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How photoperiod influences body temperature selection in *Lacerta viridis*

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Summary. European green lizards, *Lacerta viridis*, show a distinct annual cycle in their day and nighttime selected body temperature (T_b) levels when monitored under natural photoperiod. The amplitude between daily photophase and scotophase temperatures varies throughout the year. Highest body temperatures with smallest day/night variation are selected from May through July. Throughout fall, the difference between day and nighttime selected T_b levels increases. Lizards inevitably enter a state of winter dormancy which terminates daily rhythmicity patterns. Under natural photoperiodic conditions, cessation of dormancy occurs spontaneously by mid-March, regardless whether high temperatures are available or not. *Lacerta viridis* respond to an artificial long photoperiod (16 h light, 8 h dark) at all times of the year with modifications in both diel patterns and levels of selected T_b to summer-like conditions. When, however, the natural photoperiod at different phases in the annual cycle is held constant for six to eight weeks, T_b selection of *Lacerta viridis* also remains stable at the level corresponding to the prevailing photoperiod. These results implicate that the photoperiod is a more prominent Zeitgeber for seasonal cueing of temperature selection than has been surmised in the past. Further, we suggest that the large variations recorded in daily T_b cycles do not imply that this lizard is an "imprecise" thermoregulator, but rather indicates an important integral process necessary for seasonal acclimatization.

Key words: Lizard – *Lacerta* – Photoperiod – Thermoregulation – Annual cycle

An ectotherm depends highly on environmental factors for regulation of body temperature. Two main principles describe the means of gaining external heat; heliothermic reptiles bask and directly absorb solar radiation, whereas thigmothermic reptiles profit chiefly from the conductive and convective heat of hot air and substrate. Most reptiles do not, however, merely allow themselves to heat and cool passively. It is well documented that many lizards regulate T_b within a narrow, species specific range during their activity portion of the day (Brattstrom 1965; Licht et al. 1966). The physiological mechanisms which support behavioral thermoregulatory traits have not been unequivocally determined, but there is good support for a rigidly controlled cardiovascular system which regulates peripheral blood flow during episodes of heating and cooling (Morgareidge and White 1969; Baker and White 1970; White 1970, 1976; Smith 1979; Bartholomew 1982).

Even though it is well established that some lizards do indeed maintain precise T_b levels during their activity portion of the day, only a few investigations have recorded entire daily cycles of temperature selection (Hutchison and Kosh 1974; Engbretson and Hutchison 1976; Cowgell and Underwood 1979; Rismiller and Heldmaier 1982) or seasonal changes in T_b (St. Girons and St. Girons 1956; Mayhew 1963). It is contradictory that some studies report field populations of lizards showing seasonally changing levels of T_b, whereas the same species measured in thermal gradients do not (McGinnis 1966; Case 1976; DeWitt 1967). Licht (1968) suggests that such observations are directly related to environmental climatic conditions and thus T_b's measured in the field do not necessarily reflect an inherent change in the thermal preferendum of the animal at different times of the year. Mayhew (1963) has, however, reported that the T_b of *Sceloporus orcutti* shows seasonal changes which are not related to environmental conditions (e.g. ambient temperature) prevailing at the time of capture. Since ectotherms are generally considered to be thermally labile, the interaction between reptiles and fluctuations in their physical environment has mainly focused on temperature. The impact of light, or the transitioning seasonal photoperiod on behavioral and physiological modification of T_b selection has received little consideration. Indeed, most studies on reptile thermal requirements have treated heat and light synonymously (Stebbins 1963; Mcginnis 1966; Roth and Ralph 1976). The use of photo-thermal gradients as well as experiments conducted under an artificial photoperiod, i.e. a light/dark regime not coinciding with the natural photoperiod, may influence T_b selection of reptiles measured in the laboratory.

This study investigates the influence of photoperiod on T_b selection of a lizard maintained in a homogeneous microhabitat in terms of temperature and food availability. The European green lizard was chosen for the present study because it inhabits diverse ecological areas where large fluctuations in environmental temperature are common. Further, in an earlier investigation we were able to show that both patterns and levels of selected T_b change from mid-September through December when monitored under natural photoperiod (Rismiller and Heldmaier 1982). Our thesis postulates that the photoperiod plays a key role in seasonal

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cueing for T_b selection in this temperate climate lizard. Changes in T_b level may facilitate acclimatization to seasonal environmental changes confronted in nature. To investigate this paradigm on *Lacerta viridis*, we monitored T_b selection under natural photoperiod and also examined the effect of sustained or artificial photoperiod on T_b selection at different times of the year.

Methods

Lacerta viridis used in this four year study originated from a field population near Bologna, Italy (latitude 44°30′ N). Not only adult animals, but also one and two year old *L. viridis* bred in our laboratory were investigated. When not involved in experiments, groups of four to eight lizards (males and females) were housed in large terrariums (120 × 60 × 50 cm) with access to a warmer or cooler microclimate. A variety of insects were provided every other day and water supplemented with vitamin D_3 was available *ad libitum*. The terrarium room was maintained under natural photoperiod at all times, illuminated by fluorescent rods. Lights were controlled by a timer reset weekly according to sunrise and sunset and ceiling windows provided the room with a natural twilight period. In fall, all lizards not in experiments were placed in hibernation boxes (styrofoam or wooden boxes filled with dirt) and overwintered in a 5° C, natural photoperiod chamber. Termination of the hibernation period was determined for each lizard individually, according to reappearance on the surface.

Body temperature selection of *Lacerta viridis* in all experiments was monitored in thigmothermic gradient cages. The ground of these cages offered the animals a constant uniform temperature transition from 10 to 40° C (for details see Rismiller and Heldmaier 1982). Food and water were available *ad libitum*. Core body temperature of the lizards was measured telemetrically using small temperature transmitters (Mini-Mitter, model X) implanted intraperitoneally. With our system we were able to monitor and record T_b selection of twelve individually housed *L. viridis* in 3 min intervals.

To explain the system in short, transmitter pulses received via the antennas by modified car radios are amplified to a logic level pulse (+5V) that is directed to one of the input lines of a Commodore C64 user port. The time between two pulses, i.e. the time between two 0–1 transitions at the input line is measured with a machine language subroutine. Most of the environmental electrical noise interfering with the transmitter signal can be detected and eliminated by receiving the interference via an additional radio and comparing it to the transmitter signal. Selection of the 12 channels is controlled by software via three output lines of the C64 user port. After 24 h, data are stored on disk for immediate or later plotting and evaluation. For full details of this system, see Ruf and Heldmaier (1987).

Experiment I. Lizards from natural photoperiod were implanted with Mini-Mitters and placed in thermal gradients. A week was allowed for recovery and for the animal to become accustomed to the gradient cage. Body temperature selection was recorded continuously for 7–14 days under natural photoperiod. This experiment was repeated with different animals for every month of the year. Mean selected T_b during the photophase and during the scotophase was calculated for each lizard, as well as for the entire group.

Experiment II. Response to long photoperiod (16 h light/8 h dark) was determined by taking *Lacerta viridis* from natural photoperiod and placing them in an artificial long photoperiod at different times of the year. Selection of daily T_b was monitored for up to 30 days. In order to rule out the influence of handling, especially during winter experiments, we tested the effect of long photoperiod on both lizards which had been placed in the 5° C chamber for winter hibernation and later returned to the gradient, as well as lizards which had voluntarily entered winter dormancy while occupying a gradient cage.

Experiment III. Mini-Mitter implanted *Lacerta viridis* were placed in gradient cages at different times of the year, and the prevailing natural photoperiod was maintained throughout a test period of 6–8 weeks. Mean day and nighttime selected T_b's were determined for the first and last 7 days of recording and compared with T_b selection of animals measured in a transitory photoperiod. For comparison of means, the 2-way *t*-test was used for unrelated samples and the paired *t*-test for related ones. Seasonal differences were determined using simple analysis of variance and the two-way analysis of variance (ANOVA), accordingly.

Results

An earlier study has documented that *Lacerta viridis* show a diel rhythm in T_b selection during the fall, which is terminated with the begin of winter dormancy (Rismiller and Heldmaier 1982). In this study a more sophisticated monitoring system allows us closer insight not only on changing daily and seasonal levels of T_b selection, but also on their seasonally changing patterns.

Experiment I. Original recordings of voluntarily selected daily T_b under natural photoperiod are presented for every other month in Fig. 1. Whereas the mean amplitude between day and night levels of T_b in early spring and fall are large (8.9 and 10.1° C, respectively), levels of T_b in summer show only small day/night fluctuations (~4° C), and in winter they remain at a constant low level. Further, the temporal relation of T_b decline and elevation to the photoperiod varies seasonally. Whereas in spring T_b decline occurs after onset of the scotophase, in fall T_b usually decreases to a low level before sunset. On the other hand, in spring and summer photophase begin is often anticipated by an increase in T_b before lights on. In contrast, during the fall months T_b never rises until hours after the onset of the photophase. Elevation of T_b occurs increasingly later in the day as the length of the scotophase advances, until the lizards enter winter dormancy and remain for long periods at the cold end of the gradient.

Because of the distinct daily rhythms over most of the year, with higher levels of T_b chosen during the active portion of the photophase, two different mean levels were assessed. Monthly day and nighttime T_b means were determined from data of 5–10 *Lacerta viridis* for periods between 7–14 days (Fig. 2). Although an annual pattern of selected T_b level is apparent for both times of day, there is a clear split in the selection of daytime T_b levels from September through November. One group of lizards continuously decrease both day and nighttime levels of T_b, starting in August or September and usually show no day/night T_b variations after October. These animals were termed "early"

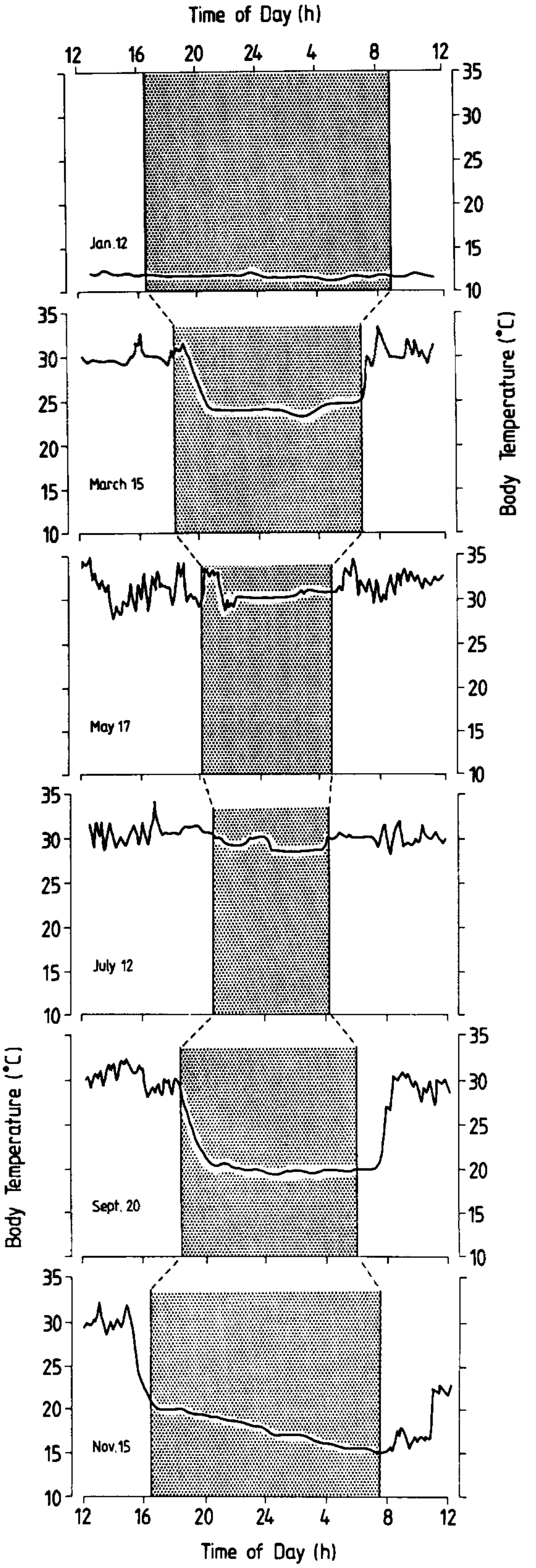

Fig. 1. Original data showing diel patterns of T_b selection at different times of the year under natural photoperiod. The shaded area represents the scotophase

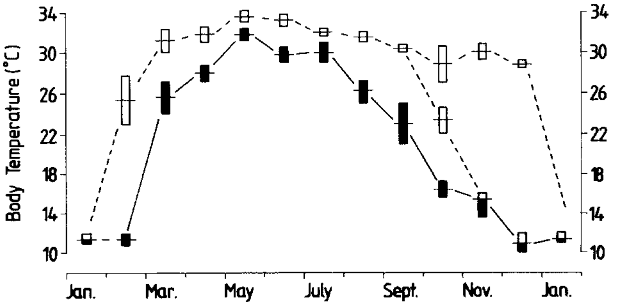

Fig. 2. Annual cycle of mean (horizontal line) selected photophase (open symbols) and scotophase (closed symbols). T_b's monitored in natural photoperiod ($N=5$–10). The vertical bars represent ±1 SEM. For explanation of split in photophase T_b's, see text

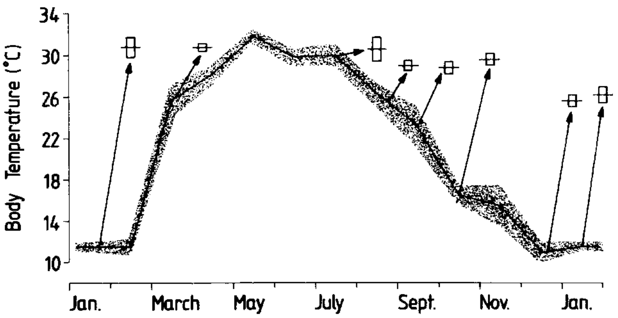

Fig. 3. Effect of long photoperiod on mean selected scotophase T_b's ±1 SEM (horizontal line with open bars) at different times of the year ($N=5$–6). The shaded area represents the course of scotophase T_b selection ±1 SEM under natural photoperiod. The arrows indicate the start and duration of each experimental period

hibernators. Those lizards who continued showing a daily elevation in T_b during the photophase until as late as mid-December were characterized as "late" hibernators. It should be noted, however, that the scotophase T_b's of these late hibernators follow the same pattern as those of the early hibernators, i.e. a continuous decrease until the onset of winter dormancy.

Evaluation of daytime selected T_b's show not only a difference in the absolute level, but also variations in the preciseness of regulation around this mean level at different times of the year. In March, for example, the mean selected photophase T_b of 6 lizards over a five day period was 31.5° C. The range of minimal to maximal T_b's selected during these days was 22.5–33.8° C. During the month of June, the mean daytime selected T_b level was 32.4° C with a range of only 31.1–33.6° C. A wider fluctuation is seen again during the fall. In one group of early hibernators in October, mean selected photophase T_b was 22.9° C and the minimum to maximum T_b's chosen over 5 days ranged from 17.8–30.2° C.

Experiment II. Lacerta viridis always responded to long photoperiod with an elevation of both day and nighttime T_b levels. The diel pattern of T_b selection was similar to that during summer, i.e. there were only very small variations in day/night levels. Because the annual cycle of mean selected T_b was more pronounced in the scotophase, it has been used as a baseline to illustrate the effect of long photoperiod at different times of the year. In Fig. 3, one sees that although long photoperiod always induced an augmentation in selected T_b, the absolute level varied according to the time of year tested. Mean scotophase T_b after 3 weeks exposure to LD 16:8 in late January, March and July was 30.9° C, which is similar to scotophase T_b levels selected in spring. The mean scotophase level after 3 weeks of long

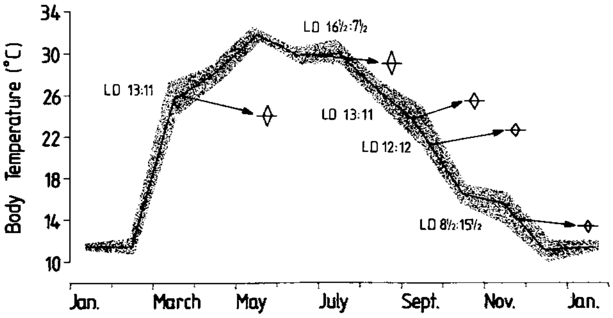

Fig. 4. Effect of sustained photoperiods at different times of the year on mean selected scotophase T_b's of *Lacerta viridis*. Other details as in Fig. 3

photoperiod in August, September and October was only slightly lower, 29.1° C. In December and early January long photoperiod also induced a significant elevation ($P < 0.001$) in selected scotophase T_b's as compared to controls under natural photoperiod (26.0 and 12.2° C, respectively). This increase in T_b was, however, significantly lower ($p < 0.05$) than the response evoked by long photoperiod at other times of the year.

Experiment III. The influence of different sustained photoperiods on voluntary T_b selection is shown again in comparison with the annual cycle of the mean selected scotophase levels (Fig. 4), the arrow denoting the beginning and end of the experimental period. Maintaining the photoperiod at LD 13:11 in March hindered the normal rapid ascent in T_b which is usual for this time of year. Diel patterns and levels of selected T_b did not change within the 8 week monitoring period and were significantly lower ($p < 0.01$) as compared to temperatures of animals under natural photoperiod. Sustained photoperiods during the descending portion of the annual cycle yielded similar results. Both daily patterns and levels of selected T_b remained relatively constant throughout the duration of the test period. Whereas *Lacerta viridis* under natural photoperiod were well on their way to winter dormancy, those maintained in LD 13:11 or LD 12:12 still had scotophase T_b's of 25.6 and 23.8° C, respectively. It was only in late November that no significant differences in T_b were found between experimental and natural photoperiod conditions.

Discussion

The direct interaction of a reptile with its thermal environment has often been considered the fundamental factor for ectothermic body temperature regulation. *Lacerta viridis* clearly show that seasonal changes in T_b levels are not solely dependent on the availability of a thermal source, but rather that the changing light/dark duration cues selection of an appropriate T_b level for the time of year. Photoperiod, the most reliable parameter for seasonal cueing in a temperate zone area, influences T_b selection of this lizard. It is, however, certainly the synergic action of environmentally changing photoperiod and ambient temperature which mediates information for seasonal acclimatization, inducing both behavioral and physiological adjustments. The annual T_b selection cycle of *Lacerta viridis*, evident under natural photoperiod, presents a new dimension to reptilian thermal ecology. We will first discuss the ecological relevance of the T_b cycle in relation to other seasonal occurrences, and second view the aspect of thermoregulatory precision.

After emergence in early spring, both day and nighttime levels of selected T_b rise rapidly, however highest levels are not selected until May through July. This is likely due to the thermoregulatory costs early in the spring. The selected photophase T_b's immediately after arousal from dormancy are in any case high enough to allow foraging and feeding. The relatively large day/night amplitude may not only benefit energy conservation, but also facilitate acclimatization and tolerance to higher temperatures which could be encountered during the forthcoming summer months.

Diel and seasonal cycles of thermal tolerance have been reported for a variety of ectotherms (Hutchison and Maness 1979). Further, some studies document that reptiles acclimated to a 24 h thermoperiod (fluctuating day/night temperature) have higher thermal tolerance than those maintained under constant ambient temperatures (Mueller 1970; Hutchison and Ferrance 1970). The integrated role of thermal preferendum and photoperiod on seasonal thermal tolerance has received little attention. Licht (1968) acclimated lizards to different temperatures and photoperiods, and found that lizards kept on longer days (14 h light) were more heat resistant than those maintained under short days (6 or 0 h light). Similarly, two groups of *Sceloporus o. occidentalis* maintained in the same thermoperiod, but exposed to either LD 16:8 or LD 8:16 responded differently to heat loads. Not only was an upward shift in thermal tolerance detected in long day animals, but they were also able to hold T_b below critical level for extended periods as compared to lizards acclimated to short photoperiod (Lashbrook and Livezey 1970). These findings justify speculation that the fluctuations in voluntarily chosen T_b levels of *L. viridis* are of physiological significance. Moreover, it is likely that increasing photophase duration (or shortening of the scotophase), cues this response.

Although reproduction has probably been studied more extensively than any other physiological process in reptiles, little is known about its correlation to selected T_b's. In the laboratory *Lacerta viridis* start to mate shortly after spring arousal, in March and April. During the following 3 months all lizards regulate T_b at levels higher than at any other time of the year, and females lay their eggs. Following this period, T_b levels, especially those in the scotophase, begin to decline. Early field studies of Mertens and Schnurre (1949) and Weber (1957) report that *Lacerta viridis* have been seen mating after sunset and that females usually lay their eggs after nightfall. It is not possible to deduce the field T_b's of gravid *L. viridis*, or speculate by which means they may retain higher T_b's for longer periods during reproduction, however this interesting point certainly deserves more attention. In analogy to our findings, closely related females of the live-bearing species *Lacerta vivipara* have highest T_b's in April and May, during mating and ovulation, but select much lower T_b's in June and July (Patterson and Davies 1978; Damme et al. 1986). The low measured T_b's of the gravid females (~26° C) corresponds to the low thermal optimum found for the in vitro development of *L. vivipara* embryos (Maderson and Bellairs 1962). From breeding *L. viridis* in our laboratory, we know that their eggs develop best when incubated between 26–28° C.

Directly following the reproduction period, the day/night amplitude of T_b selection increases. All *Lacerta viridis* show a decrease in scotophase T_b during late summer, a time at which the duration of high level T_b is still relatively long (corresponding with the photophase). The animals continue to feed in large quantities at this time of year and fat depots build up in the trunk of the tail. Whereas the older, larger lizards continue to reduce both day and nighttime selected T_b levels, the smaller, younger animals persist with a daily elevation in T_b. The significance of this daily temperature rise, whose duration often represents only a small fraction of the photophase is not known, for food intake and body weight gain are minimal. These juveniles enter winter dormancy up to ten weeks later than adults. Similar observations have been made on field populations of *Lacerta viridis* and *L. agilis*, i.e. larger adult lizards disappear earlier than smaller or younger lizards (Korsós 1982, 1984).

Very little is known about the physiological adjustments a reptile must undergo in order to survive the winter. Lack of information can be easily accounted for. A reptile's yearly hibernation period is often viewed as an involuntary result of environmental conditions, and not as a physiological necessity. Two studies have shown that the cold tolerance of lizards can be improved by acclimating the animal to a low temperature (Kour and Hutchison 1970; Spellerberg 1976). Further, we also know that an important physiological parameter, rate of heat exchange of *L. viridis* is influenced both by time of day and the phase of the annual cycle (Rismiller and Heldmaier 1985, 1986). We therefore surmise that selection of lower (predominantly scotophase) T_b's by *Lacerta viridis* during the transitional months between fall and winter dormancy help facilitate acclimatization and tolerance to low winter temperatures.

There has been some controversy on the initiating factor for winter dormancy in reptiles, although most studies report finding no correlation between entrance into hibernation and air temperature (review, Gregory 1982). The phenomenon has been attributed to food shortage, lack of adequate solar energy or air-ground temperature gradients. Our results show that the timing of disappearance from the surface and hibernation in *L. viridis* is induced by photoperiodic cueing. An age factor is partially involved, but food availability or "optimum" temperatures are certainly not factors which prompt this reaction. Our findings are in agreement with Mayhew (1965) who first speculated that reduction in photoperiod was the responsible triggering mechanism for reptile dormancy.

Even less is known about cueing for spring emergence of reptiles. Photoperiod is usually ruled out as one of the exogenous factors, since reptiles overwinter underground, where apparently no changes in illumination can be detected. *Lacerta viridis* overwintered in the laboratory in large hibernation boxes at 5° C under natural photoperiod "signal" their end of hibernation by spontaneously appearing on the surface. Lizards overwintering in gradient cages where complete submergence is not possible, respond directly to an increase in the photoperiod. Both Mayhew (1965) and Garrick (1972) noted that cessation of winter dormancy in their study animals was not temperature controlled. Endogenous circannual cycles in T_b selection, reproduction or any other seasonally occurring incident have not been extensively studied for any reptile species, so that the contribution of endogenous seasonal clocks remains obscure.

It is clear that the T_b selection of *Lacerta viridis* is not a constant that can be expressed in terms of one mean preferred or selected level. Most reported T_b's of lizards have been measured during the activity portion (usually photophase) of the day. Time of year is rarely mentioned. Each phase of the annual cycle, however, represents a characteristic physiological status, reflected by T_b level. Acclimation to an artificial photoperiod may affect a reptile's physiological condition and thus T_b selection. Hence, not only time of day, but also time of year and photoperiodic history must be taken into consideration during studies on reptile thermal biology, and with regards to any whole-animal process.

The concept of "precise thermoregulation" in reptiles was as much emphasized by early investigators (Cowles and Bogert 1944) as it was challenged by others some 20 years later (Ruibal 1961; Rand 1964). Recent literature reports findings on both "precise" and "imprecise" temperature regulators, the latter represented primarily by tropical and nocturnal species (review, Huey 1982). *Lacerta viridis* not only show varying degrees of day/night T_b level differences, but they also alter the degree of fluctuation around their mean level according to time of year. These seasonal T_b modifications must be a consequence of the photoperiod, since they occur even though the temperature regime and food availability in the microhabitat of the lizard remain constant.

Just what is "precise thermoregulation"? Although some guidelines for terminology related to reptile thermal biology have been offered (Pough and Gans 1982; Hutchison 1979), the meaning of many concepts remain ambiguous. Consequently, there is little consistency in interpretation of data throughout the literature. One primary factor related to the concept of precise thermoregulation is energetic cost versus physiological benefit. Cost-benefit thermoregulation models theorize that lizards in high-cost environments will thermoregulate less precisely than lizards in low-cost environments. Further, a lizard is predicted to thermoregulate more carefully if productivity of the habitat (e.g. food availability) is increased (Huey and Slatkin 1976; Lee 1980). Data on some lizard species seem to agree with these predictions (Lee 1980; Bowker 1984).

Although tropical and temperature-zone desert habitats support most of the lizard species studied thus far, cool-temperate zone areas and the thermoregulatory specialists occupying this environmental niche can no longer be overlooked. If availability of "optimal" ambient temperatures, an abundant food supply and lack of predators portrays conditions of a low-cost environment, then *Lacerta viridis* living in thermal gradient cages should regulate their T_b exceptionally well, i.e. within a very narrow range (accepted by many as <1° C). They do not. Body temperature data on most lizard species are inadequate to determine to what extent a lizard modifies it's T_b on a daily and seasonal basis. The over-simplified generalizations of precise and imprecise thermoregulation require revision. Analyses of reptilian thermal biology must be more directed towards evaluating species specific properties. Inherent thermal characteristics have evolved in the various congeneric groups, allowing occupation of diverse ecological niches.

The influence of maintaining reptiles in an artificial photoperiod and the resulting effects on seasonal changing behavioral or physiological functions has not yet been assessed. The fact that *Lacerta viridis* respond to long photoperiod at every time of year with an increase in both photo- and scotophase T_b's clearly demonstrates one direct effect of light/dark duration. Investigators, however, often use light/dark regimes other than extreme long or short day photoperiods, and a reptile's sensitivity to different photoperiod durations is virtually unknown. The outcome of our sustained photoperiod experiment gives us initial information on how an artificial light regime can effect one parameter, T_b selection, at different times of the year. Our results show that 13 h of light is not long enough to induce selection of higher T_b's as seen under a true long photoperiod (LD 16:8). Likewise, it is clear that LD 12:12, the photoperiod often used as a "neutral" photoperiod, yields neither long nor short day selection of T_b in this species. Although these data assess only a few points during the annual cycle, they are certainly indicative of the intricate role played by the photoperiod.

In another study where the effect of photoperiod was examined on temperature selection of a lizard, *Scleoporus undulatus*, acclimation to 12 h light in May was enough to incite selection of higher temperatures (Ballinger et al. 1969). At the same time, temperatures selected by animals exposed to 6 h light did not differ from controls. The opposite effect occurred in July. Lizards captured and maintained in 6 h light decreased selected temperatures while those kept in 12 h light did not significantly differ from controls. From these results and our own, we conclude that the response of selected T_b levels to photoperiod is correlated to physiological adaptations which underlie seasonal acclimatization to changes in environmental temperatures. Responses to different artificial photoperiods are species specific and probably vary according to the time of year.

This study has revealed that the annual cycle in T_b selection of *Lacerta viridis* is mediated and coordinated through photoperiodic information. Exposure to artificial light/dark regimes directly influences T_b selection. Hence, both photoperiod history and thermal environment must be taken into consideration in order to accurately evaluate and interpret the flexibility of thermal relationships in ectotherms. Moreover, since an unequivocal relationship between photoperiod and synchronization of seasonal T_b selection has been established, we surmise that other physiological and behavioral parameters are also affected by photoperiod history.

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