

THE METABOLIC RESPONSES OF ADULT ANGULATE TORTOISE (*CHERSINA ANGULATA*) TO VARYING AMBIENT TEMPERATURES

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ABSTRACT

Various physiological processes of ectotherms increase with increasing temperature. The effects of varying ambient temperature and gender on the metabolic rate (MR) of adult *Chersina angulata* were investigated. The tortoises were acclimated to $22 \pm 1^\circ\text{C}$ and a 14L:10D photoperiod in an environmentally controlled room prior to MR determination. Oxygen consumption (VO_2) rates were determined as index of MR in fasted and resting adult tortoises at eight experimental temperatures (14°C , 18°C , 22°C , 26°C , 30°C , 35°C , 38°C and 40°C). Gender had no significant influence on the MR of *C. angulata*. MR increased with increasing temperature, but not consistently over the whole range of temperatures tested. MR was strongly temperature dependent, with a Q_{10} value of 4.13 between 14°C and 26°C . A plateau was detected within a temperature range of 26°C – 38°C with a Q_{10} value of 1.13. The plateau may be a thermal preferendum for *C. angulata* which may render them advantage to forage at summer temperatures in their natural habitat in the Eastern Cape. Above 38°C , MR increased markedly with temperature which may indicate stress on the tortoises. At higher temperatures, the tortoises in their natural habitat may retreat to shady areas to dissipate excess heat.

Keywords: *Chersina Angulata*, Metabolic Rate, Temperature, Thermoregulation

INTRODUCTION

Temperature plays a very important role in the physiology and behaviour of ectotherms. Animals are exposed to variations in environmental temperatures in their natural habitats; hence they should thermoregulate effectively in order to cope.

Since studies of Baldwin (1925), temperature regulation of reptiles has been widely investigated (for example Sturbaum, 1982; Meek and Avery, 1988).

According to Bennett and Dawson (1976) and Angilletta *et al.*, (2002), reptiles are ectotherms and are dependent on the environment for the heat necessary for their physiological and behavioural characteristics. Many of the physiological processes of ectotherms increase linearly with increasing temperature (Hailey and Loveridge, 1997).

However, metabolic rate–temperature curves in some reptiles show plateaus with low Q_{10} values at some temperature ranges (Beaupre *et al.*, 1993; Cartland and Grimmond, 1994; Al-Sadoon, 1999; Zaidan, 2003). This could be an indication of temperature independence of metabolic rates at those temperature ranges.

Some reptiles are reported to thermoregulate physiologically by changing their heart rate and conductance to control heating and cooling rates (Bartholomew and Lasiewski, 1965; Kour and Hutchison, 1970), jugular shunts to produce head–body temperature differences (Heath, 1970), and panting (Dawson and Templeton, 1963).

The brooding python can generate heat through muscular activity (Hutchison *et al.*, 1966). The physiological heat regulation of reptiles has been mostly studied on lizards and snakes (Andrews and Pough, 1985).

Chelonians thermoregulate by a combination of behavioural and physiological means at their preferred ambient temperature. Behavioural thermoregulation has been widely investigated in tortoises (McGinnis

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and Voigt, 1971; Lambert, 1981; Perrin and Campbell, 1981; Meek and Jayes, 1982; Hailey *et al.*, 1984; Meek, 1984, 1988; Meek and Avery, 1988; Els, 1989; Zimmerman *et al.*, 1994; Bailey *et al.*, 1995; Rautenstrauch *et al.*, 1998; Rautenstrauch *et al.*, 2002; McMaster and Downs, 2006). Spotila and Standora (1985) reported that behavioural thermoregulation benefits turtles but reduces their foraging time as well as increases their metabolic demands and their exposure to predators.

Most of the work done on the physiological thermoregulation of tortoises has focused on their heating and cooling rates and on their cardiovascular and body temperature adjustments to varying ambient temperatures (Weathers and White, 1971; McGinnis and Voigt, 1971; Riedesel *et al.*, 1971; Bethea, 1972; Spray and May, 1972; Craig, 1973; Voigt, 1975; Judd and Rose, 1977; Perrin and Campbell, 1981; Els *et al.*, 1988).

There is paucity of information on the effect of temperature on the metabolism of tortoises especially those of southern Africa.

Several studies have, however, been conducted on chelonian metabolism globally, for example on turtles (Hutton *et al.*, 1960; Gatten, 1974, 1987; Prange, 1976; Herbert and Jackson, 1985; Paladino *et al.*, 1990; Lutcavage *et al.*, 1991; Henen *et al.*, 1998; Steyermark, 2002; Southwood *et al.*, 2003; Litzgus and Hopkins, 2003; Hochscheid *et al.*, 2004; Clark *et al.*, 2008; Roe *et al.*, 2008), the wood turtle (Dubois *et al.*, 2008) and tortoises (Hughes *et al.*, 1971; Neagle and Bradley, 1974; Kuchling, 1981; Kirsch and Vivien-Roels, 1984; Brown *et al.*, 2005).

Despite the great diversity of tortoises in southern Africa (Boycott and Bourquin, 2000), and the wide temperature fluctuations in some areas, for example the Nama-Karoo in South Africa (McMaster and Downs, 2006), a few studies on metabolic responses to ambient temperature have been conducted on tortoises from the region (Wood *et al.*, 1978; Hailey and Loveridge, 1997; Hailey, 1998; Scantlebury and Minting, 2006).

Most of the studies did not cover a broad range of experimental temperatures. The larger experimental temperature range with short intervals can give a better insight into the metabolic rate response to changes in ambient temperature, and enable detection of metabolic rate temperature–independence range if one exists for a particular species.

High temperatures are more hazardous to some tortoise species than cooler temperatures (Swingerland and Frazier, 1980; Meek, 1984; Peterson, 1994).

Higher temperatures have been found to decrease the activity of tortoises (Els, 1989). This ultimately leads to a lower reproductive output due to reduced food consumption (Henen *et al.*, 1998) and increased mortality (Peterson, 1994).

Lower than preferred temperatures are also known to reduce metabolic rates (Hailey and Loveridge, 1997) and the activity (Els, 1989) of tortoises.

Chersina angulata is endemic to southern Africa (Ramsay *et al.*, 2002) where it experiences a wide variation in climate and vegetation across its distribution range, for example Mediterranean climate in the Western Cape and a temperate climate in the Eastern Cape.

By understanding the metabolic responses of adult *C. angulata* to varying ambient temperatures, it may be possible to better understand how they cope in these varying environments. The species–specific metabolic relationships of *C. angulata* can also be used for comparative studies, which may cast light on their physiological adaptation (Zaidan, 2003; Litzgus and Hopkins, 2003).

From the studies on the heating and cooling rates of *C. angulata* by Craig (1973) and Perrin and Campbell (1981), an inflexion in the heating curve was noticed at a cloacal temperature range of 27–32°C, which according to Craig (1973) suggested the existence of a physiological thermoregulation mechanism. From the study of the effects of the cooling and heating rates on the heart rate of *C. angulata*, Els *et al.*, (1988) concluded that cardiovascular system plays a role in the physiological thermoregulation of *C. angulata* and that further research needed to be done to better understand the thermoregulation of *C. angulata*.

The current study was undertaken to investigate metabolic rate of adult *C. angulata* at varying experimental temperatures and the possible existence of a plateau in the metabolic rate–temperature curve.

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MATERIALS AND METHODS

Study Animal and Study Site

Chersina angulata is a medium-sized tortoise, with an adult plastron length of 150–250 mm and a mass of up to 2.1 kg. It is distinguished by its undivided gular (Boycott and Bourquin, 2000). *C. angulata* is distributed along the Cape coastal regions of South Africa and extends just into southern Namibia (Hofmeyr, 2009). The three main areas of concentration are the eastern, south-western and north-western coastal regions (Lesia *et al.*, 2003).

Seventeen adult tortoises; 8 females (mass range 358.00 to 765.55 g) and 9 males (mass range 360.02 to 867.81 g) were used in this study. Twelve of the tortoises were obtained from Sardinia Conservancy and five from a neighbouring privately owned land. Both areas are spacious and are located in the western approach to Port Elizabeth (33° 58' S, 25° 42' E) in the Eastern Cape Province of South Africa. The tortoises in both areas were free-ranging.

The sites experience temperate climate with a succession of cold fronts that move easterly along the Cape coast in winter (May to July).

The prevailing winds are west-southwesterly (Port Elizabeth Weather Bureau). Rain occurs throughout the year and the annual rainfall is 600–700 mm. The vegetation is indigenous dune thicket (Greig and Burdett, 1976; Branch, 1989).

Permits to capture, transport and keep *C. angulata* in temporary captivity at Nelson Mandela Metropolitan University (NMMU) were obtained from the Department of Economic Affairs, Environment and Tourism, Province of Eastern Cape. The protocols used in this study were non-invasive and were approved by the NMMU Research Animal Ethics Committee.

Maintenance

The tortoises were kept in an open outdoor enclosure until required for experiments. The enclosure had indigenous vegetation which provided food, shade and shelter, and also allowed sunlight for basking. The tortoises' diet was supplemented with fruits and vegetables like cabbage, carrots, tomatoes and apples. Water was made available all the time in shallow containers set into the ground.

Acclimation

A required number of tortoises were transferred into an environmentally controlled room (ECR) at a time for acclimation to experimental conditions for a period of at least one week. Inside the ECR, the tortoises were placed in an enclosure measuring 2 m x 2 m x 0.2 m. The enclosure had a sand substratum with vegetation to simulate the natural habitat. The tortoises were given fresh chopped vegetables every morning and clean water was made available *ad libitum*.

The acclimation conditions in the ECR were a temperature of 22°C ± 1°C and a light regime of fourteen hours light and ten hours darkness (14L:10D). These are mean summer temperature and photoperiod for Port Elizabeth respectively (Port Elizabeth Weather Bureau). Light was provided by the fluorescent lamps on the ceiling which were phased on automatically at 05h30, and off at 19h30. Full light or full darkness was phased in over 30 minutes to simulate sunrise and sunset respectively. Summer conditions were used in this study because the experiments were conducted in summer.

Set-up for Measuring Oxygen Consumption

The resting metabolic rates of *Chersina angulata* were determined indirectly as rates of oxygen consumption (VO₂) using an open flow through respirometry. A 5.7 litre rectangular metabolic chamber with silicone seal, four locking clips and rounded edges was used (approximately 0.26 m x 0.21 m x 0.11 m). The chamber was made of a translucent material allowing visual observation of the tortoise during VO₂ measurements.

The chamber had two holes on opposite sides, one on the lower part of the back side, for fresh air to continuously be drawn into the chamber and the other hole on the upper front side for excurrent air to be channelled to the oxygen analyzer. The chamber was connected to the oxygen analyzer by flexible oxygen impermeable tubing.

Air drawn from the metabolic chamber was pumped into an Applied Electrochemistry N37 oxygen sensor and analyzed by an Applied Electrochemistry S-3A/II oxygen analyzer. The air flow through the system

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was controlled by an Applied Electrochemistry Model R-2 air pump and a flow meter. Prior to each experiment, the oxygen analyzer was calibrated to 20.95% oxygen.

Oxygen Consumption Measurement

After acclimation and familiarization of tortoises to experimental conditions and equipment the experiments were conducted. Food was withheld from the experimental tortoise for at least forty-eight hours prior to VO₂ measurements. Water was provided *ad libitum* but withdrawn during the VO₂ measurements.

The tortoise was then taken into an adjacent ECR where VO₂ was measured. The tortoise was weighed using an electronic scale (ADAM AFP–3100L, d = 10 mg), placed into a metabolic chamber, unrestrained, and the lid of the chamber placed into position after the tortoise had settled down.

Oxygen percentage readings and behavioural observations were recorded every five minutes over a period of six hours, starting from 08h30 to 14h30. All the experiments were conducted at the same time of day to avoid a possible circadian variation in the VO₂ of the tortoises (Kirsch and Vivien-Roels, 1984). The tortoise was considered active when found scratching or walking in the chamber. After VO₂ measurements, the tortoise was weighed again and then taken to the outside enclosure, where food and water were provided. In this study, the measurements of the VO₂ were taken in quiescent and fasted tortoises during the day, hence, their resting metabolic rates (RVO₂) (Bennett and Dawson, 1976).

The VO₂ of each tortoise was measured once at each experimental temperature (14°C, 18°C, 22°C, 26°C, 30°C, 35°C and 40°C). Extra VO₂ measurements were taken on three male and three female tortoises at an experimental temperature of 38°C in an attempt to ascertain the extent of a possible metabolic rate–temperature insensitive zone. After the VO₂ measurements, the tortoises were taken to the outdoor enclosure. The tortoises were brought back to the ECR on time for acclimation prior to VO₂ measurements in the next experimental temperature.

Data Handling

The data recorded in the first two hours for all the VO₂ measurements in this study were not used in the metabolic rate calculations (Coulson and Hernandez, 1980; McCue and Lillywhite, 2002; Litzgus and Hopkins, 2003). This was done to avoid variations in the resting metabolic rates due to the handling and commencement effects on the measurements.

The resting metabolic rate of an organism is determined when the organism is resting, quiescent and in its post-absorptive state (Bennett and Dawson, 1976), as activity (Hughes *et al.*, 1971; Prange and Ackerman, 1974; Lutz *et al.*, 1989; Hailey and Loveridge, 1997) and the presence of food in the digestive tract (Hailey, 1998; Secor and Diamond, 1999) of chelonians increase their metabolic rates. The VO₂ measured while tortoises are sleeping will be an underestimate of their resting metabolic rate.

To conform to the Bennett and Dawson (1976) definition of resting metabolic rate, the recorded data of the oxygen percentage were standardized by discarding data where the tortoise was active. Data were also discarded if the experimental tortoise defaecated or urinated in the chamber. The presence of faeces resulted in wrong metabolic rates due to oxygen depletion in the chamber while movement of the tortoise in the chamber resulted in an increase in the VO₂ of the individual (Hailey and Loveridge, 1997; Hailey, 1998).

The specific resting oxygen consumption (ml O₂ kg⁻¹hr⁻¹) of each tortoise was calculated from the difference between the preset oxygen percentage (20.95%) and the recorded oxygen percentage data, the flow rate (min⁻¹) and the body mass (g) of the experimental tortoise.

Data Analysis

Student t-test was used to compare body mass between males and females. The mean specific resting oxygen consumption (sRVO₂) (ml O₂ kg⁻¹hr⁻¹) of tortoises of each sex at each experimental temperature was established and plotted against experimental temperature. RMANOVA was used to determine the effects of gender and experimental temperature on the sRVO₂ of the tortoises using Statistica Version 8. RMANOVA was used because the same animals were used at different experimental temperatures (Zar, 1998). Tukey post hoc testing was performed where necessary. The Q₁₀ values were calculated at temperature intervals. Statistical significance was assumed at P < 0.05.

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RESULTS AND DISCUSSION

Results

Body Mass

All the tortoises used in this study were adults (mass > 300 g, Branch 1984). There was no significant difference in the body mass of males and females ($P > 0.05$).

The Specific Resting Oxygen Consumption of *Chersina Angulata*

There was no statistically significant effect of gender ($F_{(1,77)} = 0.79$, $P = 0.38$) on the $sRVO_2$ of *C. angulata*. However, there was a statistically significant effect of experimental temperature ($F_{(7,77)} = 25.86$, $P < 0.001$) on the $sRVO_2$ of *C. angulata* in the population sampled. Data collected from male and female tortoises were combined for analysis. The metabolic rate–temperature curve is shown in Figure 1. The $sRVO_2$ increased with increasing temperature, but not constantly over the range of temperatures tested. The metabolic rate–temperature curves were triphasic.

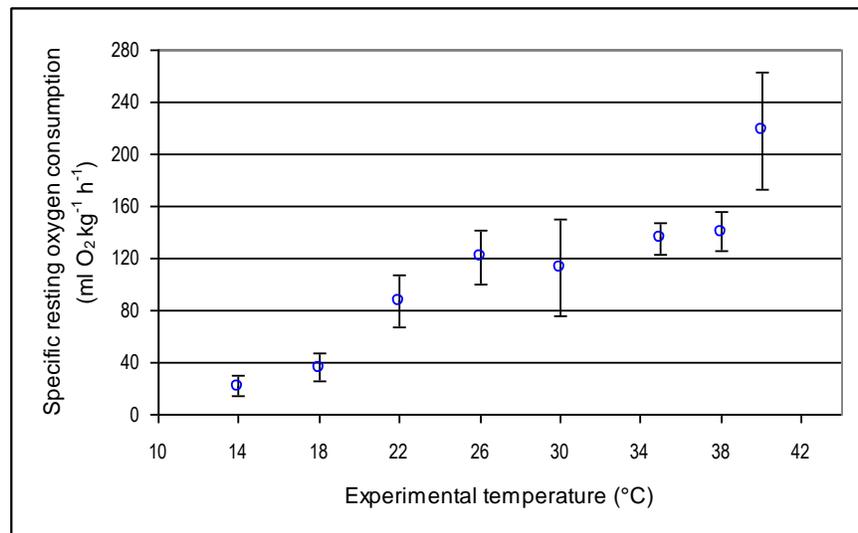


Figure 1: The Relationship of the Specific Resting Oxygen Consumption ($sRVO_2$) and Experimental Temperature in Adult *Chersina Angulata*

Ten to thirteen tortoises were used at all the experimental temperatures, except at 38°C, where only six tortoises were used. The vertical bars are standard deviations.

A post-hoc Tukey test showed that some $sRVO_2$ values at different experimental temperatures were significantly different from others while others were not. The value at 14°C was significantly different from the values at all other experimental temperatures ($P < 0.001$) except at 18°C ($P = 0.85$). The value at 22°C was significantly different from the values at all experimental temperatures, except at 26°C and 30°C. The values at 26°C–38°C were not significantly different from each other ($P > 0.05$), while the value at 40°C was significantly different from the values at all other experimental temperatures ($P < 0.05$). The relationship of the $sRVO_2$ of *Chersina angulata* and experimental temperature was redrawn to elucidate on the three observed phases (Figure 2). Regression lines were fitted to the data at each range. Three distinct stages in the metabolic rate–temperature curve of *C. angulata* are evident at the temperature ranges (i) 14°C–26°C, (ii) 26°C–38°C and (iii) 38°C–40°C. The metabolic rate increased with increasing experimental temperature at stages (i) and (iii), but levelled off at the temperature range 26°C–38°C. The regression slope was statistically significant at temperature range 14°C–26°C, with the $sRVO_2$ values decreasing with decreasing experimental temperature, the relationship can be described by the equation $sRVO_2 = 8.70 \text{ (ml O}_2 \text{ kg}^{-1} \text{ hr}^{-1}) - 107.3 \text{ (}^\circ\text{C)}$, ($P = 0.02$, $R^2 = 0.96$). The regression slope was not significant at the temperature range 26°C–38°C ($P = 0.17$). Above 38°C metabolic rate increased markedly with experimental temperature.

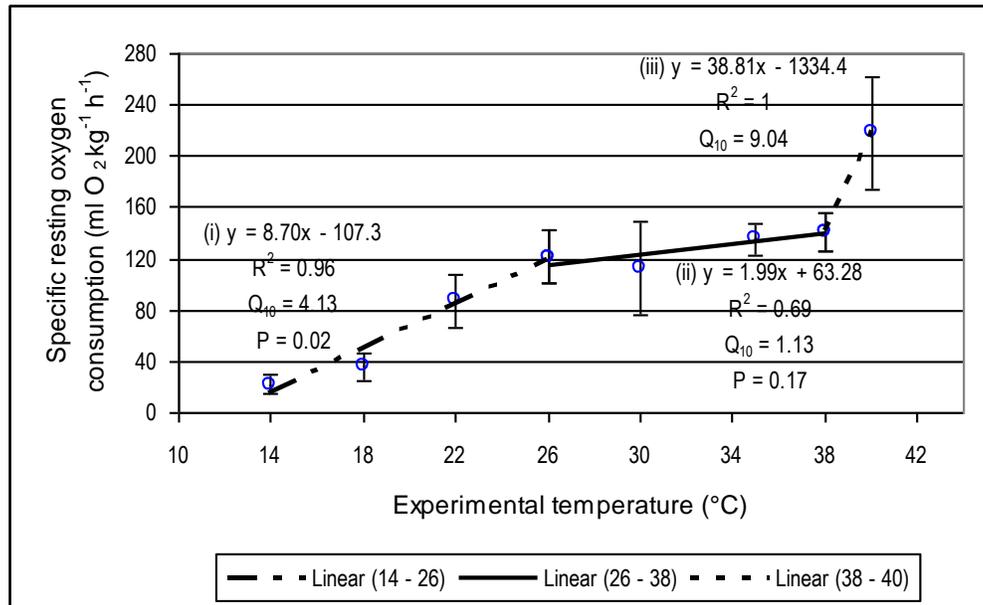


Figure 2: The Three Stages in the Relationship of the Specific Resting Oxygen Consumption (sRVO₂) of Adult *C. Angulata* and Experimental Temperature

The empty circles represent the mean sRVO₂ obtained from tortoises every 5 minutes over 4 hours at each experimental temperature. The vertical bars are the standard deviations.

The Q₁₀ values calculated from the three stages vary; 4.13, 1.13 and 9.04 for stages (i), (ii) and (iii), respectively (Figure 2). The Q₁₀ values at intervals of the entire temperatures tested (14°C–40°C) are shown in Table 1 and they change over the temperature range 14°C–40°C. The values are close to 1 at 26°C–38°C and highest at 38°C–40°C.

Table 1: Thermal Dependence of the Specific Resting Oxygen Consumption of Adult *Chersina Angulata* at Varying Experimental Temperatures (14 - 40° Expressed as Q₁₀ Values)

Experimental Temperature (°C)	Q ₁₀ Value
14-18	3.44
18-22	8.95
22-26	2.28
26-30	0.83
30-35	1.44
35-38	1.13
35-40	2.59
38-40	9.04
14-40 (over all)	2.41

Discussion

The metabolic rate of the *Chersina angulata* used in this study was not significantly influenced by gender. The metabolic rates of ectotherms are generally known to increase with increasing temperature (Templeton, 1970; Gatten, 1974; Bennett and Dawson, 1976). In this study, the metabolic rate of *C. angulata* increased with experimental temperature, but not constantly over the range of temperatures tested. The variation in the metabolic rates of tortoises at varying experimental temperatures may be an indication that the functioning of the metabolic enzymes of the tortoises is directly affected by temperature. The values of the metabolic rate of *C. angulata* are slightly higher than those of *Testudo hermanni* (Kirsch and Vivien-Roels, 1984), *Kinixys spekii* (Hailey and Loveridge, 1997) and

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Malacochersus tornieri (Wood *et al.*, 1978). The differences may be attributed to the interspecific differences among tortoises or the effects of thermal acclimation.

A metabolic depression was indicated by a steep decrease in the metabolic rate of adult *C. angulata*, with high Q_{10} values at lower temperature range (14°C–26°C). The higher Q_{10} value at the lower temperature range may be a way in which *C. angulata* conserve energy during cold nights in their natural habitat. *C. angulata* was found active at ambient temperatures greater than 17°C, with the lowest temperature at which an animal was active being 14.1°C in their natural habitat (Els, 1989). The inactivity of *C. angulata* at lower temperatures in their natural habitat may be a result of a decline in their physiological performance below their thermal preferendum. Els (1989) reported that most of the shelter exits of *C. angulata* open in an arc between North and East; and speculated that this was for the tortoises to be warmed up by the early morning sun, and to shelter from the prevailing west-south-westerly winds. The high Q_{10} values of metabolic rate calculated at the lower temperatures from this study corroborate the work of Litzgus and Hopkins (2003), who reported higher metabolic Q_{10} values at cooler temperatures than those recorded at warmer temperatures in turtles.

The mid-section (26°C–38°C), with a Q_{10} value close to 1, shows that the metabolic rate of *C. angulata* was less sensitive to temperature at this range (Bennett and Dawson, 1976; Schmidt Nielsen, 1997). This metabolic rate–temperature insensitive range or plateau may represent a thermal preferendum or a thermal performance breadth at which *C. angulata* performs best. The plateau in this study encompasses the 27°C–32°C body temperature range at which both Craig (1973) and Perrin and Campbell (1981) reported an inflexion in the heating curve of *C. angulata*. Els *et al.*, (1988) reported that during heating experiments, *C. angulata* became active at a body temperature of approximately 29°C–32°C, which is encompassed in the metabolic rate–temperature insensitive range from this study. The plateau also includes the preferred body temperature range (28°C–32°C) of *C. angulata* (Branch, 1984).

The temperature–independent metabolism at a higher temperature could be of ecological importance. The width of the temperature–insensitive range may explain the ecology and behaviour of the species (Huey and Slatkin, 1976). The plateau may also shed light on the performance breadth of *C. angulata* in their natural habitat (Huey and Stevenson, 1979). The capacity of *C. angulata* to maintain metabolic rate at such high temperatures could benefit them in foraging during summer in the Eastern Cape region where temperatures range from 18°C–27°C, with occasional bouts of up to 35°C (Port Elizabeth weather station). The temperature–independent metabolism range may support the concept of niche width (Roughgarden, 1972). The range may be the suitable temperatures at which *C. angulata* can survive and may be a contributing factor to their geographical distribution (Heatwole, 1970; Spellerberg, 1973).

From the studies that directly tested the effect of temperature on the metabolic rate of tortoises, none reported the existence of a plateau in the metabolic rate–temperature curve. Oxygen consumption has been reported to increase with increasing temperature in *Testudo hermanni* g. (Kirsch and Vivien-Roels, 1984), *Kinixys spekii* (Hailey and Loveridge, 1997), *Gopherus agassizii* and *Homopus areolatus* (Brown *et al.*, 2005), and *Geochelone sulcata* (Ligon *et al.*, 2009). From metabolic rate studies conducted on turtles, a few reported the existence of a plateau in the metabolic rate–temperature curve. Gatten (1974) reported a plateau on the metabolic rate–temperature curve of *Terrapene ornate* while Southwood *et al.*, (2003) suspected the existence of a plateau in the metabolic rate–temperature curve between 17°C and 26°C in juvenile green turtles. Penick *et al.*, (1996) measured tissue metabolic rates of juvenile green turtles and reported relatively low Q_{10} values within the temperature range of 12.5°C–27.5°C.

In other turtles, oxygen consumption has been reported to increase with increasing experimental temperature, for example, in *Trachemys scripta* (Gatten, 1974), *Chelydra serpentina* (Steyermark and Spotila, 2000) and *Kinosternon subrubrum* (Litzgus and Hopkins, 2003). Dubois *et al.*, (2008) also reported an exponential increase of metabolic rate of wood turtles (*Glyptemys insculpta*) with body temperature ranging from 15°C–35°C.

The existence of a plateau in the metabolic rate–temperature relationship has been reported in other ectotherms, like tuatara (Cartland and Grimmond, 1994), some snakes (Buikema and Armitage, 1969; Aleksuik, 1971; Seidel and Lindeborg, 1973; Al-Sadoon, 1991, 1999; Zaidan, 2003) and some lizards

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(Abe and Mendes, 1980; Patterson and Davies, 1989; Beaupre *et al.*, 1993). Jacobson and Whitford (1970) attributed the flattening of the VO_2 of *Thamnophis sirtalis* between 20°C and 30°C to reduced locomotor activity, as they reach their preferred body temperature of 28.1°C. The presence of a plateau in the metabolic rate–temperature curve of *C. angulata* from this study and from the studies of other ectotherms; show that not all ectotherms are completely dependent on ambient temperature for their functional capabilities. Some of the reptile physiological functions do not linearly increase with increasing temperature.

The highest Q_{10} value calculated in this study was at the third stage (38°C–40°C); this may be due to the tortoises being stressed and physiological thermoregulation, as well as the extension of head and limbs no longer able to cope with the need for temperature regulation. Els *et al.*, (1988) suggested that the reduction in the heart rate of *C. angulata* at higher temperatures may be a physiological strategy of retarding further heat gain.

In their natural habitat, *C. angulata* may have applied more behavioural thermoregulation strategies, like retreating to shady areas and extending their heads and limbs so as to dissipate heat. Els *et al.*, (1988) reported that *C. angulata* forage within ten metres of their shelters or shade, which renders them a short distance to shuttle between shade and sun.

The spurred tortoise (*Testudo graeca L.*) was found to employ evaporative cooling at high ambient temperatures, with salivatory thermoregulation starting at 39.5°C ± 0.4°C (Cloudsley–Thompson, 1974). From this study, and that of *Testudo graeca* (Cloudsley–Thompson, 1974) it is clear that ambient temperatures above 38°C may stress tortoises. Avoidance of extreme ambient temperatures may conserve energy.

Conclusion

The specific resting oxygen consumption ($sRVO_2$) of adult *C. angulata* increased with increasing experimental temperatures, but not constantly over the range of temperatures tested (14°C–40°C). A plateau exists at a temperature range of 26°C–38°C. Beyond the plateau, the specific resting oxygen consumption increased markedly with temperature. The study shows that *C. angulata* has the ability to thermoregulate physiologically to some degree. The study has shown that *Chersina angulata* although considered an ectotherm also shows endothermic characteristics. *C. angulata* may better be classified as a heterotherm since it exhibits combinations of ectothermy and endothermy. This implies that the common interpretations were an oversimplification. *C. angulata* are neither purely ectothermic nor purely endothermic. They are dependent on their surroundings but also seem to have an internal physiological mechanism for thermoregulation. *C. angulata* from this study acted as a conformer at a temperature range of 14 – 26°C and a thermoregulator at a temperature range of 26 – 38°C.

ACKNOWLEDGEMENTS

The authors thank the Department of Economic Development and Environmental Affairs for permits to capture *C. angulata* at Sardinia Bay, transport to Nelson Mandela Metropolitan University (NMMU) and keep them in captivity; Mr. Gavin Allen of Sardinia Conservancy for granting access into the conservancy and loaning most of the tortoises used in this study; Dr P.E.D. Winter, for loaning some of his tortoises used in this study, and NMMU and Botswana College of Agriculture for financial support.

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