et al., 1995). The  $T_{sel}$  for *P. melisellensis* (33.5–36.5 C) was measured during summer for lizards from the study population (unpubl. data). The  $T_{sel}$  for *P. muralis* (31.9–36.5 C) was determined during summer for lizards from central Spain (Bauwens et al., 1995). By using the latter estimate, we explicitly assume that lizards from different geographic areas have similar thermal preferences. This assumption is supported by the absence of variation in  $T_{sel}$  among populations living along pronounced altitudinal gradients in each of two species of lacertid lizards (Van Damme et al., 1989, 1990).

We use two indices to determine how well a  $T_b$  or  $T_c$  distribution conformed to  $T_{sel}$ . First, we determine the percentage of  $T_b$  or  $T_c$  readings

that fell within  $T_{sel}$ . Second, we calculate the absolute value of each deviation of  $T_b$  or  $T_c$  from the bounds of  $T_{sel}$  ( $d_b$  and  $d_c$ , respectively). When  $T_b$  or  $T_c$  is within  $T_{sel}$ , the corresponding  $d_b$  or  $d_c$  equals 0 (details in Hertz et al., 1993). The accuracy of temperature regulation estimates the extent to which lizards achieve  $T_b$ s within the target range, and is indexed by mean  $d_b$ ; low values indicate high accuracy, that is, that  $T_b$ s are maintained within or close to  $T_{sel}$ . The thermal suitability of the habitat quantifies the deviation of the  $T_c$ s from  $T_{sel}$  and is estimated by mean  $d_c$ . Low values of mean  $d_c$  imply that the environmental temperatures are close to  $T_{sel}$ , such that environmental conditions allow attainment of  $T_b$ s within  $T_{sel}$  without much regulatory efforts.

The effectiveness of temperature regulation quantifies the extent to which  $T_b$ s are closer on average to  $T_{sel}$  than are the  $T_c$ s and is estimated by the index  $E = 1 - (d_b/d_c)$ . Values of  $E$  that approach one indicate that lizards maintain  $T_b$ s close to  $T_{sel}$  in an environment where the  $T_c$ s deviate considerably from  $T_{sel}$  (Hertz et al., 1993).

A prerequisite for using the procedures of Hertz et al. (1993) is that the  $T_c$ -models sample all microclimates present, and each of the microclimates in proportion to its availability (Hertz et al., 1993). As a first base to distribute the models, we used estimates of the availability of solar microclimates collected in another Mediterranean area (Palagruža, Croatia) during September 1998 (sun: 50%; partial shade: 40%; shade: 10%; unpubl. data). To account for the difference in study periods (late October vs September) and the higher coverage by shrubs and trees in the actual study area, we intentionally decreased the proportion of models in sun (sun: 37%; partial shade: 42%; shade: 21%). The availability of solar microclimates also changes during the course of a day. Thus, to achieve representative sampling of the solar microclimates, models should either be relocated throughout the day, or estimates of solar microclimate availability at different times of day should be used to adjust the  $T_c$ -distribution (e.g., by a weighting procedure; Bauwens et al., 1996). We regret that time constraints (intensified by a nonforecasted autumn storm) impeded our collection of this information.

To assess the robustness of our estimates of  $d_c$  and  $E$  to variations in the availability of solar microclimates, we performed a sensitivity analysis. We varied availabilities by some hypothetical scenario's, used the estimated availability coefficients to weigh the original  $T_c$ -values, and then recalculated  $d_c$  and  $E$ . Our procedure

changed the putative availability of sunlit sites and assumed that the remaining area was covered for 75% by partially shaded and for 25% by fully shaded microclimates. We varied both the maximal availability of sunlit sites (at midday) and the amplitude of diel changes in the availability of solar microclimates. The availability of sunlit sites at midday was changed from 30% to 80% (in steps of 10%). For each of these values, we simulated hour-by-hour variation in the availability of sunny sites by a sinusoidal function, with the set maximum value at midday and minimal values (at 0900 h and 1500 h) that were one of four possible fractions (0.10, 0.25, 0.50 and 0.75) of the midday availability. Low fractions (e.g., 0.10) simulate large diel differences in the availability of sunlit sites (e.g., from a low 5% at 900 and 1500 h, to a maximum of 50% at 1200 h), whereas high fractions (e.g., 0.75) mimic relatively small hour-to-hour variation in the sunlit area (e.g., from a low 37.5% at 0900 and 1500 h, to a maximum of 50% at 1200 h).

*Estimates of relative performance at the activity  $T_b$ s.*—

Data on the temperature dependence of burst sprinting speed were available for *P. muralis* (Bauwens et al., 1995). These authors measured sprint speed in a laboratory racetrack at a series of controlled  $T_b$ s. For each  $T_b$  of *P. muralis* measured in the field, we estimated the corresponding relative sprint speed [percent of maximum sprint speed (= 174 cm/sec at  $T_b = 35.2$  C)] by interpolation on the thermal sensitivity function (sprint speed vs experimentally set  $T_b$ ). The resulting distribution provides an estimate of the relative (percent of maximum) sprinting performance that lizards are predicted to exhibit at their activity  $T_b$ s in the field.

## RESULTS

*Operative temperatures.*—We analyzed variation in  $T_c$ -profiles of different models by a repeated measurements ANOVA, after checking for homogeneity of variances, with the hourly average  $T_c$ s as dependent variables (within subjects factor = time), and solar microclimate and microhabitat type, nested within solar microclimate, as between subjects factors. Both the interaction between solar microclimate and time, and solar microclimate, had significant effects on variation in  $T_c$ s ( $P < 0.001$ ). However, we found no significant effects of the interaction between microhabitat and time ( $P > 0.05$ ) and of microhabitat ( $P > 0.10$ ). Hence, microhabitat type, within each solar microclimate category, did not significantly influence diel variation in  $T_c$ s. This

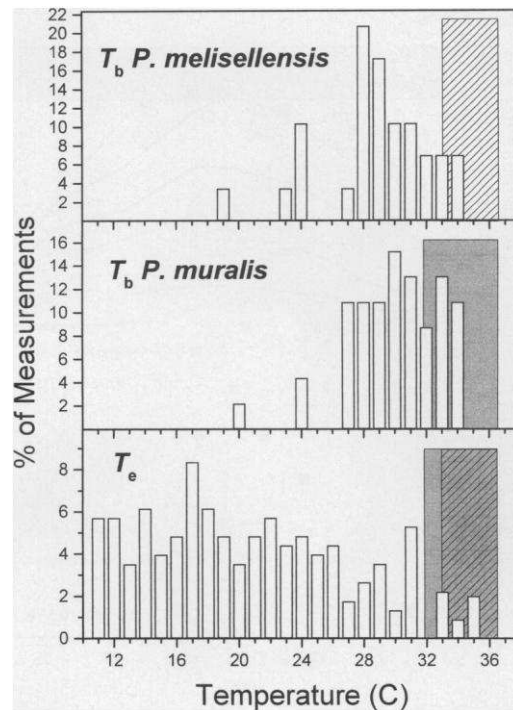


Fig. 1. Distributions of body temperature ( $T_b$ ) of field-active *Podarcis melisellensis* and *Podarcis muralis* and of available operative temperatures ( $T_c$ ) in autumn. The hatched and shaded areas denote the selected temperature ranges ( $T_{sel}$ ) of, respectively, *P. melisellensis* and *P. muralis*.

analysis indicates that exposure to sunshine, rather than structural microhabitat, is the primary factor inducing variation in  $T_c$ s, and justifies our grouping of models in the distinct solar microclimate categories.

As expected for the time of the year (autumn),  $T_c$ s were generally low ( $21.6 \pm 0.4$  C,  $n = 228$ ) and never exceeded the lizards' selected temperature ranges (Fig. 1). Moreover, most  $T_c$  measurements were far from the  $T_{sel}$  of *P. melisellensis* (3% of  $T_c$ s within  $T_{sel}$ ; mean  $d_c = 11.9 \pm 0.4$  C) and of *P. muralis* (8% of  $T_c$ s within  $T_{sel}$ ; mean  $d_c = 10.4 \pm 0.4$  C). Thus, the thermal environment posed strong overall restrictions on the lizards to achieve  $T_b$ s within their  $T_{sel}$ .

The  $T_c$ s as well as the  $d_c$ s for both species varied considerably throughout the day (one-way ANOVAs, all  $P < 0.001$ ). None of the  $T_c$ s fell within the  $T_{sel}$  of either species before 1000 h and after 1330 h (Fig. 2). During the other intervals  $\leq 10\%$  of  $T_c$ s was within the  $T_{sel}$  of *P. melisellensis*. During the interval 1100–1300 h, 15–25% of  $T_c$ s was within the  $T_{sel}$  of *P. muralis* (Fig. 2).

Models that were exposed to full sun had the

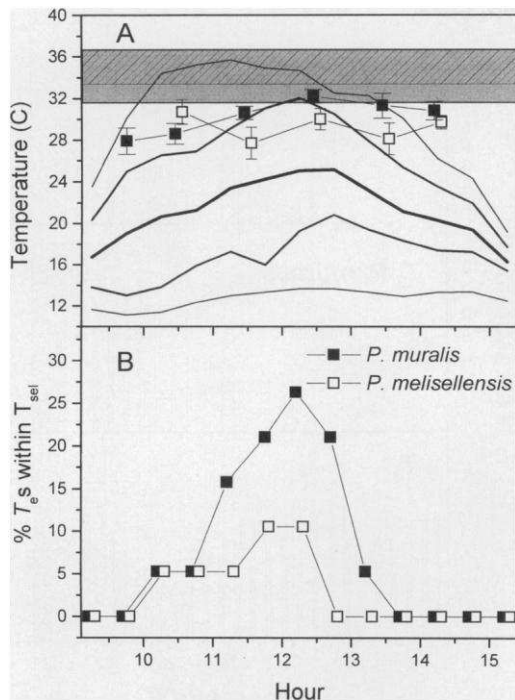


Fig. 2. (A) Summary statistics of diel variation in body temperatures ( $T_b$ ; mean  $\pm$  1 SE) of *Podarcis melisellensis* (open squares) and *Podarcis muralis* (solid squares), and of operative temperatures ( $T_e$ ; lines from bottom to top: minimum, first quartile, mean, third quartile, and maximum temperatures recorded during 30-min intervals). The hatched and shaded areas denote the selected temperature ranges ( $T_{sel}$ ) of, respectively, *P. melisellensis* and *P. muralis*. (B) Diel variation in the percentage of  $T_e$ -readings that fell within the  $T_{sel}$  of *P. melisellensis* (open squares) and *P. muralis* (solid squares).

highest and the most variable  $T_e$ s during the course of the day (Fig. 3). In the sampling periods between 1000 and 1330 h, the percentage of models in sun that achieved  $T_e$ s within the  $T_{sel}$  of *P. muralis* varied between 14% and 71%. During the same interval, the proportion of models with  $T_e$ s within the  $T_{sel}$  of *P. melisellensis* varied between 0% and 29%. Only models that were perpendicular to direct solar radiation had  $T_e$ s within the  $T_{sel}$  of either species. The  $T_e$ s measured in partially shaded or shaded sites never approached  $T_{sel}$  (Fig. 3). Thus, lizards encounter suitable thermal conditions only between 1000 and 1330 h, exclusively in sunlit microhabitats, and only when they orient themselves perpendicular to the sun.

*Body temperatures and indices of thermoregulation.*—The  $T_b$ s of active lizards in the field did not differ significantly between males and females in

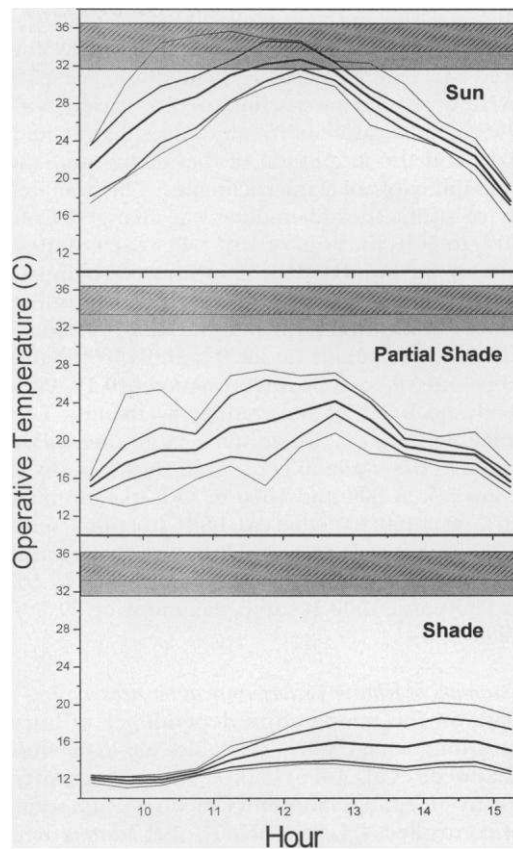


Fig. 3. Summary statistics of diel variation in operative temperatures ( $T_e$ ) in different solar microclimates. Curves (from bottom to top) indicate the minimum, first quartile, mean, third quartile, and maximum operative temperatures recorded during 30-min intervals. The hatched and shaded areas identify the selected temperature ranges ( $T_{sel}$ ) of, respectively, *Podarcis melisellensis* and *Podarcis muralis*.

either of both species (two-way ANOVA,  $P > 0.10$  for the effects of sex and the interaction between sex and species). We therefore lumped data for the two sexes in further analyses.

The mean  $T_b$  for *P. melisellensis* (mean  $\pm$  1 SE =  $29.1 \pm 0.6$  C,  $n = 29$ ) and *P. muralis* ( $30.4 \pm 0.4$  C,  $n = 46$ ) did not differ significantly (one-way ANOVA:  $F_{1,73} = 2.96$ ,  $P > 0.05$ ). Only a relatively small proportion of the  $T_b$ s fell within  $T_{sel}$  (*P. melisellensis*: 7%; *P. muralis*: 33%) and none of the recorded  $T_b$ s exceeded  $T_{sel}$  (Fig. 1). The mean deviation of the  $T_b$ s from  $T_{sel}$  (i.e.,  $d_b$ ) was significantly higher in *P. melisellensis* ( $4.4 \pm 0.6$  C) than in *P. muralis* ( $2.0 \pm 0.4$  C; one-way ANOVA:  $F_{1,73} = 13.29$ ,  $P < 0.001$ ). Thus, *P. muralis* maintains  $T_b$ s closer to  $T_{sel}$  than *P. melisellensis*. Because both species maintained similar  $T_b$ s, this difference is largely because of the higher

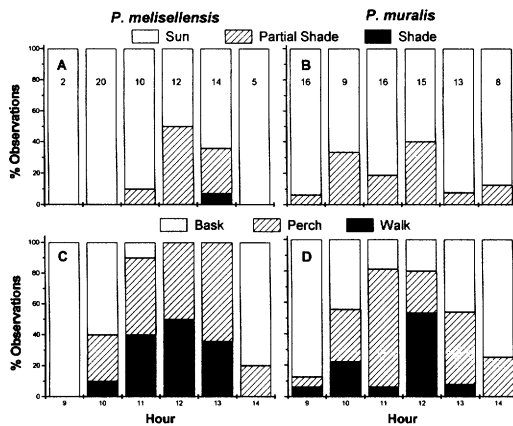


Fig. 4. Diel variation in the relative use of solar microclimates (A, B) and in the relative number of lizards observed basking, perching or walking (C, D) in *Podarcis melisellensis* (A, C) and *Podarcis muralis* (B, D). Numbers in panels A, B indicate sample sizes.

value of the lower limit of  $T_{sel}$  in *P. melisellensis* (33.5 C vs 31.9 C in *P. muralis*).

Neither the  $T_b$ s nor the  $d_b$ s of both species varied significantly among hours of the day (two-way ANOVA, both  $P > 0.50$ ). Hence, lizards maintain their  $T_b$ s at about similar levels throughout their daily activity period (Fig. 2). At different times of day, the  $T_b$ s were within the range of  $T_s$ s except during the last hourly period (Fig. 2). During the interval 0900–1000 h,  $T_s$ s increased quickly; all lizards were caught near the end of this period, when some of the  $T_s$ s equaled or exceeded the measured  $T_b$ s. Note that only *P. muralis* was sampled at this time; very few *P. melisellensis* had emerged before 1000 h (Fig. 4). Although the  $T_s$ s dropped abruptly from 1330 h onward, both species maintained  $T_b$ s well above the  $T_s$ s after 1400 h. Putative reasons for this discrepancy are that we caught most lizards during the interval 1400–1430 h, that most lizards were basking to increase the rate of heat gain (Fig. 4; our models did not mimic this posture), and that we may have failed to sample  $T_s$ s at the very warmest microhabitats available at that time of the day.

Although  $T_b$ s of both species were rather low relative to their  $T_{sel}$ , they were closer to the  $T_{sel}$  than were the  $T_s$ s, indicating that lizards actively thermoregulated. The  $E$ -indices (*P. melisellensis*:  $E = 0.63$ ; *P. muralis*:  $E = 0.81$ ) indicate that both species thermoregulated with moderate to high effectiveness.

The sensitivity analysis showed that our estimates of  $d_c$  and  $E$  are robust to variations in microclimate availability. Differences in the amplitude of diel changes in microclimate avail-

ability at a set midday maximum had only minor effects on estimates of  $d_c$  (range of maximal differences: 0.6–1.5 C) and  $E$  (range of maximal differences: 0.01–0.08) for both species. Variation in the maximal availability of sunlit areas (30–80%) also had small effects: estimates of  $d_c$  varied between 9.3–12.8 C (*P. melisellensis*) and 7.8–11.3 C (*P. muralis*), whereas estimates of  $E$  varied between 0.52–0.66 (*P. melisellensis*) and 0.75–0.82 (*P. muralis*). The highest values correspond to the lower estimates for maximal availability of sunlit sites. In short, all hypothetical scenarios, including those that assumed unrealistically high values for the availability of sunlit sites (e.g., maximal availability 70–80%), yielded  $d_c$ s that were much larger than the  $d_b$ s for either species. Thus, it is highly unlikely that any possible failure to sample  $T_s$ s in proportion to microclimate availability has affected our conclusion that lizards were actively thermoregulating.

*Use of solar microclimates and basking behavior.*—The vast majority of lizards (81% in both species) were fully exposed to sun when first seen. Virtually all others were in partial shade (Fig. 4). The proportion of lizards observed in full sun declined significantly around midday in *P. melisellensis* ( $\chi^2 = 16.86$ , 5 df,  $P < 0.01$ ; Fig. 4) but was approximately constant throughout the day in *P. muralis* ( $\chi^2 = 8.32$ , 5 df,  $P > 0.10$ ). Because the availability of sunlit sites in terrestrial habitats is lowest during morning and afternoon and highest around midday (Huey et al., 1977), the observed pattern of solar microclimate usage is opposite to that expected when lizards would use patches of sun and shade randomly.

The proportion of lizards seen basking was highest in the morning and afternoon (Fig. 4). During the midday hours (1100–1400 h), most lizards were either perching or walking. The majority of lizards that were fully exposed to sun were basking or perching (*P. melisellensis*: 80%; *P. muralis*: 90%), the rest were walking. In contrast, about half of those that were in partial shade or shade were actively moving (*P. melisellensis*: 58%; *P. muralis*: 47%), the remaining were perching.

*Estimates of relative performance at the activity  $T_b$ s.*—Combination of the observed  $T_b$ s with data on the thermal dependence of sprinting speed in *P. muralis* indicated that the observed  $T_b$ s were associated with a mean relative performance of  $82 \pm 1\%$  (range: 50–97%). Only a minor fraction of the  $T_b$ s (2%) was conducive to a speed  $\geq 95\%$  of the maximum. Nevertheless, a major-

ity (65%) of the  $T_b$ s would allow lizards to run at  $\geq 80\%$  of their maximal capacities and an additional 22% of the recorded  $T_b$ s were associated with relative sprint speeds of 75–80%.

#### DISCUSSION

The  $T_b$ s maintained by surface-active lizards during autumn were rather low, relative to both those recorded for the same species during summer and to the range of selected temperatures. Body temperatures recorded during this study for *P. muralis* (mean  $\pm 1$  SE =  $30.4 \pm 0.4$  C) were lower than those measured during summer in two populations in northern Spain (both  $33.8 \pm 0.2$  C; Braña, 1991) and in one population in central Spain ( $32.0 \pm 0.4$  C; Martín-Vallejo et al., 1995). Only 33% of the  $T_b$ s that we measured were within the selected range. Similarly, body temperatures of *P. melisellensis* ( $29.1 \pm 0.6$  C) were considerably lower than those recorded during July in the same population ( $35.1 \pm 0.2$  C; I. Grbac, D. Bauwens and B. Lazar, unpubl. data). A very low proportion (7%) of the  $T_b$ s measured in autumn was within the selected temperature range.

Although both species maintained relatively low  $T_b$ s, several lines of evidence indicate that lizards were actively thermoregulating. First, the  $T_b$ s of field-active lizards were well above the available  $T_c$ s and much closer to the  $T_{sel}$  than were the  $T_c$ s. Thus, lizards actively regulated  $T_b$ s toward the selected range. Second, our behavioral observations indicate that lizards clearly selected the sunlit microclimates, especially during early morning and late afternoon when they were least available. In addition, large proportions of lizards seen during early morning and late afternoon were basking (i.e., flattened body, and perpendicular orientation to sun), a behavioral mechanism that increases the rate of heat gain (Heath, 1965; Avery, 1976; Bauwens et al., 1996). The concordance between the behavioral observations and the finding that  $T_b$ s were much closer to  $T_{sel}$  than were the  $T_c$ s, indisputably demonstrates that lizards were actively thermoregulating.

The discrepancy between the  $T_b$ s measured in autumn and those maintained during summer in the field and in laboratory thermogradients, might be the result of two factors (Van Damme et al., 1987, 1989; Christian and Weavers, 1995). First, restrictions imposed by the thermal environment may impede the achievement of  $T_b$ s at summer levels. Second, lizards might actively shift thermoregulatory set points, which may itself be either an immediate response to the thermal conditions or an acclimatization re-

sponse (i.e., a shift of the range of selected temperatures).

Our  $T_c$  measurements clearly indicate that environmental conditions severely constrain the lizards to achieve  $T_b$ s within their selected range. The cool air temperatures and low radiation intensity during autumn make that only a very small proportion ( $< 10\%$ ) of the  $T_c$ -records fell within the  $T_{sel}$ . Moreover, only models that were fully exposed and perpendicularly oriented to the sun achieved  $T_c$ s within  $T_{sel}$  and only during a relatively short period of the day (approximately 1000–1330 h). Partially shaded and shaded microclimates did not offer suitable thermal conditions at any time of the day. Thus, the maintenance of relatively low  $T_b$ s can be attributed, at least in part, to thermal restrictions imposed by cool ambient conditions during autumn. This situation differs from that documented for a number of other lizards, where a preponderance of hot rather than cold conditions imposes severe constraints on activity levels and patterns of microhabitat usage (e.g., Grant and Dunham, 1988; Grant, 1990; Bashey and Dunham, 1997). Nevertheless, findings similar to ours were reported for the temperate zone lacertid *Lacerta vivipara*, where cool thermal conditions during early spring force adult males to maintain  $T_b$ s well below their  $T_{sel}$  (Van Damme et al., 1987).

Do environmental constraints alone explain the maintenance of relatively low  $T_b$ s? Although thermal restrictions were paramount, some of the microhabitats offered thermally suitable conditions at least during part of the day. Hence, during that interval, lizards were theoretically able to maintain  $T_b$ s within  $T_{sel}$ . However, at all times of day only a fraction of the lizards did so. Rather, they most often maintained  $T_b$ s approximately 2–4 C below  $T_{sel}$ . We interpret this as an indication for a behavioral shift in thermoregulatory set points.

A possible reason for this putative regulatory response is that the achievement of  $T_b$ s within  $T_{sel}$  poses serious restrictions on other behaviors. If maintaining  $T_b$ s within  $T_{sel}$  would be the primary or only determinant of lizard behavior, we expect lizards to restrict activity to times and places that offer thermally suitable conditions (Bauwens et al., 1996; Bashey and Dunham, 1997). Favorable microclimates were offered exclusively by some of the sites that were fully exposed to sunshine. Although most lizards were seen in full sun, about 20% of them were in partial shade and hence exposed to  $T_c$ s that were well below  $T_{sel}$ . Interestingly, about half of the lizards seen in partial shade, but merely 10–20% of those in sun, were actively moving. This

suggests that lizards visit partially shaded microclimates for foraging, either because food is more abundant there or because invertebrate prey have reduced escape abilities because of the cool thermal conditions. Thus, we suggest that foraging visits to thermally suboptimal sites induce the lizards to regulate their  $T_b$ s at levels below their  $T_{sel}$ . In other words, we hypothesize that maintaining  $T_b$ s within  $T_{sel}$  would be possible only at the expense of other behaviors.

In general, lizards are hypothesized to regulate their  $T_b$ s at levels that are a compromise between the costs in terms of time and energy expended in regulatory behaviors and the benefits associated with maximizing physiological performances (Huey and Slatkin, 1976; Huey, 1982). When the time spent thermoregulating becomes so long, or restrictions imposed by selecting thermally favorable habitats so stringent that they jeopardize other behaviors, lizards should either forego activity or change regulatory set points. However, because physiological and whole-animal performances are temperature dependent (Huey and Stevenson, 1979; Huey, 1982; Van Damme et al., 1991), a behaviorally based shift in set-point temperatures will inevitably alter performance capacities. For instance, the predicted relative sprint speed of *P. muralis* at the observed  $T_b$ s was on average 82%, whereas maintaining their  $T_b$ s within  $T_{sel}$  would have allowed them to run at 95% of maximal levels (Bauwens et al., 1995). Thus, the relatively low  $T_b$ s that lizards maintained in autumn are associated with a reduction in performance capacities. However, in the absence of a yardstick, it is difficult to judge whether this represents a severe reduction in predicted performance capacities. Predicted performances of active diurnal lizards are often > 95% of maximum levels (Hertz et al., 1983; Huey et al., 1989). Nevertheless, lower levels (80–90%) were observed in several species of *Anolis* (Hertz et al., 1993) and in high-altitude populations of the lacertids *Lacerta vivipara* and *P. tiliguerta* (respectively, 65% and 80%; Van Damme et al., 1989, 1990).

Because we did not determine the selected temperatures during autumn, we cannot assess whether regulation of  $T_b$ s below the summer  $T_{sel}$  represents a short-term response to ambient factors, or reflects acclimatization to seasonally changing conditions. Few studies have explored seasonal differences in the selected temperatures of lizards (review in Christian and Bedford, 1995). In lizards from subtropical areas in Australia seasonal (wet–dry seasons) differences in  $T_{sel}$  amounting to  $\approx$  3–4 C were found in some species (Christian and Bedford, 1995, 1996) but not in another (Schäuble and Grigg,

1998). The temperate zone lizards *Crotaphytus collaris* (Sievert and Hutchison, 1989) and *Tiliqua rugosa* (Firth and Belan, 1998) exhibit seasonal variation in  $T_{sel}$ , but this was not related to environmental temperatures; the  $T_{sel}$  were lower during summer than in other seasons. Similarly, in the lacertid lizard *Lacerta vivipara*, month-to-month variation in the  $T_{sel}$  of adult males and nonpregnant females was restricted in magnitude and not related to among-month differences in ambient temperatures (Van Damme et al., 1986). Thus, there is little evidence that shifts in  $T_{sel}$  reflecting acclimatization to seasonal variation in environmental conditions are a widespread phenomenon in lizards. Nevertheless, we encourage future efforts to examine this hypothesis in our study species.

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