

Heating and cooling rates and their effects upon heart rate in the angulate tortoise, *Chersina angulata*

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The heating and cooling rates of adult *Chersina angulata* were investigated to ascertain whether these tortoises can physiologically alter their rates of heat exchange. In addition, heart rates were recorded to provide an insight into the control of heat exchange. *C. angulata* heats significantly faster than it cools. Heart rates increase with increasing body temperature, and for all body temperatures heart rates were greater during heating than during cooling. This suggests that the cardiovascular system plays a role in the heat exchange of the tortoises, but further study is required to completely understand the thermoregulatory process.

Die tempo van verhitting en afkoeling van volwasse *Chersina angulata* is ondersoek om vas te stel of hierdie skilpaaie fisiologiese veranderinge in die tempo van hitteuitruiling teweeg kan bring. Harttempo is ook gemeet om insig in die kontrole van hierdie uitruiling te kry. *C. angulata* verhit vinniger as wat dit afkoel. Harttempo vermeerder met 'n verhoging in liggaaamstemperatuur, en vir alle liggaaamstemperature is harttempo hoër gedurende verhitting as gedurende afkoeling. Dit dui aan dat die kardiiovaskulêre stelsel dalk 'n rol speel in die hitteuitruiling van die skilpaaie, maar verdere studies is nodig om hierdie termoregulatoriese proses volledig te verstaan.

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Many studies have demonstrated that several reptile species have the ability to physiologically alter their rates of heat exchange. Studies of lizards have shown that many species heat faster than they cool (Bartholomew & Tucker 1963, 1964; Bartholomew & Lasiewski 1965; Weathers 1970, 1971; Wilson & Lee 1970; Spellerberg 1972; Claussen & Art 1981; Fraser 1985). Similar results were obtained with crocodiles and alligators (Grigg & Alchin 1976; Smith 1976; Boland & Bell 1980; Chater 1984; Smith, Standora & Robertson 1984). However, the terrapins do not follow this general pattern. It would appear that in water the terrapins heat faster than they cool, but experiments conducted in air give conflicting results (Weathers & White 1971; Spray & May 1972; Lucey 1974). In general the tortoises heat faster than they cool (Weathers & White 1971; Voigt & Johnson 1977; Perrin & Campbell 1981) although faster cooling than heating rates have been recorded for some species (Spray & May 1972; Bethea 1972; Craig 1973).

One of the causative mechanisms implicated in these altered rates of heat exchange is blood flow between the core and periphery of the animal. The heart rate is often used as an indication of cardiovascular change, although it is not a direct measure of blood flow to the periphery (Bartholomew & Tucker 1963, 1964; Bartholomew & Lasiewski 1965; Wilson & Lee 1970; Weathers & White 1971; Bethea 1972; Gatten 1974; Lucey 1974; Voigt 1975; Smith 1976; Adams & deCarvalho 1984). Heart rates have not been measured in any of the South African tortoise species.

Although southern Africa hosts one of the richest terrestrial tortoise populations in the world, very little is known about the thermoregulatory abilities of these animals. Only Craig (1973) and Perrin & Campbell (1981)

have investigated aspects of thermoregulation, but the results obtained are contradictory, and no heart rate measurements were done. The purpose of this study was to investigate the heating and cooling rates of the angulate tortoise, *Chersina angulata*, in the eastern Cape Province, South Africa. In addition, heart rates were measured to provide greater understanding of the thermoregulatory response of these animals to changing ambient temperatures.

Materials and Methods

Two male and two female *C. angulata* were used for the experiments. The animals were housed in an outdoor enclosure until one week before the experiments, all of which were conducted during July and August.

Deep body temperatures were monitored using model X 'Minimitter' radio-transmitters, which have a temperature-dependent pulse frequency. Signals were received on an AM transistor radio. The transmitters used were calibrated in a water bath before and after the experiments. The means of these values were used to construct calibration curves. The transmitters were inserted orally into the stomachs of the tortoises. A muscle relaxant, Flaxedil (gallamine triethiodide), was injected intramuscularly at a dosage of 1,5 mg/kg. Relaxation was immediately overcome after the insertion of the transmitters by injecting the antagonist neostigmine methyl-sulphate (50 µg/kg), preceded by atropine sulphate (25 µg/kg). The tortoises were then kept in an indoor enclosure for one week prior to experimentation to ensure complete recovery. X-ray photographs confirmed that the transmitters remained in the stomachs of the tortoises throughout the experiments. Experimental

animals were starved for two days prior to the experiment to standardize conditions.

Heart rates were obtained by placing two platinum wires through a hole in the plastron to the pericardium. The holes were sealed using dental acrylic. The position of the wires was confirmed using X-ray photography. Only the heart rates of non-active tortoises were used.

The heating and cooling experiments were conducted in a Vötsch Climatic Chamber. The tortoises were exposed to 10°C for approximately 16 h prior to measuring the heating rate, after which the temperature of the chamber was changed to 35°C (this took a maximum of 10 min to stabilize). When the deep body temperatures approximated the ambient temperature, the ambient temperature was changed to 10°C (the temperature again stabilized within 10 min). The tortoise was then cooled for a maximum of 4 h. The tortoise remained within the chamber for the duration of the experiment.

The deep body temperature and heart rate were recorded every 10 min during the first hour of the experiment, and thereafter every 20 min. The tortoises were unrestrained throughout the experiment, and their behaviour was noted at regular intervals. It was not possible to control accurately the humidity in the experimental chamber during the experiments, but it remained lower than the 60% considered critical by Weathers (1972) during heating experiments.

No control experiments on dead animals were performed. Both Craig (1973) and Perrin & Campbell (1981) found that there was no significant difference in the heating and cooling rates of dead *C. angulata*. Any differences in the rate of heating and cooling of live animals would thus indicate some physiological control of heat exchange.

Rates of heating and cooling were calculated by the method of Bartholomew & Tucker (1963), using the formula

$$dT_b/dt = 2,303 S \Delta T$$

where S is the slope of the line relating the natural log of the difference between Ta and Tb to time, and ΔT is the difference between Ta and Tb at the body temperature to be evaluated. In all cases the rate was determined at the midpoint of the temperature range i.e. ΔT = 12,5 °C, because the comparison between heating and cooling rates is only meaningful if ΔT is the same. The results obtained using this method are highly dependent upon the experimental procedure, but it was used in other experiments and repeated in order to enable valid comparisons to be made with previous work.

Heart rates during heating and cooling were compared for each animal using paired sample t tests. The mean heart rates at 3°C intervals were calculated and the values during heating and cooling compared.

Results

For all the heating and cooling experiments, the relationship between ΔT and time was determined by the method of least squares (Figure 1). The slopes of the regression lines were then used to calculate the heating

and cooling rates. It would appear that the heating rates show some inflexions in, for instance, Figure 1b. However, considering the good regression coefficient (r = 0,98) all the data were included in a single regression equation. The body temperature at which the heating rate was determined (22,5°C) was reached within the first hour i.e. before the inflexion point. During the heating experiments the tortoises were initially still, with limbs and head retracted. As the body temperature increased they gradually extended their limbs, and at a body temperature of approximately 29–32°C were active for a short while. Thereafter, as body temperatures increased further, the animals became very still, with all limbs extended, either partially or fully. Conversely, during the cooling experiments, the tortoises very soon became still and tucked their heads and limbs inside the shell. They remained in that position for the duration of the experiments. In all experiments, the regression coefficient indicated a better fit for the cooling than the heating rates.

For all four *C. angulata* the rates of heating are greater than the rates of cooling (Table 1), although variations occur between individuals. *C. angulata* heat between 1,40 and 2,06 times faster than they cool. Mean heating and cooling rates are 0,196 (SE = 0,015) and 0,124 (SE = 0,010) °C / min respectively. The heating and cooling rates are statistically significantly different for

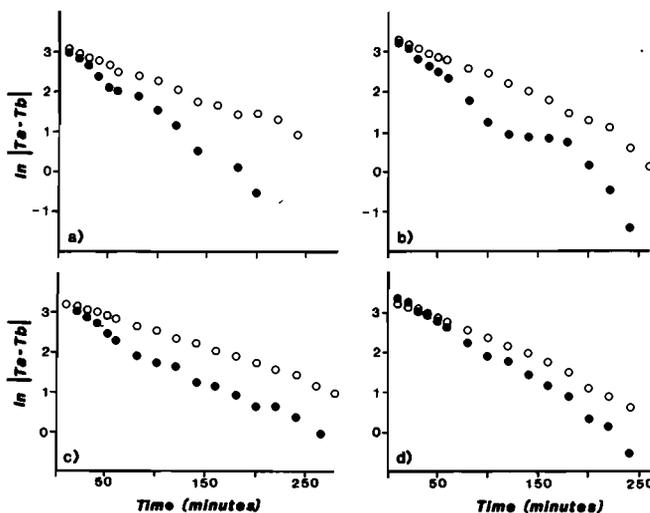


Figure 1 Heating (●) and cooling (○) curves for *C. angulata*. (a) Female, 744g; (b) Male, 787g; (c) Female, 754g; (d) Male, 775g. Tb = body temperature, Ta = ambient temperature (35°C during heating, 10°C during cooling).

Table 1 Heating and cooling rates (°C/min) for *C. angulata*

No.	Sex	Mass (g)	Heating rate	Cooling rate	Ratio (H:C)
1	F	744	0,222	0,108	2,06
2	M	787	0,218	0,145	1,50
3	F	754	0,147	0,101	1,46
4	M	775	0,198	0,141	1,40

each tortoise when compared by analysis of covariance ($p < 0,0001$ in all cases) (Table 2).

Heart rates of *C. angulata* increased with an increase in body temperature, with some fluctuations at body temperatures greater than 30°C during heating experiments (Figure 2). For all body temperatures heart rate was statistically significantly greater during heating than during the cooling experiments (t tests; $p < 0,002$). The minimum rate recorded (at 10°C) was 4 beats/minute, with a maximum heart rate of 53 beats/minute recorded during the heating experiments (Figure 2).

Discussion

C. angulata in this study had a faster rate of heating than of cooling. Craig (1973) reports contradictory findings i.e. greater cooling than heating rates for *C. angulata*, whereas the present results support Perrin & Campbell (1981). However, the rates obtained in this study are approximately 25 and 20 times greater than those of Perrin & Campbell (1981) for the heating and cooling rates respectively (Table 3). The values reported by Craig (1973) are approximately double (for the heating experiments) and four times as high (for the cooling experiments) as in this study (Table 3). Neither author states the method of calculation of the heating and cooling rates reported. It was assumed that the same method as in this study i.e. that of Bartholomew & Tucker (1963), was used in both cases.

Both Craig (1973) and Perrin & Campbell (1981) report an inflexion in the heating curve at body temperatures of 27–32°C. Although the data from these experiments

Table 3 Summary of mean heating and cooling rates (°C/min) for *C. angulata*

Heating rate	Cooling rate	<i>n</i>	Source
0,43	0,49	14	Craig 1973
0,0079	0,0062	3	Perrin and Campbell 1981
0,196	0,124	4	This study

show apparent inflexion points, these are not clearly defined in all the cases. Craig (1973) also reported an inflexion in the cooling slope in 10 out of 14 experiments, although none were obtained either by Perrin & Campbell (1981) or in this study.

C. angulata spends much of its time under cover, and it is rare to find a tortoise foraging more than 10 m from cover. The preferred active body temperature for this species is 28–32°C (Branch 1984). Considering that summer temperatures in this region fluctuate between 17 and 27°C (with occasional peaks of up to 35°C), a physiological mechanism which would increase the heating rate and/or decrease the cooling rate would be of value to attain and retain optimal body temperatures. Heat dissipation when the body temperature exceeds preferred levels is generally behavioural i.e. *C. angulata* retreats to shady areas and assumes a posture similar to that adopted during basking. The retardation of heat loss is important during the night when ambient temperatures are low. The shell is also an effective insulator (Mackay 1964; McGinnis & Voigt 1971) and acts as a shield against heat loss when all the limbs are tucked inside.

The heart rate of *C. angulata* increases with increasing body temperature, and at all body temperatures the rate during heating was significantly greater than that during cooling. Unfortunately, no data on other possible changes in circulation or on metabolic heat production are available for this species. However, the large changes in heart rate would imply that in *C. angulata* the heart rate plays a role in heat exchange. The apparent reduction in heart rate at higher body temperatures is possibly a mechanism to retard further heat gain. It is also possible that the maximum heart rate for the tortoise had been reached.

The desert tortoise, *Gopherus agassizii* was found to heat faster than it cooled in the field, although rates of heating and cooling were equal under laboratory conditions (Voigt 1975). Heart rates were significantly faster during heating than cooling at any particular body temperature, with a sharp increase in heart rate at body temperatures exceeding 27,5°C. A state of continuous vasodilation is suggested as a possible explanation (Voigt 1975).

Faster heating than cooling rates have also been recorded for *Geochelone carbonaria* (Weathers & White 1971), *Gopherus berlandieri* (Voigt & Johnson 1977), *Geochelone pardalis* and *Homopus areolatus* (Perrin & Campbell 1981).

Table 2 Comparison of heating and cooling rates for *C. angulata* using analysis of covariance (Zar 1985)

No.	<i>df</i>	F	<i>p</i>
1	1; 24	67,18	< 0,0001
2	1; 27	30,88	< 0,0001
3	1; 27	61,31	< 0,0001
4	1; 26	81,95	< 0,0001

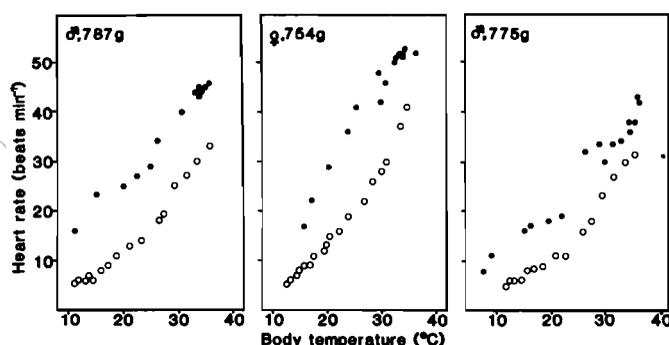


Figure 2 Heart rates of *C. angulata* during heating (●) and cooling (○). Ambient temperatures during heating and cooling were 35 and 10°C respectively.

Spray & May (1972), in contrast, found that *Gopherus polyphemus* and *Terrapene carolina* cooled significantly faster than they heated, with cooling/heating ratios of 1.4 and 2.2 respectively. Conflicting results are reported for the ornate box turtle, *Terrapene ornata*. Significantly faster cooling than heating rates were recorded by Bethea (1972), while no significant differences were found by Adams & deCarvalho (1984). In fact, they state that, in general, the animals warm slightly faster than they cool. However, the experiments of Bethea (1972) were conducted in air, while those of Adams & deCarvalho (1984) were conducted in water.

Heart rates of *T. ornata* increase with increasing body temperature, with no significant differences in the rates recorded during heating and cooling (Bethea 1972; Gatten 1974; Adams & deCarvalho 1984). Cardiovascular changes do not therefore appear to have a significant effect upon the rate of heat exchange in these turtles.

There is no doubt that most reptiles have the ability to alter rates of heat exchange with the environment, using a combination of behavioural and physiological mechanisms. The most important factors affecting these rates in the laboratory are: (i) evaporative water loss, (ii) metabolic heat production, (iii) changes in surface area and (iv) changes in blood flow.

Evaporative water loss has been shown to be of importance, especially in aquatic forms (Bentley & Schmidt-Nielsen 1966). In lizards, metabolic heat can account for many of the differences between heating and cooling rates, particularly at lower temperatures. Unfortunately, few data are available for the tortoises and the importance of this factor is as yet uncertain. Changes in surface areas of experimental animals are not well documented, and in many cases the animals are restrained and unable to retract their limbs. It would seem that for terrestrial tortoises changes in blood flow are very important in heat exchange. Although changes in heart rate have most commonly been used as an indication of cardiovascular change during heating and cooling, an increased heart rate does not necessarily imply increased heating rates. Likewise, changes in the rates of heat exchange can occur without any concomitant effect on heart rate. Differential heating and cooling effects in some species are primarily due to changes in blood flow to the skin and carapace. Changes in stroke volume are also a possibility, although one not yet measured. It is important, therefore, to investigate a combination of these factors simultaneously, before any conclusions can be drawn.

Conclusions

C. angulata exercises some control of its rate of heating and cooling in the laboratory by changing its heart rate and surface area. During heating, the heart rate is elevated and surface area generally increased. While cooling, heart rate is depressed and surface area decreased. Rates of heating are greater than those of cooling, which confirms the findings of Perrin & Campbell (1981). While laboratory experiments cannot duplicate conditions in the field, it can be expected that *C. angulata*

can exercise some control over its rate of heating and cooling, with both physiological and behavioural mechanisms playing a role.

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