

PHYSIOLOGICAL THERMOREGULATION OF THE CANARY LIZARD *GALLOTIA GALLOTI*

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Abstract—1. The Canary Island lizard *Gallotia galloti*, tested in still air between 5 and 35°C, heated faster than it cooled. The ratio between heating and cooling thermal time constants shows no dependence on body weight and its value was 0.50 on average.

2. Regression equations for the relationship between the thermal time constant (τ) and body weight (W) during heating (h) and cooling (c) are:

$$\tau_h = 1.74 W^{0.56}$$

$$\tau_c = 2.42 W^{0.66}$$

3. During heating the core and subcutaneous body regions heat at the same rate, while during cooling the core cools more slowly than the subcutaneous area.

4. Heart activity differences during heating and cooling were restricted at body temperature range 7–20°C. The increased heart activity during heating appears to be a physiologically controlled response, as opposed to the decreased heart activity during cooling, which appears to be a passive response.

INTRODUCTION

The existence of physiological thermoregulation in several reptilian species has been established through the analysis of undergoing changes in the animal's body temperature, when heating or cooling in a thermostated chamber. Thus, by measuring the rate of temperature change (Bartholomew and Tucker, 1963) or the thermal time constant (Smith, 1976) from the time versus body temperature curves obtained during such experiments, it has been shown that most reptiles investigated heated faster than they cooled (Bartholomew and Tucker, 1963, 1964; Bartholomew and Lasiewski, 1965; Grigg *et al.*, 1979; Smith, 1976; 1979; Smith *et al.*, 1984; Weather, 1970; McKenna and Packard, 1975; Spray and May, 1972; Claussen and Art, 1981). This fact, and another reported by some of these authors to the effect that dead animals heat and cool at the same rate, have been considered as evidence of the existence of a certain degree of physiological thermoregulation in reptiles.

In lizards and other reptiles, body weight is a decisive factor influencing the value of heating and cooling rates (see review by Claussen and Art, 1981). On the other hand, in alligators, the time for cooling as opposed to the time for heating is greater in larger specimens; this fact has been considered by Smith (1976) as indicating that larger alligators are better physiological thermoregulators than small ones. Nevertheless, in some small lizards in which the heating rate is greater than the rate of cooling, the ratio between the heating and cooling rates does not show weight dependence (Weathers, 1970; Claussen and Art, 1981).

Cardiovascular adjustments appear to be primarily responsible for the differences between heating and

cooling in most of the reptiles investigated; in this sense, higher heart rate during heating than during cooling, and peripheral blood flow changes have been the main features reported in lizards (Bartholomew and Lasiewski, 1965; Bartholomew and Tucker, 1964; Weathers, 1971; Morgareidge and White, 1969; Baker *et al.*, 1972) and other reptiles (Smith, 1976; Grigg and Alchin, 1976; Smith *et al.*, 1984). The extent to which these mechanisms control the heat exchange during heating and cooling may be of different importance for the various groups and reptilian species, therefore determining their particular capacity of physiological thermoregulation.

To date, most of the work in physiological thermoregulation of reptiles has been done on American and Australian reptilian species; we think that the knowledge of the physiological thermoregulation in reptiles of other regions can be important from the comparative point of view.

In this work the capacity of physiological thermoregulation of the Canary Island lizard *Gallotia galloti* is investigated. Thus, the thermal time constant was measured in several specimens of different weights during heating and cooling in still air. Again, core and subcutaneous temperatures differences and cardiac activity changes during heating and cooling were measured to determine some features of cardiovascular involvement in the control of heat exchange in these lizards.

MATERIALS AND METHODS

The experimental animals used in this work were *Gallotia galloti* lizards weighing from 15 to 74 g and of undefined sex. The lizards were captured in Tenerife (Canary Islands, Spain). The Canary Islands belong to a biogeographically well defined region called Macaronesia (lat. 39°45' N and

14°49' N; long. 31 17' W and 13°20' W). The animals were kept in terraria, the bottoms of which were covered with sand and where ambient temperature ranged from 20 to 25°C during the day and 17 to 20°C at night. The relative humidity ranged from 50 to 60%. Water and food consisting of small pieces of banana and tomato were provided *ad libitum*.

The heating and cooling experiments were carried out in two identical chambers (40 × 40 × 30 cm) the ambient temperature of which could be controlled by a thermostat. The cooling chamber was maintained at $5 \pm 0.5^\circ\text{C}$, and the heating chamber at $35 \pm 0.5^\circ\text{C}$. The chamber floors were covered with cork and the animals were free to run on it. Relative humidity in both chambers ranged between 35 and 40%. All the experiments were carried out in still air.

In the heating experiments, the lizards were previously cooled to 5°C and then transferred to the heating chamber after which data recording started. Once the body temperature of the lizards reached 35°C, they were transferred to the cooling chamber, the cooling experiment following till lizard body temperature came down to 5°C.

Several experiments designed to take measurements at different stable ambient temperatures ranging between 5 and 35°C were carried out in which the corresponding chamber was thermostated at the chosen temperature. In these experiments the animal was kept within the chamber during a 24 hr habituation period, after which the measures were made.

Core and subcutaneous body temperature were recorded by an electrical thermometer (Nihon Kodhen MGA III-219) fitted with small thermistor probes. To record core temperature one of the probes was inserted through the animal's cloaca 2 cm deep, and thermistor leads were attached to the tail to prevent the probe coming off. Subcutaneous recording was achieved by inserting the probe through a small cut done on the dorsal tegument (beside the last dorsal vertebrae), and thermistor leads were attached to the caudal region.

Bipolar electrocardiogram (ECG) recording was carried out by means of two small stainless steel electrodes inserted below the skin to the right and left of the lizard dorsal region, one of them anterior to the heart and the other posterior to the heart. A third electrode situated at the caudal region near the tail served as earth electrode.

The DC output voltage from the thermistor thermometer and the ECG signal from the electrodes were led to the recorder system (Nihon Kodhen polygraph) to be filtered and amplified; polygraph output was connected to an automatic data acquisition and processing system for small animals (González and Vera, 1984). This system is based on a North Star microcomputer equipped with two minifloppy disk drivers, an 8 bit Analog to Digital converter with 16 multiplexed channels, a real time programmable clock, a printer (Centronics 779), an X-Y plotter (Houston), an oscilloscope (Hewlett Packard 1201A) and a video terminal (Heathkit H19). Voltages from the polygraph were input to the system A/D converter and manipulated by software. So, to get body temperature versus time data during heating and cooling experiments, a BASIC program was developed that sampled the DC temperature voltage every 2 sec and stored the data samples together with the current time in the computer memory. Once the experiment finished, data were saved in a file on a diskette. A calibrated program computed the actual body temperature values and with another program, the regression equations were obtained of the decimal logarithm of the difference between ambient temperature and body temperature versus time by the least squares method. Thermal time constant was obtained from the latter. The slopes of the fitted straight lines to the data were compared by *t*-test for slopes.

We measured the heart activity from the RR interval of the lizard ECG, as the computerized system allowed us a precise on-line measurement of the consecutive RR intervals

by a BASIC program and an ASSEMBLER subroutine for detection of ECG peak R. The RR intervals were stored in the computer memory at the same time as the current value as DC temperature voltage. The RR value assigned to a given temperature corresponded to the average of the RR intervals recorded at that temperature. RR mean and body temperatures were stored on diskette at the end of the experiment. This procedure was also used for obtaining RR intervals in the experiments carried out at stable ambient temperatures. RR mean values during heating and cooling were compared by *t*-test. One-way analysis of variance was used when comparing RR mean values at a given temperature obtained during heating, cooling and stable temperatures. *F*-test for slopes was used to compare regression coefficients of the RR-body temperature fitted curves in those three situations.

RESULTS

Figure 1 shows a semilog plot of the absolute value of the difference between body cloacal temperature (core temperature T_B) and ambient temperature (T_A) during heating and cooling in one lizard. Linear regression was significant ($P < 0.01$) for both heating and cooling data and the slopes of the fitted straight lines were significantly different ($P < 0.01$).

Values of the thermal time constant were always greater during cooling than during heating and are shown in Fig. 2 versus body weight in a log-log plot. In both cases linear regression was significant ($P < 0.01$). The regression equations are:

$$\tau_h = 1.74 W^{0.56} \quad (r = 0.89)$$

$$\tau_c = 2.42 W^{0.66} \quad (r = 0.93).$$

There were no differences between the slopes of the straight lines fitted to the data. No linear regression was found between the τ_h/τ_c ratio and body weight; the average value of that ratio for 15 specimens was 0.50 (2 SD = 0.12).

In four specimens where records were carried out of subcutaneous and cloacal temperature, no significant differences were found during heating between the cloacal and subcutaneous thermal time constants; however, during cooling, the cloacal thermal time constant was significantly greater ($P < 0.01$)

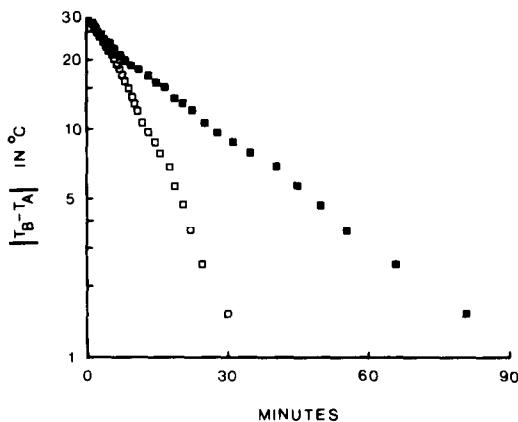


Fig. 1. Thermal response in a 35 g *Gallotia galloti* tested in still air, during heating (open squares) and cooling (closed squares).

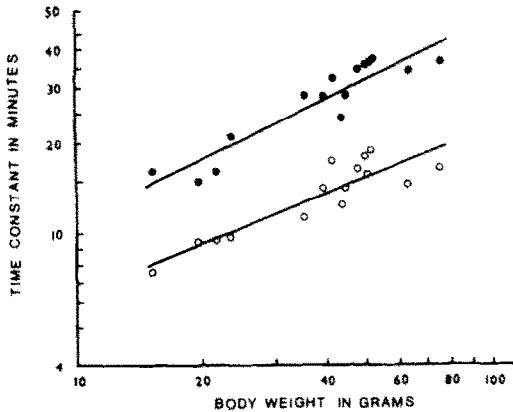


Fig. 2. The relationship between thermal time constant and body weight. Open circles represent values obtained during heating and closed circles values obtained during cooling. Straight lines fitted by least squares method.

than the subcutaneous one. These results are summarized in Table 1.

The mean values of electrocardiogram RR intervals obtained during heating and cooling experiments are shown in Fig. 3. In both cases RR-body temperature data were significantly fitted ($P < 0.01$) to a decreasing exponential. The regression equations are:

$$RR(h) = 7.53 \exp(-T/11.6) \quad (r = -0.97)$$

$$RR(c) = 9.81 \exp(-T/10.7) \quad (r = -0.98)$$

(h = heating; c = cooling; T = body temperature; r = correlation coefficient).

Cooling RR mean values were significantly greater ($P < 0.01$) than heating ones only at the body temperature range from 7 to 20°C.

RR mean values obtained at different stable temperatures are shown in Fig. 4 together with those obtained during heating and cooling at the same body temperatures. A decreasing exponential was also significantly fitted ($P < 0.01$) to the RR-body temperature data obtained at stable temperatures. The regression equation is:

$$RR = 12.35 \exp(-T/10.2) \quad (r = -0.99).$$

Comparing the regression coefficients of the exponentials fitted to RR-body temperature data obtained during heating, cooling and stable temperatures, significant differences ($P < 0.05$) were only found between heating and stable temperatures. Moreover, in the range of body temperature from 5 to 25°C, RR mean values obtained at different stable temperatures were significantly greater ($P < 0.001$) than those obtained during heating and cooling at the same body temperatures. Above 25°C no significant

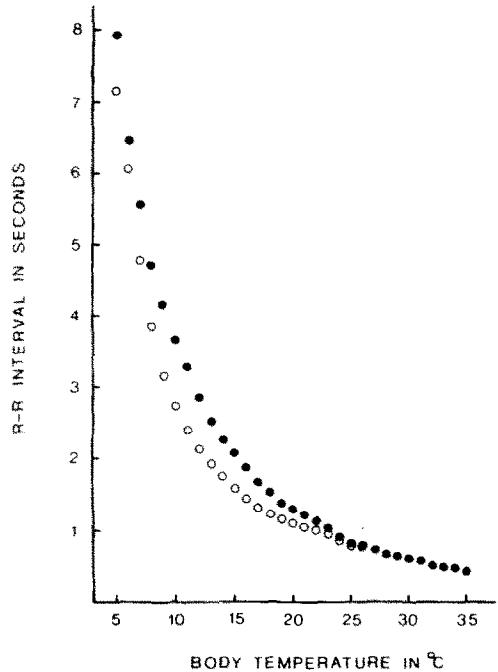


Fig. 3. Mean RR interval versus body (cloacal) temperature in 11 lizards, during heating (open circles) and during cooling (closed circles). To avoid confusion, ranges and SE are plotted in Fig. 4 for the RR means at every 5°C of body temperature.

differences between RR mean values were found in any of the three situations investigated.

DISCUSSION

Gallotia galloti lizards, like many other reptiles, heat faster than they cool. More specifically, in these lizards tested in still air the time for heating is approximately half the time for cooling. Moreover, the ratio τ_h/τ_c appears to be independent of body weight. This result has also been reported in other small lizards tested under similar experimental conditions (Weathers, 1970; McKenna and Packard, 1975; Claussen and Art, 1981). However, in some alligators (Smith, 1976; Smith *et al.*, 1984) and agamids (Grigg *et al.*, 1979) the ratio τ_h/τ_c decreases with body weight as larger specimens increase their cooling time as opposed to the time for heating. We think that the discrepancy between lizard results and those found in alligators may be related to the characteristics of biological species, since in ours and the other lizards reported, without taking into account their individual

Table 1. Thermal time constants in four *Gallotia galloti* lizards computed from cloacal and subcutaneous temperatures during heating and cooling experiments

Animal No.	Body weight (g)	Thermal time constants			
		Cloacal		Subcutaneous	
		Heating (min)	Cooling (min)	Heating (min)	Cooling (min)
1	41	10.64	27.30	11.03	23.87
2	46	12.54	24.41	11.92	19.00
3	50	12.66	29.64	13.31	21.73
4	54	14.12	26.11	14.42	22.19

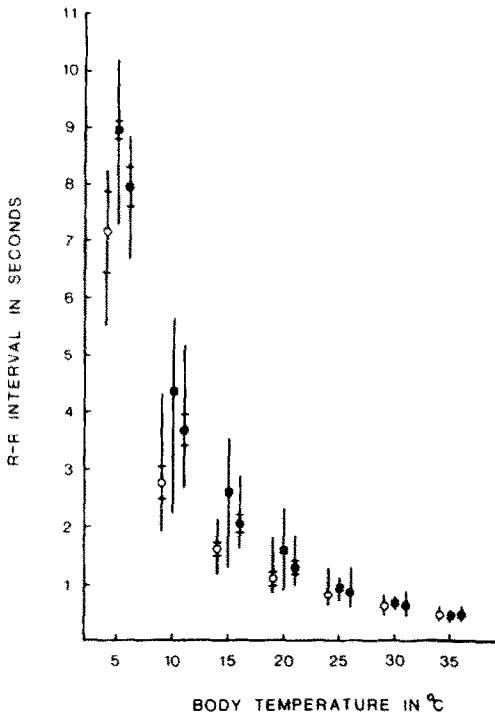


Fig. 4. Mean RR interval versus body (cloacal) temperature at different stable ambient temperatures (closed rectangles), during heating (open circles) and during cooling (closed circles). Vertical lines indicate ranges and horizontal marks indicated $\pm 2SE$. To avoid overlap, only mean values every 5 degrees have been plotted, and mean heating and cooling RR values have been displaced to the right and to the left of each temperature considered, respectively. Means correspond to 11 lizards.

biology, their body weight range is smaller than that of alligators reported and this fact may give rise to surface/volume relationships or other size-related physical relationships that may influence the body heat exchange and be particular to each species of reptiles.

On the other hand, if the value of the ratio τ_h/τ_c is taken as an index of the capacity of physiological thermoregulation (Smith, 1979) then the lizard *Gallotia galloti*, whose average value for this ratio is 0.5, would have a greater physiological capacity of thermoregulation than the lizards reported by Bartholomew and Tucker (1963), Weathers (1970), McKenna and Packard (1975), and Claussen and Art (1981), tested under similar conditions and in those the ratio τ_h/τ_c inferred from their heating and cooling rate data ranged approximately from 0.64 to 1.07 (0.85 on average) but would, however, be comparable to that of alligators whose weights fall between 5 and 50 kg (Smith *et al.*, 1984) and have a ratio of 0.51 on average.

Concerning the body weight dependence of the thermal time constant: the exponents of the regression equations for τ_h and τ_c in our animals fall within the range 0.21–0.68 reported by Claussen and Art in their revision on species of several reptilian groups, although they are greater than the value of 0.33 based on geometric similarity reported by these authors; however, they are near those reported by

Smith *et al.* (1984) in alligators, thus indicating a similar weight dependence of the thermal time constant in our lizards and in the reptiles studied by Smith.

Core and subcutaneous temperature measurements indicated that during heating both body regions heat at the same rate, but during cooling the core cools more slowly than the subcutaneous area; similar results have also been found in alligators (Smith, 1976). These cooling and heating differences are indicative of changes in the thermal conductivity produced by changes in the blood flow between the core and the periphery, probably governed by some kind of thermal vasomotor control system: during heating, the increase in peripheral blood flow would increase the thermal conductivity between core and periphery, thus reducing their temperature differences, but during cooling peripheral vasoconstriction would reduce blood flow and thermal conductivity of the periphery, thus preventing a quick cooling of the core. Some results in this sense have been observed in several species of Squamata (Morgareidge and White, 1969; Weathers, 1971; Weathers and Morgareidge, 1971) and Crocodylia (Grigg and Alchin, 1976; Smith *et al.*, 1984).

Differences in the cardiac response during heating and cooling were only observed for body temperatures ranging from 7°C to 20°C. This result is in part different from that reported in other reptilian species where the heart rate during heating was always greater than during cooling in all the body temperature range investigated (Bartholomew and Lasiewski, 1965; Smith, 1976; Grigg and Alchin, 1976). Moreover, the cardiac intervals measured at different stable temperatures (Fig. 4) were greater than those obtained during heating and cooling at the same body temperatures in the range from 5–25°C only, thus suggesting that cardiac adjustments begin to take place on the one hand during heating, through an increasing of central blood flow that, together with a parallel increase in the peripheral blood flow, would help lizards to reach quickly their preferred temperature. On the other hand, during cooling, the lower heart rate and more probably peripheral vasoconstriction would prevent their departure from their thermal preferendum. It can be observed that above 25°C no differences in cardiac response were found in any of the situations investigated, indicating that over 25°C mechanisms other than cardiac adjustments are responsible for maintaining heating and cooling rate differences.

Finally, we have only found differences between the rate of RR change during heating and that obtained at stable temperatures and no differences between the latter and that obtained during cooling. It seems, therefore, that during heating an active heart acceleration exists that may be centrally controlled, while during cooling the heart rate appears to decrease in a passive manner. In fact RR values during cooling are close to those measured at stable temperatures.

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