Seasonal variation in the contribution of different behavioural mechanisms to lizard thermoregulation

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Summary

1. We studied seasonal changes in the thermoregulatory behaviour of the lacertid lizard *Psammodroums algirus* in a Mediterranean evergreen forest. Body temperatures (T_b), environmental operative temperatures (T_e) and upper and lower limits of the selected thermal range (T_{sel}) were lower in May than in July.

2. On average, mean deviations of T_b from T_{sel} (0·7 °C in both seasons) were much smaller than those of T_e (8·3 °C in both seasons). Thus both the accuracy (average difference between T_b and T_{sel}) and effectiveness (the extent to which T_b are closer than T_e to T_{sel}) of thermoregulation were high, and similar in both seasons.

3. However the thermoregulatory contribution of two distinct behavioural mechanisms varied markedly between seasons. Daily activity contributed significantly to the regulation of T_b in May (when a population of T_e thermometers matching lizard activity patterns would be, on average, 1·0 °C closer to T_{sel} than were randomly available T_e), but not in July (when such a population would be only 0·2 °C closer to T_{sel} than were randomly available T_e). The selection of sun–shade patches, the contribution of which was larger than that of daily activity in both seasons, was more important in July (when it produced a distribution of T_e that would be, on average, 3·1 °C closer to T_{sel} than were randomly distributed T_e) than in May (when a population of thermometers matching the lizards' pattern of exposure to sunlight would be 1·3 °C closer to T_{sel} than were randomly available T_e).

4. These changes are discussed in the light of seasonal differences in the daily patterns of among-patch variation in T_e. In spring, lizard activity was low in the early morning because even the selection of sunlit patches was of limited utility to attain T_b within T_{sel}; in summer, lizards could remain active at midday, despite low overall thermal suitability, by selecting shaded patches. Thus the contribution of patch selection to thermoregulation was important in the early basking period of both seasons, and at summer midday hours.

5. Our data suggest that shuttling between sun and shade, rather than selecting sun or shade, may be an additional mechanism of behavioural thermoregulation, the importance of which would be greatest at times of day when lizards use patches at random (e.g. spring midday hours), and that their mean T_b is closer to the grand mean of full sun and full shade T_e than to the mean equilibrium T_e within any type of patch.

Key-words: daily activity, operative temperatures, patch selection, selected range, shuttling behaviour

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Introduction

Thermoregulation is an active process by which animals maintain their body temperature (T_b) as close as possible to an independently defined target range (the

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selected temperature range, T_{sel}) at which their performance tends to be maximal (Heath 1970; Huey 1982; Hertz, Huey & Stevenson 1993; Bauwens *et al*. 1995). The consequences of thermoregulation are important because T_b affects all levels of physiology, from enzyme reactions to growth and locomotion (Huey 1982; Sinervo & Adolph 1994; Bauwens *et al*. 1995). All these processes perform relatively well over a range of T_b that usually encompasses T_{sel}, but decline rapidly outside that range (Huey & Stevenson 1979; Huey & Kingsolver 1989).

Reptiles thermoregulate mainly by behavioural means (Cowles & Bogert 1944; Huey 1982). Behavioural adjustments include habitat or microhabitat shifts (Hertz 1981; Hertz & Huey 1981; Christian, Tracy & Porter 1983; Adolph 1990; Bauwens, Hertz & Castilla 1996; Webb & Shine 1998); retreat-site selection (Huey *et al*. 1989; Webb & Shine 1998; Kearney & Predavec 2000; Kearney 2002); changes in activity times (Huey, Pianka & Hoffman 1977; Hertz 1981; Hertz & Huey 1981; Carrascal & Díaz 1989; Van Damme *et al*. 1989; Bauwens *et al*. 1996); variations in the frequency and duration of stays in full sun (Huey *et al*. 1977; Carrascal & Díaz 1989; Van Damme *et al*. 1989; Díaz 1991, 1994); and postural adjustments (Martín *et al*. 1995; Bauwens *et al*. 1996; Kearney & Predavec 2000).

The relative contributions of these behavioural mechanisms to thermoregulation, and the very existence of an active thermoregulatory process, cannot be evaluated without the use of appropriate null hypotheses (Heath 1964; Huey *et al*. 1977; Hertz 1992; Hertz *et al*. 1993; Díaz 1994; Bauwens *et al*. 1996; Díaz 1997; Schauble & Grigg 1998; Kearney & Predavec 2000). Such 'no-thermoregulation' hypotheses can be obtained by computing environmental operative temperatures (T_e) that represent the equilibrium temperatures of inanimate objects whose heat-transfer properties approximate those of study animals (Bakken & Gates 1975; Bakken 1992). Thus the random distribution of T_e in a habitat describes the null distribution of T_b expected in non-regulating animals (Hertz *et al*. 1993). Operative temperatures can be estimated directly using physical models of the study organism (Bakken & Gates 1975; Grant & Dunham 1988; Hertz 1992; Hertz *et al*. 1993; Bauwens *et al*. 1996; Belliure, Carrascal & Díaz 1996; Díaz 1997; Kearney & Predavec 2000).

These conceptual and analytical advances have fostered the evaluation of thermoregulation by field-active lizards. Hertz *et al*. (1993) developed a research protocol that combines data about T_e, body temperature (T_b) and selected thermal range (T_{sel}) to estimate quantitative indexes of the accuracy (the average difference between T_b and T_{sel}) and effectiveness (the extent to which T_b is closer to T_{sel} than is T_e) of temperature regulation. This protocol offers the additional advantage that it allows the relative contributions of the behavioural mechanisms listed above to be measured by considering how far the T_e of a population of models whose distribution matches that of lizards is closer to T_{sel} than are randomly distributed T_e (Bauwens *et al*. 1996).

Here we analyse the changes between spring and summer in the relative contributions to behavioural thermoregulation of activity times and selection of sun–shade patches by a lacertid lizard. Although it is well known that both the thermal environment and the thermoregulatory behaviour of lizards show seasonal variation (Huey *et al*. 1977; Christian *et al*. 1983; Van Damme, Bauwens & Verheyen 1987; Hertz 1992; Hertz *et al*. 1993; Christian & Bedford 1995; Schauble & Grigg 1998), no previous studies have quantified seasonal changes in the relative importance of various behavioural adjustments. Specifically, we address the following questions: Do activity times and the selection of sun–shade patches contribute to thermoregulation in both seasons? Are there seasonal changes in the relative contribution of these mechanisms, or in the accuracy or effectiveness of thermoregulation? Which mechanism is more relevant in each season? Is there any evidence of the importance of other adjustments?

Materials and methods

STUDY ORGANISM AND STUDY AREA

Psammodromus algirus is a medium-sized (adult snout-vent length 60–85 mm; mass 6–15 g) lacertid lizard inhabiting shrub and woodland habitats of the western Mediterranean region (Arnold 1987; Díaz & Carrascal 1991). Lizards were sampled at El Pardo (Madrid, central Spain: 40°31′ N, 03°47′ W; 650–700 m elevation), a Holm Oak (*Quercus ilex*) broad-leaved, perennial forest in which offshoots of *Q. ilex* dominate the shrub layer together with the Rock Rose *Cistus ladanifer*. Meteorological conditions vary widely among seasons; mean temperature and precipitation are 15·0 °C and 54·0 mm in May *vs* 23·4 °C and 14·8 mm in July. *Psammodromus algirus* is the most abundant lizard species in the area. Several predators, including birds and snakes (*Malpolon monspessulanus* and *Elaphe scalaris*), are common at the study site.

FIELD SAMPLING

Field sampling took place over 12 days in the activity season of 1997, six in spring (9–31 May) and six in summer (17–31 July). Data were collected on sunny days between 07.00 and 20.00 h (Mean European Time), covering the whole daily activity period of the species. In both seasons, data about T_e, T_b, and mechanisms of behavioural thermoregulation were simultaneously collected.

OPERATIVE TEMPERATURES AND BODY TEMPERATURES

Data on T_e were obtained using unpainted copper cylinders (models: 5 cm long × 1 cm diameter), closed at both ends except for a small fissure that allowed insertion of the sensing tip of an electronic digital thermometer (Osaka electronic equipments, ±0·1 °C precision). These copper models are suitable for measuring the T_e experienced by *P. algirus* because, under the same conditions of radiant heat load (100 W bulb at different heights), the mean temperatures at equilibrium of lizards and models were highly correlated ($r^2 > 0.99$; Belliure *et al*. 1996) and the resulting regression equation had a slope and intercept that did not differ significantly from 1 and 0, respectively ($P > 0.25$ in both cases). The adequacy of the T_e thermometers was confirmed experimentally (Walsberg & Wolf 1996).

In each season, 15 copper models per sampling day were placed at randomly selected intervals (1–9 m, distance determined by one-digit numbers from a table of random numbers) along the transects employed to measure daily variations in lizard activity; each sampling day there was a new scatter of models. Each model was dropped on the ground and positioned with its inferior surface contacting the substrate. Temperatures from all models were registered at hourly intervals. In addition to T_e the following were also recorded: time of day; weather at moment of measurement (cloudy *vs* sunny); and, if sunny, exposure to sun (full sun, sun filtered by vegetation or full shade). The distribution of models with respect to sun–shade patches provides a 'no-thermoregulation' hypothesis with which the lizards' exposure to sunlight can be compared.

Data on cloacal T_b were obtained from lizards captured by hand or with a noose, and measured to the nearest 0·1 °C with a Miller–Weber quick-reading thermometer using standard precautions (Avery 1982). Sex, time of day, weather and sun exposure at the moment of capture were also recorded. A constant effort was made to ensure captures were evenly distributed over the daily activity period.

LIZARDS' ACTIVITY PATTERNS AND USE OF SUN–SHADE PATCHES

Lizard activity was estimated by taking 15 min censuses, repeated hourly between 07.00 and 20.00 h. These censuses took place along six different transects per season (one per sampling day). We counted all lizards seen within 2·5 m of the progression line to control for potential differences in visibility between sites. When first sighted, lizards were scored into categories of sex, sunny *vs* cloudy weather, and sun exposure. To increase sample sizes, data concerning exposure to sunlight were obtained from all lizards observed, including those captured to measure their T_b, after checking that the distribution into categories of sun exposure did not differ significantly between lizards seen within and outside census bands (χ^2, df = 2, $P > 0·1$ in both cases).

SELECTED TEMPERATURE RANGES

The T_{sel} that lizards attempt to maintain in the field in the absence of physical and biotic constraints (Licht *et al*. 1966) was estimated in the laboratory (Facultad de Ciencias Biológicas, Universidad Complutense) using standard precautions. Food and water were supplied *ad libitum*; the photothermal gradient employed offered a wide range of T_e (23·4–51·7 °C); T_b was measured at different times of day on lizards of both sexes; and no social interactions that could have limited accessibility to the heat source were observed. Selected temperature ranges were estimated for each lizard as the central 80% of all T_b selected in the thermogradient (Bauwens *et al*. 1995; Gvodzik 2002). Detailed analyses of seasonal variation in T_{sel} will be reported elsewhere. The

average T_{sel} varied between seasons, increasing ≈2 °C from May (30·9–34·7 °C) to July (32·8–36·9 °C).

DATA ANALYSES AND EVALUATION OF MECHANISMS OF TEMPERATURE REGULATION

The thermal suitability of microsites (Hertz *et al*. 1993; Bauwens *et al*. 1996; Díaz 1997) was indexed by the mean of the absolute values of deviations of T_e from the T_{sel} of the corresponding season ($\bar{d}_e$). Similarly, the accuracy of thermoregulation was indexed by the mean of the absolute values of deviations of T_b from T_{sel} ($\bar{d}_b$). The effectiveness (E) of thermoregulation (improvement of accuracy with respect to non-regulating models) was evaluated using the formula $E = 1 - (\bar{d}_b/\bar{d}_e)$ (see Hertz *et al*. 1993 for details).

The relative importance of distinct behavioural mechanisms in each season was evaluated using the protocol followed by Bauwens *et al*. (1996). Thus the random distribution of models (T_e and d_e) provides a null hypothesis of no thermoregulation, representing the T_b of a lizard population with constant activity levels throughout the day, and with patterns of use of sun–shade patches proportional to their availability. The thermal consequences of the observed daily variations in activity were estimated by calculating the distribution of T_e expected if the number of models measured at each time of day had been proportional to the number of lizards that were actually observed. The resulting distribution of d_e (d_{act}; deviations from T_{sel} weighted for activity times) represents the d_b of a lizard population using activity levels as the only mechanism of temperature regulation. If the contribution of activity times to thermoregulation (equal to the difference $\bar{d} - \bar{d}_{act}$) is important, $\bar{d}_{act}$ must be significantly smaller than $\bar{d}_e$. Similarly, the thermal consequences of the observed patterns of sun–shade selection within each hourly period were estimated by weighting T_e and d_e by the number of lizards seen in full sun, filtered sun, or full shade in that hourly period. The resulting distribution of d_{sun} represents the deviations from T_{sel} of a lizard population using the selection of sun–shade patches as its only thermoregulatory behaviour. The contribution of patch selection to thermoregulation will be equal to $\bar{d}_e - \bar{d}_{sun}$, assuming that $\bar{d}_{sun}$ is significantly smaller than $\bar{d}_e$. The weighting coefficients were L_i/M_i, where L_i is the proportion of lizards in the ith hourly period or using the ith category of sun–shade patch (excluding lizards observed during cloudy intervals when no selection could occur); and M_i is the proportion of models in that hourly period or in that category of sun exposure. We used the WEIGHT procedure of SPSS/Windows to weight the T_e data because this algorithm allows introduction of fractional values as weighting coefficients (Bauwens *et al*. 1996). Thus the weighted distributions of d_{act} and d_{sun} can be analysed using standard parametric tests.

The intensity of selection for categories of sun exposure within each hourly period was estimated as $1 - O_{lm}$,
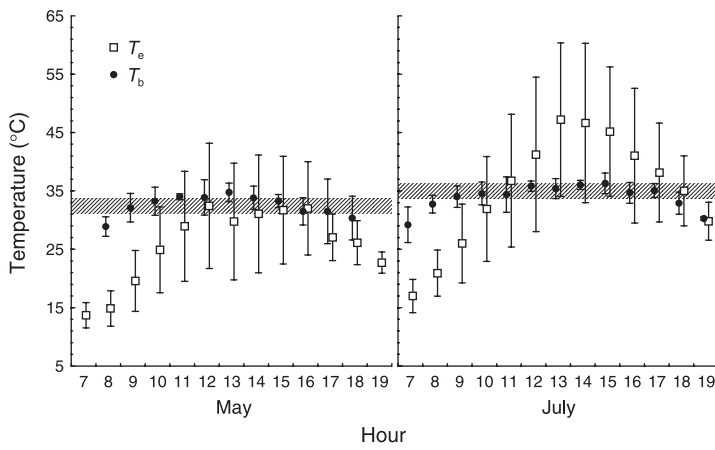
Fig. 1. Diel variation (mean ± SD) of environmental operative temperatures (T_e) and body temperatures (T_b) in each study season. Sample sizes are shown in Table 1. Hatched areas, position of selected temperature range.

where O_{lm} is Pianka's symmetrical overlap index applied to the distributions of lizards and models. The extent of selection varies between 0 (maximum overlap between model and lizard distributions) and 1.

Data were analysed using standard parametric techniques and log-linear analyses. We used $P \leq 0.05$ as a standard criterion of statistical significance.

Results

OPERATIVE TEMPERATURES AND THERMAL SUITABILITY

Operative temperatures were lower in May (mean ± SD = 25·8 ± 9·5 °C) than in July (31·5 ± 13·3 °C), showing significant hourly variation in both seasons (Fig. 1). The midday increase of T_e was less pronounced in May than in July (two-way ANOVA with the T_e data in Fig. 1;

season, $F_{1,2314} = 716·78$, $P < 0·001$; hour, $F_{12,2314} = 157·15$, $P < 0·001$; interaction, $F_{12,2314} = 10·13$, $P < 0·001$).

The deviations of T_e from T_{sel} (d_e) varied significantly with time of day in both seasons, but the patterns of hourly variation were markedly different in May and July (Table 1). Thus in spring, average d_e were smallest (thermal suitability was highest) at midday, whereas in July the midday T_e were far too high (Fig. 1); summer d_e were smallest, and thermal suitability was highest, at 10.00–12.00 and 17.00–20.00 h. As a result of these contrasting patterns of hourly variation, overall thermal suitability did not change significantly from May to July (two-way ANOVA with the d_e data in Table 1; season, $F_{1,2314} = 0·056$, $P = 0·814$; hour, $F_{12,2314} = 60·37$, $P < 0·001$; interaction, $F_{12,2314} = 14·36$, $P < 0·001$).

Seasonal differences in T_e and hourly patterns of thermal suitability were associated with a greater incidence of cloudy intervals in spring (33·8% of all models measured in May) than in summer (12·2% of all models measured in July; $\chi^2 = 152·28$, df = 1, $P < 0·001$). Sun availability, indexed by the proportion of models exposed to full or filtered sun, was higher in July ($\chi^2 = 12·58$, df = 2, $P = 0·0018$). In both seasons deviations from T_{sel} were lowest in patches of filtered sun, but in spring thermal suitability was lowest in the shade (97·7% of models with $T_e < T_{sel}$), whereas in summer it was lowest in full sun (85·7% of $T_e > T_{sel}$).

BODY TEMPERATURES

Body temperatures varied seasonally (mean ± SD = 32·6 ± 2·6 °C in May vs. 34·0 ± 2·7 °C in July) and with time of day, being higher at midday than in the early morning and late afternoon (Fig. 1, two-way ANOVA; season, $F_{1,102} = 22·63$, $P < 0·001$; hour, $F_{10,102} = 7·25$, $P < 0·001$; interaction, $F_{10,102} = 0·50$, $P = 0·887$). Lizards thermoregulated accurately (mean $d_b < 1$ °C) except

Table 1. Diel deviations (mean ± SD, °C) from the selected temperature range of lizards (the target of thermoregulation) of environmental operative temperatures (d_e) and body temperatures (d_b). For d_e sample size (N) = 90 measurements per hour in both seasons

	d_e		d_b			
	May	July	May		July	
Hour	Mean ± SD	Mean ± SD	Mean ± SD	N	Mean ± SD	N
07.00–08.00	17·2 ± 2·2	15·8 ± 2·9	–	–	3·6 ± 3·1	6
08.00–09.00	16·0 ± 3·0	12·1 ± 3·1	2·1 ± 1·4	6	0·6 ± 0·9	6
09.00–10.00	11·5 ± 4·8	8·3 ± 4·0	0·6 ± 1·1	6	0·3 ± 0·6	4
10.00–11.00	7·8 ± 4·7	6·1 ± 4·8	0·5 ± 0·8	6	0·2 ± 0·4	6
11.00–12.00	7·2 ± 4·6	6·5 ± 7·7	0·0 ± 0·0	3	0·8 ± 1·1	6
12.00–13.00	7·1 ± 5·8	9·1 ± 9·5	0·9 ± 1·3	4	0·0 ± 0·0	5
13.00–14.00	6·3 ± 6·4	12·1 ± 11·2	0·6 ± 0·9	6	0·0 ± 0·1	5
14.00–15.00	6·0 ± 6·5	11·1 ± 12·3	0·3 ± 0·4	6	0·0 ± 0·0	5
15.00–16.00	5·7 ± 5·4	9·5 ± 9·8	0·0 ± 0·1	7	0·4 ± 0·5	6
16.00–17.00	4·7 ± 4·6	7·3 ± 9·2	0·7 ± 1·1	6	0·3 ± 0·7	6
17.00–18.00	4·7 ± 2·4	4·5 ± 6·3	2·0 ± 1·8	2	0·0 ± 0·0	6
18.00–19.00	5·3 ± 2·7	2·6 ± 3·9	1·6 ± 2·3	2	0·8 ± 1·1	6
19.00–20.00	8·2 ± 1·8	3·4 ± 2·5	–	–	2·5 ± 0·3	3
Total	8·3 ± 6·0	8·3 ± 8·3	0·7 ± 1·1	54	0·7 ± 1·4	70

for the first and last hourly periods (Table 1). Although T_b increased seasonally, T_{sel} was also higher in summer (Fig. 1). Thus the accuracy of thermoregulation was similar in both seasons (two-way ANOVA with the d_b data in Table 1; season, $F_{1,102} = 2·47$, $P = 0·119$; hour, $F_{10,102} = 3·44$, $P = 0·0006$; interaction, $F_{10,102} = 0·650$, $P = 0·766$).

EXTENT OF THERMOREGULATION

In both seasons, T_b were closer to T_{sel} than were T_e, that is, $\bar{d}_b$ was significantly smaller than $\bar{d}_e$ (May, $t = 9·25$, df = 1222, $P < 0·001$; July, $t = 7·70$, df = 1238, $P < 0·001$), providing unequivocal evidence of active thermoregulation. The total amount of thermoregulation achieved, estimated by the difference $\bar{d}_e - \bar{d}_b$, was nearly identical in both seasons (7·54 °C in May *vs* 7·65 °C in July). Not surprisingly, the effectiveness of thermoregulation was also similar in spring ($E = 0·910$) and summer ($E = 0·917$).

SEASONAL VARIATION OF ACTIVITY TIMES AND SELECTION OF SUN−SHADE PATCHES

Overall times of activity, based on the lizards seen within census bands, were slightly different in both seasons. In July activity was somewhat bimodal, with a clearer
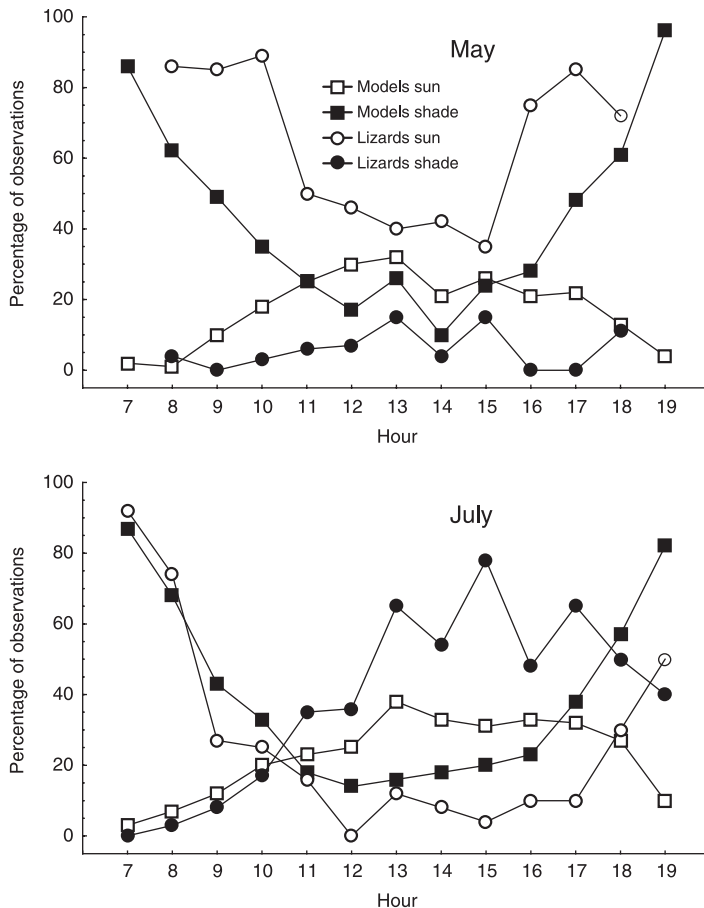
decrease in the number of lizards seen at midday hours and with a higher proportion of sightings in the two first (07.00–09.00) and the two last (18.00–20.00) hours of the daily activity period (May, 11% of 210 observations; July, 27% of 207 observations; $\chi^2 = 15·56$, df = 1, $P < 0·001$).

Selection of sun–shade patches was analysed by means of a log-linear analysis on the complete data set of lizard and model observations, classified according to season, time of day and exposure to sun (Fig. 2; observations made during cloudy intervals were excluded from this analysis). The final model obtained ($G = 54·71$, df = 48, $P = 0·235$) included three interactions: model or lizard × season × hour (partial association: $G = 27·53$, df = 12, $P = 0·006$); model or lizard × sun exposure × hour ($G = 276·20$, df = 24, $P < 0·001$); and model or lizard × sun exposure × season ($G = 128·33$, df = 2, $P < 0·001$). The first interaction shows that midday activity was higher in May, whereas the formation of diurnal clouds, much commoner in May than in July, reduced the number of utilizable models from 13.00 h onwards. The second interaction suggests that, in both seasons, selectivity varied with time of day: for lizards the proportion of observations in full sun was highest in the early morning, whereas for models it was highest at midday. The third, more relevant interaction shows that selectivity changed significantly from May, when sunlit sites were selected throughout the day (64% lizards *vs* 16% models in full sun) to July, when there was a pronounced selection of shaded sites at midday (11.00–18.00 h, 46% lizards *vs* 21% models in full shade).

MECHANISMS OF BEHAVIOURAL THERMOREGULATION

To evaluate the contribution of activity times to temperature regulation, the distribution of d_e of a non-thermoregulating population (mean ± SD = 8·28 ± 5·98 °C in May, 8·34 ± 8·30 °C in July; Table 1) was compared with the deviations from T_{sel} of a hypothetical lizard population using the observed times of activity as its only thermoregulatory mechanism ($\bar{d}_{act}$ ± SD = 7·31 ± 5·67 °C in May and 8·13 ± 8·24 °C in July). In May $\bar{d}_{act}$ was smaller than $\bar{d}_e$ ($t = 4·02$, df = 2338, $P < 0·001$), whereas in July $\bar{d}_{act}$ and $\bar{d}_e$ did not differ significantly ($t = 0·61$, df = 2338, $P = 0·539$). Mean d_{act} was smaller in May than in July ($t = 2·80$, df = 2338, $P = 0·005$). Thus activity times contributed significantly to thermoregulation in spring, but not in summer; their contribution ($\bar{d}_e - \bar{d}_{act}$) was 0·97 °C in May (12·9% of the difference $\bar{d}_e - \bar{d}_b$) and 0·21 °C in July (2·7% of the difference $\bar{d}_e - \bar{d}_b$).

Similarly, the thermoregulatory contribution of sun–shade selection was tested by comparing the distribution of d_e with the deviations from T_{sel} of a hypothetical population using the observed daily patterns of patch selection as its only thermoregulatory mechanism ($\bar{d}_{sun}$ ± SD = 6·99 ± 6·30 °C in May and 5·22 ± 5·97 °C in July; $N = 775$ and 1027, respectively, due to the

Fig. 2. Diel variation of the percentage of lizards and models in full sun and full shade in each study season.

exclusion of T_e measured during cloudy periods). In both seasons lizards selected patches that allowed them to maintain their T_b closer to T_{sel} than expected under the null hypothesis of no thermoregulation ($\bar{d}_{sun}$ was significantly smaller than $\bar{d}_e$; May, $t = 4\cdot13$, df = 1548, $P < 0\cdot001$; July, $t = 9\cdot78$, df = 2052, $P < 0\cdot001$). However, $\bar{d}_{sun}$ was smaller in May ($t = 6\cdot04$, df = 1800, $P < 0\cdot001$), indicating a seasonal increase in the importance of patch selection. The contribution of this mechanism ($\bar{d}_e - \bar{d}_{sun}$) was 1·29 °C in May (17·1% of the difference $\bar{d}_e - \bar{d}_b$) and 3·12 °C in July (40·8% of the difference $\bar{d}_e - \bar{d}_b$).

The intensity of patch selection within each hourly period (estimated as 1 – Pianka's index) varied with time of day in both seasons (Fig. 3), as did the amount of thermoregulation attributable to patch selection ($\bar{d}_e - \bar{d}_{sun}$); these variables were positively correlated ($r = 0\cdot751$ and $0\cdot708$ in May and July, respectively; $n = 13$ and $P < 0\cdot01$ in both cases), showing that the influence of patch selection on thermoregulation was greatest when lizards used sun–shade patches less randomly. In May lizards actively selected sunlit patches (Fig. 2), and the contribution of patch selection to thermoregulation was appreciable ($\bar{d}_e - \bar{d}_{sun} > 1$ °C) in the early morning and late afternoon, but not at midday (11.00–17.00 h), when lizards used patches randomly and $\bar{d}_e$ was smaller than $\bar{d}_{sun}$ (Fig. 3). In July, however, the distribution of lizards was non-random due to the selection not only of sunlit patches (07.00–10.00 h) but also of shaded ones (12.00–18.00 h); the contribution of patch selection was appreciable ($\bar{d}_e - \bar{d}_{sun} > 1$ °C) at all times of day except 10.00–12.00 and 18.00–20.00 h, and $\bar{d}_e$ was smaller than $\bar{d}_{sun}$ only at 18.00–19.00 h (Fig. 3).

The total amount of thermoregulation attributable to activity times and selection of sun–shade patches ($\bar{d}_{act} + \bar{d}_{sun}$) was 2·26 °C in May (30·0% of the difference $\bar{d}_e - \bar{d}_b$), and 3·33 °C in July (43·5% of the difference $\bar{d}_e - \bar{d}_b$). Thus other adjustments must account for the unexplained portion of observed thermoregulation in spring and, to a lesser extent, also in summer.
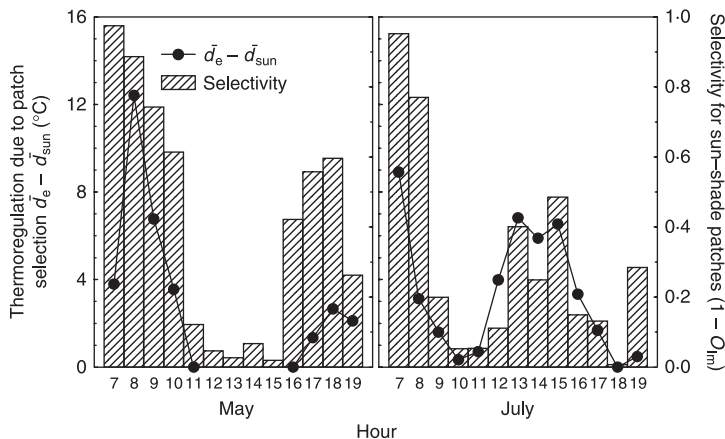

Fig. 3. Diel variation in the contribution of patch selection to temperature regulation ($\bar{d}_e - \bar{d}_{sun}$, where $\bar{d}_{sun}$ is the distribution of deviations of T_e from T_{sel} weighted for the selection of sun–shade patches; see text for details) and in the extent of selectivity (hatched bars) measured as $1 - O_{lm}$, where O_{lm} is Pianka's symmetrical overlap index between the distributions of lizards and models in full sun, filtered sun or full shade patches.

Discussion

According to our results, the behavioural mechanisms used by lizards to regulate their T_b varied considerably between seasons, although the accuracy and effectiveness of thermoregulation did not. This is in contrast with previous reports of other lizard species such as *Anolis cristatellus* from Puerto Rico (which thermoregulated more effectively in August than in January; Hertz *et al.* 1993) and *Pogona barbata* from northern Australia (which thermoregulated in summer but not in autumn; Schauble & Grigg 1998).

We first discuss the relative importance of activity times and patch selection as thermoregulatory mechanisms (Tracy & Christian 1986; Bauwens *et al.* 1996), and the factors that might explain the observed seasonal variation in their contribution. Second, we argue that shuttling between sun and shade, rather than selecting sun or shade, may be an important thermoregulatory behaviour.

SEASONAL VARIATION OF THERMOREGULATORY MECHANISMS

Daily activity contributed significantly to thermoregulation in May but not in July, whereas the selection of sun–shade patches, the contribution of which was larger than that of daily activity in both seasons, was more important in July than in May Although overall thermal suitability did not vary between seasons, the interaction between the effects of season and time of day on d_e was highly significant. Thus changes in the relative importance of various behavioural mechanisms might be related to seasonal differences in the variation of T_e among times of day and among patches within times of day.

In May, deviations of T_e from T_{sel} were high in the early morning, when lizard activity was lowest; at midday d_e was smaller and less variable than in July. On average, thermal suitability was exceptionally low ($\bar{d}_e > 10$ °C) only during the first three sampling hours, and during that period patches in full sun (those closest to T_{sel}) were not only in short supply (4·1% of models) but also of low thermal quality (mean $T_e = 26\cdot2$ °C and mean $d_e = 5\cdot2$ °C). Therefore lizard activity was low in the early morning because even the selection of the warmest microsites was of limited utility to elevate their T_b. These small thermal benefits were probably associated with important costs (Huey 1974; Huey & Slatkin 1976): the scarce sunlit patches available might be easy to locate by the numerous predators inhabiting the study area, which could take advantage of the low T_b and impaired escape performance of lizards (Christian & Tracy 1981; Huey & Kingsolver 1989; Bauwens *et al.* 1995). Not unexpectedly, the contribution of activity times to thermoregulation was significant: activity was low in the early morning and late afternoon when hardly any other thermoregulatory options were available, and high at midday hours when thermal suitability was higher.

In July deviations of available T_e from T_{sel} were large ($\bar{d}_e > 10$ °C) not only in the early morning but also at midday. However, this did not preclude a relatively large availability of shaded microsites (23·9% of models in full shade between 13.00 and 16.00 h) that offered quite favourable thermal opportunities (mean $T_e = 35 \cdot 3$ °C and mean $d_e = 1 \cdot 2$ °C). Moreover, shaded microhabitats also provide refuge against predators, at least inside Holm Oak shrubs (Díaz 1992). As a consequence, lizards could remain active at midday despite the large deviations from T_{sel} attributable to the large number of models in full sun. Not surprisingly, activity times did not contribute significantly to summer thermoregulation as lizards could remain active at midday in our Mediterranean forest, thus differing from previous reports of lizard thermoregulation in desert environments (Cowles & Bogert 1944; Grant & Dunham 1988). Only 5·5 and 21·7% of the models in May and July, respectively, attained T_e above 43·5 °C, which is the critical thermal maximum for *P. algirus* (Bauwens *et al.* 1995).

Concerning the selection of sun–shade patches, its contribution increased from May to July. It is well known that lizards modify their use of sunlit and shaded areas among seasons, times of day and/or localities in response to changes in the thermal environment (Huey *et al.* 1977; Hertz 1981; Hertz & Huey 1981; Christian *et al.* 1983; Grant & Dunham 1988; Carrascal & Díaz 1989; Díaz 1994, 1997). Thus lizards selected sunlit patches more intensively in spring, when there were more and lower T_e below T_{sel} (Huey & Webster 1976; Huey *et al.* 1977). But the most pronounced seasonal difference in the contribution of this mechanism to thermoregulation occurred, as for activity times, at midday hours. The selection of sunlit patches during the early morning basking period, and its contribution to thermoregulation, were evident in both seasons (see $\bar{d}_e - \bar{d}_{sun}$ values in Fig. 4 at 08.00–09.00 h in May and at 07.00–08.00 h in July), whereas at midday the behaviour
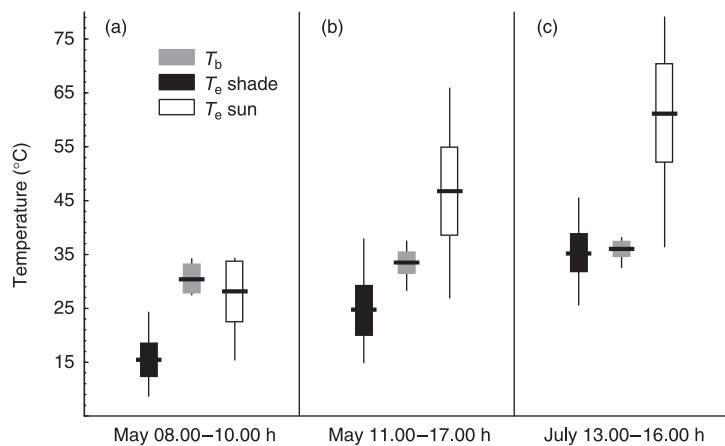
of lizards was clearly different in May and July. In May the distribution of lizards was random with respect to sun and shade between 11.00 and 16.00 h, and the selection of sun–shade patches did not contribute to thermoregulation ($\bar{d}_e \leq \bar{d}_{sun}$; Fig. 4). In July lizards actively selected shaded patches between 13.00 and 16.00, as expected from their high thermal suitability, and such selection produced temperatures that were, on average, 6·4 °C closer to T_{sel} than were T_e. In summary, the contribution of patch selection to thermoregulation increased from May to July because in the latter season it was important not only in the early morning, but also at midday.

Similarly, the contribution of patch selection was larger than that of activity time because at the hourly periods when its thermoregulatory significance was highest (e.g. 08.00–10.00 h in May; 07.00–08.00 and 13.00–15.00 h in July), selected patches were the only ones that provided temperatures close to or within T_{sel}. Thus patch selection produced a precise distribution of non-random temperatures that contributed to the elevation of T_b above randomly sampled T_e in the early morning (in both May and July) or to their descent below randomly sampled T_e at summer midday hours. At the same time, patch selection allowed lizards to remain active despite low levels of overall thermal suitability, hindering the contribution of activity times to thermoregulation.

CONTRIBUTION OF SHUTTLING TO TEMPERATURE REGULATION

In May, midday T_e had mean values not far from the lizards' T_{sel}, but their variability was very high. In addition lizards used sunlit and shaded patches almost at random, and the contribution of patch selection to thermoregulation was negligible. Between 11.00 and 17.00 h the observed distribution of lizards into sun and shade patches produced temperatures that were, on average, 2·1 °C further from T_{sel} than were randomly available T_e. However, lizard thermoregulation was both accurate and effective during that time interval, as lizard T_b were, on average, 5·8 °C closer to T_{sel} than were T_e (Table 1). Therefore other mechanisms must account for this large amount of unexplained thermoregulation.

We suggest that shuttling (moving back and forth frequently between sunlit and shaded patches) may be regarded as an additional mechanism of behavioural thermoregulation. Our methodological approach assumes that lizards achieve thermal equilibrium at the microsites they occupy (Hertz *et al.* 1993; Bauwens *et al.* 1996), but this assumption may not be valid if they move so rapidly between sun and shade that their T_b, rather than equilibrating to the T_e within each type of patch, approximates the mean T_e of the patches through which they move (Tracy & Christian 1986; Bauwens *et al.* 1996). This is exactly what our data suggest (Fig. 4). In May the mean T_b of lizards between 11.00 and 17.00 h (33·5 °C) was closer to the grand mean of T_e in full sun and in full shade (35·7 °C) than to the mean equilibrium

Fig. 4. Mean, SD and range of body temperatures (T_b) and operative temperatures in full sun (T_e sun) and in full shade (T_e shade) under three different circumstances of patch selection: (a) May, 08.00–10.00 h, when lizards actively select sunlit patches; (b) May, 11.00–17.00 h, when their distribution is random with respect to sun and shade; (c) July, 13.00–16.00 h, when they seek patches in full shade.

T_e within any type of patch (full sun 46·7 °C; full shade 24·7 °C; partial sun 29·8 °C). This contrasts with the situation observed when lizards actively selected patches in full sun (e.g. 08.00–10.00 h in May) or in full shade (13.00–16.00 h in July), and their T_b approached the mean T_e of the selected patch type (Fig. 4).

Shuttling would be of particular importance at those times of day when the distribution of lizards is unselective and the contribution of patch selection to thermoregulation is smallest (Fig. 3). Its involvement would be larger in spring, consistently with the larger proportion of thermoregulation unexplained in that season by the mechanisms discussed above. The thermoregulatory significance of shuttling has been considered by previous researchers (Tracy & Christian 1986; Hertz *et al*. 1993; Bauwens *et al*. 1996), but we know of no formal method to quantify its contribution directly (e.g. combining information about environmental temperatures and heat-exchange rates; Díaz 1991; Carrascal *et al*. 1992; Gvodzik 2002). Previous studies have shown that lizards from a nearby population of *P. algirus* use sunlit patches more often, but during shorter periods, after the early morning basking period, when heating rates in the sun equal cooling rates in the shade (Díaz 1991).

In conclusion, the high accuracy and effectiveness of lizard thermoregulation in Mediterranean open forests, which remained constant throughout the activity season, may conceal substantial variation in the relative contribution of the different behavioural mechanisms employed to thermoregulate. Some of these mechanisms, such as daily activity, are probably less important than previously thought; whereas others, such as shuttling movements between sun and shade that impede body temperature equilibrating to the environmental temperature within any type of patch, may have greater significance than previously thought.

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