



High body temperatures in an arid, winter-rainfall environment: Thermal biology of the smallest tortoise

Victor J.T. Loehr*

Homopus Research Foundation, Kwikstaartpad 1, 3403 ZH IJsselstein, Netherlands

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ABSTRACT

Herbivorous tortoises in arid, winter-rainfall regions need to forage in seasons that provide relatively little heat for their ectothermic metabolism. To help understand how tortoises exploit resources in winter-rainfall areas, I recorded ambient, soil, and body temperatures for *Homopus signatus* in four spring seasons, and in one summer, autumn, and winter. The spring thermal environment enabled *H. signatus* to maintain body temperatures that were high compared to other small tortoise species. Mature females had higher spring body temperatures than males and immature individuals, probably because mature females were developing eggs. In summer, autumn, and winter, body temperatures differed between males and females, relating to sexually different activities and retreat uses. The relatively high body temperatures of *H. signatus* in winter and spring, along with a non-isometric relationship between body temperature and soil temperature, suggest that tortoises thermoregulated and may need considerable time to gain heat. Additional studies should compare body temperatures of *H. signatus* to operative temperatures, and determine the vulnerability of the taxon to human interferences that affect behavioural time budgets and body temperatures.

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1. Introduction

Tortoises occur on all continents except Australia and Antarctica, and their range includes several arid regions (Ernst et al., 2000). In these low rainfall environments, herbivorous tortoises need to take advantage of favourable conditions and feed when primary production is available (Henen, 1997; Loehr et al., 2009; Peterson, 1996). As a result of the ectothermic physiology of tortoises, body temperatures depend on opportunities for thermoregulation. When such opportunities are scarce in seasons with primary production, important fitness consequences may result (Huey and Berrigan, 2001) because chelonian body temperatures affect locomotion (Ben-Ezra et al., 2008; Claussen et al., 2002), food intake (Zhang et al., 2009), metabolism (Penick et al., 2002; Schmidt, 2003), reproduction (Lapid et al., 2004) and possibly other performance indicators. Generally, performance increases with body temperature, and drops rapidly when optimal temperature is exceeded (Huey and Kingsolver, 1989). Nevertheless, performance curves imply that ectotherms may function at a range of temperatures, as suggested by active angulate and desert tortoises (*Chersina angulata* and *Gopherus agassizii*, respectively) at ambient

temperatures below 10 °C (Keswick et al., 2006; Wilson et al., 1999). Furthermore, chelonians may acclimatise biochemical processes to increase performance at relatively low body temperatures (Seebacher et al., 2004).

The Succulent Karoo, in north-western South Africa, is a winter-rainfall region that usually receives less than 150 mm per annum (Cowling et al., 1999). Winter is the primary growing season for plants (Cowling et al., 1999; Esler and Rundel, 1999), at daily average ambient minimum and maximum temperatures of 8.0 and 16.4 °C, respectively, for July (data for 1990–2004 in Springbok; South African Weather Services, unpublished data). Primary production decreases in spring, at daily average minimum and maximum temperatures of 9.5 and 20.9 °C for September. In summer, little plant growth occurs, and daily average minimum and maximum temperatures rise to 15.8 and 29.2 °C for January. The Succulent Karoo harbours several tortoise species (Boycott and Bourquin, 2000) that need to exploit primary production in winter and spring.

One of the tortoise species in the Succulent Karoo is the Namaqualand speckled tortoise, *H. signatus*. This tortoise is very small and sexually dimorphic; maximum straight carapace lengths of males and females are 93 and 110 mm, respectively (Loehr, 2002; Schmidt and Engelbrecht, 2006). It is associated with a rocky environment (Boycott and Bourquin, 2000), where it frequents shallow rock crevices as spring retreats (Loehr, 2002). Females are opportunistic in the acquisition of resources, and may be

* Tel.: +31 30 6888616.

E-mail address: loehr@homopus.org.

particularly active in spring, with additional activity in other seasons (Loehr et al., 2009). The opportunistic foraging behaviour of females has evolutionary significance, because female foraging should enhance their body condition, which influences their reproductive success, affecting both egg size and whether they reproduce, the former which probably enhances offspring survival (Loehr et al., 2011). It is not known what seasonal body temperatures females maintain, and if body temperatures differ between males and females.

To help understand how arid-region tortoises exploit primary production in winter-rainfall environments, I examined ambient, soil, and body temperatures in a population of *H. signatus* during four spring seasons, and in one summer, autumn, and winter. I interpreted body temperatures in relation to the ecology of *H. signatus*, and analysed sexual differences.

2. Materials and methods

2.1. Study site and measurements

In each spring from 2001 to 2004, a 3.7 ha study site near Springbok, South Africa, was methodologically inspected for tortoises daily (circa 08:00–19:00 h) by two to five persons (see Table 1 for sampling dates). Springbok weather station, located 2.5 km north of the study site, provided ambient temperature data (i.e., air temperature 1.5 m above the ground) for 1990–2004.

For each tortoise encountered, I recorded the temperatures of the carapace at the second vertebral scute, the centre of the plastron, and in one of the inguinal areas, to the nearest 0.1 °C, using an infrared thermometer (Pyropen L, Calnex Electronics Ltd., Bedfordshire, U.K., emissivity set at 0.95). I moved the tortoise aside and recorded the temperature of the soil in a circle (circa 10 cm diameter) at the spot where the tortoise was found, using the same thermometer. All these measurements were completed within 1 min. To verify that shell and inguinal temperatures correlated with body temperatures, I also measured cloacal temperatures with a type K thermocouple (GTF101-5/GMH 3230, Greisinger electronic, Regenstauf, Germany) for 156 encounters (straight carapace lengths [SCL] 34.3–104.6 mm, cloacal temperatures 12.5–38.1 °C), in 2003–2004. Each tortoise had its SCL, maximum shell height (SH), and maximum shell width (SW) measured to the nearest 0.01 mm, and these parameters estimated shell volume ($SV = \pi * SCL * SH * SW / 6000$; Loehr et al., 2004). I categorised the activities that tortoises were engaged in as basking (stationary, head and/or limbs stretched and exposed to heat radiation), feeding, hiding (inactive in retreat), or walking. Males were distinguished from females by the longer tails, concave plastrons and smaller body sizes of males; small individuals without clear sexual dimorphisms were recorded as juveniles (Boycott and Bourquin, 2000). Before release, tortoises were marked uniquely

Table 1

Daily average minimum and maximum ambient study period and long-term temperatures, and average study period soil temperatures at the sites where tortoises were found. Different superscript letters indicate statistically different annual ambient minimum, maximum^a, or soil temperatures^b.

Year	Ambient temperature (°C)		Soil temperature (°C)
	Minimum	Maximum	
2001 (7 Sep–1 Oct)	8.6 ^b	18.5 ^b	22.8 ^b
2002 (13 Sep–7 Oct)	12.0 ^a	24.1 ^a	27.1 ^{ac}
2003 (5 Sep–7 Oct)	8.6 ^{bc}	19.7 ^{bc}	24.4 ^d
2004 (2 Sep–30 Sep)	9.7 ^{abc}	21.8 ^{abc}	26.9 ^c
1990–2000 (2 Sep–7 Oct)	10.6 ^{abc}	21.7 ^{abc}	–

^a One-way ANOVA, $F_{4,149} \geq 3.35$, $P \leq 0.012$.

^b One-way ANOVA, $F_{3,1162} = 12.93$, $P < 0.001$.

with combinations of black nail polish dots on the carapace (2001 and 2002), or by notching the marginal scutes (2003 and 2004; Cagle, 1939).

Some of the tortoises (1–9 males and 6–15 females) were equipped with thread-trailing or radio-tracking devices and tracked for 6–28 days each spring. At each tracking occasion, I recorded body temperatures, soil temperature, and tortoise activity.

In addition to the infrared technique used in spring, I used quick-setting epoxy to glue iButtons (DS1921L-F50, Dallas/Maxim, Dallas, USA) to the third costal scute of nine adult male and ten adult female tortoises in 2003. iButtons recorded and logged the temperature, to the nearest 0.5 °C, every 3 h. Six females with iButtons were tracked in 2003 and 2004. One male was recovered dead, but iButton recordings showed a marked change in temperatures with maxima over 40 °C from 8 March 2003, which I assumed was the date of death. The date of death for a recovered female could not be deduced, and recordings after the date it was last seen alive were discarded. In order to verify that iButton temperatures correlated to body temperatures, I compared recordings with (infrared) inguinal temperatures, as my sampling design did not include cloacal measurements for tortoises with iButtons.

2.2. Statistical analysis

I used infrared temperatures to calculate average body temperatures for males, females and juveniles in each spring. My experimental design combined independent sampling with replacement and repeated measures, but the repeated measures were severely imbalanced (i.e., varying numbers of tortoises were tracked over different periods, and samples included missing values). Therefore, I compared average body temperatures of independently sampled males, females, and juveniles (i.e., after removing tracked tortoises) among years and tortoise activities. In addition, I scaled body temperatures on soil temperatures and used ANCOVA to compare regressions for independently sampled males, females, and juveniles.

iButton temperatures allowed me to calculate averages for 3-hour intervals in spring (September–November), summer (December–February), autumn (March–May), and winter (June–August). iButton recordings represented repeated measures, but I was unable to use repeated measures (RM) tests on the complete dataset because iButtons did not record during the same periods. Therefore, I used independent tests to compare male and female iButton temperatures among seasons, and supplemented these tests with RM tests for three males and five females in summer, autumn, and winter (1 December 2003 to 31 July 2004), and for four males and six females in spring (18 September to 30 November 2003).

All tests were performed in SigmaStat 2.03 (SPSS Inc., Chicago, USA), except ANCOVA (Quinn and Keough, 2002; Zar, 1999) and chi-square tests (Zar, 1999), which were completed in Microsoft Excel 2007. Student–Newman–Keuls (SNK) post hoc tests followed ANOVA and ANCOVA, and differences were considered significant at $P < 0.05$.

3. Results

3.1. Ambient and soil temperatures

Ambient temperatures in the spring study periods ranged from 1.3 to 33.3 °C. The daily average minimum and maximum study period temperatures differed among years (Table 1). Post hoc tests indicated that all years had daily minimum and maximum temperatures that were similar to the long-term average (Table 1). However, the 2002 study period was warm compared to 2001 and 2003. Soil temperatures at the sites where a tortoise was found

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