Some aspects of thermoregulation in three species of southern African tortoise

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Behavioural and physiological thermoregulation were studied in *Chersina angulata, Homopus areolatus* and *Geochelone pardalis*. Results on behavioural thermoregulation (response to thermal gradient) suggest it to be of greatest significance in *H. areolatus*. Physiological thermoregulation was studied in terms of individual capacities to control thermal conductance. All three species showed definite capacities to thermoregulate by altering conductance. *H. areolatus* appears to possess greatest physiological control of conductance and has a higher maximum preferred temperature than the other two species studied. Large specimens of *G. pardalis* show little physiological control of heat flux and this decreases with increasing size. *C. angulata* has a greater degree of control over conductance than *G. pardalis*. It is concluded that size alone can not explain all the different thermoregulatory characteristics. The study demonstrates the need for a holistic theory of physiology and ecology of thermoregulation in tortoises.

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Gedrags- en fisiologiese hittebeheer is bestudeer in *Chersina angulata, Homopus areolatus* en *Geochelone pardalis*. Resultate oor gedrags-hittebeheer (reaksie tot 'n hittegradient) dui aan dat dit van die grootste belang is by *H. areolatus*. Fisiologiese hittebeheer is bestudeer in terme van individuele vermoëns om hittegeleiding te beheer. Al drie spesies wat bestudeer is, het besliste vermoëns getoon om fisiologies hittebeheer toe te pas deur geleiding te verander. Dit kom voor asof *H. areolatus* die beste fisiologiese beheer oor geleiding het en het 'n hoër maksimum verkose temperatuur as die ander twee spesies wat bestudeer is. Groot voorbeelde van *G. pardalis* toon weinig fisiologiese beheer oor hittewisseling en dit neem af na mate die grootte toeneem. *C. angulata* het 'n groter mate van beheer oor geleiding as *G. pardalis*. Daar word afgelei dat grootte alleen nie al die verskillende hittebeherende kenmerke kan verklaar nie. Die studie toon duidelik die behoefte aan 'n holistiese teorie van die fisiologie en ekologie van hittebeheer by skilpaaie.

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Many reptiles are known to possess varying capacities to maintain temperature differentials between their bodies and the environment. Reptiles, having the characteristics of low metabolic rates and high thermal conductances (McNab 1978), must attain thermal constancy by non-endothermic mechanisms. The thermoregulatory capacities of terrestrial chelonians have received surprisingly little attention (Cloudesley-Thompson 1968, 1970, 1974). A capacity to alter thermal conductance and hence control rates of heat flux is a physiological mechanism of thermoregulation present in a number of terrestrial testudinids (Weathers & White 1971, Bethea 1972). Thermoregulation by behavioural means has been reported in a number of tortoise species (McGinnis & Voight 1971, Voight & Johnson 1977). In addition the phenomenon of large body size is recognized as an important factor in the maintenance of thermal constancy in ectothermic organisms (McNab & Auffenberg 1976).

Studies of thermoregulation in tortoises have largely been restricted to New World species, but this preliminary investigation considers three species which co-exist in the Eastern Cape of South Africa. They are the small, areolate tortoise *Homopus areolatus* (Thunberg 1787), the angulate tortoise *Chersina angulata* (Schweigger 1812), and the large mountain tortoise *Geochelone pardalis* (Bell 1828). Evidence for thermoregulation in *C. angulata* has previously been reported by Craig (1973).

Methods and Material

Care of Tortoises

Specimens were collected from the Andries Vosloo Kudu Reserve 30 km northeast of Grahamstown, (33° 8′S; 26° 39′E), and housed in an outdoor enclosure until required, whereupon they were transferred to a constant environment room for a period of at least two weeks prior to experimentation. The constant environment room was maintained at a temperature of approximately 25 °C during periods of light and 20 °C during darkness, (14L:10D). Humidity was uncontrolled and varied between 30% and 90%. Temperature and humidity were monitored continuously with a thermohygrograph. The tortoises were housed in a large arena with straw for cover. All tortoises were observed to eat grasses, vegetables and *Opuntia* and water was always available. Table 1 gives details of the specimens studied.

Table 1 Number, mass, and sex of the tortoises studied

G. pardalis					
Number	Gp1	Gp2	Gp3	Gp4	Gp5
Mass (kg)	11,105	6,930	1,585	0,752	0,695
Sex	Female	Male	Male	Female	Female
C. angulata					
Number	Ca1	Ca2	Ca3		
Mass (g)	914	855	890		
Sex	Male	Male	Male		
H. areolatus					
Number	Ha1	Ha2	Ha3	Ha4	
Mass (g)	212	79	240	71	
Sex	Female	Male	Female	Male	

Behaviour experiments

The experimental procedure used involved observing the animal's response to a thermal gradient. A box was constructed 180 cm by 60 cm with a depth of 33 cm (Fig. 1). It was lined with 2-cm thick polystyrene sheeting for insulation but was open at the top. A 2-kW electric heater at one end was used as a heat source, providing a temperature gradient of approximately 15 °C to 60 °C when operated in a constant environment room set at 10 °C. Divisions 20 cm apart were marked along the length of the gradient. A sand substrate, partially covered with straw, was used.

Tortoises were equilibrated at 10 °C for approximately 10 h, and placed in the gradient at position 5 (Fig. 1) where the temperature was 25 °C. The positions of the tortoises in the thermal gradient apparatus were recorded every 15 min. Body temperatures were recorded at 30-min intervals, or more frequently, during the course of the experiment. Three specimens of each species were tested individually in the thermal gradient for at least six trials. The large size of specimens Gp1 and Gp2 precluded their testing in this manner.

The maximum body temperature recorded for each tortoise during this experiment was used as an estimate of the maximum preferred body temperature. The total distance moved by the tortoise in moving towards and away from the heat source was used as an indicator of the extent of its behavioural thermoregulation.

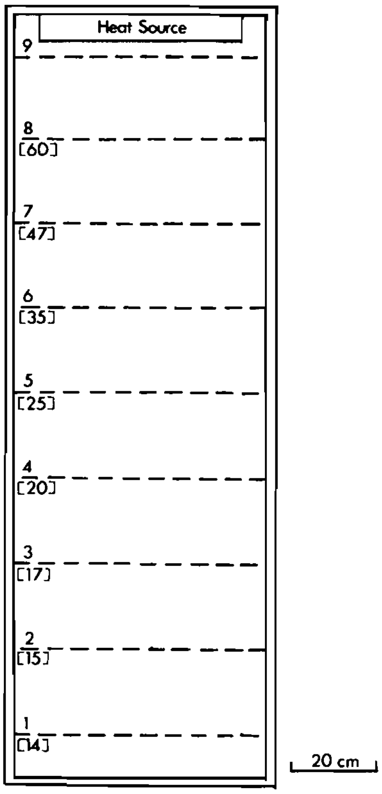

Fig. 1 Plan of the thermal gradient apparatus. The heat source is a 2-kW electric heater. Numbers in parenthesis indicate approximate air temperature (°C) at each position of the thermal gradient.

Temperature monitoring apparatus

Deep body temperatures of *G. pardalis* and *C. angulata* were monitored using a model X 'Minimitter' radio transmitter. Its pulse rate is determined by a temperature sensitive element in its circuit, and was received on an AM transistor radio. The power source was provided by a 1,4-volt mercury cell battery. The size of the transmitter plus battery was 9 mm × 15 mm and it weighed 1,2 g. The transmitters used were initially calibrated in a water bath against a standard mercury thermometer (accuracy 0,1 °C) and stop-watch.

On the completion of all experiments the transmitters were recalibrated. The means of these values were used to construct calibration curves, which provided a realistic accuracy to 0,5 °C. For protection the transmitters were covered in paraffin wax before being inserted orally into the tortoises. An anaesthetic, Sagatal (pentobarbitone sodium), was injected intramuscularly at a dosage of 15 mg/kg. No experiments were performed on the tortoises for at least five days. Postmortems revealed that in all specimens the transmitter had remained in the stomach during the experimental period.

As the transmitters were too large to use with *H. areolatus*, body temperatures were recorded using thermistors inserted into the cloaca when a reading was required. Thermistors were calibrated in a water bath against a standard mercury thermometer (accuracy 0,1 °C) before and after all experimentation and calibration curves were constructed.

Heating and cooling experiments

The capacity of tortoises to thermoregulate physiologically was determined using a standard method for reptiles (Johnson, Voight & Smith 1978, Ellis & Ross 1978).

Tortoises were cooled in a constant environment room at 10 °C for approximately 10 h prior to measuring heating rates, after which they were rapidly transferred to a second constant environment room set at approximately 35 °C. The increase in body temperature was monitored regularly.

For *H. areolatus* temperatures were recorded at 10-min intervals initially with later readings every 15 or 30 min. For the two larger species, initial readings every 15 min with later readings every 30 min were found to be sufficient. When the body temperature approximated the ambient temperature, the tortoises were returned to the constant environment room set at approximately 10 °C. Changes in body temperature for the cooling experiments were recorded in the same manner as for the heating experiments. Tortoises were unrestrained during heating and cooling experiments.

The ambient temperatures of the experimental rooms were recorded accurately (0,1 °C). The mean of these regular values was taken as the ambient temperature for the analysis of data (maximum range 2,5 °C). It was not possible to control the humidity of experimental rooms.

The relative humidity for all heating experiments ranged between 25% to 35%, with the range of relative humidity for cooling experiments being 85% to 90%. There were no significant fluctuations in humidity during the course of each experiment.

To serve as controls, tortoises were killed (by injection of 10 mg/kg suxamethonium chloride) on the completion of all experiments and the heating and cooling experiments repeated.

Results

Behaviour experiments

When introduced into the thermal gradient, specimens of different species consistently showed characteristic patterns of activity. *H. areolatus* normally adopted a basking posture with head and legs extended, or moved towards the heat source. Patterns of activity involved irregular movements before the tortoise buried itself in the straw at the coolest end of the thermal gradient. At this point experiments were terminated. *C. angulata* and *G. pardalis* particularly showed little tendency to move towards the heat source or adopt a basking posture; the only consistent movement was to the cooler end of the thermal gradient.

Table 2 shows the mean values for the total distance moved and the maximum body temperature reached in the thermal gradient over all trials for all specimens of the three species studied. The total distance moved is given in terms of the distances marked in the thermal gradient (Fig. 1); the distance between the two divisions being one unit. Figure 2 is a graphical representation of the movement in the thermal gradient for one trial of Gp4 and Ha2. In these particular trials movement was monitored continuously over the experimental period. The results in Table 2 however are all derived from trials in which the position of the tortoises was recorded every 15 min.

Table 2 Means of maximum body temperatures and distances moved in response to the thermal gradient. (Error estimates have been excluded)

	G. pardalis	*C. angulata*	*H. areolatus*
Maximum body temperature (°C) ($n = 18$)	28,7	29,3	34,8
Distance moved ($n = 21$)	5,2	6,3	16,4

Distance moved is in units marked on the thermal gradient apparatus. (n = Number of trials X number of individuals of each species.)

While this would not affect the validity of results for patterns of movement as shown by *G. pardalis*, it would result in lower estimates of the responses of *H. areolatus*.

A two-level nested analysis of variance (Parker 1973) showed a significant ($P < 0,01$) difference between species for both maximum body temperature and total distance moved. Because the mean value for total distance moved by *H. areolatus* is somewhat greater than that of *C. angulata* and *G. pardalis*, the differences between pairs of means was tested using the method of least significant range for *a posteriori* comparisons (Sokal & Rohlf 1969). The differences in mean values between *C. angulata* and *H. areolatus* and between *G. pardalis* and *H. areolatus* are significant at the 5% level. The difference between the mean values of *C. angulata* and *G. pardalis* are, however, not significant at this level.

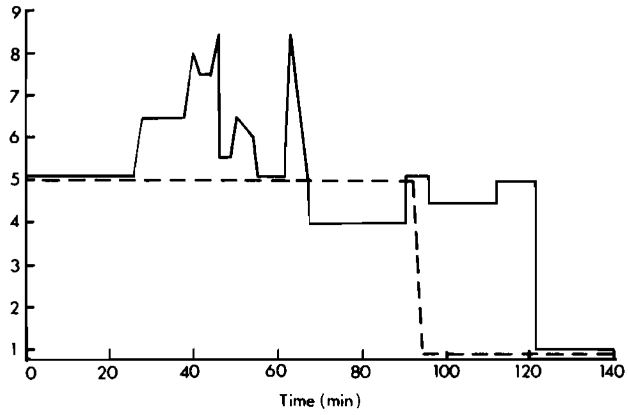

Fig. 2 Patterns of movement in the thermal gradient of Gp4 (dashed line) and Ha2 (solid line). Position is the distance along the length of the thermal gradient.

Hence for comparative purposes, recording the position of tortoises at intervals of 15 min has little effect on the overall results.

Heating and cooling experiments

The heat loss or gain of an inert body shows an exponential relationship with time. The relationship is linear if $\log(T_a - T_b)$ (T_a = ambient temperature, T_b = body temperature) is plotted against time, with rates of heating and cooling (*i.e.* the gradients) being equal.

Hence a plot of $\log(T_a - T_b)$ against time for dead tortoises should be linear with equal rates of heating and cooling. Any departure from this relationship in live tortoises will indicate physiological thermoregulation by altering thermal conductance.

Results for all tortoises were initially plotted in this manner. Where the plots were linear, regression lines were fitted by the method of least squares. For rates that showed a definite inflexion, regression lines were fitted independently to the sets of values on either side of the inflexion.

a) G. pardalis

Table 3 gives the results for *G. pardalis* and Figure 3 demonstrates the exponential relationship of body temperature with time for Gp2 when dead. The ratio of heating rates to cooling rates of the dead specimens all approximate unity (range 1,02 – 1,11; mean value 1,06, n = 5) as expected if heat exchange is entirely passive.

The ratios of heating rate to cooling rate in live specimens are all greater than unity, (Fig. 4). Using the heating and cooling rates prior to the inflexion (for specimens Gp4 and Gp3) the mean heating/cooling ratio value for the five specimens studied is 1,46. Hence on average live specimens of *G. pardalis* cool 68% slower than they heat.

Whether this is due to an active enhancement of heat influx or an active retardation of heat efflux, or both, can be determined by comparing heating and cooling rates of

Table 3 Heating and cooling rates (°C/min) for *G. pardalis*, *C. angulata* and *H. areolatus* when alive and dead

	Dead		Alive					
			Heating	Cooling	Heating	Cooling	Inflexion temperature (°C)	
	Heating	Cooling	(Before inflexion)		(After inflexion)		Heating	Cooling
G. pardalis								
Gp1	2,40	2,36	2,97	2,65	–	–	–	–
Gp2	3,61	3,44	4,21	2,91	–	–	–	–
Gp3	6,04	6,06	6,94	3,66	–	1,89	20,0	–
Gp4	10,70	9,65	12,17	7,03	8,11	–	35,0	–
Gp5	11,58	11,03	11,93	10,47	–	–	–	–
C. angulata								
Ca1	10,28	10,79	8,57	6,19	2,86	–	30,0	–
Ca2	12,78	12,51	7,13	5,19	3,50	–	31,0	–
Ca3	12,32	11,62	8,05	5,63	3,21	–	30,5	–
H. areolatus								
Ha1	26,71	16,52	21,41	21,05	5,23	8,11	34,5	14,5
Ha2	41,80	24,41	28,54	15,84	–	3,03	–	12,0
Ha3	24,44	16,74	20,41	18,29	3,89	6,74	29,5	16,0
Ha4	35,95	40,42	33,08	23,54	28,25	10,72	31,5	13,5

All values are negative and are shown 10^3 greater than actual values.

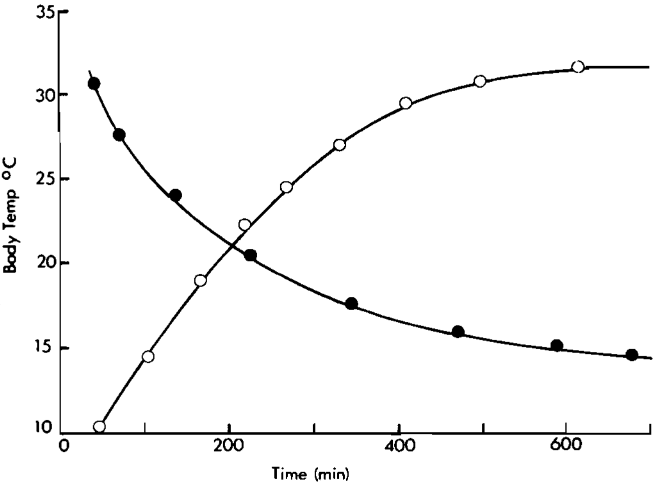

Fig. 3 Body temperatures during heating (open points) and cooling (solid points) for specimen Gp2 when dead. Ambient temperature when heating 31,1 °C, and for cooling 9,2 °C.

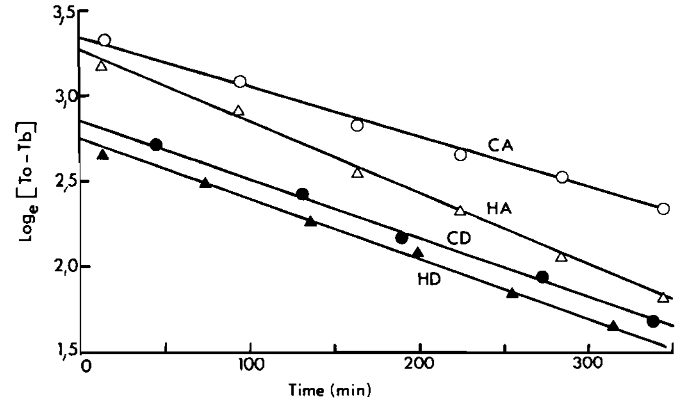

Fig. 4 Heating and cooling curves for Gp2. Curves are arranged for greatest clarity, and intercepts with the ordinate are of no significance. CA = cooling alive; HA = heating alive; CD = cooling dead; HD = heating dead.

live specimens with those of tortoises when dead. All tortoises heated faster alive than dead (mean value, heating rate alive/heating rate dead = 1,16) indicating a capacity to augment heat influx (Fig. 4). In addition four of the five specimens cooled at a slower rate when alive than when dead (mean value, cooling rate alive/cooling rate dead = 0,82); meaning that active retardation of heat efflux is also important in this species (Fig. 4).

Two specimens showed definite inflexions in their heating and cooling curves. The cooling curve of Gp3 shows an inflexion indicating a further retardation of heat loss below a body temperature of 20 °C (Fig. 5). The heating curve of Gp4 shows an inflexion indicating a decreased rate of heat influx above 35 °C (Fig. 6). Before the inflexion the heating rate is greater than when dead, after the inflexion the heating rate is less than when dead. This suggests that *G. pardalis* is able to both enhance and retard heating rates when necessary.

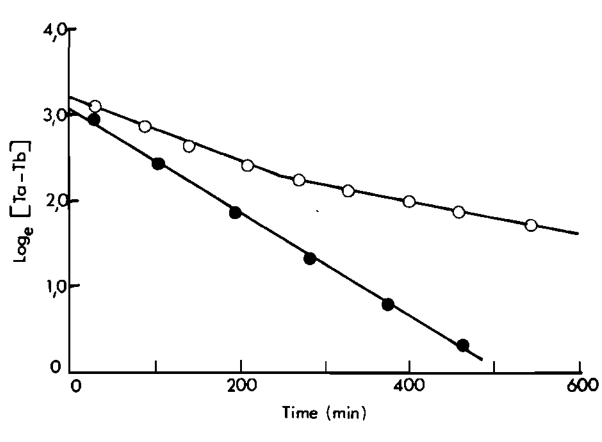

Fig. 5 Cooling curves for Gp3 when dead (solid points) and alive (open points).

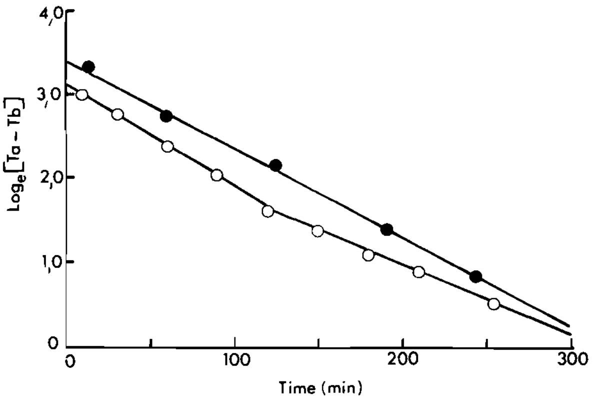

Fig. 6 Heating curves for Gp4 when dead (solid points) and alive (open points).

b) *C. angulata*

Table 3 shows the results for *C. angulata*. In all three specimens an inflexion occurs in the heating curve at a mean body temperature of 30,5 °C. For all specimens the heating rate prior to the inflexion is greater than the cooling rate, but is less than the heating rate of dead tortoises (Fig. 7). This means that unlike *G. pardalis, C. angulata* retards heat uptake; heat influx being further reduced after the inflexion.

All three specimens cooled at a faster rate when dead than alive indicating a capacity to retard heat loss.

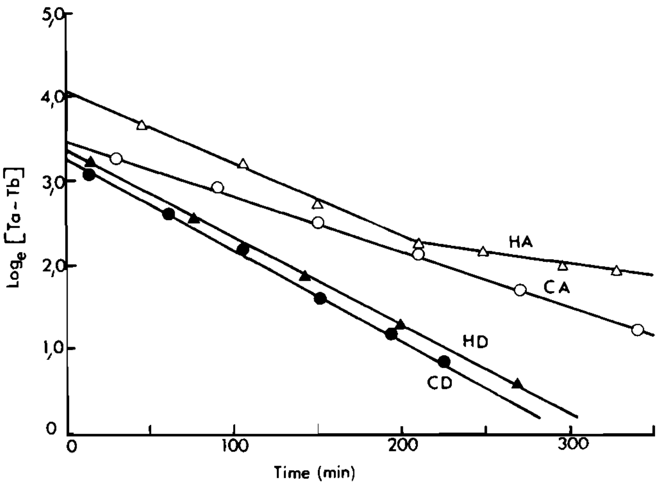

Fig. 7 Heating and cooling curves for Ca1. Curves are arranged for greatest clarity, and intercepts with the ordinate are of no significance. CA = cooling alive; HA = heating alive; CD = cooling dead; HD = heating dead.

c) *H. areolatus*

Table 3 gives the heating and cooling rates of *H. areolatus*. The heating to cooling ratios of dead specimens vary considerably from unity (mean value 1,42) suggesting any further comparisons of heating and cooling rates to be of limited value. Even assuming the rates of live tortoises to be indicative of the animal's physiology, few conclusions can be drawn as there are no base values with which to compare these values. Hence it is not possible to determine whether differences in rates are due to thermoregulatory capacities or to technical artifact. This clearly demonstrates the importance of using dead animals as controls.

Of significance however is the departure from linearity in the cooling curves of all four specimens indicating a reduction in the rate of heat loss at lower body temperature. A similar departure from linearity occurs in the heating curves of three of the four specimens demonstrating a decreased rate of heat influx at higher body temperatures. Specimen Ha2 is the only specimen to show a constant heating rate over the entire body temperature range ($r < -0,99$). While some heating and cooling curves show a definite inflexion, rates of temperature change of other specimens show a curved relationship with time (Fig. 8). For curved heating and cooling plots regression lines were fitted as if an inflexion was present. The mean body temperatures at which inflexions occurred during heating and cooling were 31,8 °C and 14,0 °C respectively.

Results suggest active retardation of heat gain in all specimens. Cooling rates of specimens Ha1 and Ha3 are actively enhanced at high body temperatures and retarded at lower body temperatures. Comparisons for Ha2 and Ha4 demonstrate greater rates of cooling when dead than alive indicating that cooling is retarded through the entire body temperature range.

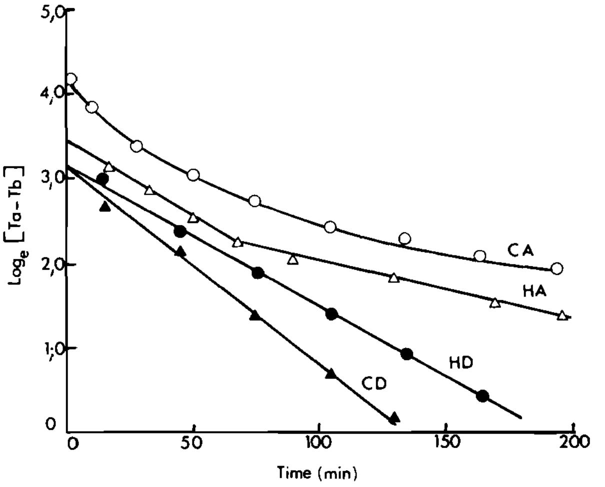

Fig. 8 Heating and cooling curves for Ha4. Curves are arranged for greatest clarity, and intercepts with the ordinate are of no significance. CA = cooling alive; HA = heating alive; CD = cooling dead; HD = heating dead.

The effect of large size

Large body size contributes to thermal constancy as the decreased surface area to volume ratio effectively decreases thermal conductance (Ellis & Ross 1978). This is demonstrated by the low rates of heat exchange of large tortoises. The relationship given by the regression of body mass and cooling rates for the five specimens of *G. pardalis* when alive is described by the equation,

$°C/min = 0,12M^{-0,421}$, where M = mass in g.

This can be stated alternatively as,

$\log (°C/min) = -0,421 \log M - 0,90$ ($r < 0,90$)
(Fig. 9).

However, the corresponding relationship for dead tortoises describes the effect of mass on cooling rates without the effects of control of conductance, and is represented by,

$°C/min = 0,12M^{-0,512}$, where M = mass in g ($r < -0,99$) (Fig. 9).

The exponent of this relationship is smaller than that expected ($-0,33$) if the cooling rate is determined only by surface area-volume relations and all tortoises have similar proportions (Bartholomew & Lasiewski 1965).

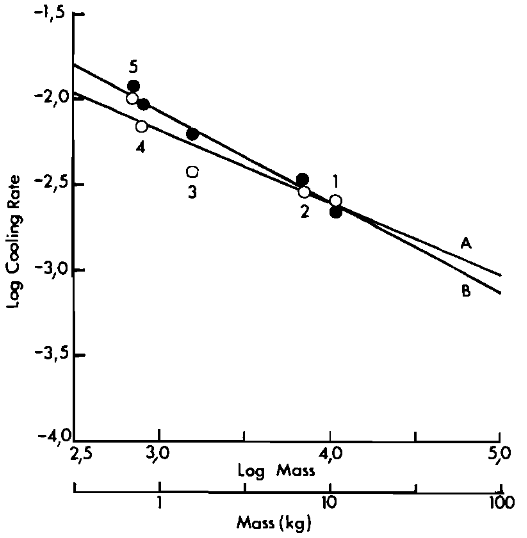

Fig. 9 Regression lines for mass and cooling rate when alive (line A), and mass and cooling rate when dead (line B) for *G. pardalis*. The number below each pair of points indicates the specimen. Open points are cooling rates when alive, solid points when dead.

Discussion

Behaviour

Few workers have attempted to compare experimentally the significance of thermoregulatory behaviour between different species. This is partly because many considerations of reptilian thermoregulation are based on the assumption that thermoregulation through behavioural means is of primary importance in most reptile species, and that thermoregulation is normally beneficial (Huey & Slatkin 1976).

Recent studies on lizards indicate that some species are frequently passive to ambient conditions and that behavioural thermoregulation in terms of costs involved and benefits gained is not always explicable in terms of energetics (Huey & Slatkin 1976). Thermoregulatory behaviour patterns utilized by testudinids include: moving between sun and shade and hot and cold environments, which alters heat flux (Voight & Johnson 1977); modifying postures which alter surface areas exposed to heat sources and sinks (Voight & Johnson 1976); and regulating activity times (Bourn 1976). While all these factors should be considered when evaluating a species' tendency to thermoregulate behaviourally, experiments to test the extent of behaviour patterns are difficult to conduct.

Movement in response to heat was considered in this study because, first, of the three thermoregulatory behaviour patterns mentioned, this is the most readily controlled under laboratory conditions, and secondly, this factor could conceivably be of importance to tortoises. Movement between warm and cool regions necessitates a significant expenditure of energy (Pianka & Pianka 1970) an important consideration for tortoises as large as *G. pardalis*. Such activity could increase susceptibility to predation (Pianka & Pianka 1970) which might be important in small species such as *H. areolatus*.

All experiments using thermal gradients must be interpreted carefully. Artificial thermal gradients provide a steepness of temperature range unlike anything to be encountered in the field (Cowles & Bogert 1944). Cloudesley-Thompson (1970) found basking behaviour in *Testudo (Geochelone) sulcata* to be temperature-mediated rather than light-mediated. Under field conditions high light intensities might normally be associated with warm temperatures and low light intensities as in shaded regions with low temperatures.

That levels of light intensity could be important is suggested by specimens of *G. pardalis* and *C. angulata* that tended to seek out the darkest regions of the experimental room when body temperatures became high. Basking behaviour was most apparent in *H. areolatus*. Craig (1971) found this behaviour pattern to be common in *G. pardalis* but infrequent in *C. angulata*.

During the behaviour experiments, maximum body temperature was recorded for each tortoise. It was not possible to measure the mean preferred body temperature or the lower limit of preferred body temperature range due to short activity times (< 4 h) of the tortoises, and the lack of response shown by *G. pardalis* and *C. angulata*. The most frequent movement of *G. pardalis* was a direct movement to the coolest region of the gradient. The upper limit was greatest in *H. areolatus* (34,8 °C) with lower values for *G. pardalis* (28,7 °C) and *C. angulata* (29,3 °C). While this suggests that *H. areolatus* is likely to be more active at higher temperatures than the other two species, a number of studies (De Witt 1967, Pianka & Pianka 1970) have found little correlation between (laboratory determined) preferred body temperatures and actual field (eccritic) temperatures. Short term climatic conditions might prevent a reptile reaching its preferred body temperature range, yet activities such as feeding and predator avoidance must continue.

Consequently the actual body temperatures at which a reptile is active in the field do not necessarily match those determined in a thermal gradient (Cowles & Bogert 1944), eccritic temperatures being a compromise between physiology and ecological reality (Huey & Slatkin 1976). The results presented here suggest greater importance of behavioural mechanisms of thermoregulation in *H. areolatus* than in either *G. pardalis* or *C. angulata*.

Physiology

The purpose of the heating and cooling experiments was to determine if physiological control of conductance is an important thermoregulatory mechanism in the three species of tortoise studied. All three species showed some control of conductance by retarding and/or enhancing overall heating and cooling rates, and by differentially altering rates of heat exchange during heating and cooling.

The humidity in the experimental rooms could not be controlled. Although the humidity remained constant during the course of each experiment, the relative humidity in the heating experiments (25% – 35%) was considerably less than the relative humidity during the cooling experiments (85% – 90%). Weathers (1972) tested the effect of humidity on heating and cooling rates of lizards and found relative humidities greater than 60% to significantly increase heating rates and cause deviation from linear relationships with time. Cooling rates, however, were not affected. The humidity level during all the heating experiments was lower than that considered critical by Weathers (1972).

The comparatively large surface area to volume ratio of *H. areolatus* could mean that heating rate depression through evaporative water loss might be significant. Sturbaum & Riedesel (1977) have proposed the carapace of testudinids to be a significant region of water loss. In addition, the greater activity of *H. areolatus* during the heating experiments and the inability of this species to retract completely within its shell (Loveridge & Williams 1957) means a proportionally larger surface area is exposed for potential evaporative water loss than in either *C. angulata* or *G. pardalis.*

G. pardalis was found to enhance heat uptake and retard heat loss, with differential rates of heat exchange apparent in only two specimens. An inflexion occurred in the cooling curve of only one specimen of *G. pardalis*; Craig (1971) found a similar inconsistency in the cooling curves of *C. angulata. C. angulata* differentially retards heat influx with increasing body temperature; Craig (1973) similarly found an inflexion to occur at 27 – 32 °C. However, unlike the results of this study, Craig (1973) found the heating rates of live *C. angulata* to be less than the cooling rates. *H. areolatus* was the only species to consistently show differential rates of heat exchange during both heating and cooling. The irregularities in the results of the control experiments for *H. areolatus* however meant that limited conclusions could be drawn. The reasons for these irregularities are possibly explained by the small size and hence comparatively large surface area to volume ratio of *H. areolatus.*

Few terrestrial chelonians have been found to enhance heat influx actively, a characteristic of most other reptiles (Voight & Johnson 1977). Frequent exposure to temperatures that could invoke heat stress has been proposed as the reason for *Chersina angulata* (Craig 1973), *Terrapene ornata* (Bethea 1972), *Terrapene carolina* and *Gopherus polyphemus* (Spray & May 1972) to actively retard heating. Previous to this study *Geochelone carbonaria* (Weathers & White 1971) and *Gopherus berlandieri* (Voight & Johnson 1977) were the only species studied to show the more typical reptilian characteristic of having a faster heating than cooling rate.

The ratio of the heating rate to the cooling rate tends to obscure rather than elucidate the physiological capacities of a reptile to alter thermal conductance. Weathers & White (1971) concluded that the turtle species they studied heated on average 25% faster than they cooled. However, unless compared with dead animals it is not possible to state whether this is due to active enhancement of heating, active retardation of cooling, or due to both factors. Such ratios ignore the significance of any inflexions that might be present in the rate curves. The importance of this is shown in the heating curves of specimen Gp4 (Fig. 6). The heating rate when alive is greater than the heating rate when dead before the inflexion, but the heating rate when dead is greater after the inflexion. This suggests a capacity to both enhance and retard heat gain. To present such data in the form of a heating to cooling ratio would obscure this possibly significant feature.

The experiments of this study examined control over conductance which is only one mechanism by which reptiles can exert physiological thermoregulation. Other mechanisms include: changes in radiative properties of the integument (Louw, Young & Bligh 1976), although colour change is unknown in chelonians except for breeding colour changes in *Geochelone travancorica* (Auffenberg 1964); changes in rates of ventilation, although this effect appears to be negligible in lizards (Bartholomew & Tucker 1963); altered evaporation rates, which are known to be of significance at high temperatures in *Testudo (Geochelone) sulcata* (Cloudsley-Thompson 1970), and changes in metabolic rate. Bartholomew, Tucker & Lee (1965) found that the difference in heating and cooling rates of the lizard *Tiliqua scinoides* could be accounted for entirely by metabolic heat production. However heat production due to metabolism will tend to increase the rate of heating and decrease the rate of cooling (Louw *et al.* 1976). Thus metabolism could be a factor in the apparent differences in heating and cooling rates in *G. pardalis* but not in *C. angulata* since in this species metabolic heat, if sufficiently high, would tend to decrease the difference between heating and cooling rates.

The effect of large size

It is of interest to compare the mass-cooling rate regression for dead and living *G. pardalis*. For a tortoise of any given mass, the difference between the cooling rates when dead and alive is due to physiologically altered thermal conductance. For *G. pardalis* the two regression lines intersected at a mass of approximately 11,1 kg due to actively retarding heat loss, this effect increasing with decreasing mass. Hypothetically, a tortoise of mass 11,1 kg should cool with equal rates when dead and alive; that is, it should show no physiological retardation of heat loss. The largest specimen tested (Gp1) had a mass of 11,1 kg and as predicted shows almost equal rates of cooling when dead and alive (cooling alive/cooling dead = 1,01). If it is realistic to extrapolate the regression lines past the point of intersection, it would mean tortoises of mass greater than 11,1 kg should actively enhance cooling; the degree of this enhancement increasing with size. This implies that specimens of *G. pardalis* over this size might face problems of overheating.

Conclusion

All three tortoise species studied showed definite capacities to thermoregulate physiologically by altering conductance. *H. areolatus* probably shows greater thermoregulatory capacities through behavioural means than do either *G. pardalis* or *C. angulata. H. areolatus* also appears to possess greater physiological control of conductance and has a higher maximum preferred temperature than the other two species. Large specimens of *G. pardalis* show little physiological control of heat flux, this decreasing with increasing size, while it is possible that *C. angulata* shows little reliance on behavioural mechanisms to enhance heating. The capacity of *H. areolatus* to control heat exchange differentially when both heating and cooling might suggest greater physiological control of conductance than in the other species. In addition, the tendency of some of the heating and cooling curves of *H. areolatus* to show a curved rather than a simple inflected linear relationship, could mean a more sensitive mechanism for controlling conductance. The presence of inflexions in all heating curves but not in the cooling curves of *C. angulata* suggests a lesser degree of control of conductance than in *H. areolatus* but greater than in *G. pardalis.*

Interpretation

Three species of tortoises that occur sympatrically have been found to have different thermoregulatory mechanisms, and hence it appears that inter-specific differences in physiological and behavioural thermoregulation can not be explained by climatic factors alone.

If a single ancestral stock of tortoises colonized southern Africa, differences in thermoregulation strategies could be due to differential habitat selection, local adaptation, and hence allopatric speciation. This idea is not negated by current sympatric distributions, which might have occurred subsequent to speciation. Alternatively the single ancestral stock may always have been sympatric, in which case size differentiation (character divergence) would have resulted from competition, *e.g.* for food of different size, nutrient content, or availability within the single habitat, to promote speciation. The different sizes of the species would then necessitate different thermoregulatory strategies.

Geographical and seasonal changes in climate in southern Africa necessitate some thermoregulatory capacity in tortoises. Many environmental variables could influence body size of a tortoise, and size would determine its thermoregulatory strategy. Large species with great thermal inertia might be subjected to less selective pressure for thermoregulatory mechanisms. They would be limited by particularly high temperatures and unsuited to exploiting heat influx by behavioural means because of their limited mobility. Physiological thermoregulation would be favoured over behavioural mechanisms owing to the high energy costs of movement in large-sized species. The higher incidence of predation on small (adult) tortoises, and timely basking behaviour, could lead also to selection for physiological thermoregulation in these species. Behavioural thermoregulation utilizes 'free' energy but is time-wasting.

The evolution of an optimal size for a tortoise species in a given habitat is undoubtedly controlled by many factors, and even from a thermoregulatory standpoint, several conflicting points emerge. Behavioural responses of an organism to environmental change may be very rapid but internal reorganisations of genetic material take longer. Any response of the organism involves some commitment of the organism's resources, including time and energy. The response to an environmental change may include gene frequency changes in the population and these gene frequency changes may themselves alter the response of the population to a further selective pressure. This is the 'genetic homeostasis' phenomenon of Lerner (1954). It may be expected for example, that strong selection for a specific anatomical feature may result in a lowering of overall physiological flexibility or that selection for a specific behavioural feature may be accompanied by morphological changes (Slobodkin 1968).

This study clearly demonstrates the need for a holistic theory of the ecology of thermoregulation. Huey & Slatkin (1976) provide such a model but it is restricted to a cost-benefit analysis of different lizard species' tendencies to thermoregulate behaviourally. An alternative to this would be a theory emphasising the different mechanisms by which reptiles can achieve thermal independence and under what environmental situations the different strategies should be employed.

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