Oecologia (Berl) (1982) 53:222–226

Oecologia

The Effect of Photoperiod on Temperature Selection in the European Green Lizard, *Lacerta viridis**

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Summary. Voluntary body temperature selection of unrestrained *Lacerta viridis* revealed consistant photoperiod entrained diel patterns. Each daily cycle was characterized by an elevation in body temperature (T_b) to a high level plateau which declined at the onset of scotophase to a low level; both of which were maintained within narrow ranges.

Under natural photoperiod in fall, lizards responded to shorter days by sinking low level T_b's and expanding the duration of these low levels until no rhythmicity was shown. Subsequent exposure to long day, LD 16:8, induced self-arousal and a slightly altered diel T_b selection with significantly higher T_b's being chosen at both the elevated and lower daily levels. Changes in the relations of diel T_b selection due to a shift in photoperiod, suggest that photoperiod acts as a seasonal indicator for thermal adaptation.

Introduction

Lizards are usually associated with warm climates, but can be found as far north as latitude 70°, which is north of the Arctic Circle (Andersen 1971). It would seem reasonable for lizards confronted with seasonal extremes to display overt thermoregulatory measures. In a review on adaptation of reptiles to cold, Spellerberg (1976) stated that very little reliable information is available on thermal relations of European reptiles and on temperate climate lizards in general. The family Lacertidae represents an important group of European lizards with 180 species distributed from southern Greece to northern Scandinavia.

The ability of lizards to effectively thermoregulate, primarily by behavioral means, was recognized at the beginning of the century, but it was not until 1944 that Cowles and Bogert published a series of papers establishing general terminology for practical comparison of reptile thermobiology. Studies pertaining to temperature measurements in reptiles have been numerous and include many various methods, e.g. mercury and quick-reading thermometers, thermocouples and transmitter telemetry. Only the latter allows deep core T_b monitoring of totally unrestrained animals. Employment of telemetry monitoring has for the most part been limited to fairly large lizards, e.g. lace monitor (Stebbins et al. 1968), Galapagos marine iguana (Mackay 1964) and the western fence lizard (McGinnis 1970), but advanced models can be implanted in small lizards (< 50 g). In the past, many investigations on lizards' T_b have been performed in photothermal gradients, which when shut down at night assume room temperature, thus permitting no voluntary selection of temperature during the scotophase. The importance of usage of thigmothermal gradients employing a wide temperature regime has been stated by Engbretson et al. (1976), since only these allow a lizard voluntary thermal selection throughout its entire daily cycle.

Lacerta viridis is one of the largest European lizard species, primarily inhabiting northern Spain, France and central Italy, but also found in areas of Germany even as far north as the Mark Brandenburg, latitude 52°. It was our aim to develop a method of continuous long term T_b monitoring and to collect T_b data from this temperate climate lizard under as natural as possible conditions. This was carried out by following the daily voluntary temperature selection by means of radio telemetry in unrestrained *Lacerta viridis* under natural photoperiod during fall, in winter and after subsequent exposure to artificial long day.

Material and Methods

European green lizards from field populations of southern France and northern Italy were purchased from commercial suppliers in summer. All animals were held in single cages at a constant room temperature of 23° C, and fed a diet of fly maggots, mealworms and crickets. Fresh water was supplied daily in shallow dishes. *Lacerta viridis* were exposed to natural photoperiod during late summer and fall, thus experiencing ever shorter daylight hours. Following winter solstice an artificial long day LD 16:8, was initiated. During maintenance under natural photoperiod, illumination was provided by a window facing ENE and fluorescent lighting, controlled by a timer which was reset weekly according to sunrise and sunset. Long day conditions were maintained soley under artificial lighting. Mean light intensity in the animal room varied between 60 and 200 lux.

In order to test voluntary temperature selection, five identical thigmothermal gradient cages (70 × 40 × 35 cm) were constructed. The gradient, a solid sheet of aluminum with copper tubing attached to the bottom side, was heated and cooled at opposite ends by circulating water baths. A uniform transition from 10 to 40° C was herewith established in all gradient cages. These temperatures are representitive of those which *Lacerta viridis* experience in nature and were maintained throughout the experiment. A thin layer of sand covered the floor of the cage and shelving across the entire back length provided the lizards with

* This research was carried out in partial fulfillment of a diploma degree at the J.W.G. University, Frankfurt/Main

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0029-8549/82/0053/0222/$01.00

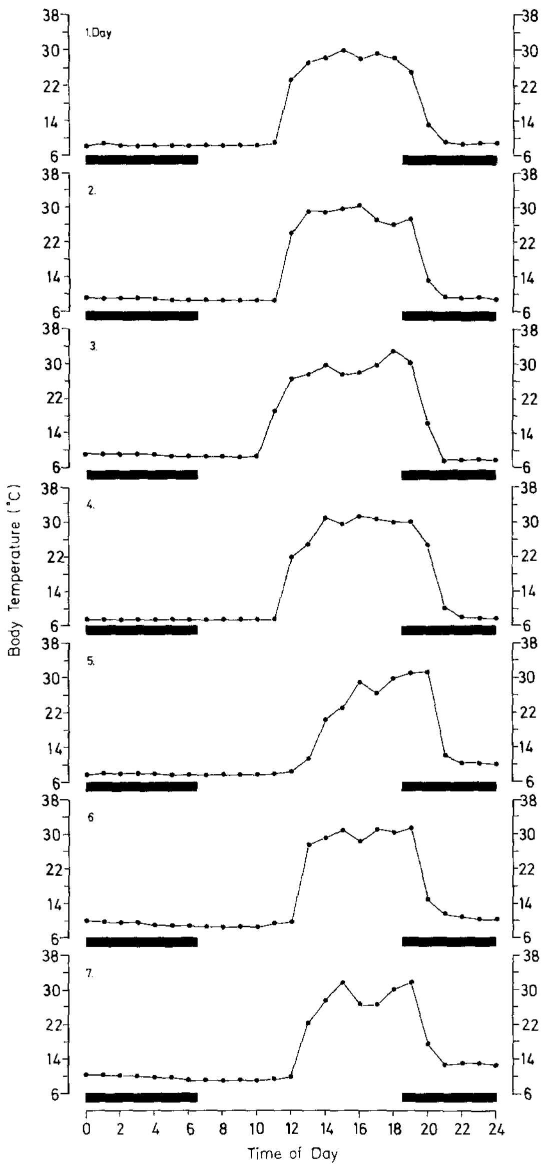

Fig. 1. Voluntary body temperature selection of a single lizard monitored over 7 consecutive days in mid Sept. under natural photoperiod. Each point represents the hourly mean T_b. Black bars indicate the scotophase

shelter at any given temperature of the gradient. Air temperatures within the cages, measured 5 cm above the floor approximated those of ambient ($23 \pm 1°$ C).

Temperature sensitive radio transmitters (Mini-mitter, model X), 1.4 cm long, 0.5 cm in diameter and weighing 1.3 ± 0.1 g, were used to obtain lizards'deep core body temperature. Animals were anesthetized with Halothane and the transmitters were implanted intraperitoneally. Observations showed that the implants had no affect on normal behavior, and transmitters were replaced without complications. Mean body weight of *Lacerta viridis* used in this experiment was 33.6 g.

Mini-mitter implanted lizards were placed singly in gradient cages, and remained therein throughout the entire experimental period. Body temperature emitted signals perceived through an antenna and modified by a simultaneous digital-analog transformer were registered continuously on a recorder, thus allowing exact T_b determination for each ten minutes. Mean hourly T_b's were then graphically charted for each day. Five *Lacerta viridis*

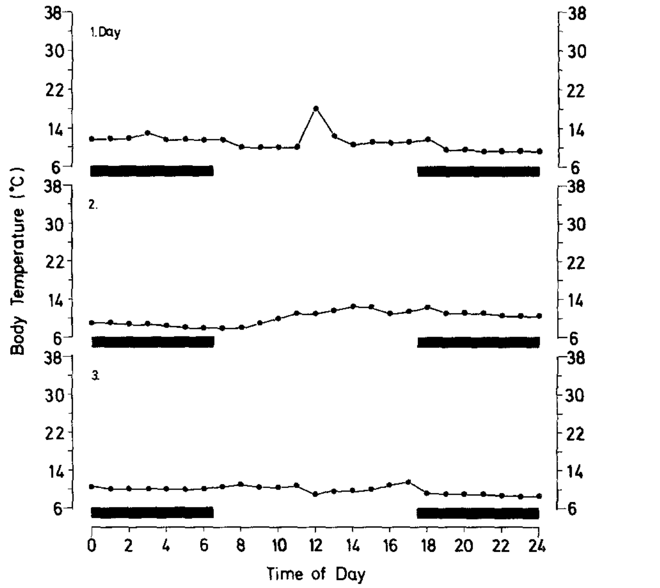

Fig. 2. Hourly mean T_b's of a single lizard living in a thigmothermal gradient cage under natural photoperiod. Data was collected over 3 consecutive days at the end of Oct. and represents the lizards' brumation period. Black bars indicate scotophase

were monitored successivily for 7 to 14 consecutive days beginning Sept. 13 by LD 12:12, and continuing through the naturally decreasing photoperiod to LD 8:16 on Dec. 21. At this time LD 16:8 was introduced, and after several weeks, transmitters were exchanged for renewal of batteries and registration was begun anew. In this manner, daily voluntary thermal selection data were gained from unrestrained *Lacerta viridis* during fall, i.e. transition to short day, and during an artifical long day.

Tests of significance were made using the paired t-test.

Results

All *Lacerta viridis* demonstrated similar daily rhythms of thermal selection. Figure 1 is a typical example of a single lizard registered over seven consecutive days during fall. Each diel cycle is typified by two distinct plateau levels of body termperature, which are maintained within a fairly narrow range. During fall monitoring, a rapid rise in T_b occurred 3.5 to 5.5 h after the onset of photophase and remained at this elevated level for 8 to 9 h; then descending as rapidly as it had risen shortly after scotophase begin. Mean T_b over the 7 recorded days was 28.7 and 8.9° C for the high and low level, respectively.

Registration of the same lizard later in fall revealed altered behavior in thermal selection. Body temperatures no longer displayed the clear temporal cycle shown earlier. Not only the onset of T_b elevation, but also the duration of the different levels varied greatly from day to day. This irregular pattern of temperature selection was followed by an absence of T_b rhythmicity (Fig. 2). As lizard's T_b remained at a stable low level over many days (mean T_b 10.8° C), we equated this period to brumation. Subsequent exposure to artificial long day induced self-arousal from the brumation state and a renewed cyclic pattern of T_b selection ensued. Figure 3 shows seven consecutive days of thermal selection in the same lizard pictured for fall and brumation. In the first four days of registration, a higher and lower level plateau in daily T_b selection can clearly be distinguished. Elevation in T_b is usually concurrent with the onset of the photophase and the rapid decline to lower level tempera-

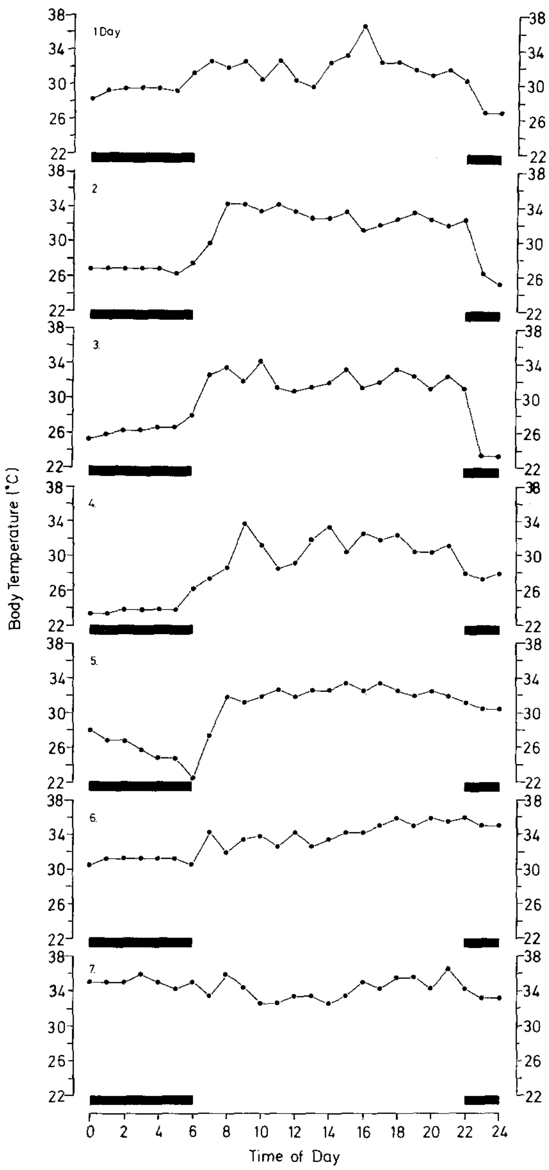

Fig. 3. Seven consecutive days of voluntary T_b selection of a single lizard after 6 weeks acclimation to long photoperiod (LD 16:8). Other features as in Fig. 1

tures occurs shortly after scotophase begin. The duration of the elevated plateau is therefore approximately 16 h. Mean T_b for the different levels over these four days was 32.7 and 26.1° C. Days 5 through 7 demonstrate that the lizard abandons its daily rhythmic pattern at some time under the influence of long photoperiod, and maintains its T_b at a constant high level. During this prolonged high level period, T_b never falls below 32° C and temperatures even greater than this were prevalent.

Comparison of high and low T_b for individual lizards during fall, brumation and long day are presented in Fig. 4. For each period, T_b's are displayed as the mean with range indicated. All individuals voluntarily selected distinct high and low levels of T_b which conform to a temporal pattern. This pattern was present not only during fall, but also under long day conditions. It was only during brumation that no clear cyclic repetition could be detected. Moreover, T_b calculated for individual lizards during the brumation state was in most cases lower than low level temperatures during fall.

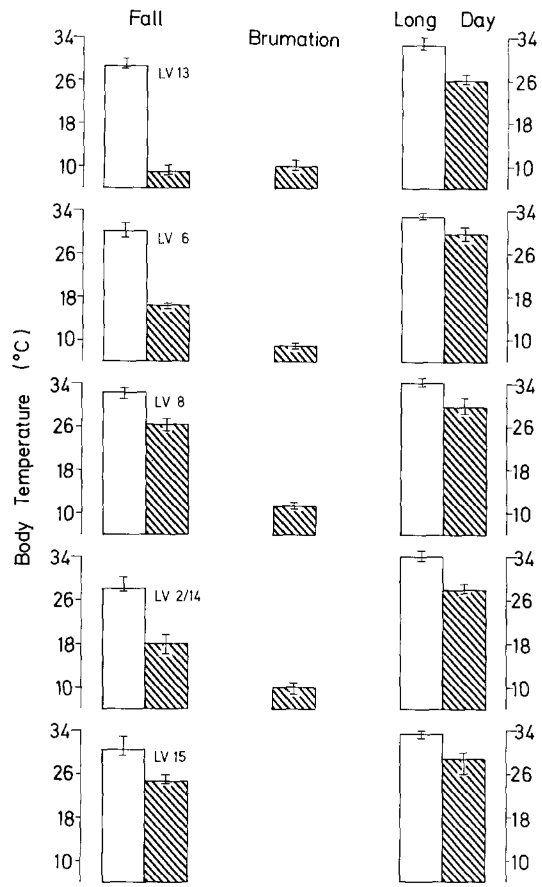

Fig. 4. Mean high (*open columns*) and low (*hatched columns*) level T_b's of individual lizards during fall, brumation and long day. Values for fall and long day were calculated from data for 5 to 7 consecutive days. Horizontal lines represent the range

Table 1. Phase relations of T_b rhythmicity in individual *Lacerta viridis*, measured under natural photoperiod in fall and artificial long day. Values are means over 5 to 7 consecutive days, ±SD. Phase angle (h) for onset of high level T_b as related to onset of photophase

Animal Nr.	ψ onset (h)		Duration of high level T_b (h)	
	Fall	Long day	Fall	Long day
LV 13	−4.8 ±0.8	+0.6 ±0.5	8.4 ±0.5	16.4 ±0.5
LV 6	−2.5 ±1.7	−0.3 ±1.0	7.0 ±2.6	16.2 ±1.2
LV 8	−0.8 ±0.4	−0.2 ±0.4	12.0 ±0.4	16.3 ±0.8
LV 2	−2.0 ±1.3	+2.0 ±0.4	5.7 ±1.0	16.2 ±0.7
LV 15	−0.4 ±0.2	0.0	11.5 ±2.9	15.7 ±0.5

Voluntary T_b selection during fall and long day photoperiods was characterized by subtle differences. Whereas the range for elevated T_b's in fall lies between 28.3 and 32.4° C for individuals, this level during long day increased to between 32.7 and 34.2° C. Likewise, lower level T_b ranges for fall and long day differ, and lie between 8.9 to 26.5° C and 26.1 to 29.8° C, respectively. Both levels of T_b were significantly higher under long day ($p<0.005$ and $p<0.02$). Long photoperiod was also accompanied by an increased duration of high level T_b. During fall lizards maintained elevated T_b's for 5.7 to 12.0 hours daily, and under long day this increased to 14.5 to 17.0 h. Elevated levels of T_b during long day are more strongly coupled with the photophase than in fall. This is characterized by a more positive phase angle between onset of high level T_b and onset of photophase (Table 1).

Discussion

European green lizards living in a semi-natural environment displayed a distinct diurnal pattern of thermoregulatory behavior. Diel thermal selection in other lizards has also been documented, e.g. in *Anolis carolinensis* (Hutchison et al. 1974; Underwood 1980), *Lacerta sicula* (Spellerberg et al. 1974) and *Scelophorus magister* (Engbretson et al. 1976). In all studies a daily rhythm was evident, with higher temperatures selected in the photophase and lower temperatures selected in the scotophase. Furthermore, the results presented on voluntary thermal selection in *Lacerta viridis* illustrate that changes in photoperiod produce changes in the diurnal pattern of temperature selection. Registration of T_b during fall under naturally transitioning photoperiod revealed that the number of h a lizard maintained an elevated T_b was reduced from 12 to 4 from mid September through mid November. Occurrence of daily voluntary hypothermia in other lizards has been reported (Regal 1967) and may indicate a purposeful energy saving measure for the animal. However, the significance of periodic hypothermia to a lizards' thermophysiology has not been fully investigated. This aspect is especially vital in respect to preparation for brumation in lizards living in temperate climate zones.

The importance of photoperiod as a seasonal cue is emphasized by the fact that all *Lacerta viridis* entered brumation despite a constant air temperature of 23° C, availability of food and high gradient temperatures permitting normal activity. During this period of dormancy individuals had mean daily T_b's between 8.8 and 11.3° C, indicating that no activity took place. Little research has been carried out on the aspect of winter dormany in reptiles, nonetheless both facultative and obligatory hibernators are known. *Lacerta viridis* would seem to belong to the latter of these.

Artificial long day LD 16:8, stimulated self-arousal and a renewed, but slightly altered diurnal rhythm of T_b selection. Whereas lizards maintained high T_b's a mean of 8.5 h during the transitioning photoperiod of fall, this high level duration almost doubled during long day, 16.2 h. Moreover, both high and low levels of T_b were significantly elevated during long day. Whereas the level of high and low T_b between fall and long day increased, the amplitude between the levels decreased. Mean differences in amplitude for fall and long day were 10.9 and 4.9° C, respectively (Fig. 4). The significance of changes in T_b level as a response to photoperiod may represent an important physiological adaptation for lizards in temperate climate areas. All findings suggest that the length of the daily light period acts as a seasonal synchronizer for Lacerta viridis' thermal behavior. Use of daylength as an indicator of seasonal change can be especially advantageous for reptiles living in temperate areas where other parameters such as weather or food availability are not so readily predictable. This is supported by studies on the annual testis cycle in three species of *Uma* (Mayhew 1964) and *Anolis carolinensis* (Licht 1967, 1971) which have also been found to be regulated by photoperiod.

The concept of preferrred body temperature in reptiles is probably the most widely documented aspect of reptile thermobiology. However, various often ambiguous methods under which temperature data have been collected, have lead to an abundance of contradictory findings. For the most part, T_b's of active individuals recorded during the diurnal portion of the day have been presented as the preferred body temperature for many species. As a result of the rhythmicity in voluntary T_b selection shown by *Lacerta viridis*, with a distribution of high and low temperatures that do not occur randomly, but constitute two well-defined levels of thermal selection, we suggest that two different preferred body temperatures per daily cycle should be acknowledged. Furthermore, it has been indicated that not only the time of day, but also the time of year, i.e. photoperiodic history of the animal, is important when considering a reptiles preferred temperature. In this study, the mean preferred body temperatures of *Lacerta viridis* for the two different levels in fall were 30.0 and 18.9° C, and during long day, 33.5 and 28.5° C. Although no locomotor activity was registered, it is postulated that these high and low T_b levels correspond to the activity and rest phases of the lizard, as they also strongly correlate with the photo- and scotophase. Observations of continuous high level T_b's after extended exposure to long day suggest mating unrest. This is confirmed by a field study on *Lacerta viridis* (Weber 1957) documenting that many animals were active after dark during the summer months. Mating was observed even at dusk and females were seen laying their eggs at night. Removal of temperature transmitters after completion of the experiments revealed that females had well-developed eggs and the male testicles were much larger than at the initiation of long photoperiod.

Few attempts have been made to investigate seasonal variation in thermoregulatory behavior and preferred body temperature in lizards. In a field study on *Sceloporus orcutti* (Mayhew 1963), mean T_b measured during January and Fabruary was found to be significantly lower than in any succeeding month. In contrast, laboratory investigations concerning seasonal preferred body temperatures in *Sceloporus occidentalis* (McGinnis 1966) and *Sceloporus virgatus* (Stebbins 1963) found no shift in preferred temperatures. It should be noted that both studies were conducted using photothermal gradients under non-varying photoperiodic conditions.

European green lizards responsed to long day photoperiod acclimation with a significant increase in preferred body temperatures over fall. An investigation by Ballinger et al. (1969) on *Sceloporus undulatus* also suggests an adjustment of preferred temperature due to photoperiod acclimation. However, Licht (1968) found no differences in the preferred temperatures of *Anolis carolinensis* after acclimation to various photoperiods. The thermoregulatory responses shown by *Lacerta viridis* in this study indicate that the photoperiod plays an important role not only in daily thermal selection, but that it may also act as a primary cue to seasonal changes in T_b selection.

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Received December 9, 1981