

THERMAL BEHAVIOR AS A FUNCTION OF THE TIME OF DAY:
HEAT EXCHANGE RATES AND OXYGEN CONSUMPTION
IN THE LACERTID LIZARD *LACERTA VIRIDIS*¹

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The European green lizard *Lacerta viridis* heats more rapidly than it cools when tested during the activity portion of its daily cycle. In contrast, slower rates of cooling relative to heating are not typical when lizards are tested during their normal scotophase rest period. Furthermore, *L. viridis* cools at a slower rate than do other lizards of equal size. Simultaneously measured oxygen consumption displayed an inverse pattern during daytime heating and cooling with significantly higher metabolic rates during 75% of the entire cooling process, whereas nighttime metabolic responses were practically identical during both heating and cooling. Responses to acute heating and cooling varied according to the time of day tested, coinciding with the activity and rest phases.

INTRODUCTION

Although it is well established that most reptiles gain heat more rapidly than they lose it, there are no data available on rates of heating and/or cooling for European lacertids. This family of lizards has an extensive range distribution, with *Lacerta vivipara* found as far north as latitude 70° N (Andersen 1971). It is to be expected that lizards living in areas with seasonal temperature extremes would possess precise thermoregulatory mechanisms, allowing not only behavioral but also physiological control over such important factors as the rate of body temperature change. In a review on thermoregulation, metabolism, and social behavior in Lacertidae, Avery (1976) reports that the behavioral complexity among European lacertid lizards is inversely related to latitude. He suggests that thermoregulation occupies a greater portion of the daily time budget in lizards inhabiting higher latitudinal areas. One can further conclude that efficient thermoregulatory responses are of vital necessity for such animals.

An equally important aspect of reptile thermobiology, and one that is often overlooked but deserves consideration, is the

influence of daily activity and rest phases on the energy budget. Voluntary hypothermia during the rest phase of a lizard's daily cycle has often been documented (Regal 1967; Hutchison and Kosh 1974; Spellerberg and Smith 1975; Engbretson and Hutchison 1976; Rismiller and Heldmaier 1982); however, there has been little more than speculation concerning the ecological significance of this behavior. Physiological parameters affecting the control of body temperature have never been studied for that portion of the day when a lizard voluntarily seeks out temperatures lower than those of its activity period. Physiological rates of reptiles are not completely dependent on ambient temperature (for a review, see Bartholomew [1982]), and we further suggest that control of physiological processes may be related to the time of day, that is, to whether the animal is in its activity or rest phase.

Lacerta viridis viridis primarily inhabits parts of France, northern Italy, Spain, and a few areas of Germany but can also be found as far north as the Channel Islands (latitude 49°27' N). Since *L. viridis* is the largest lacertid native to latitudes above 40° N, it was chosen as the subject for this investigation of the effects of acute heating and cooling on rates of body temperature change and oxygen consumption. To date, simultaneous measurements of these two parameters have been reported for only one other lizard (Bartholomew and Vleck 1979) and one snake (Dmi'el

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and Borut 1972). Our study presents data on physiological control of body temperature change for a lacertid lizard, compares data on heat exchange rates from *L. viridis* with findings of studies of other lizards, and considers the significance of the daily body temperature selection cycle on the rate of heat exchange during daytime and nighttime tests of heating and cooling.

MATERIAL AND METHODS

The five male *Lacerta viridis* lizards used in this experiment were field caught in the area of Vendée, France (latitude 46°40' N), in May 1982 and transported to Marburg, Federal Republic of Germany (latitude 50°49' N). The animals were maintained under local natural photoperiod conditions and overwintered in hibernation boxes in an unheated frost-free room (3–7 C) from November 1982 through March 1983. The lizards were then held in single cages and given food and water ad lib. Illumination was provided by fluorescent lighting controlled by a timer that was reset weekly according to sunrise and sunset and by a window facing SSW. The mean light intensity of this room at midday was 800 lx, and the ambient temperature remained constant at 23 ± 1 C.

During heating and cooling experiments, rates of oxygen consumption and body temperature were registered simultaneously for the five lizards, whose body weights ranged from 26.7 to 45.5 g. In order to obtain deep core body temperature on unrestrained animals, temperature-sensitive radio transmitters (Mini-mitter, model X) 1.4 cm \times 0.5 cm and weighing 1.2 g were implanted intraperitoneally. These transmitters respond at the rate of 4 C/min and enable accurate body temperature (T_b) monitoring to ± 0.1 C. Tests were conducted in a climate chamber (Weiss 500 SD/50–60 DU) whose temperature could be changed rapidly (2 C/min) and controlled with an accuracy of ± 0.1 C. Lizards were placed in individual Plexiglas metabolic boxes (0.5-liter vol), and the airflow was adjusted to 20 liters/h. Oxygen consumption measurements were made with an open system consisting of a paramagnetic oxygen analyzer (Oxytest S, Hartmann and Braun) and an infrared

CO₂ analyzer (Uras 2T, Hartmann and Braun). These two channel systems allowed direct comparison between the effluent and influent air, with an accuracy of ± 0.01 vol%. The response time of this system, i.e., time needed for the gas sample to travel from the source to the sensor, was 40 s. All measured gas volumes refer to standard temperature and pressure. The $\dot{V}O_2$ (ml/[g \cdot h]) was calculated according to the method of Heldmaier and Steinlechner (1981). Ambient temperature was monitored by means of a copper-constantan thermocouple located inside the metabolic boxes. Time, ambient temperature, body temperature, and measurements from the gas analyzers were listed on-line (Tektronix 4051) and stored on disk.

A 60-W light bulb encased in Plexiglas illuminated the chamber. An aluminum shield was hung under the lamp so that the lizards received no direct radiation and the mean light intensity was 82 lx. For daytime experiments, animals were placed in the 20 C climate chamber after sunrise and at least 1 h prior to the beginning of the test. Visual monitoring of locomotor activity was registered throughout the testing periods. At time 0, the chamber temperature was elevated to 38 C and stabilized within 10 min. When all animals had reached a body temperature within 0.5 C of ambient temperature, the chamber was cooled to 20 C. For nighttime experiments, the lizards were placed in the 20 C chamber 1 h before the beginning of the scotophase, and the light was turned off at "sunset." The same heating and cooling procedure was performed as had been performed during the day, except that no visual control of activity could be made. To provide a control for radiant heat absorption, we monitored heating and cooling rates of a dead lizard under daytime conditions, (i.e., with the light on) and at night (i.e., with light off).

Normal distribution of the sample differences was tested according to the method of Pearson and Stephens (1964), and data were statistically analyzed using the paired-sample *t*-test.

RESULTS

Figures 1 and 2 show real-time plots for body temperature and oxygen con-

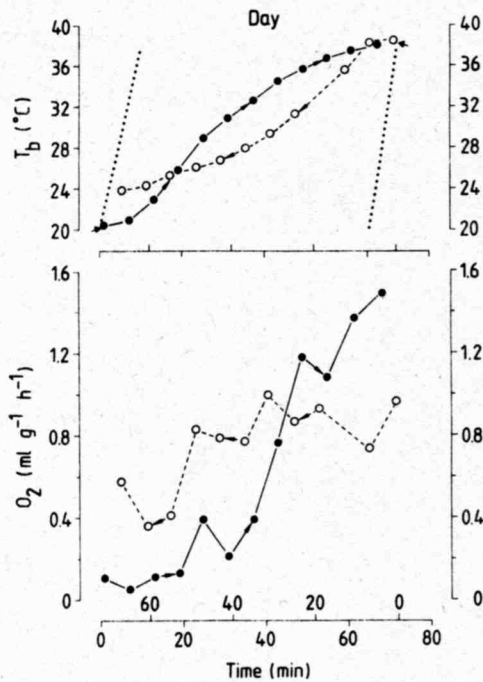


FIG. 1.—Real-time plot of body temperature (upper graph) and oxygen consumption (lower graph) for a single lizard during daytime heating (●) and cooling (○). Direction of time course is indicated by arrows. Lower time scale corresponds to heating and upper scale to cooling phase. At time 0, the chamber temperature was either raised from 20 to 38 C or lowered from 38 to 20 C as indicated by the dotted line.

sumption against test duration in minutes during heating and cooling for day and night, respectively. These plots illustrate the data of one lizard (37.6 g) but are typical of all lizards tested. The difference in duration for day- and nighttime heating and cooling is striking. Whereas during the day lizards needed 49–72 min to raise their T_b to within 1 C of ambient temperature, 71–92 min were required for equivalent results at night. All curves can be assigned a sigmoid form, with their relative steepness or flatness indicating the velocity with which the temperature change occurred. The rapid ascent of T_b during daytime heating and its quick decline at the onset of cooling during the night are noteworthy. There is an exponential augmentation of oxygen consumption during daytime heating as the lizards' T_b rises above 31 C, but nighttime metabolic rates show a sharp increase only after T_b has

exceeded 36 C. During daytime heating, animals struggled briefly as T_b increased above 35 C but again became quiescent as their temperatures continued to rise. Accordingly, the rate of O_2 consumption increased sharply but then fell from 1.5 to 0.96 ml/(g·h) while the T_b of the lizard was 38 C. Moreover, the metabolic rate then remained relatively high (0.76–0.91 ml O_2 /(g·h)) until T_b decreased below 23 C. With one exception, all lizards exhibited augmented metabolic rates during daytime cooling within a 10–12 C body temperature range of between 21.5 and 33.3 C. In contrast, the nighttime plot reveals little difference in O_2 consumption during heating and cooling.

When the mean oxygen consumption of all lizards is plotted against T_b (fig. 3), two patterns of metabolism can be distinguished. The gradual increase in metabolic rate as T_b rises from 20 to 30 C during daytime heating represents 42% of the time required to complete the entire heating cycle and yields a Q_{10} of 2.3. A sharp increase in oxygen consumption then coincides with the elevation in T_b from 30 to 38 C. During cooling, metabolic rates remain relatively high—that is, between 0.57 to 0.76 ml O_2 /(g·h)—as T_b drops from 38 to 25 C (i.e., during 75% of the cooling process). At paired body temperatures of 31–25 C, metabolic rates during cooling are significantly higher than during

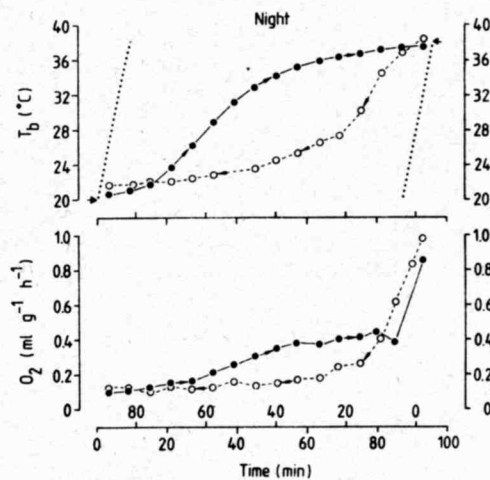


FIG. 2.—Real-time plot for the lizard in fig. 1 during nighttime testing. All symbols are as in fig. 1.

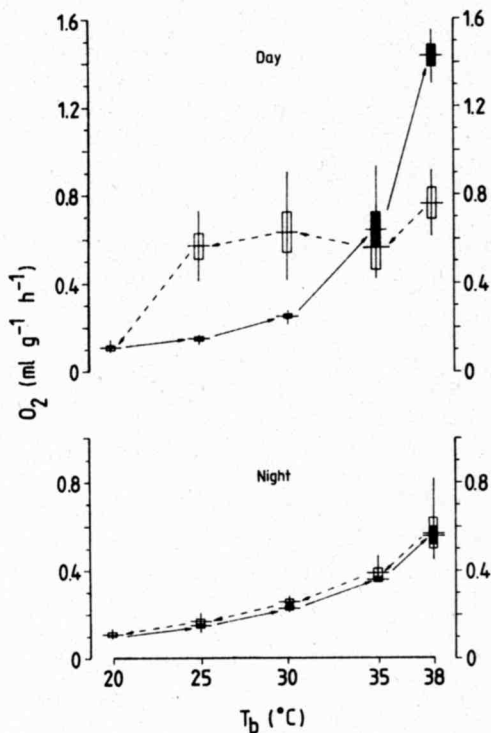


FIG. 3.—Mean oxygen consumption (horizontal lines) of lizards during heating (closed symbols) and cooling (open symbols) for day ($N = 4$) and night ($N = 5$). Boxes represent ± 1 SEM and vertical lines indicate the range. Arrows indicate direction of time course.

heating. Mean respiratory quotients (RQ) measured during daytime were 0.71 and 0.81 for heating and cooling, respectively. At night (fig. 3, bottom), the pattern for the metabolic rate during heating and cooling is nearly identical. The steady increase in O_2 consumption as body temperatures rise from 20 to 35 C constitutes 68% of the heating process and has a Q_{10} of 2.2. During cooling, decreasing metabolic rates likewise accompany decreasing T_b 's, from 35 to 20 C with a Q_{10} of 2.3. There is no point at which nighttime heating and cooling metabolic rates differ more than 0.03 ml O_2 /(g·h). Mean RQ values are 0.68 and 0.57 for heating and cooling, respectively. For T_b 's at 20–30 C, there are no significant differences between daytime and nighttime O_2 consumption rates during heating; however, at 35–38 C, daytime values are more than double those at night (1.43 vs. 0.57 ml O_2 /(g·h),

respectively). Moreover, at every $T_b \geq 25$ C, metabolic rates during daytime cooling were greater than during nighttime cooling.

In order to standardize and compare our results with those of other studies, we plotted heating and cooling data semilogarithmically as the difference between T_b and T_a against time (fig. 4). All slopes were calculated by the method of least squares, with $r > -.97$ for all regressions. Daytime heating and cooling data for *Lacerta viridis* show that these lizards heat more rapidly than they cool, as indicated by the steepness of the slope. Indeed, all lizards heated significantly faster ($P < .02$ for one animal and $P < .001$ for all others). The nighttime plot is of particular interest because the typical reptilian pattern of slower cooling relative to heating is no longer evident. Of the five lizards tested, three heated significantly faster, but the pattern of rate change differs from that of the daytime. Testing for differences between day- and nighttime heating proved significant ($P < .002$) for all but one lizard, whereas the difference between day- and nighttime cooling was not significant in four of the five animals. The rates of heating and cooling for all lizards are presented in table 1 as both the instantaneous change in T_b at $\Delta T_b/2$ (calculated by the method of Bartholomew and Tucker [1963]) as well as by the thermal time constant (τ ; calculated according to the method of Smith [1976]). Paired-sample t -tests showed that nighttime cooling/heating ratios are significantly higher ($P < .02$) than those of the daytime. Whereas τ for all lizards is significantly greater during daytime cooling than it is during daytime heating, there is no significant difference between nighttime heating and cooling.

Also included in table 1 are the results using one dead lizard. Although the rates of change between heating and cooling are not equal, data for heating during day and night as well as cooling day and night are essentially the same, indicating that the lighting in the test chamber supplied no significant source of radiant heat. Furthermore, as has been shown in other studies (Weathers 1970; Spray and May 1972; McKenna and Packard 1975), the dead lizard heated more slowly during daytime testing than did the live animals.

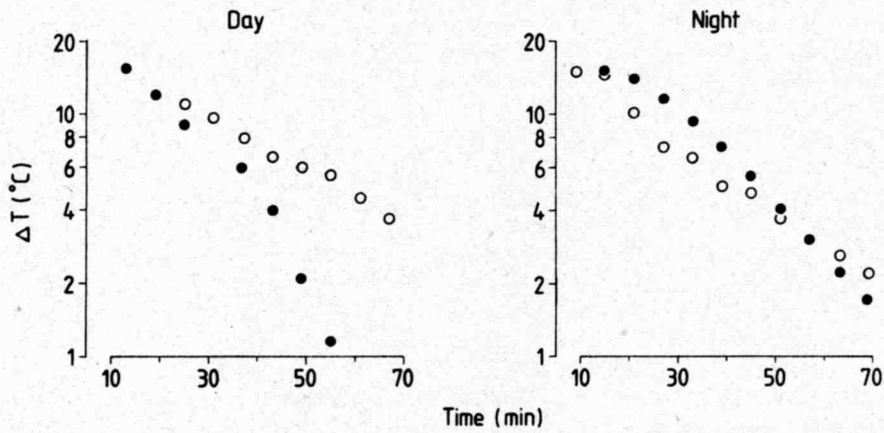


FIG. 4.—Semilog plot for rates of heating (●) and cooling (○) presented as the relation of difference between T_a and T_b (ΔT) and time for both day and night testing.

DISCUSSION

Lacerta viridis, a primarily heliothermic lizard, can control its rates of heating and cooling even in the absence of radiant heat. The ability to exercise limited physiological thermoregulation has been demonstrated in many species of lizards that inhabit desert or semitropical regions; however, data on northern European species are lacking completely (table 2). Lizards native to higher latitudes must meet demands of prolonged low-temperature

conditions and reduced breeding time; therefore, the degree to which lizards can control body temperature may be partially dependent on geographical distribution.

Since rate of change in T_b (expressed as $^{\circ}\text{C}/\text{min}$) is highly dependent on the experimental method used and varies continuously throughout the testing period, it is given at the body temperature midpoint mainly for comparison with previous studies (table 1). Weathers (1970) investigated the heating and cooling responses of *Dipsosaurus dorsalis*, a lizard comparable

TABLE 1
HEATING RATES (at $\Delta T_b/2$), THERMAL TIME CONSTANTS, AND THEIR RATIOS FOR INDIVIDUAL LIZARDS

ANIMAL	BODY WEIGHT (g)	DAY			NIGHT		
		Heating	Cooling	Cooling/Heating	Heating	Cooling	Cooling/Heating
Rate of change at $T_b/2$ (C/min)							
C	45.4	.380	.223	.59	.259	.232	.89
S	37.8	.517	.210	.41	.366	.278	.76
N	30.3	.755	.336	.44	.402	.216	.54
D	29.0	.695	.486	.70	.499	.473	.95
F	27.0	.580	.272	.47	.372	.268	.72
Dead ..	30.0	.397	.285	.72	.392	.290	.74
Thermal Time Constant (min)							
		Heating	Cooling	Heating/Cooling	Heating	Cooling	Heating/Cooling
C	45.4	22.20	36.16	.61	31.35	33.40	.94
S	37.8	17.48	38.88	.45	22.98	30.38	.76
N	30.3	12.67	26.34	.48	20.58	38.84	.53
D	29.0	14.35	19.59	.73	19.67	19.41	1.01
F	27.0	15.59	30.0	.52	23.01	31.72	.73
Dead ..	30.0	21.01	27.91	.75	21.94	28.62	.77

TABLE 2

GEOGRAPHICAL DISTRIBUTION OF LIZARDS FOR WHICH RATES OF HEAT EXCHANGE HAVE BEEN DETERMINED

Lizard Species	Latitude	Native to	Body Weight (g)
<i>Sphenomorphus quoyi</i>	35°00' S	Southeast Australia	4.5–32.6 ^a
<i>S. tympanum</i>	35°00' S	Southeast Australia	3.4–11.8 ^a
<i>S. kosciuskoi</i>	35°00' S	Southeast Australia	6.5–10.4 ^a
<i>Varanus punctatus</i>	32°00' S	Queensland, Australia	186 ^b
<i>V. gouldi</i>	27°28' S	Brisbane, Australia	94–1060 ^b
<i>V. varanus</i>	27°28' S	Brisbane, Australia	735–4008 ^b
<i>Tiliqua scincoides</i>	26°00' S	Queensland, Australia	512–560 ^c
<i>Amphibolurus barbatus</i>	26°00' S	Queensland, Australia	294–605 ^d
<i>Physignathus lesueurii</i>	26°00' S	Queensland, Australia	141–588 ^e
<i>V. acanthurus</i>	20°00' S	Charter Towers, Australia	16 ^b
<i>Amblyrhynchus cristatus</i>	1°00' S	Galápagos Islands	652–1360 ^f
<i>Anolis carolinensis</i>	31°15' N	Louisiana	1.7–6.3 ^g
<i>Dipsosaurus dorsalis</i>	33°80' N	Palm Springs, California	29–88 ^h
<i>Callisaurus draconoides</i>	39°00' N	Central Nevada	6.1–13.2 ⁱ
<i>Cnemidophorus sexlineatus</i>	39°23' N	Waterton, Colorado	3.5–7.7 ^j
<i>Sceloporus undulatus</i>	40°35' N	Ft. Collins, Colorado	6.3–12.3 ^j
<i>Lacerta viridis</i>	46°40' N	Vendée, France	26.7–45.4 ^k

^a Spellerberg (1972).^b Bartholomew and Tucker (1964).^c Bartholomew, Tucker, and Lee (1965).^d Bartholomew, and Tucker (1963).^e Grigg, Drane, and Courtice (1979).^f Bartholomew and Lasiewski (1965).^g Claussen and Art (1981).^h Weathers (1970).ⁱ Muth (1977).^j McKenna and Packard (1975).^k Present study.

in size to *L. viridis*, and plotted the relation of rate of change ($^{\circ}\text{C}/\text{min}$) to body weight. Data obtained for *L. viridis* during daytime heating fitted well into Weathers's regression for heating in still air. In contrast, the daytime cooling rates for *Lacerta* (mean = 0.3 C/min) fall well below those rates measured for *D. dorsalis*, even at zero wind velocity. Spray and May (1972) summarized data from one species of snake and several species of terrestrial and aquatic basking lizards and turtles ranging in weight from 50 to 300 g in a log-log plot of the rate of heat exchange as a function of body weight and found that, in general, larger reptiles exhibit a slower rate of change in T_b during both heating and cooling. Mass-specific equations for heating and cooling were calculated separately for terrestrial and aquatic reptiles. Rates of heat exchange calculated from the equation for terrestrial reptiles— $dT/dt = 1.505 W^{-.383}$ for heating—yield values that are similar to those found during

nighttime heating of *L. viridis*; however, daytime rates for *L. viridis* were much higher. Cooling rates calculated from the cooling equation for terrestrial reptiles— $dT/dt = 1.420 W^{-.384}$ —were greater than those actually measured for both day and night cooling, i.e., the cooling rate of *L. viridis* is slower than that in other reptiles of equal size.

The thermal time constant, which is the time required for an object to travel 63% of the way to the applied temperature, is independent of the magnitude of the temperature step used and remains stable with time throughout the response. Its application and advantages over midpoint temperature change in calculating heat-rate exchange have been discussed by Smith (1976), Boland and Bell (1980), and Grigg, Drane, and Courtice (1979); moreover, Smith (1976) introduced an equation for recalculating rate changes at the midpoint temperature to τ , and Grigg et al. (1979) employed this method for a comparative

study. The relation between the thermal time constant in minutes and body mass in grams was plotted as a log-log function for nine lizard and three crocodylian species ranging from ca. 50 g to 30 kg. The calculated slopes for heating and cooling in air intersect at a body mass of ~46 g, suggesting that reptiles below this weight cannot heat more rapidly than they cool. Table 1 includes the thermal time constants calculated for *L. viridis* during heating and cooling during both day and night. The daytime values range from 12.67 to 22.20 min and 19.59 to 38.88 min for heating and cooling, respectively, which, when one is calculating for body mass from Grigg's allometric relation, would represent animals with body masses 156.6 and 743.5 g for daytime heating and 332.6 to 1,339.3 g for daytime cooling, respectively.

Claussen and Art (1981) investigated the heating and cooling rates of a small lizard, *Anolis carolinensis*, and found that it heats more rapidly than it cools. They then incorporated data to present an allometric relationship between heating and cooling rates ($^{\circ}\text{C}/\text{min}$) and body mass (including data for many lizards smaller than 80 g). Heating rates for *L. viridis* estimated from this equation conform with those found for daytime heating; however, estimates of cooling rates are in every case higher than those actually measured. In all mass-specific equations presented, *L. viridis* demonstrates the typical rate-of-heating pattern expected for a lizard of its size, but it cools at a much slower rate than expected. This supports the idea that control over rates of heat transfer is perhaps more closely correlated with the ecological niche of a lizard than with its size; moreover, the even lower rates of change found for heating and cooling during the night (i.e., the rest phase) serve to document the frugality of this lizard with regard to energy expenditure.

The contribution of endogenous heat production to observed differences between heating and cooling constants of the same magnitude has received considerable attention (Bartholomew 1982). Our data on thermal conductance were evaluated and adjusted for metabolism by the method of Bartholomew and Tucker (1963)— $C = C'$

— $M/(T_b - T_a)$, where C is the corrected thermal conductance, C' is the apparent conductance calculated directly from the slopes of the heating or cooling curve, and M is the metabolic rate. A stipulation for the usage of this equation is the quantification of metabolism during heating and cooling. The uncorrected and corrected thermal conductances and their ratios for heating and cooling during both day and night test conditions are presented as the mean for all lizards tested at various body temperatures (table 3). Conductance during daytime cooling was found to be significantly lower than that during heating, supporting findings of a slower cooling rate during the daytime. For nighttime testing, there were generally no significant differences between heating and cooling conductance values, except for the smallest lizard, which showed a significantly higher thermal conductance during cooling. One can further observe that nighttime ratios are much larger than those found during the day. Indeed, thermal conductance during daytime heating is in every case significantly higher than that calculated for nighttime heating. *Lacerta viridis* can and does vary its thermal conductance, which in turn alters the thermal time constant of the animal.

The oxygen consumption pattern of *L. viridis* during daytime heating and cooling is very similar to that displayed by *Spaleirosophis cliffordi* (Dmi'el and Borut 1972), i.e., a fairly low $\dot{V}\text{O}_2$ level persisted until an increase in body temperature above the preferred level was accompanied by a sharp rise in oxygen consumption. The reverse then occurred during cooling, that is, a high level of metabolism endured until T_b dropped below the normal activity temperature. Simultaneous measurements of oxygen consumption and T_b have been reported for only one other lizard, the semiaquatic Galápagos marine iguana (Bartholomew and Vleck 1979). These findings likewise documented that, at any given body temperature, rates of metabolism during cooling were usually higher than those during heating. Values of RQ for *L. viridis* varied between 0.68 and 0.71 during heating and 0.57 and 0.81 during cooling. These values are within the normal range reported for reptiles (for

TABLE 3

MEAN UNCORRECTED AND CORRECTED THERMAL CONDUCTANCES AND THEIR RATIOS AS CALCULATED AT VARIOUS TEMPERATURES DURING HEATING AND COOLING FOR BOTH DAY- AND NIGHTTIME TESTING

BODY TEMPERATURE (C)	UNCORRECTED			CORRECTED		
	Heating	Cooling	Cooling/Heating	Heating	Cooling	Cooling/Heating
Day:						
25	.562	.477	.79	.552	.570	1.03
28	.756	.420	.56	.735	.485	.66
30	.726	.422	.58	.694	.475	.68
33	.833	.401	.48	.755	.445	.59
35	.856	.374	.44	.630	.407	.65
Night:						
25	.292	.458	1.57	.281	.492	1.75
28	.480	.402	.84	.462	.430	.93
30	.470	.413	.88	.443	.438	.99
33	.535	.382	.71	.482	.404	.84
35	.547	.394	.72	.436	.419	.96

a review, see Bennett and Dawson [1976]; Grigg [1978]).

From all data presented on the thermal behavior of *L. viridis* during heating and cooling, it is concluded that this lizard exercises certain physiological control over the rate of its body temperature change. Increasing thermal conductance during daytime heating would result in decreased time needed to obtain a high body temperature level, which would also be reflected by the small thermal time constant found for this phase. In contrast, decreasing conductance during cooling may aid in prolonging the time that *L. viridis* maintains its preferred body temperature. Low thermal conductance during nighttime heating may help throttle heat transfer

and subsequent increase in body temperature. The large conductance ratio indicates that the acquired heat is eliminated as rapidly as possible. Day- and nighttime oxygen consumption can be regarded similarly. Increased metabolic rates during daytime cooling and low oxygen consumption during nighttime cooling reflect physiological control of body temperature that is important to a lizard's energy budgeting; furthermore, allometric relationships of heating and cooling for *L. viridis* support the hypothesis that there are species-specific rates of heat exchange (Clausen and Art 1981), which may in turn be related to geographically dependent thermal requirements.

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