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THERMOREGULATORY RESPONSES TO ENVIRONMENTAL SEASONALITY BY THE LIZARD *LACERTA VIVIPARA*

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ABSTRACT: Seasonal patterns of body temperatures and thermoregulatory behavior were studied in the temperate zone lizard *Lacerta vivipara* Monthly mean body temperatures of free-ranging lizards varied seasonally Body temperatures were positively correlated with corresponding mean air temperatures but were most elevated above ambient temperatures during the cool early spring months In early spring, body temperatures recorded in the field were considerably lower than those that the animals maintained in a laboratory thermal gradient (selected temperatures) During the colder months, the time of activity was restricted, and lizards increased basking frequency and actively sought warmer microhabitats A biophysical model was used to calculate equilibrium temperatures that a lizard could achieve by maximizing, respectively minimizing, its heat gain under the prevailing environmental conditions. Estimates of the "maximal operative temperature" demonstrate that environmental conditions often forced lizards from their selected temperatures during the cooler months Calculated "minimal operative temperatures" seldom approached selected temperatures Lizards regulated body temperatures near selected levels, or if these could not be achieved for physical reasons, they regulated near maximal operative temperatures During the coolest periods, activity was highest in adult males We suggest that a main benefit of thermoregulation under these suboptimal conditions may be the maximization of mating success, through an increase of the rate of sperm development

Key words: Activity times; Basking; Behavioral thermoregulation; Body temperature; *Lacerta vivipara*; Microhabitat utilization; Seasonal variation; Thermal environment

SINCE the discovery of behavioral thermoregulation in lizards (Cowles and Bogert, 1944), data on lizard body temperatures have accumulated (reviews in Avery, 1982; Brattstrom, 1965) The relevance of these data for comprehensive analyses of thermoregulation is, however, limited (Huey and Slatkin, 1976) In most studies, body temperature measurements were listed without much documentation on associated behavior, and the measurement of environmental temperatures was often crude and poorly standardized The recent development of biophysical techniques has illustrated the complexity of lizard-microclimate interactions (Bartlett and Gates, 1967; James and Porter, 1979; Porter and Gates, 1969; Porter et al , 1973; Tracy, 1982) and has helped in providing a means of quantifying the thermal environment (Christian et al , 1983; Roughgarden et al , 1981; Waldschmidt and Tracy, 1983) In addition, activity of field workers has been restricted both in the geographical localization and in the timing of their studies Most work has been performed in neotropical and warmer temperate areas (Avery, 1982) and is often restricted to the summer months Knowledge of the nature and flexibility of thermoregulatory responses to the general climatic and the seasonal variation in weather conditions is therefore limited and biased (Huey et al , 1977)

Thermal environments in the colder parts of temperate zones are characterized by cool mean air temperatures and a strong seasonal and diel thermal variability Ectotherms can respond to such changes in

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environmental temperatures by physiological acclimatization, that is shifting optimum temperatures (Christian et al., 1983) or by adjusting thermoregulatory behavior, so that body temperatures are maintained at the same level (Huey and Slatkin, 1976). Success of the latter strategy will depend on the investment in thermoregulatory activities (Huey and Slatkin, 1976) and on constraints imposed by the thermal environment.

Observations on the thermal biology of the temperate zone lizard *Lacerta vivipara* in laboratory and outdoor enclosures have shown that this diurnal basking lizard maintains activity temperatures around 30–33 C (Avery, 1971, 1976; Patterson and Davies, 1978; Spellerberg, 1976; Van Damme et al., 1986). However, this lizard, which inhabits the subarctic and Atlantic climatic regions (Spellerberg, 1976), occupies a thermal environment subject to strong seasonal and daily fluctuations, where the costs of maintaining a constant body temperature are likely to be high (Avery, 1976; Huey and Slatkin, 1976). Therefore, this species is well suited for a study of responses to seasonal changes in the thermal environment. These considerations prompted us to examine changes in body temperatures and thermoregulatory behavior of *L. vivipara* along a seasonal time gradient of changing environmental conditions. To discriminate among possible mechanisms inducing changes in body temperatures, we here integrate field and laboratory temperature measurements, behavioral observations, and biophysical modeling.

MATERIALS AND METHODS

Animals

Lacerta vivipara Jacquin is a small (adult body length: 50–60 mm; mass: 3–4 g), ground-dwelling lizard that behaves like a typical heliotherm (Avery, 1976). It is livebearing and reproduces once a year, having a distinct annual reproductive cycle. Mating and ovulation occur in April and May respectively; the young are born during the last week of July and the first half of August (Bauwens and Verheyen, 1985).

Three age classes can be distinguished by body length: juveniles (born in the current activity season), subadults (born during the previous year), and adults (in at least their third activity season). Sexual dimorphism (vent color, presence or absence of a swelling at the tail base) is most pronounced in the adult lizards.

Field Study

The field study was carried out at a site (150 × 40 m) in the Belgian national nature reserve 'de Kalmthoutse Heide' [Kalmthout (51°25′ N, 4°25′ E), province of Antwerp, Belgium]. The vegetation is characteristic of moist heathland, dominated by crossleaved heath (*Erica tetralix*), purple moor-grass (*Molinia caerulea*), and bog asphodel (*Narthecium ossifragum*). Birch (*Betula pendula*) and pine (*Pinus sylvestris*) stand isolated and form small bushes. The lizards bask on clumps of purple moor-grass and accumulations of vegetation around the base of trees, and during warmer periods they retreat to shade provided by the birches.

Observations on some aspects of thermoregulatory behavior were made from March–September in 1978, 1979, 1982, 1983, and 1984. The study area was crossed systematically throughout the day, and upon each observation of a lizard, we recorded time of day, sex, age class, estimated amount of solar radiation at the spot of first sighting (full sun, sun filtered by vegetation, shade, overcast), the approximate duration of sunshine before capture (either <5 or ≥ 5 min), and whether or not the lizard was basking (dorsoventral flattening of the body and orientation towards the sun).

In 1982–1984, we captured lizards by hand and measured body (cloacal = T_b) and air (shaded bulb, 1 cm above substrate, = T_a) temperatures to the nearest 0.1 C with a thermocouple connected to an electronic thermometer. To avoid physical damage to the lizards, body temperatures of juveniles (body size: 20–30 mm) were not recorded, and this age group is not considered in this study.

The precision or extent of thermoregulation (sensu Huey, 1982; Huey and Slatkin, 1976) was estimated by the slope of the regression line of T_b on T_a A slope ≈ 0 suggests precise thermoregulation, whereas a slope approaching 1 indicates thermal passivity (Huey, 1982; Huey and Slatkin 1976)

Selected Body Temperatures

We obtained monthly estimates of body temperatures selected by lizards in a laboratory thermal gradient (see Van Damme et al , 1986, for a detailed account) We assume that body temperatures in the thermal gradient represent estimates of the temperatures that lizards would attempt to achieve in the field in the absence of physical and biotic restrictions (Licht et al., 1966) This view can be questioned (Huey, 1982; Huey and Stevenson, 1979), mainly because of possible effects of acclimation (Bradshaw and Main, 1968; Graham and Hutchison, 1979; Wilhoft and Andersen, 1960) and the intraspecific variability in selected temperatures (Case, 1976; Mayhew, 1963; Mueller, 1969; Patterson and Davies, 1978) However we believe that these major objections can be circumvented by using recently caught animals and by referring exclusively to the appropriate age/sex class, reproductive condition, and period

Maximal and Minimal Operative Temperatures

For each T_b measured in the field, we calculated two corresponding body temperatures that could be attained under ambient environmental conditions The "maximal operative body temperature" (T_{max}) was simulated assuming that the lizard was in full sun and oriented so that it maximized solar radiation input The "minimal operative temperature" (T_{min}) was estimated assuming that the the lizard was in deep shade and thereby minimizing the absorption of solar radiation

Estimates were obtained by using the steady-state energy balance equation of Tracy (1982) and solving it for body temperature Air temperature was estimated by the measured T_a Radiation flux density at the date and time of capture was calculated as described in McCullough and Porter (1971) The amount of solar radiation absorbed by the lizard was estimated as in Campbell (1977) using geometrical formulae for horizontal cylinders to calculate body areas exposed to radiation (Monteith, 1973) and a short wave absorption coefficient equal to 0 84 (Knotig, 1964). For the calculation of T_{min}, the amount of direct solar radiation absorbed was assumed to be zero Thermal radiation was computed from the Stefan-Boltzman equation (Tracy, 1982) Convection was estimated as in Roughgarden et al (1981) Wind velocities were obtained from a nearby weather station (Antwerp, 25 km southeast) and adjusted for low heights using the wind profile equation (Campbell, 1977) Metabolic heat production, evaporative heat loss, and conductive heat flow were considered to be negligible (Muth, 1977; Porter et al., 1973; Tracy, 1982)

As our approach of estimating maximal operative temperatures assumes that the animal is in steady state with its environment and maximizes heat gains, the T_{max} values were estimated only for lizards that were captured after a ≥5 min period of continuous sunshine [5 min is the approximate time taken by an adult *L vivipara* to heat from 15–25 C under cloudless conditions and at an ambient temperature of 15 C (Avery, 1976)]

Our calculations of T_{max} and T_{min} are based on indirect estimates of radiation intensity and wind speed The calculated temperatures should therefore be regarded as crude estimates, and we emphasize that our aim is not to obtain accurate estimates for each corresponding T_b-measurement, but rather to detect general patterns in the variation of the range of temperatures that lizards can attain Note that the maximal operative temperature is identical to the "grey body temperature index" of Roughgarden et al (1981) for objects that maximize heat gains

Statistical Procedures

We used *t*-tests (two-tailed) or one way analyses of variance (ANOVA) and Student-Newman-Keuls tests to evaluate differences among group means, three way G-tests for contingency tests of indepen-

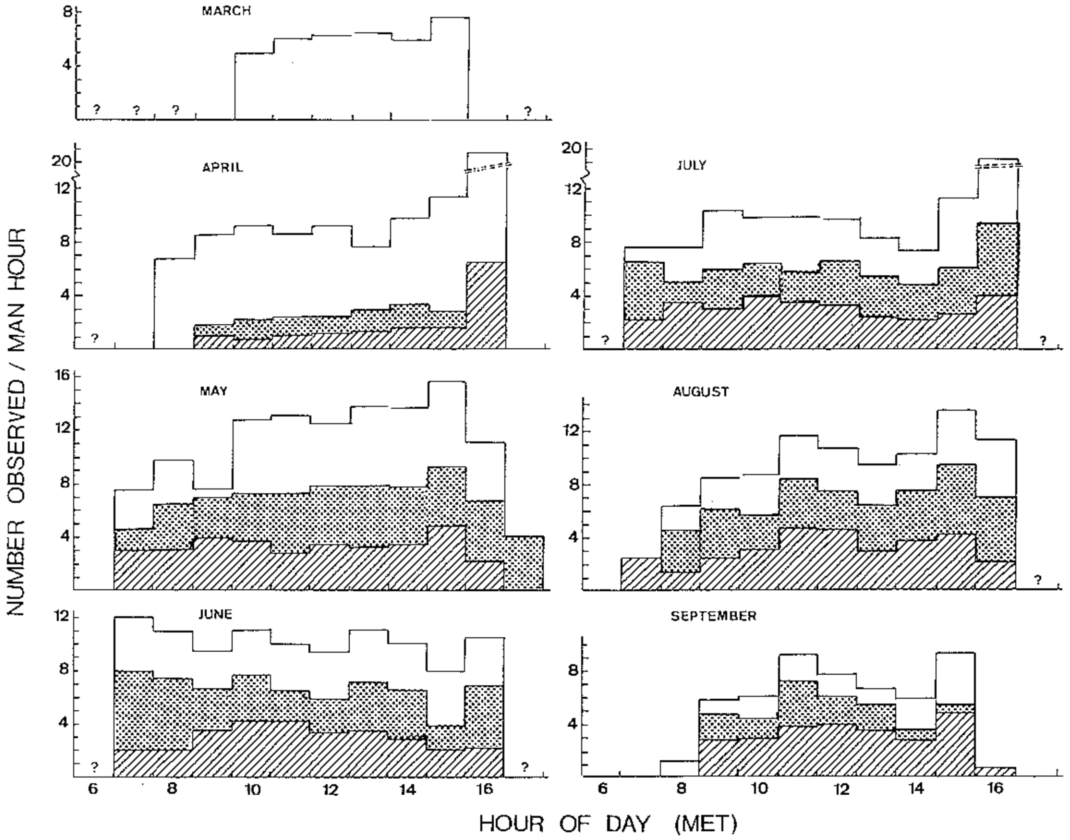

Fig. 1.—Number of lizards observed per man hour at different times of day during each month. Open = adult males; hatched = adult females; stippled = subadults; ? = no data available.

dence (Sokal and Rohlf, 1969), analyses of covariance (ANCOVA) to test for differences among slopes of regression lines (Snedecor and Cochran, 1967), and Spearman rank correlations (r_s). The standard criterion of statistical significance was $\alpha = 0.05$.

RESULTS

Activity and Thermoregulatory Behavior

Daily activity patterns of this heliothermic lizard were largely dependent on prevailing weather conditions, particularly the level of solar radiation (see also Avery, 1971, 1976; Hailey, 1982; House et al., 1980). Generally, lizards did not emerge on cloudy days. On changeable days, lizards responded to prolonged cloudy periods by retreating underground, but they quickly resumed activity when direct sunshine was available again. Observations in outdoor enclosures and field census data indicate that all individuals are active when thermal conditions are suitable for activity (R. Van Damme and D. Bauwens, unpublished data).

L. vivipara responded to seasonal variation in environmental conditions by adjusting their time of activity. Lizards emerged earlier and retreated later in midsummer than during spring and late summer (Fig. 1). There was a marked difference in activity patterns among age/sex classes during spring: adult males emerged from hibernation 1 mo before the adult females and subadults. Throughout April, males also appeared earlier in the morning and were seen more frequently than other groups (Fig. 1).

The proportion of lizards observed in

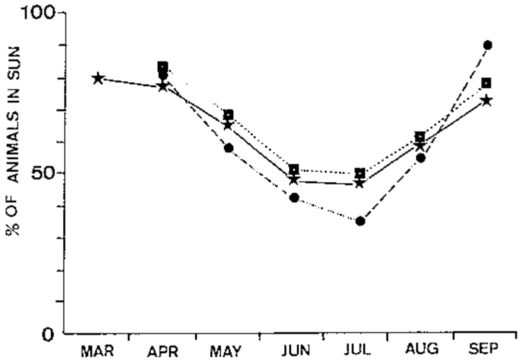

FIG. 2.—Percentage of lizards that were seen in full sun when first sighted during different months (sunny weather samples only). Star = adult males; black dots = adult females; square = subadults.

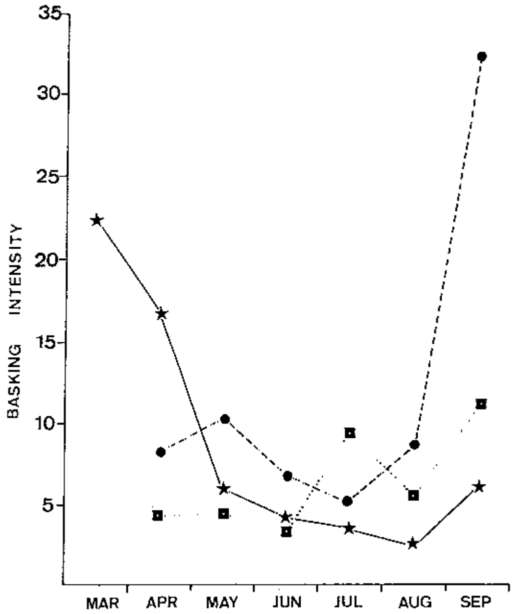

FIG. 3.—Percentage of lizards that upon first sighting were basking ("basking intensity") during different months (sunny weather samples only). Star = adult males; black dots = adult females; square = subadults.

full sun, filtered sun, and shade (Fig. 2) differed significantly among months (three way G-test: $P \ll 0.001$—observations during overcast weather excluded). Microhabitat utilization differed also among age/sex groups ($P < 0.001$): adult females were seen less frequently in full sun than the other lizard groups during most of the months (Fig. 2).

The proportion of animals that was seen basking (Fig. 3) varied significantly among months (three way G-test: $P \ll 0.001$—observations during overcast weather excluded). The seasonal pattern of basking intensity also varied among age/sex groups, as evidenced by the significant difference among lizard groups ($P < 0.005$) and the significant interaction between age/sex class and month ($P \ll 0.001$) on the relative number of lizards that were basking. During spring, males basked more frequently than other lizards, whereas basking incidence was highest in subadults and especially in adult females during August and September (Fig. 3).

Variation in Air and Body Temperatures

Active lizards in the field had mean body temperatures of 29.9 C (1 SD = 3.51, n = 1063, range: 16.2–37.8 C). About 71% of all temperatures were between 28.0 and 33.0 C. Air temperatures ranged from 5.6–32.1 C ($\bar{x}$ = 20.3, 1 SD = 4.93, n = 1063).

Table 1 summarizes monthly values of T_b and T_a. Differences between median and mean body temperatures were small (<1.0 C) for all months and lizard groups, indicating but a low to moderate degree of skewness of the T_b-records. A considerable seasonal variation in T_b was evident in all three lizard groups (ANOVA, all values of $P \ll 0.001$). Mean body temperatures were low during March and April, higher in midsummer, and slightly lower again in September. Monthly mean T_b was correlated with monthly mean T_a (r_s = 0.651, $P < 0.01$, combined correlation for all groups). The difference between T_b and T_a in a given month and lizard group is negatively rank correlated with mean air temperature ($r_s = -0.865$, $P < 0.001$), indicating that T_b was high relative to T_a during the cooler months.

A comparison of the monthly mean body and air temperatures of the three age/sex groups reveals few significant differences. In April, both T_b and T_a were higher in adult females than in adult males and subadults ($P < 0.05$). In June, gravid females were observed at air temperatures that were lower than in adult males and sub-

TABLE 1.—Mean (±1 SE) and median (in parentheses) body temperatures (T_b) and air temperatures (T_a) in the field, and selected body temperatures (T_s) in a laboratory thermogradient (data from Van Damme et al. 1986); n = number of temperature measurements.

	Field study			Thermal gradient	
	T_b	T_a	n	T_s	n
Adult males					
March	24.2 ± 0.4 (24.0)	11.5 ± 0.3	63	33.3 ± 0.2	70
April	28.5 ± 0.3 (29.2)	16.1 ± 0.3	205	32.8 ± 0.1	126
May	29.9 ± 0.4 (30.0)	19.5 ± 0.4	43	32.1 ± 0.1	236
June	31.3 ± 0.5 (31.8)	19.2 ± 0.4	61	32.3 ± 0.2	100
July	31.9 ± 0.3 (32.2)	24.2 ± 0.4	58	33.3 ± 0.1	128
August	31.2 ± 0.2 (31.0)	23.8 ± 0.5	44	33.1 ± 0.2	106
Sept	30.2 ± 0.5 (30.5)	20.9 ± 0.5	27	32.5 ± 0.3	54
Adult females					
April	30.3 ± 0.5 (30.2)	21.1 ± 0.6	32	32.1 ± 0.2	93
May	30.4 ± 0.4 (30.8)	20.3 ± 0.3	52	32.1 ± 0.5	54
June					
Gravid	33.4 ± 0.6* (33.2)	23.2 ± 0.6	12	30.3 ± 0.3	74
Non-gravid	31.3 ± 0.4 (32.1)	21.2 ± 0.4	66	34.0 ± 0.3	19
July					
Gravid	30.6 ± 0.4* (30.6)	24.2 ± 0.6	32	30.0 ± 0.4	10
Non-gravid	31.3 ± 0.4 (31.5)	24.3 ± 0.5	30	32.7 ± 0.3	60
August	31.5 ± 0.4 (32.1)	24.4 ± 0.5	44	33.3 ± 0.2	85
Sept	30.0 ± 0.6 (30.5)	22.8 ± 0.5	31	32.2 ± 0.2	97
Subadults					
April	28.0 ± 0.5 (28.8)	18.8 ± 0.7	38	31.1 ± 0.2	114
May	29.3 ± 0.4* (29.7)	20.7 ± 0.6	40	29.9 ± 0.2	116
June	31.2 ± 0.4* (32.2)	20.3 ± 0.5	43	30.5 ± 0.3	77
July	30.8 ± 0.3 (31.2)	24.2 ± 0.4	49	32.4 ± 0.3	70
August	30.6 ± 0.3 (30.8)	24.3 ± 0.4	61	32.1 ± 0.2	97
Sept.	30.4 ± 0.5 (31.0)	22.3 ± 0.5	32	32.0 ± 0.3	71

* Field body temperatures that were not significantly lower than the corresponding selected temperatures.

adults, but not different from those of non-gravid females. Mean body temperatures of gravid and non-gravid females did not differ significantly (lumped data for June and July: *t*-test, $P > 0.10$).

Precision of Thermoregulation

The slopes of the regression equations of T_b on T_a did not vary significantly among subpopulations within each month (ANCOVA, all values of $P > 0.05$). Therefore, our further analysis is based upon combined samples. A highly significant difference between the slopes of the monthly regression lines was evident (ANCOVA, $P < 0.001$; Fig. 4A), suggesting a considerable seasonal variation in the extent of thermoregulation. Slope values were highest in March, June, and September, suggesting thermal passivity during these months.

We considered measurements that were made after a ≥5 min period of continuous sunshine separately. The lizards involved probably had sufficient opportunities to bask and to regulate their T_b. In most months, regression slopes of T_b on T_a were lower, but not significantly so, for this subset of data than for the total samples (Figs. 4A,B). Significant differences (ANCOVA, $P < 0.001$) were evident during June, when a considerable fraction of the T_b-readings was taken during cloudy and variable weather, and during July.

Correlates of Body Temperatures

Monthly mean T_b values for the distinct lizard groups show a marginally non-significant rank correlation with basking incidence ($r_s = -0.428$, $P = 0.06$), and a highly significant negative rank correlation with the proportion of lizards observed in full sun ($r_s = -0.768$, $P < 0.001$).

We compared body temperatures recorded in the field with temperatures selected by lizards in a laboratory thermal gradient (Table 1, data from Van Damme

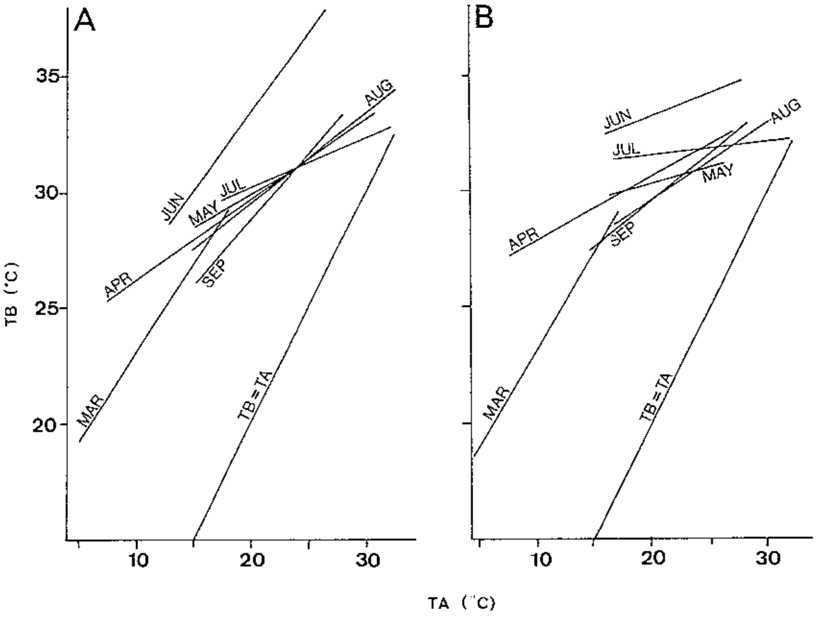

FIG. 4.—Regression lines for body (T_b) vs. air temperatures (T_a) in different months (combined regressions for all lizard groups). (A) Total samples; (B) lizards captured after ≥5 min of continuous sunshine only.

et al., 1986). In most of our monthly samples, mean T_b values were significantly lower than the corresponding mean selected temperatures (Table 1). These differences were largest during the early spring months (particularly in the adult males) and were negatively rank correlated with mean monthly T_a ($r_s = -0.429$, $P = 0.05$), indicating that especially during the cool months lizards were active at body temperatures well below their selected levels. Also, the differences between mean selected body temperature and the actual mean field T_b were positively correlated with both basking incidence ($r_s = 0.487$, $P < 0.05$) and the proportion of lizards seen in full sun ($r_s = 0.771$, $P < 0.001$). Hence, the differences between temperatures selected in the laboratory and those maintained in the field were highest during the cooler months, even though lizards tended to be in the sun and basked most frequently during these periods.

Maximal and Minimal Operative Temperatures

Our estimates (Table 2) indicate a considerable seasonal variation in maximal operative temperatures. In March and April, the adult males in particular were most often physically unable to attain their selected temperatures. It should be noted, however, that during the spring months mean body temperatures closely approached mean values of T_{max}, at least when the latter did not exceed selected levels (Tables 1 and 2). During the period June–September, T_{max}-values most often exceeded selected levels. Estimates of T_{min} were always close to the measured T_a and hence considerably lower than the selected temperatures, suggesting that microhabitats where lizards could eventually cool down were readily available.

DISCUSSION

The observed body temperatures of free-ranging *Lacerta vivipara* show considerable seasonal variation related to changes in environmental temperatures. Selected temperatures maintained in a laboratory thermogradient were unrelated to environmental temperatures (Patterson and Davies, 1978; Van Damme et al., 1986). In contrast, selected temperatures in the adult lizards were generally highest during

TABLE 2.—Mean (±1 SE) body temperatures (T_b) and maximal operative temperatures (T_{max}) in different lizard groups (lizards captured after ≥5 min of continuous sunshine only), and the percentage of T_{max} estimates lower than the corresponding mean selected temperature (see Table 1); *n* = number of temperature measurements

	T_b	T_{max}	% < T_s	*n*
Adult males				
March	24.5 ± 0.5	25.1 ± 0.4	100	45
April	29.9 ± 0.3	29.6 ± 0.4	79	131
May	30.5 ± 0.3	33.3 ± 0.4	34	35
June	34.2 ± 0.3	35.6 ± 0.6	0	22
July	32.1 ± 0.2	37.1 ± 0.5	4	47
August	31.3 ± 0.3	38.8 ± 0.5	4	27
Sept	30.8 ± 0.3	35.3 ± 1.1	26	23
Adult females				
April	30.9 ± 0.6	34.6 ± 0.6	19	27
May	30.8 ± 0.3	33.9 ± 0.4	25	48
June				
Gravid	33.4 ± 0.7	37.9 ± 1.0	0	9
Non-gravid	33.9 ± 0.4	36.2 ± 0.8	22	18
July				
Gravid	31.3 ± 0.4	38.4 ± 0.7	0	21
Non-gravid	31.8 ± 0.3	38.2 ± 0.6	0	22
August	32.3 ± 0.4	38.8 ± 0.6	7	31
Sept	30.6 ± 0.4	38.8 ± 0.9	7	28
Subadults				
April	29.1 ± 0.5	31.6 ± 1.0	43	26
May	29.9 ± 0.3	34.4 ± 0.6	10	31
June	32.9 ± 0.4	35.3 ± 0.7	6	18
July	31.3 ± 0.3	37.4 ± 0.6	0	34
August	31.0 ± 0.3	38.7 ± 0.5	6	48
Sept.	31.1 ± 0.4	38.7 ± 0.7	4	27

the cooler months. The observed variation in field values of T_b can therefore not be attributed to seasonal differences of selected temperature levels, but seems to be a response to environmental seasonality.

During periods with low ambient temperatures, costs of raising body temperature are high. An ectotherm then can either abandon thermoregulation or can meet the costs and elevate its temperature as high as possible (Huey and Slatkin, 1976). Hence, the question is: to what extent does the variation in field values of T_b reflect an active shift in thermoregulatory strategy and to what extent is it merely induced by changing environmental conditions?

Slopes of regressions of T_b on T_a and differences between monthly mean selected and mean field T_b were highest during the cooler months. These data might suggest that lizards shift from thermoregulation to thermal conformity as ambient temperatures fall. Other results clearly contradict this interpretation. Mean values of T_b were more elevated above air temperatures during the cooler months than in midsummer, indicating that lizards actually raise their body temperature above ambient levels. Maximal operative temperatures were periodically below selected levels, demonstrating that environmental constraints prevented the achievement of selected temperatures during the early spring months. The close agreement between field values of T_b and maximal operative temperatures during the cooler months shows that lizards do not shift to thermoconformity; rather they maintain their body temperatures as high as it is physically possible.

The following reasons support the view that short-term behavioral shifts are the main mechanism that enables individuals of *L. vivipara* to maintain their temperature near maximal levels during cool periods (1) The time of activity varies seasonally and is highly dependent on ambient weather conditions during all months. Lizards are only active in the presence of direct sunshine (Avery, 1971; House et al., 1980) and activity is restricted to the midday hours during the cooler months; this reduces the variation in external conditions to which lizards are actually exposed. (2) The most conspicuous aspects of behavioral thermoregulation in these lizards are shuttling between sun and shade and the alternation of activity bouts with periods of overt basking (Avery, 1978; Hailey, 1982; House et al., 1980). Lizards are most frequently seen in sun during spring and late summer and most often seen in shaded sites in the summer months. Although changes in microhabitat utilization do not necessarily imply thermoregulatory movements (Huey et al., 1977), the observed seasonal pattern of utilization of sunlit sites is opposite to the ∩-shaped distribution that is expected if lizards move randomly with respect to patches of sun and shade in terrestrial habitats (Huey et al., 1977). Hence, lizards seem to seek sunlit areas during the cooler months and appear to retreat frequently to shaded sites in summer. Basking incidence also tends to be highest in spring and late summer.

The physical environment periodically prevents this species of lizard from achieving its selected temperature. It should, however, be stressed that only the adult males during March and April showed major discrepancies between selected and body temperatures attained in the field. In other months and for other groups of lizards, activity was restricted to times when environmental conditions seemingly allow the animals to approach their selected temperatures. Thus it appears that by their early emergence on a seasonal and daily basis during March–April, adult males are exposed to unfavorable conditions which cause them to devote a considerable amount of time to activities which elevate body temperatures. Why do males, but not the other lizard groups, incur these costs? Knowledge of the reproductive biology of this non-territorial species helps to identify possible benefits. Spermatogenesis, which terminates during the weeks following emergence from hibernation (Courty and Dufaure, 1979), is temperature-dependent in *L. vivipara* (Joly and Saint Girons, 1981). Elevation of body temperatures hence increases the rate of sperm development and probably enhances mating opportunities, because females are receptive soon after or upon emerging from hibernation (Bauwens and Verheyen, 1985). The latter suggestion is supported by the finding that mating success is highest in those males that emerge earliest from hibernation (D. Bauwens, unpublished data). Maximization of reproductive success seems therefore to be a major benefit that males derive from elevation of body temperatures near maximal levels during the thermally unfavorable early spring period.

The observation that lizards periodically maintain body temperatures around maximal attainable levels has some implications for the estimation of the extent of thermoregulation by slopes of regressions of T_b on T_a. If values of T_b are near maximal, the regression slope will equal 1 as the maximal operative temperatures are linearly dependent on air temperature (R. Van Damme, unpublished data). Therefore, regression slopes alone cannot discriminate between this strategy and thermoconformity (slope = 1). Examination of the intercepts might then be helpful: the intercept will be zero in thermoconformers ($T_b = T_a$) but will exceed zero when lizards regulate their temperature around maximal attainable levels ($T_b = T_m > T_a$). These considerations supplement previous comments on the limitations of using regression slopes as measures of thermoregulatory precision (Dreisig, 1984; Hertz and Huey, 1981; Huey, 1982; Huey and Slatkin, 1976). In general, we believe that this study illustrates Huey's (1982) statement that a comprehensive analysis of thermoregulation requires consideration of behavior, body temperature, and environmental conditions (see also Christian et al., 1983).

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