EVIDENCE FOR THERMOREGULATION IN THE TORTOISE
CHERSINE ANGULATA

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ABSTRACT

The results of experiments on *Chersine angulata* suggest that a mechanism exists for controlling rate of change of body temperature over the range 20–35°C. Active retardation of heat uptake close to the upper temperature is a prominent feature as measured by cloacal temperature. Unlike other reptiles so far studied, *Chersine angulata*, when alive, cools more rapidly than it heats up. Dead animals heat and cool at the same rate, and more rapidly than live animals. It is suggested that overheating is the critical factor in the thermal relations of the tortoise.

INTRODUCTION

Reptiles have long been known to exploit variations in their thermal environment in order to exercise a considerable degree of control over their body temperature. Cowles and Bogert (1944) and Bogert (1948) among others have shown the importance of such thermoregulatory behaviour.

However, in recent years detailed work, in particular by Bartholomew and his associates (1963, 1964, 1965 and 1966), has shown conclusively that in many lizards there are physiological mechanisms for controlling body temperature. Circulatory factors other than heart rate, such as changes in peripheral circulation, seem to be the most important components of the system.

Most of the above work has dealt with lizards from the arid regions of America and Australia, while the Chelonia have been rather neglected. The only recent temperature records for a terrestrial form are those of Mackay (1964), who monitored body temperature in free-living Galapagos tortoises. The Chelonia are of particular interest, since containment within a rigid shell must limit the effectiveness of postural changes during behavioural thermoregulation as practised by other forms. It thus seems probable that tortoises would be more dependent on physiological mechanisms than other reptiles.

MATERIALS AND METHODS

Four specimens of *Chersine angulata*, two males weighing 810 gm and 575 gm, and two females weighing 750 gm and 600 gm, were used for the readings. Cloacal temperatures were measured with 3 mm diameter thermistor probes (STC F23) linked to a battery-powered portable Wheatstone bridge ammeter. Readings were obtained as degrees of deflection from the zero mark of the ammeter, and this value was converted to degrees Celsius by referring to a calibration curve, prepared from readings in a water-bath at known temperatures over the range required. Before use the thermistors were checked against this curve. When readings were taken, they were inserted to a depth of 7 cm in the cloaca.

The experiments investigated the rates of heating and cooling under controlled conditions

FIGURE I

RESULTS FOR 810 GM ANIMAL
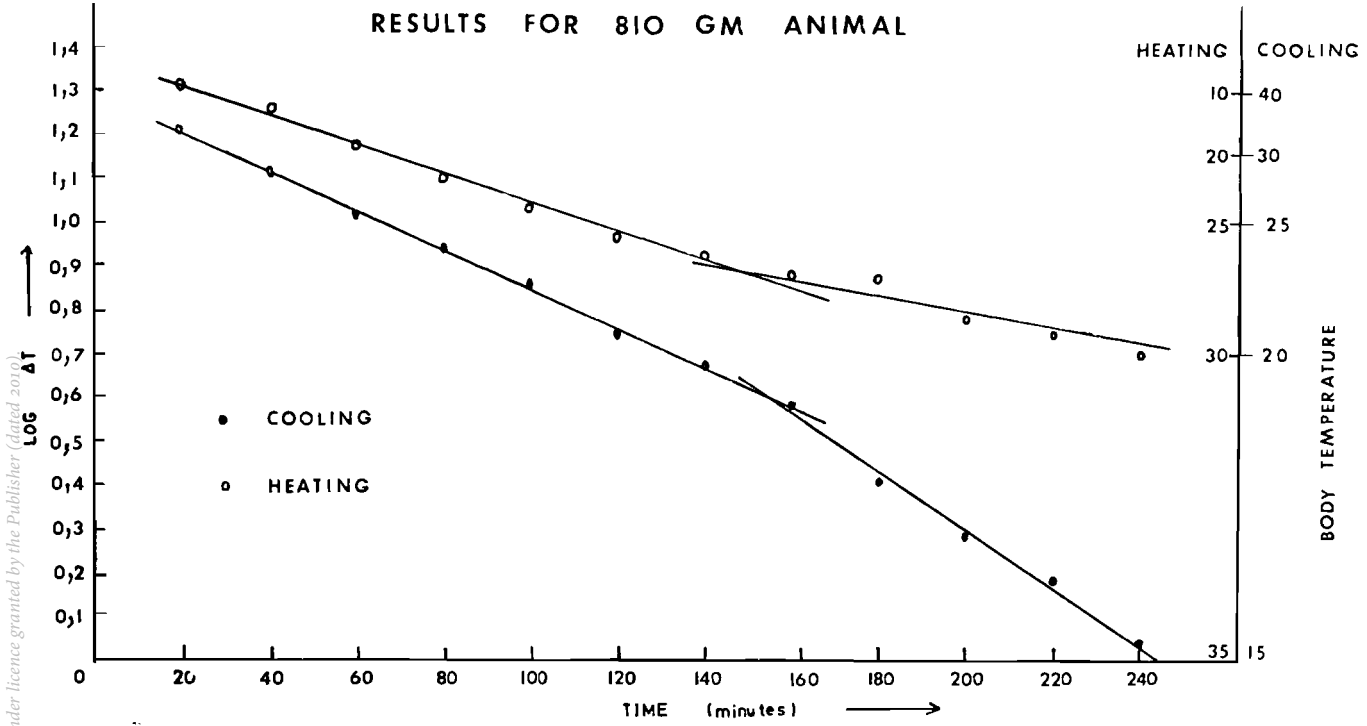
in still air, over the temperature range 15–35°C. A cold room set at 15°C, and an oven chamber set at 35°C were used. After a six-hour equilibration period at one temperature, the animals were transferred to the other chamber, and cloacal temperature was measured at twenty-minute intervals over a four-hour period. The same procedure was followed with two of the animals after death. Fourteen heating and fourteen cooling experiments were performed with live animals; three heating and three cooling experiments with dead animals.

Representative individual experiments on two of the animals are shown in the figures. In all graphs a semi-logarithmic plot was used: the log of $\triangle t$, the difference between cloacal temperature and ambient temperature, was plotted against time.

RESULTS AND DISCUSSION

In all experiments when the live animals were being heated, the graph showed a clear inflexion point as illustrated in Fig. 1. The point at which the change of slope occurred varied for individual animals, ranging from 27 to 32°C (cloacal temperature). The rate of cooling in four cases showed no change in slope, but in the other ten experiments there was an inflexion indicating an increase in the rate of cooling, as shown in Fig. 1. This occurred between cloacal temperatures of 19 and 21°C. The change in gradient during the heating experiment represents a marked reduction in the rate at which the animal is taking up heat. In the graphs of cooling experiments, however, the change in slope represents an increase in the rate of cooling.

Comparisons between experiments on the same animal alive and dead (Fig. 2) show that for dead animals the slope is linear throughout. Therefore the change of slope in the case of living animals must be a phenomenon due to some physiological process.

The gradients of all heating and cooling graphs were calculated from the slope prior to inflexion, and from the mean values, the ratio cooling slope : heating slope was calculated.

TABLE 1

MEAN GRADIENTS FOR ALL EXPERIMENTS

	Cooling slope	Heating slope	C/H
Alive	0,49	0,43	1,14
Dead	0,81	0,79	1,02

It is obvious that the dead animal is both heating and cooling more rapidly than the live animal, and the C/H ratio is very close to unity, as would be expected if heat transfer were entirely passive.

Bartholomew and Tucker (1963, 1964) measured heating and cooling rates over the temperature range 20–40°C for the Australian lizards *Amphibolurus barbatus* and *Varanus gouldii*. For the latter they obtained a C/H ratio of 0,88 while for *A. barbatus* the ratio was 0,75. In the Galapagos marine iguana a C/H ratio of 0,5 has been recorded (Morgareidge and White 1969),

FIGURE 2

RESULTS FOR 575 GM ANIMAL
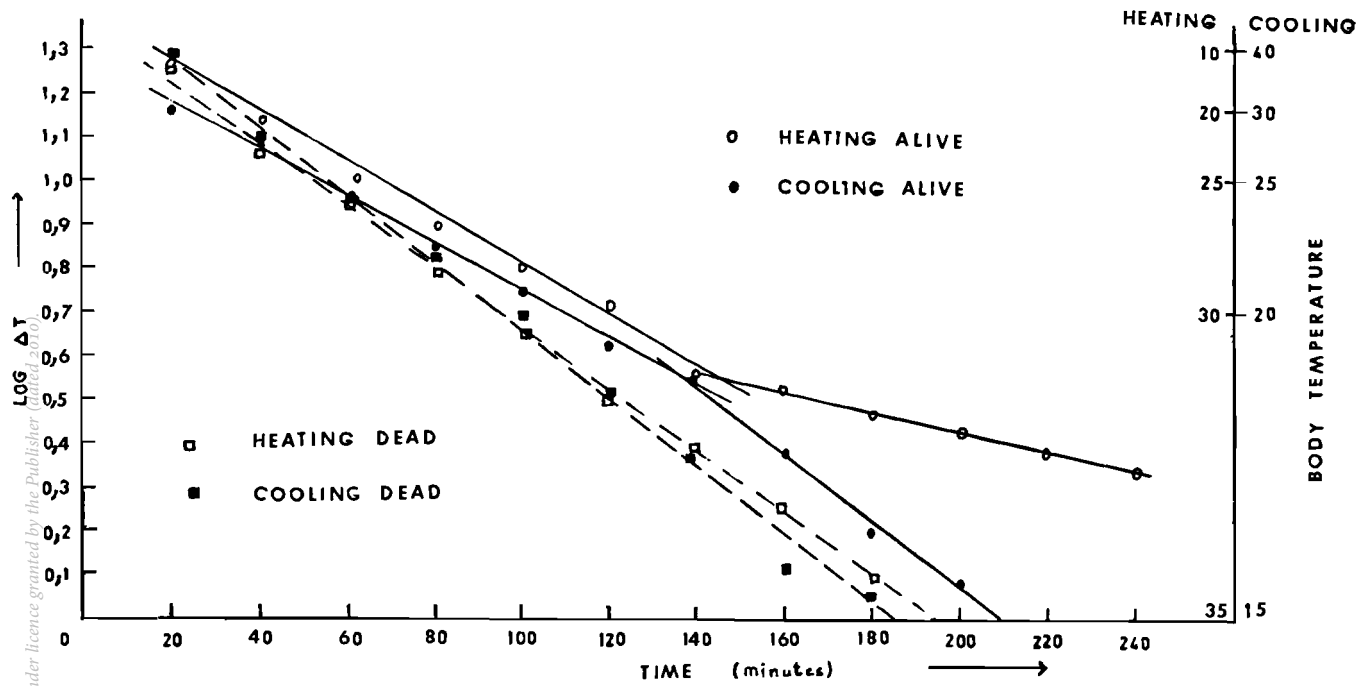
and Sapsford (unpublished) found ratios as low as 0,34 for the fresh-water turtle *Pelomedusa subrufa*. Thus in all cases the animals were heating noticeably faster than they were cooling. In contrast, the value of 1,14 for *Chersine angulata* indicates that it is cooling more rapidly—an ecological explanation may be suggested for this.

C. *angulata* is a herbivore, relatively slow-moving and confined to a shell, which restricts its behavioural responses to temperature. With a relatively innutritious diet, it will require longer periods of active feeding than insectivorous or carnivorous forms such as most lizards. Consequently it would be advantageous for the animal to retard the rate of heat uptake, and so be able to spend more time in the open. While overheating may prove fatal, cooling merely leads to inactivity.

On the other hand, herbivorous matter requires a longer digestion period, so that rapid cooling at night would be a distinct disadvantage. It is possible that the increased rate of cooling recorded in these experiments was due to peripheral vasoconstriction affecting the cloacal region, while a higher core temperature was maintained.

It should be noted that these results were obtained with animals under artificial conditions, and that the cloacal temperatures measured may not reflect the true core temperatures. In this case the inflexions on the graphs would merely be the result of a change in the circulation rate. Nevertheless, the data collected to date strongly suggest that active thermoregulation occurs in *Chersine angulata*.

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