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Seasonal Responses to Heating and Cooling in *Lacerta viridis*

Peggy D. RISMILLER and Gerhard HELDMAIER

Dept. of Biology, Philipps University,
D-3550 Marburg, F. R. Germany

INTRODUCTION

Lacerta viridis, a primarily heliothermic lizard, demonstrates augmented rates of heating and diminished rates of cooling when tested during their activity portion of the day in May /Rismiller and Heldmaier, 1985/. This lizard also displays a strong circadian rhythm in body temperature selection, whereby both level and amplitude shift with the seasonally changing photoperiod. Although decades of studies have documented hysteresis between heating and cooling rates of both large /Bartholomew and Tucker, 1963/ and small lizards /Classen and Art, 1981/, seasonal changes in physiological control of thermoregulation have not been considered. Since the voluntary shift in T_b preference shown by L. viridis most likely involves modification of other physiological parameters, we decided to compare spring rates of heating and cooling with those found in the fall.

MATERIALS AND METHODS

Field caught Lacerta viridis from the area of Bologna, Italy were obtained in summer /1984/ and housed under natural photoperiod in large terrariums. Ambient temperature of the room was 22°C and infrared lamps provided supplement heating during daylight hours. Lizards used in experiments were transferred to individual thigmothermic gradient cages /for details see Rismiller and Heldmaier, 1982/ at least ten days prior to testing and maintained under natural photoperiod throughout the test series. All step function heating and cooling experiments were performed on unrestrained L. viridis weighing between 32.0 and 48.0 g. Telemetric monitoring of T_b was possible using temperature sensitive radio transmitters /Mini-mitter, model X/ implanted intraperitoneally. Lizards' metabolic rates were measured in 0.5 liter transparent plastic metabolic boxes at an airflow of 20 liters/h using a paramagnetic oxygen analyzer /Oxytest S/ and an infrared CO_2 analyzer /Uras 2T/. Metabolic boxes were placed in a climate chamber with indirect lighting, i.e. the lizards received no direct radiant heat. It was possible to elevate or decrease the temperature in the chamber very rapidly /more than 3°C per min./; consequently animals were not disturbed for temperature step shifts. Oxygen consumption and body temperature were registered simultaneously and along with time, ambient temperature and RQ, listed on-line /Tektronix 4051/. Experiments were performed during the animal's normal activity period and lizards in individual metabolic boxes were placed in the 20°C chamber at least one hour prior to test begin.

The paired-sample t-test was used to analyze statistical differences in heating and cooling within one testing period, and the two-way analysis of variance was used to determine seasonal differences in the evaluated parameters.

RESULTS

The course of T_b and O_2 consumption as a function of time during heating and cooling are presented for single lizards as real time plots in Figs 1 and 2 for March and November, respectively. Whereas the lizard in March needed 55 min. in order to heat to a T_b within 0.5°C of T_a, L. viridis tested under the same conditions in fall required 115 min. Time needed for cooling to within 1°C of ambient was 96 min. during spring and 84 min. during fall testing. Metabolic response to daytime heating during March shows a linear increase with increasing T_b, augmenting sharply at temperatures above 34°C. During the beginning of cooling O_2 consumption decreases with decreasing T_b until, in this case, T_b falls below 32°C. The metabolic rate is then augmented above corresponding heating rates and remains at an increased level until T_b falls below 23°C. In contrast, O_2 consumption during heating in November remains at a relatively low level augmenting as T_b increases above 32°C, and declining rapidly during the cooling phase.

Elevated metabolism during daytime cooling in March becomes more evident when the mean O_2 consumption is plotted at different T_b's /Fig. 3/. During cooling metabolic rate remains at a fairly high level, between .42 and .58 ml $O_2/(g*h)$ as T_b drops from 35 to 25°C. Indeed at paired T_b's between 25 and 33°C, metabolic rates are significantly higher /$p < 0.05$/. O_2 consumption values during heating and cooling in November /Fig. 3/ do not differ from one another. Mean RQ's determined during these experiments were .72 and .66 for heating and cooling in March, as well as .66 and .63 November.

Rates of heating and cooling expressed as the thermal time constant / τ / were determined by plotting the difference between T_b and T_a semilogarithmically against time. Heating and cooling slopes as well as the corresponding τ values /calculated according to the method of Smith, 1976/ are shown in Fig. 4. During both March and November values for cooling were significantly higher than for heating $p < 0.01$ and $p < 0.05$, respectively. However, whereas slopes for heating and cooling in March were statistically different, demonstrating higher heating rates and diminished rates of cooling, no slope differences were found in November.

DISCUSSION

Responses of Lacerta viridis to heating and cooling differ when measured during the spring as compared to fall. Whereas a large hysteresis exists between spring heating and cooling, with a mean of 62 min. needed to heat as compared to more than 132 min. needed to cool to within 0.5°C of ambient, lizards during fall testing required a mean of 79 and 87 min. for heating and cooling, respectively. Consequently, τ derived from the slopes of the exponential rate of heating or cooling is significantly greater for cooling in March /$p < 0.05$/ i.e., the rate of T_b change during cooling was slower than in November. Lizards generally displayed more rapid heating rates in March, however neither differences in regression slopes nor τ could be statistically confirmed.

The role of endogenous heat production expressed as the metabolic rate, and its influence on changes in thermal conductance have been discussed at length /review by Bartholomew, 1982/. In order to assess the contribution of O_2 consumption to heat exchange rates, thermal conductance was calculated and adjusted for metabolism by the method of Bartholomew and Tucker /1963/. Results are presented in Tab. 1. In March both uncorrected and corrected thermal conductances at all temperatures were significantly higher during heating /$p < 0.01$/. Indeed, metabolic rate could account for only 53 to 70% of the difference in rate of temperature change at T_b's greater than 25°C. In November however, only at T_b's 28,33 and 35°C was the conductance significantly higher during heating, and these differences diminished when correction for metabolism was made. Differences in rate changes were fully compensated at T_b's 25 and 35°C,

Table 1. Mean thermal Conductance ml O_2 /g^{-1} h^{-1} $^{\circ}C^{-1}$/.

	UNCORRECTED			CORRECTED		
Tb (°C)	Heating	Cooling	Cooling/ Heating	Heating	Cooling	Cooling/ Heating
March						
25	.421	.333	.791	.398	.405	1.017
28	.617	.292	.473	.548	.349	.598
30	.605	.298	.492	.561	.351	.626
33	.689	.284	.414	.600	.316	.527
35	.705	.308	.437	.484	.335	.692
November						
25	.464	.436	.939	.448	.504	1.125
28	.555	.382	.688	.530	.421	.794
30	.544	.390	.717	.506	.430	.849
33	.619	.367	.593	.559	.392	.701
35	.633	.475	.750	.465	.494	1.062

whereby O_2 accounted for 70 to 85% of differences found at other temperatures. Moreover, at temperatures above 25°C thermal conductance in March was significantly greater during heating than in November /$p < 0.01$/ and significantly lower during cooling /$p < 0.01$/. The differences between rates of heat exchange are reduced in fall and consequently reflect a greater contributing effect of metabolic rate, although O_2 consumption was substantially less /Fig. 5/ than during spring testing. In order to more clearly quantify the role of metabolism during heating and cooling hysteresis, the metabolic scope of L. viridis must be determined at different times of the year. It is clear that endogenous heat production is not solely responsible for all changes in thermal conductance, and as suggested by other authors, we believe that changes in peripheral circulation are important as a mechanism of hysteresis.

L. viridis has a preferred daytime T_b of 33.0°C during spring /corresponding to the mating season/ and voluntarily shifts to lower preferred T_b in fall. This study has shown that rates of heat exchange, O_2 consumption and thermal conductance are likewise modified in fall, suggesting a change in the animal's energy budget strategy. This linkage between perferred T_b and physiological functions is ecologically meaningful, indicating the capacity of L. viridis to adapt to changing seasonal conditions. We conclude that consideration of seasonal variations in all physiological parameters should receive more attention in future studies.

REFERENCES

BARTHOLOMEW, G. A. /1982/: Physiological control of body temperature. - In: GANS, C. /ed./: Biology of the reptilia. Vol. 12, pp. 167-211. Academic Press, New York.

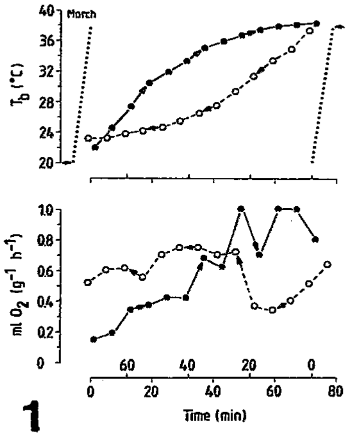
BARTHOLOMEW, G. A., TUCKER, V. A. /1963/: Control of changes in body temperature, metabolism, and circulation by the agamid lizard, Amphibolurus barbatus. - Physiol. Zool., 36 /3/ : 199-218.

CLAUSSEN, D. L., ART, G. R. /1981/: Heating and cooling rates in Anolis carolinensis and comparison with other lizards. - Comp. Biochem. Physiol., 69A : 23-29.

RISMILLER, P. D., HELDMAIER, G. /1982/: The effects of photoperiod on temperature selection in the European green lizard, Lacerta viridis. - Oecologia, 53 : 222-226.

RISMILLER, P. D., HELDMAIER, G. /1985/: Thermal behavior as a function of the time of day: heat exchange rates and oxygen consumption in the lacertid lizard Lacerta viridis. - Physiol. Zool., 58 /1/ : 71-79.

SMITH, E. N. /1976/: Heating and cooling rates of the American alligator, Alligator mississippiensis. - Physiol. Zool., 49 : 37-48.



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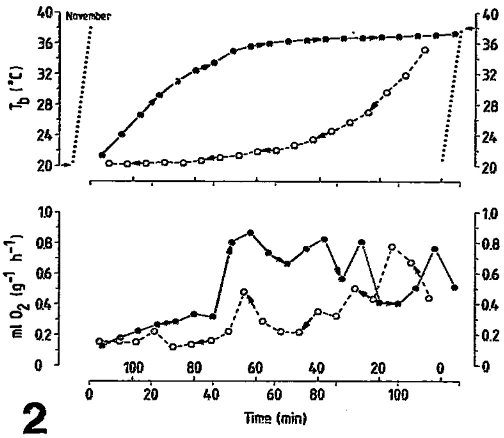

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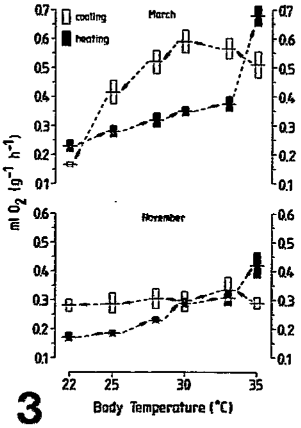

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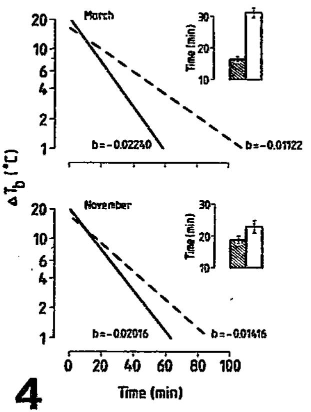

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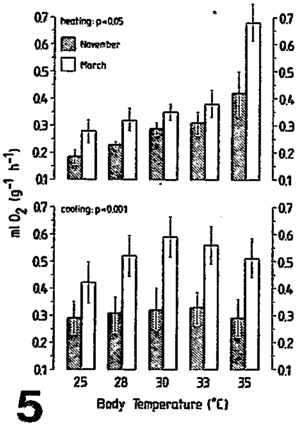

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Fig. 1: Real time plot for March of O_2 consumption and T_b against time. /●/ and lower time scale represent heating, and /○/ and upper time scale is for the cooling phase. Arrow and dotted line indicate step function temperature change. Fig. 2: Real time plot for fall, all symbols as in Fig. 1. Fig. 3: Mean O_2 consumption at different T_b's for heating and cooling during spring and fall. Fig. 4: Semilog plot for heating /solid line/ and cooling /broken line/ as well as corresponding thermal time constant /hatched column: heating, open column: cooling/. Fig. 5: Mean metabolic rates at different T_b's during spring and fall.