

## HEAD-BODY TEMPERATURE DIFFERENCES IN THE AUSTRALIAN BLUE-TONGUED LIZARD, *TILIQUA SCINCOIDES* DURING RADIANT HEATING

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(Received 4 September 1978; accepted 5 April 1979)

**Abstract**—When heated radiantly, head-body temperature gradients developed in both live and dead *Tiliqua scincoides*. The gradients were consistently larger in live than in dead individuals, indicating they were enhanced by a physiological component superimposed on the more basic physical components. Large gradients in the initial phases of heating represented a lag effect, the head core beginning to receive heat before the body core because it is closer to the heated surface. Once this lag effect subsided, the body heated more rapidly than the head because it presented a greater incident surface area per unit mass than did the head. Living lizards appeared to maintain head-body temperature differences until the maximum voluntary temperature was approached.

### INTRODUCTION

MANY studies have shown that reptiles exert considerable control over the net rate of flow of thermal energy between their bodies and the environment (see reviews by Templeton, 1970 and Heatwole, 1976) but to what degree they can control heat distribution within their bodies is far from clear. The many implications of reptiles being able to utilize thermal gradients, in particular to regulate head temperature independently of body temperature, have led to a series of studies which have examined these gradients in lizards (Heath, 1964; Johnson, 1972; Webb *et al.*, 1972; Spray & Belkin, 1973; Pough & McFarland, 1976; Crawford *et al.*, 1977), snakes (Webb & Heatwole, 1971; Johnson, 1973, 1975; Hammerson, 1977) turtles (Riedesel *et al.*, 1971; Webb & Johnson, 1972) and crocodilians (Johnson, 1974). Unfortunately, these studies have seldom been able to demonstrate the degree to which the head-body temperature differences can be physiologically controlled.

The present study was designed to determine the magnitude of head-body temperature gradients which developed in blue-tongued lizards (*Tiliqua scincoides*) subjected to uniform radiant heating. By comparing individuals when both alive and dead, it was possible to determine the degree to which the gradients were the result of physical and/or physiological processes. An attempt was also made to determine the degree to which the gradients could be considered as being physiologically "controlled".

### MATERIALS AND METHODS

Four *Tiliqua scincoides* captured in the vicinity of Melbourne, Victoria, were obtained from an animal dealer. They were housed in an open enclosure on the roof of the Biological Sciences Building, University of Queensland, and maintained on a diet of banana, land snails, new-born mice and canned dog food. Until sacrificed, the specimens appeared healthy.

To restrict head and trunk movements during experiments, each lizard was strapped to a board with a narrow

strip of clear, adhesive, cellophane tape across the base of the tail and just anterior to the front legs. Temperatures were measured with thermocouples (48 s.w.g. copper/constantan), the voltages being amplified with a Rikadenki Kogyo d.c. Microvoltmeter (model A10) and recorded on a monopen chart recorder of the same brand (model B-1); an ice bath supplied the reference temperature. The equipment was calibrated against a mercury thermometer and the absolute accuracy of stated temperatures is  $\pm 0.5$  deg C (discrimination between any two thermocouples was  $\pm 0.5$  deg C). The rectal probe was inserted via the cloaca so that the junction was approx 6 cm from the cloaca and 1.8 cm below the dorsal surface; a thin rod was used to position the probe. For the head probe, a hole was drilled through the skull where the second and third supraoculars met the right fronto-parietal. The thermocouple was inserted such that the junction was 0.85 cm from the dorsal surface of the head; it lay in contact with the optic blood sinus. The probe was secured in place with a drop of resin.

Each trial was started by placing an implanted, restrained lizard in a refrigerator, and allowing it to cool to the desired initial temperatures ( $T_h^0$  and  $T_b^0$ ; Table 1). When the head and body temperatures were within 0.5 deg C of each other and at the desired magnitude, the lizard was removed from the refrigerator and positioned 30 cm below a horizontally oriented 1000 W bar radiator, which effected radiation of approximately equal intensity along the lizard's length. When the radiator was switched on, head and body temperatures were recorded alternately for 2 min intervals until the Maximum Voluntary Temperature (MVT; Rubial, 1961; Ballinger *et al.*, 1970) was reached, i.e. the first intense struggles, but see results. The same procedure was used for dead lizards, except that they were heated until their temperatures exceeded the range of MVT's of the live lizards (Table 1). The lizards were killed by cooling to the lethal minimum because it was felt that injection of liquid agents may have altered the physical conditions of heating.

To determine the effect of initial temperature on the head-body temperature gradients, one lizard was heated six times with the same radiant heat load, but from a range of initial temperatures (5–18°C). The lizard was allowed time between consecutive heatings to make good its water loss. Unfortunately, dehydration precluded repeated heating of dead lizards.

Table 1. Results of uniform radiant heating of a restrained *Tiliqua scincoides* specimen.

LIZARD	$T_h^0$	$T_b^0$	$\Delta T_{\max}$	$T_e$	MVT	$T'_h$	$T'_b$
1 alive	4.9	5.1	5.9 (min 10)	27.5 (min 21)	34.1	0.84	1.11
1 alive	8.1	8.0	4.1 (min 8)	23.0 (min 14)	32.4	0.92	1.29
1 dead	7.5	7.5	3.5 (min 4)	22.7 (min 12)	-	0.81	1.13
2 alive	7.5	6.5	5.4 (min 9)	33.4 (min 31)	33.2	0.71	1.01
2 dead	3.9	4.0	4.3 (min 6)	20.7 (min 16)	-	0.67	1.11
3 alive	6.0	6.0	7.3 (min 11)	33.5 (min 34)	33.7	0.64	0.95
3 alive	7.1	7.1	8.4 (min 10)	35.4 (min 36)	34.2	-	-
3 alive	9.4	9.4	6.6 (min 8)	37.3 (min 28)	36.4	-	-
3 alive	11.6	11.6	4.7 (min 8)	34.3 (min 20)	34.9	-	-
3 alive	16.2	16.2	2.8 (min 4)	35.5 (min 21)	34.2	-	-
3 alive	17.8	17.7	2.3 (min 7)	35.3 (min 21)	34.4	-	-
3 dead	5.6	5.6	4.5 (min 8)	23.7 (min 18)	-	0.72	1.15

$T_h^0$ —initial head temperature;  $T_b^0$ —initial body temperature;  $\Delta T_{\max}$ —maximum head-body temperature difference reached;  $T_e$ —value at which head and body temperatures became equal; MVT—temperature at the onset of violent struggling;  $T'_h$ ,  $T'_b$ —average rates of increase in head and body temperatures, respectively. Numbers in parentheses represent minutes of heating before the temperature immediately above was reached. Temperatures—°C; rates of heating estimated subsequent to  $\Delta T_{\max}$  being reached—°C/min.

The relative incident areas of both the head and body were estimated for lizards 2, 3 and 4 by photographing each lizard from the direction of the incoming radiation received during the experiments. The images of the head (including the neck) and body were cut from the prints and separately weighed. The ratio of these weights very nearly equals the ratio of incident areas for both the head and body and thus could be used to compare the amount of radiation falling on both regions. Differences in the curvature of the dorsal surface of the head and body do not alter the respective incident areas, which are normal to the direction of incoming radiation.

The total surface areas of the head and body of lizard 4 were estimated after death by applying a paint-on-peel-off cosmetic coating (Helena Rubenstein 2239D) to the entire surface, and removing it in roughly planar sections when it was completely dry; these were laid on graph paper and the areas estimated by counting the enclosed squares.

A Siemens Cardiomat (model T) was used to monitor the heart rate of lizard 3 during two heatings.

## RESULTS

### 1. A physical basis for head-body temperature gradients

Dead lizards typically heated as shown in Fig. 1A. with substantial head-body temperature differences occurring ( $\Delta T_{\max}$  in Table 1). The head core began heating before the body core, which merely reflects the differing depths of the head and body probes below the surface receiving radiation (0.85 cm and 1.8 cm respectively), with the shallower head probe receiving heat via conduction before the rectal probe. Once this initial effect subsided, body temperature rose in all cases more rapidly than head temperature ( $T'_b > T'_h$

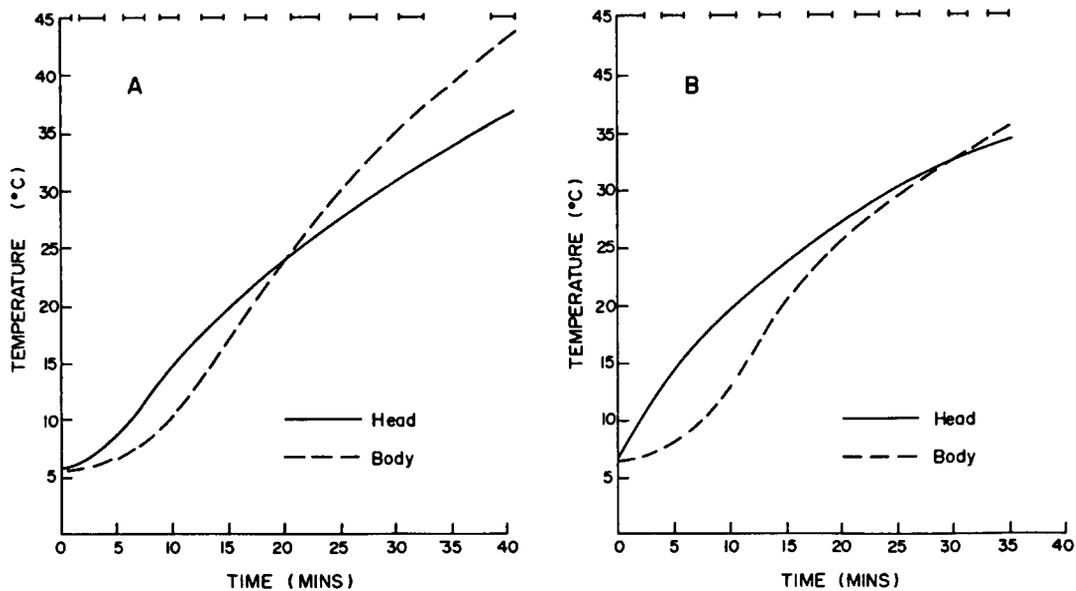


Fig. 1. Head temperature and body temperature plotted against time for a *Tiliqua scincoides* specimen during radiant heating from above. "A" depicts the heating curves for the specimen when dead; "B" when alive. The horizontal bars represent measurement of body temperature.

in Table 1), a result consistent with predictions that can be made from the incident area to mass ratios (Table 2). The body heated faster, principally because it presented a greater incident area per unit mass to the incoming radiation than did the head. The differences in heating rates of the head and body are not fully accounted for by the differences in incident area to mass ( $C \neq D$  in Table 2) which suggests that other physical parameters are also not equivalent for head and body (e.g. absorptivity, emissivity, specific heat, conductivity, convection and evaporation—see Spotila *et al.*, 1972).

Total surface areas of the head and the body of lizard 4 were 58 cm<sup>2</sup> and 227 cm<sup>2</sup> respectively, with respective weights of 38 g and 156 g. Heat uptake during radiant heating depends on the area receiving radiation, whereas heat uptake during convective heating is roughly proportional to total surface area. Quite different heating curves would result if convective heating was used since unlike incident area, total surface area per unit mass was not significantly different for head and body (1.53 cm<sup>2</sup>/g and 1.46 cm<sup>2</sup>/g respectively); this indicated that results of experiments using different heating methods cannot be readily compared.

The curvature of the head and body heating traces (after the initial effect) for both live and dead lizards (Figs. 1A and B) probably reflects a gradual reduction in the temperature difference between the core and the irradiated surfaces, as core temperatures rise; the temperature of the irradiated surfaces equilibrate at a relatively high value soon after heating commences (see Heath, 1964). There is also a continuous decrease in the uptake of heat by the non-irradiated surfaces of the lizard (i.e. convective heat uptake) which when lizard temperature surpasses air temperature, becomes a source of heat loss. This source of heat exchange is dependent on total surface area minus incident area.

## 2. A physiological contribution to head-body temperature gradients

Typically, the pattern of heating in live lizards (Fig. 1B) was considerably different from that in dead ones. Maximum head-body temperature differences were of greater magnitude and occurred after more minutes of heating in the live lizards even though heating was started at the same temperature when they were both alive and dead (Table 1). Transport of heat from the hotter head to the cooler body by the circulatory system must significantly hinder the development of head-body temperature differences in live lizards—despite this, the gradients which developed in live lizards were larger than those which developed in the same lizards when dead. This indicates a physiological contribution to head-body temperature gradients in *T. scincoides*.

Table 2. Values of some physical parameters related to the heating rates of the head and body of *Tiliqua scincoides*.

LIZARD	A	B	C	D	Wt
1	-	-	-	-	197g
2	4.27	6.23	1.46	1.66	258g
3	4.68	5.76	1.23	1.60	205g
4	4.12	5.71	1.39	-	196g

A—the ratio of the mass of the body to the mass of the head; B—the corresponding ratio for incident area; C—the corresponding ratio for incident area to mass; D—the corresponding ratio for observed rates of heating; Wt—total weight.

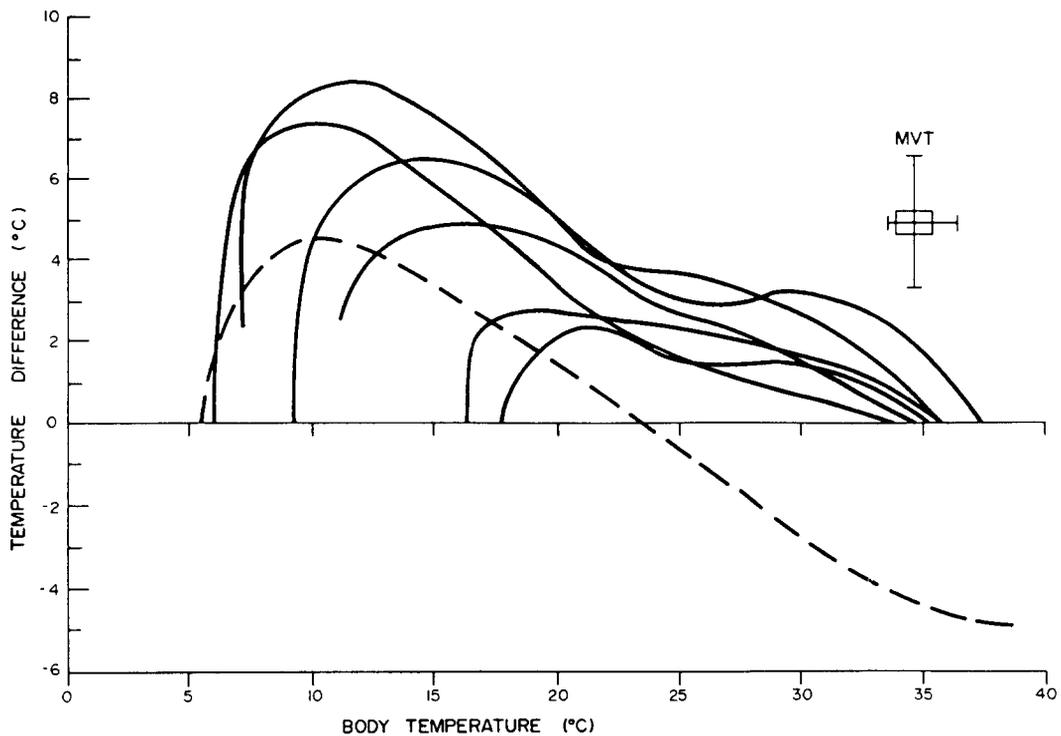


Fig. 2. Head-body temperature difference plotted against body temperature for repetitive heatings of a *Tiliqua scincoides* specimen from a range of initial temperatures. Solid lines represent heating while the lizard was alive; the broken line represents heating of the dead lizard. The vertical bar represents the mean MVT; the horizontal bar, the total range of MVT values and the box encloses one standard deviation of the MVT values.

### 3. Physiological control of head-body temperature gradients

During heating, the lizards remained virtually motionless until an obvious and determined attempt to escape was made. The latter behaviour occurred within a narrow range of temperatures and its onset is taken to indicate the Maximum Voluntary Temperature (MVT) (Ruibal, 1961; Ballinger *et al.*, 1970). Using this estimate, lizard 3 had a mean MVT of 34.6°C (SD = 0.95,  $n = 6$ ).

Figure 2 depicts a series of six trials (lizard 3) each with a different initial temperature. Low initial temperatures generally resulted in large head-body temperature differences, but more importantly, a positive head-body temperature difference was always maintained in the live lizard, but not in the dead one, until a narrow range of internal temperatures was reached. This range ( $\bar{X} = 35.2^\circ\text{C}$ , SD = 1.28; head and body temperatures equalized) overlaps the MVT's for lizard 3 which strongly suggests that in living lizards a mechanism operates to enhance head-body temperature gradients until the MVT is approached. The mechanism does not involve sudden adjustment of heart rate, and it was not possible to determine whether the mechanism resulted in adjustment of head temperature or body temperature or both.

In one heating of lizard 1, the heating pattern of the live lizard was similar to that produced when it was dead, the head being 2.0°C cooler than the body at MVT. The significance of this exception is un-

known, though it may suggest the mechanisms which regulate head-body temperature gradients are not strictly obligatory.

### DISCUSSION

Head-body temperature gradients in reptiles are known to be influenced by exposure of the head and body to different microclimates (De Witt, 1967), and many reptiles make use of this by adopting appropriate behavioural orientation during basking (Heath, 1964; Webb & Johnson, 1972; Hammerson, 1977; Webb, 1978). Physiological control, as opposed to behavioural control of the gradients, is more difficult to demonstrate, nevertheless possible mechanisms have been proposed (Heath, 1964, 1966; Webb, 1972; Crawford *et al.*, 1977). In contrast to these studies, Pough & McFarland (1976) reported that the magnitude of head-body temperature gradients in *Iguana iguana* was consistently greater in dead than in live lizards; they concluded that the gradients could result from physical factors alone and be independent of the animals control. The results of the present study support the contention that physical factors play an important role, but the fact that the gradients in the live *T. scincoides* were consistently larger than those in the dead one indicates a substantial physiological component superimposed on the more basic physical components. Reasons for the lack of agreement between Pough & McFarland's (1976) results and those presented here are unknown but possibly reflect

the different heating methods (see also Voigt & Johnson, 1977) and/or different ratios in the exposed surface areas of the head and body in the two species.

The apparent control of head-body temperature gradients demonstrated by the *T. scincoides* individual which was repeatedly heated from different initial temperatures (Fig. 2) is particularly interesting. It did not seem to be brought about by sudden increases in heart rate (though stroke volume changes could have increased cardiac output), and there were no sudden changes in the heating rates of either the head or body. Eyebulging, which would indicate the use of cephalic shunts (Heath, 1964, 1966), was also not observed so the mechanism of control remains essentially obscure.

Given the range of initial temperatures used in the present study (5–18°C), and the fact that the heating was radiant from above, it may well be that the pattern of heating demonstrated in Fig. 2 characterizes many heliothermic lizards when they are basking. The magnitude of the head-body temperature gradient could represent largely the physical and behavioural characteristics of the lizard within its thermal environment, but coupled also, in many lizard species, with a tendency to enhance the gradient until the MVT is reached.

In general, the results of the present study support the conclusions of Pough & McFarland (1976), that head-body temperature gradients *per se* are of little value to an understanding of reptilian thermoregulation unless presented in the context of the physical factors which have contributed to their occurrence. In addition, however, it has been shown that substantial head-body temperature gradients do occur during heating, which means that considerable error can be introduced in experiments which attempt to precisely relate phenomenon of neural temperature dependence such as Critical Thermal Maximum to body temperature (see Webb & Witten, 1973).

*Acknowledgements*—I wish to thank Tony Thulborn for the guidance he gave during the course of the study. I am also particularly indebted to Grahame Webb who initially stimulated my interest in the topic and later assisted greatly in the formulation of my ideas. Tony Thulborn, Grahame Webb, Chris Drane and Jeff Lang offered many useful manuscript suggestions.

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*Key Word Index*—Thermoregulation; head-body temperature differences; *Tiliqua scincoides*.