Thermoregulatory factors in the Karoo dwarf tortoise, *Chersobius boulengeri*

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ABSTRACT

Tortoises are ectothermic and they are dependent on environmental temperature and behaviour for controlling their body temperature within their preferred optimal temperature zone (POTZ). The IUCN-status of *Chersobius boulengeri* is in January 2018 updated to "Endangered". More knowledge about this species is necessary for managers to take appropriate conservation measures. To get more insight in the thermoregulatory ecology of *Chersobius boulengeri*, sex, behaviour, carapace, plastron and cloacal temperatures and environmental temperatures were recorded during a fieldwork period of about six weeks in February and March. The carapace, plastron and cloacal temperatures were not significantly different in *C. boulengeri*. No difference was found between males and females and active tortoises had a significantly higher temperature than inactive tortoises. Most of the time, the tortoises were hiding in crevices. The body temperature of hiding tortoises relies most on the ceiling, soil and ambient temperatures respectively. The usage of crevices by *C. boulengeri* results thus in options for controlling their body temperature by radiation, convection and conduction. This species seems to be a thermoconformer by adopting the ambient temperatures in the crevices.

INTRODUCTION

Thermoregulation is an important aspect in the behaviour of reptiles. Reptiles are ectothermic and depend on environmental temperature and behaviour for controlling their body temperature within a preferred optimal temperature zone (POTZ) (Divers, n.d.). Within the POTZ, reptiles may attempt to achieve a specific body temperature for metabolic activities (Divers, n.d.). The metabolic rate of reptiles is on average much lower than the metabolic rate of mammals and correlates with ambient temperature (Heijnen, 2016; Lei & Booth, 2014). Besides metabolic rates, body temperature influences locomotion (Ben-ezra, Bulté, & Blouin-Demers, 2008), food intake (Zhang, Du, Shen, & Shu, 2009) and reproduction (Telemeco, Radder, Baird, & Shine, 2010).

Tortoises are reptiles of the order Chelonia which can live in a wide variety of habitats. In South Africa a big part of the known species are endemic and they have to deal with extreme circumstances (Rhodin et al., 2017). There are multiple ways for tortoises to adjust their behaviour for controlling body temperature, such as: restriction of activity times, shuttling between hot and cool microhabitats, postural modifications that alter the rates of heating and cooling, and diel and seasonal cycles of activity (Bauwens, Castilla, & Mouton, 1999; Bauwens, Hertz, & Castilla, 1996; Hertz & Huey, 1981; Oromí, Sanuy, & Sinsch, 2010; Pianka, Huey, & Hoffman, 1977; Stevenson, 1985).

This research is focussed on the thermoregulation of the Karoo dwarf tortoise (*Chersobius boulengeri*). *Chersobius boulengeri* is a small tortoise (up to 13 cm) which lives in parts of the Eastern Cape (South Africa) to Touwsrivier in the Western Cape. The range in the Northern Cape extends to Calvinia in the northwest and beyond Carnarvon in the northeast (IUCN, 2017). Their habitat consists of rocky landscapes and dolerite ridges (IUCN, 2017). *Chersobius boulengeri* is listed as Near Threatened on the IUCN Red List of Threatened Species and even proposed Endangered since January 2018 (Loehr, personal communication). This indicates a decrease in the population of this species. There are no published ecological studies on *C. boulengeri* done yet.

Chersobius boulengeri lives in an habitat with a summer rainfall season ("Klimaat Williston," 2018; Loehr, 2017). Their dry habitat (180 mm of rain a year) provides only enough food in the summer. The relatively high ambient temperatures in summer result in warm circumstances for foraging in *C. boulengeri*. Their small body size results in a fast adaptation on environmental temperatures, but this also gives risks for overheating (Coulson, 1996; Loehr, 2018). The additional difficulty is thus to prevent overheating while foraging. By adapting their behaviour to these circumstances, the tortoise will meet his needs, by sheltering under rock slabs on rocky plateaus and dolerite ridges (Swingland & Klemens, 1989).

To enable managers to take appropriate conservation measures, we urgently need more insight in the ecology of *C. boulengeri*, including its thermoregulation. In this study, the measured body temperatures of the tortoises were overviewed and the regressions and correlations of those body temperatures were investigated. Then the dependency of predicted cloacal temperatures was analysed on internal factors, such as sex, behaviour, activity and time of the day. After that, the influence of external factors on the body temperature was investigated (type of rock and environmental temperatures). Eventually, the cloacal temperature of *C. boulengeri* was determined with a calculated linear model of significantly affected variables.

METHODS

Study site and weather conditions

Chersobius boulengeri was studied in the austral summer, from the 14th of February till the 21th of March 2018, near Williston, South Africa. Fieldwork took place at a 16 ha northern-easterly facing hill, including ridges, rocky slopes, dry riverbeds and plateaus, with sandstone and dolerite rocks. Ambient temperatures vary usually between 15.7 and 32.3 °C in February and between 13.5 and 29.3 °C in March. The mean rainfall in February is 22 mm and in March 37 mm ("Klimaat Williston," 2018). Daily minimum and maximum ambient temperatures, rainfall and relative humidity were obtained by a weather station with dataloggers situated in the centre of the study site.

Survey and measurements

The site was methodically searched for tortoises. At every encounter with a tortoise, date, time, specimen number, behaviour, sex, microhabitat, soil temperature and carapace temperature were recorded. Males were distinguished from females by external characteristics (males have longer tails, have a concave plastron and have a smaller body size (Anders et al., 2017). Behaviours were categorised as shown in *Table 1*.

Table 1: Explanation of the behaviours of C. boulengeri.

Behaviour	**Explanation**
Hiding	Tortoises in a rock crevice or concealed under a shrub
Basking	Tortoises sitting still with extremities and/or head extended
Walking	Tortoise walking
Feeding	Tortoise feeding
Courtship	The behaviour of male tortoises at attracting a mate

The carapace temperature, the plastron temperature and the temperatures of the environment of the tortoise were measured with a calibrated infrared thermometer (Amprobe IR-450, Beha-Amprobe GmbH, Glottertal, Germany) at max. distance of 0.5 cm.
For several encounters, the cloacal temperature was also measured, with a calibrated thermocouple (type K thermocouple, GTF101-5/GMH 3230, Greisinger electronic, Regenstauf, Germany). All these measurements were completed within one minute. Each tortoise was notched for future identification. Nine males and 16 females were equipped with radio transmitters (max. 10% of body mass for males (9 g) and females (13.7 g) and attached to the carapace with epoxy glue). Telemetered tortoises were located every 3-4 days using a receiver.

Statistical analysis

In this study, minimum, maximum, mean cloacal, carapace, soil, and ambient temperatures were calculated with the related standard deviations or 95% confidence intervals of the mean.
Cloacal temperatures were compared with carapace and plastron temperatures using a regression analysis. Because carapace temperatures had been recorded at different locations on the carapace, carapace temperatures among locations were also compared using one-way ANOVA.
After that, the regression line was used to predict the cloacal temperatures with carapace temperatures. Then, the effects of sex, time of the day, activity, and behaviour on the predicted cloacal temperatures were tested. The relations of the external factors (such as stone type under which a tortoise was hiding, environmental temperatures and microhabitat) were also determined. The relationship between these variables and the predicted cloacal temperature was determined using regression and correlation analysis for continuous variables, and using independent t-tests or ANOVA for qualitative variables.
The relation of the predicted cloacal temperature and the soil temperatures were analysed with a regression analysis. With the resulting regression line of the hiding tortoises was calculated when the predicted cloacal temperature was equal to the soil temperature. This was repeated for hiding tortoises.
At last, all the aforementioned variables were used to identify and select the variables that significantly affected the predicted cloacal temperature. For this, a multiple linear regression was applied. First, all the variables, which are expected to be independent, were included in a Univariate general linear model. This resulted in a table with Tests of between-subjects effects, where the added value of the individual variables is described. The model was then simplified by excluding the unnecessary variables (the less significant variable) until all the variables contribute significant to the predicted cloacal temperature. The statistical software used was SPSS. Differences were considered statistically significant when $P<0.05$ and tests were checked on normality, homogeneity and constant variance.

RESULTS

1. *Descriptive statistics*

Ambient temperatures, for the moments on which a tortoise was encountered, varied between 6.0 and 34.7 °C. The relative humidity was between 4.2 and 94.4%, with a mean value of 35.2%. The mean soil temperature was 26.1 °C, with a minimal temperature of 11.4 °C and a maximum temperature of 53.4 °C.

During the study period, 50 tortoises were found. Some individuals were encountered multiple times and some were only found once. The sample population contains 25 males, 23 females, one juvenile and one hatchling. Including all the recaptures, the total data set contains 310 measurements, 244 carapace temperatures, 91 plastron temperatures, 32 cloacal temperatures and 254 soil temperatures.

From the 244 measurements including a carapace temperature, 197 tortoises were hiding, 21 tortoises were walking, 23 tortoises were basking, one tortoise was feeding, one tortoise was courting and from one tortoise, the behaviour was unknown.

The descriptives of the cloacal, carapace and plastron temperatures are described in *Table 2*.

Table 2: Minimum, maximum and mean temperatures of the body temperatures of C. boulengeri in Celcius degrees.

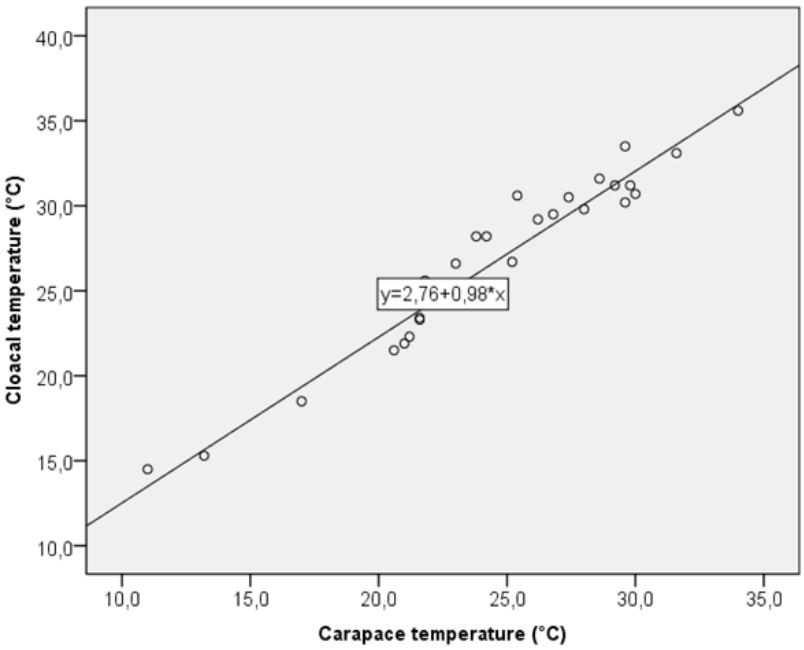
Location of temperature measurement	Minimum	Maximum	Mean	95% confidence interval for mean
Cloaca	14.5	35.6	26.55	24.74 – 28.36
Carapace	10.6	38.0	26.44	25.78 – 27.102
Plastron	13.2	36.2	26.29	25.38 – 27.19

2. *Relationships between temperatures of the plastron, carapace and cloaca*

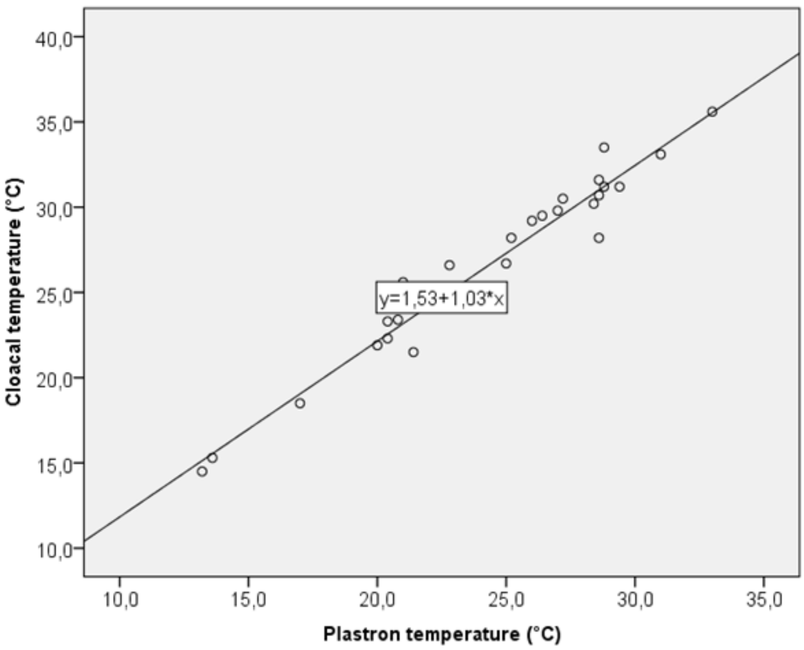
The temperatures of the carapace and plastron were correlated to cloacal temperatures (*Table 3, Figure 1A/B*). There was little difference between the correlation coefficients for plastron and carapace temperatures (carapace temperature: R=.967, p=.000; plastron temperature R=.971 p=.000).
In this study, carapace temperatures were used to predict cloacal temperatures for all carapace temperature measurements. This because there were more carapace temperature recordings than plastron temperature recordings.
Predicted cloacal measurements were used in all further analyses.

Table 3: Results of regressions on the plastron and carapace temperatures with the cloacal temperature.

Dependent variable	N	F	Regression equation	R^2	Std. Error of the Estimate	P
Plastron temperature	31	491.003	Tcloaca = 1.526 + 1.031 * Tplastron	.944	1.2155	.000
Carapace temperature	32	428,703	Tcloaca = 2.756 + .976 * Tcarapace	.935	1.3083	.000



A.



B.

Figure 1A/B: Regression lines of the cloacal temperature correlated with the (A) carapace and (B) plastron temperatures of C. boulengeri.

Measurements on multiple locations on the carapace of individual tortoises (dorsally, laterally, anteriorly and posteriorly) were not significantly different from one another (one-way ANOVA, $F(3,241)=1.468$ and $p=.224$), so the location of measurement of the carapace temperature were disregarded when calculating predicted cloacal temperatures.

3. Dependency of predicted cloacal temperature on internal factors
    a. Sex

The mean predicted cloacal temperature of males was 27.58 °C (SD=4.858, N=90) and the mean predicted cloacal temperature of females was 28.67 °C (SD=4.687, N=142). There was no significant difference in the mean predicted cloacal temperatures between males and females (independent samples t-test*,* *t*(230)=-1.713, *p*=.088).

    b. Behaviour

The mean predicted cloacal temperatures of tortoises that where basking, courting, feeding, hiding and walking were 30.97 °C (SD=2.88, N=23), 28.33 °C (SD=-, N=1), 15.83 °C (SD=-, N=1), 27.96 °C (SD=5.13, N=197) and 31.86 °C (SD=4.02, N=21), respectively. There was one feeding tortoise found and one courting tortoise. These data are not included in the statistical analysis.
There was a difference between the mean temperatures associated with the behaviours (Kruskal Wallis test, *H*(2)=12.213, *p*=.002). The post-hoc tests showed a significant difference in hiding compared to walking (*U*=1107.500, *Z*=-2.493, *p*=.012) and basking (*U*=1370.000, Z=-2.671, *p*=.007).

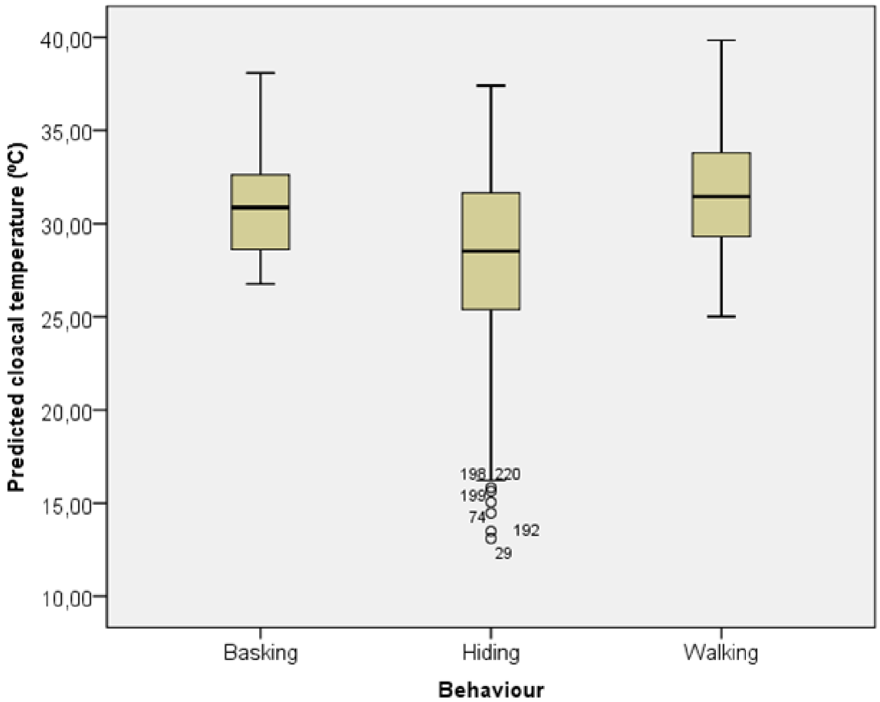


Figure 2: Predicted cloaca temperatures engaged in different observed behaviours.

The mean soil temperatures for hiding, walking and basking tortoises were respectively, 25.10, 29.33 and 29.55 °C. There is a significant difference between these soil temperatures (F(2,239)=11.014, *p*=.000). The soil temperature of hiding tortoises is significant different from the basking and walking tortoises.

    c. Activity

All the measurements of hiding tortoises were defined as inactive. Inactive tortoises had a mean cloacal temperature of 27.96 °C (SD=5.13) and active tortoises had a mean cloacal temperature of 30.99 °C (SD=4.10). The mean difference of 3.03 °C was significant (Mann-Whitney test, *U*=2761.000, *z*=-3.161, *p*=.002).

d. Time of day

When projecting the predicted cloacal temperatures in time, the cloacal temperature tended to increase until early in the afternoon, after which it appeared to level (*Figure 3*).

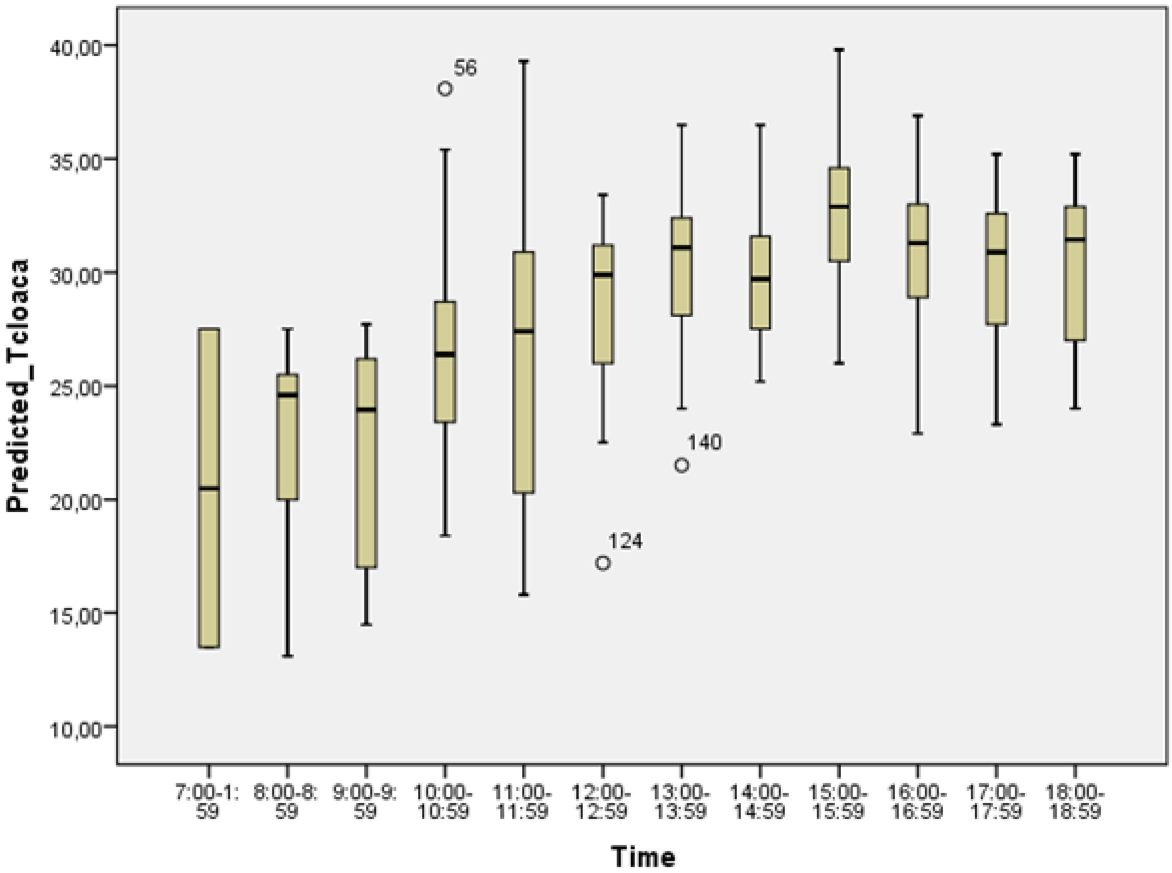


Figure 3: The course of the predicted cloacal temperatures over the day from single measurements from a tortoise per day.

When testing the difference of the temperatures in the time budgets, the temperatures from the time groups starting on 10:00 h and ending on 18:59 h are not significantly different. The time groups from 7:00 till 9:59 h are significantly different from the temperature at 18:00-18:59 h (mixed model ANOVA, p>.05).

4. *Dependency of predicted cloacal temperature on external factors*

A. Type of rock

The mean predicted cloacal temperature was 28.76 °C (*SD*=4.22 *N*=37) for tortoises hiding in sandstone retreats and 28.31 °C (*SD*=3.73 *N*=135) for dolerite retreats. The variance between the groups is equal (p=.065) and there was no difference in variance between the groups (t(141)=.556, p=.579).

B. Environmental temperatures

The predicted cloacal temperature was most strongly correlated with the ceiling temperature, followed by respectively the soil temperature, the ambient temperature and the temperature at top of the stone (*Table 3*).

Table 3: Correlation and number of measurements of the predicted cloacal temperature with environmental temperatures.

Location of environmental temperature	Correlation with predicted cloacal temperature	N
Ceiling temperature	.845	174
Soil temperature	.827	229
Ambient temperature	.607	219
Temperature on top of the stone	.572	175

Soil temperature

The predicted cloacal temperature and the soil temperature for the total dataset were closely related (*Figure 4A*). The data points imply a linear correlation. The predicted cloacal temperatures remained higher than the soil temperature during the whole spread in soil temperature. The regression analysis was not executed due to the non-normal distribution of the data set.

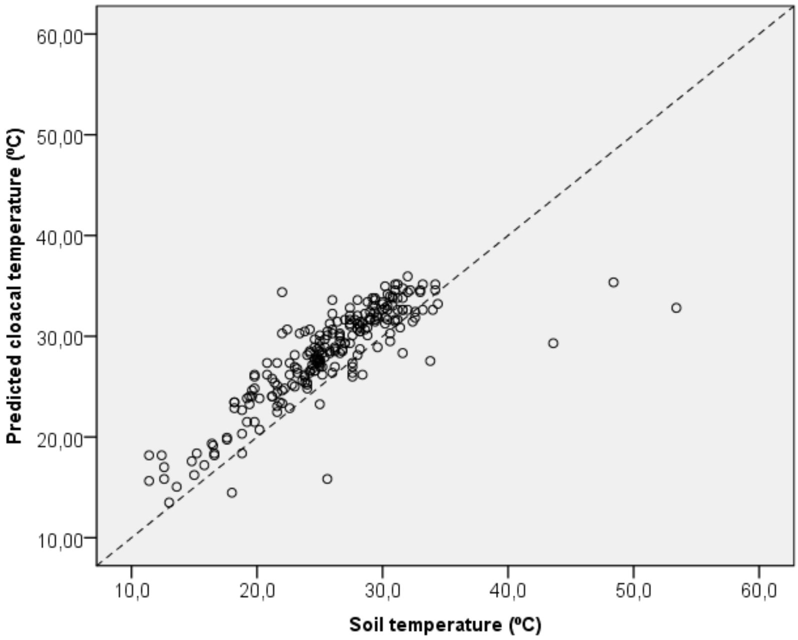


Figure 4A: Relationship between soil temperature and predicted cloacal temperatures for all encounters. Dotted line is isometric line (x=y).

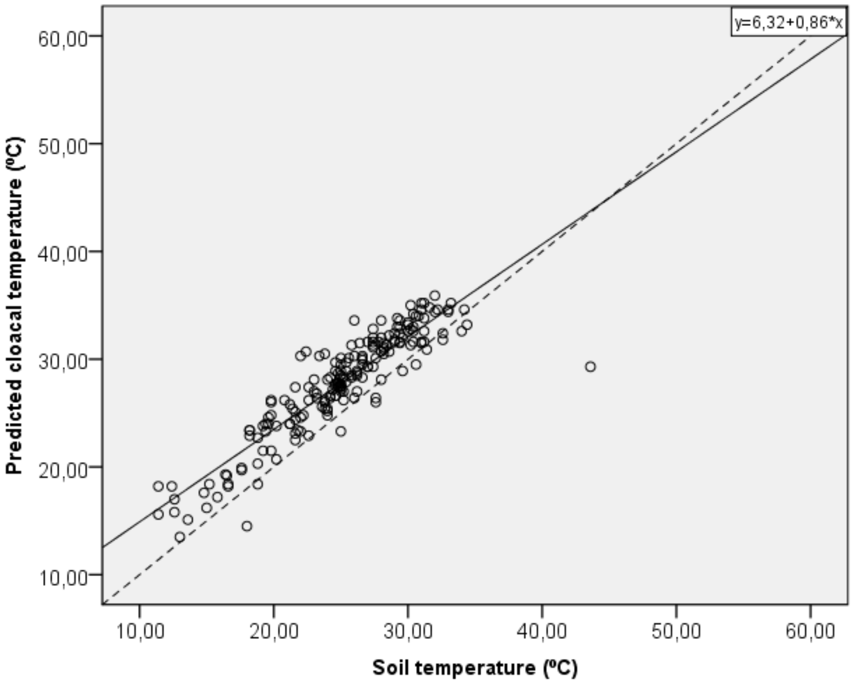


Figure 4B: Relationship between soil temperature and predicted cloacal temperatures for encounters with tortoises that were hiding in rock crevices. Line is regression; dotted is isometric line (x=y).

For tortoises that were hiding in rock crevices, most outliers of the dataset were excluded. The regression line for the hiding tortoises is given by the following formula (*Figure 4B*). The regression was tested on normality, linearity and constant variance (F(188)=828.061, p=.000, R^2=.816)

$$T_{\text{predicted cloaca}} = 6.318 + .859 * T_{\text{soil}}$$

Ceiling temperature

The predicted cloacal temperature and the ceiling temperature in a crevice were closely related (*Figure 5*). This regression satisfied the conditions and resulted in the following formule (p<.001):

$$T_{\text{predicted cloaca}} = 11.999 + .572 * T_{\text{ceiling}}$$

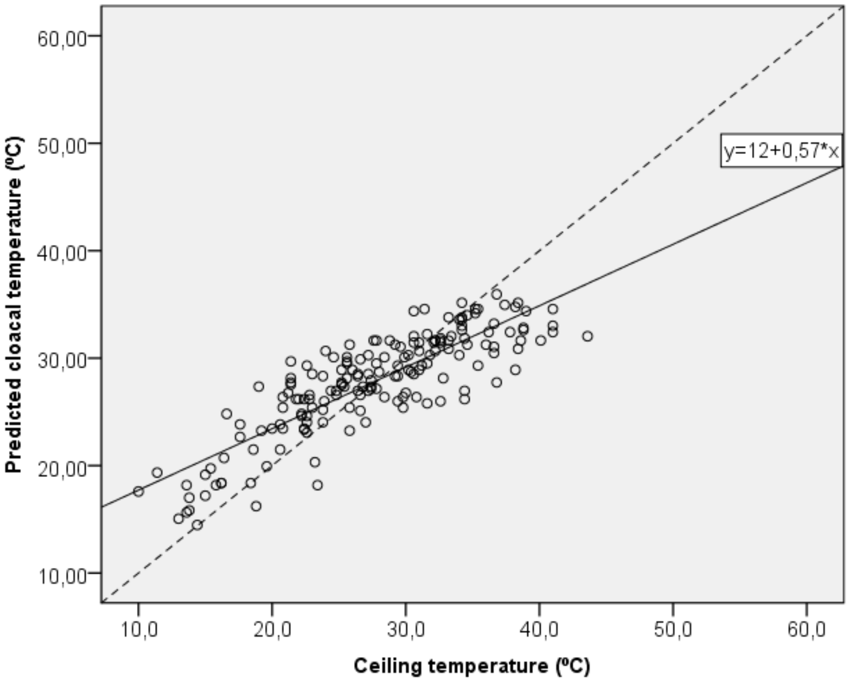


Figure 5: Relationship between the predicted cloacal temperature and the ceiling temperature in a crevice. Line is regression; dotted is isometric line (x=y).

In this figure 5, we see a linear pattern without outsiders. This predicted cloacal temperature is equal to the ceiling temperature on 28.04 °C. At ceiling temperatures beneath 28.04 °C, the predicted cloacal temperature remains higher than the ceiling temperature.

5. Dependency of multiple variables on the carapace temperature

A multiple linear regression was calculated to predict the cloacal temperature based on the soil temperature and the difference between soil temperature and ambient temperature. A significant regression equation with an R^2 of .689 was found (p<.005). The multivariable regression was checked for normality, linearity constant variance. This analysis resulted in the following formule:

$$T_{predicted\ cloaca} = 7.379 + .811 * T_{ambient} + .521 * (T_{soil} – T_{ambient})$$

With an ambient temperature increase of one degree Celsius, the predicted temperature increased .811 °C at a constant difference between soil temperature and ambient temperature. If the difference between the soil temperature and the ambient temperature increased with one degree, then the predicted cloacal temperature increased .521 °C at a constant ambient temperature.

A multiple linear regression was also calculated to predict the cloacal temperature based on the soil temperature, the ambient temperature and the ceiling temperature. These variables statistically significantly predicted the cloacal temperature with an R^2 of .815 (p<.005). All the variables added statistically significantly to the predicted cloacal temperature.
For tortoises which are hiding in a crevice, the following formule can be used:

$$T_{predicted\ cloaca} = 7.064 + .472 * T_{soil} + .139 * T_{ambient} + .198 * T_{ceiling}$$

If the soil temperature increased with one degree, then the predicted cloacal temperature increased with .472 °C. With an ambient temperature increase of one degree Celcius, the carapace temperature increased .139 °C. And if the ceiling temperature rises with one degree Celcius, then the carapace temperature will rise with .198 °C. A side mark is that this only counts if the other temperatures in this model stay constant.

CONCLUSION AND DISCUSSION

1. Body temperatures

The mean cloacal temperature for *C. boulengeri*, between 7:45 h and 18:50 h, was 26.55 °C. This mean temperature is lower compared to *Chersobius signatus*, which had a range from 28.9 to 30.9 °C during activity in spring (Loehr, 2012). Either, minimum and maximum ambient temperatures during the study period of *C. signatus* varied between 9.9 and 21.8 °C. These ambient temperatures were low compared to the ambient temperatures in this study period (Loehr, 2012).

The carapace temperatures reached high temperatures (maximum of 38 °C). The critical maximum temperature (the thermal point at which locomotory activity becomes disorganized and the animal loses its ability to escape from conditions that will promptly lead to its death) could be between 39.00 and 43.90 °C in testudines (Hutchison, Vinegar, & Kosh, 1966). Smaller tortoises have higher critical thermal maximum compared to larger turtles (Webb & Johnson, 1972), so for *C. boulengeri*, this could be above 39°C. The exact critical maximum temperature of *C. boulengeri* is unknown.

The temperatures before 7:45 h and after 18:50 h were not measured and thus cannot be included in the mean temperature. The true mean cloacal temperature is hypothesised to be lower, because of cold ambient temperatures at night. To determine the true cloacal temperature of this species, temperatures should be measured during 24 h, because the current time interval is not sufficient to calculate a mean cloacal temperature.

2. Transformation of the carapace temperature to a cloacal temperature

The cloacal, carapace and plastron temperatures were highly correlated and there was no significant difference between the temperatures on these locations. The cloacal temperature can function as representative of core temperatures for small tortoises (McMaster & Downs, 2013). The number of recorded measurements of cloacal temperatures was limited, so I decided to transform the carapace temperature into a cloacal temperature with a linear regression. The cloacal temperatures were not measured at every encounter, because of the invasive handling when recording a cloacal temperature.

The carapace temperatures were transformed to predicted cloacal temperatures by using a linear regression. The small body size of *C. boulengeri* probably helped reduce differences among measurements, and likely between cloacal and core body temperatures (Loehr, 2012; Mcmaster, 2007; McMaster & Downs, 2013; Webb & Johnson, 1972). The correlations between cloacal, plastron and carapace temperature and the high proportion of explanations of the regressions confirmed that de carapace temperature measurements could function as a parameter for the cloacal temperature. This approach is similar to the application of Loehr (2012).

3. Internal factors

Sex:

The results of this study indicate that there is no sexual difference in mean cloacal temperatures and in mean predicted cloacal temperatures between males and females. Because no significant difference was found between the sexes, I assumed that this equality applied to all other variables. This to prevent too small groups for further analysis. For more knowledge about sex differences in thermoregulation, future research may be needed.

Behaviours:

The behaviours seemed to have a significant difference in predicted cloacal temperature. The hiding tortoises turned out to have a lower mean predicted cloacal temperature than the walking and basking tortoises. Most of the hiding tortoises were hiding in a crevice. It seems that the soil temperature is higher when walking and basking. This results in higher body temperatures of active tortoises.

However, the sample size for feeding and courtship only consist of one measurement each. The sample size is thus too small to make a statement about these behaviours.

Activity:

The mean predicted cloacal temperature during activity is 30.99 °C. This is in accordance with the mean body temperatures for nine tortoise species from different regions during activity (27.0 to 34.7 °C) in Hailey & Coulson (1996). There was a significant difference in predicted cloacal temperatures between active and inactive tortoises. This can be explained by the changed environmental influences. First, the tortoises which were inactive, were most of the time in a crevice. They were almost never exposed to sun and the soil temperatures in the crevice were significant lower than the soil temperatures of active tortoises.

Inactivity is often observed during the measurements; 197 out of 244 measurements were from hiding tortoises. There could be multiple reasons for tortoises to remain inactive during the day. One of these arguments could be the risk for overheating (Loehr, 2012). Another, nonthermal, reason is the risk of predation by crows (Fincham & Lambrechts, 2014). Most animals modify their behaviour and reduce their activity levels in the presence of predators (Webb & Whiting, 2005).

The tortoises were named as inactive when they were hiding in a crevice or under a bush. The linkage of these locations with inactivity can be wrong. When we looked in a crevice in which a tortoise was hiding, multiple times, the tortoise was standing or walking in the crevice. Because the view in the crevice was limited and measurements were short period observations, it is unknown what was the pattern of behaviour inside the crevices. This can be studied with cameras in the crevices in future research.

Time of the day:

We can explain the course of the cloacal temperature over the day by the behaviour of the tortoises. For tortoises which are in direct sunlight, we expect them too cool down faster when ambient temperature decrease compared to hiding tortoises (Bauwens et al., 1999). The temperatures in the crevices are hypothesised to be more constant than the environmental temperatures, so the tortoises can be exposed to a more equal environmental temperature (Christian, Tracy, & Tracy, 2006). I assume that the tortoises did reach their temperature in the POTZ and that they attempt to keep their temperature constant, by choosing their microhabitats.

In *Figure 3* a lot of spread is visible. This can be explained by the method of measuring. These measurements are derived from multiple tortoises, on multiple days. Individual differences and variance between hot and cold days are not been taken into account in this figure. For future research, the usage of iButtons can give solutions for a more reliable diagram of the course over the day.

4. **External factors**

There is no influence found in type of rock on the predicted cloacal temperatures. For hiding tortoises, the ceiling temperature has the biggest correlation with the predicted cloacal temperature followed by the soil temperature and the ambient temperature.

For a regression between predicted cloacal temperature and the soil temperature, the data was not normally distributed, even after trying with transformed variables. For hiding tortoises, the normality, linearity and variance of the predicted cloacal temperature was acceptable for the regression.

When we look at the hiding tortoises, their predicted cloacal temperature is higher than the soil temperature. Their body temperature is closely related to their environment, so we can conclude that *C. boulengeri* is rather a thermoconformer than a thermoregulator. Apparently, the temperature of the ceiling of the stones has a big effect on the body temperature. Maybe, applying only the soil temperature in the determination of the FPBT is incomplete. A tortoise can thermoregulate by responding to heat transfer by conduction, radiation, convection and evaporation. When hiding in a crevice, the conduction takes place with the soil. The radiation comes from heat as a result by warming by the sun directly derived from the ceiling. The influence of convection on thermoregulation is expected to be small in crevices, because airflow is limited. No evaporation by panting or salivation is observed during the study period.

The temperature on which the predicted cloacal temperature meets the soil temperature, is expected to be the field preferred body temperature (FPBT). The FPBT of hiding tortoises is calculated on 41.81 °C. This is not realistic, because this exceeds the maximum critical temperature for tortoises. So this calculated temperature is excluded from the results.

In the graph with the ceiling temperature a linear correlation is found. These points cross the isometric line at 27.91 °C. Above this temperature, tortoises try to maintain a colder cloacal temperature. Under 27.91 °C, the cloacal temperatures are warmer than the ceiling. This can be caused by either another way of heat transfer (e.g., extending or withdrawing extremities) or by (physiologically) retaining heat or by shuttling between cool and warm sites in a crevice.

5. **Multivariable regression and thermoregulation**

The dependency of multiple variables on the carapace temperature was determined with a multivariable linear regression analysis. The analysis was started with the following variables: sex, behaviour, ambient temperature, difference between soil and ambient and the predicted cloacal temperature. Only the significant influences were included in the model. The soil temperature and the ambient temperature seemed to have most influence on the carapace temperature. For hiding tortoises, soil temperature, ambient temperature and ceiling temperature affected the predicted cloacal temperature most. The effects of the soil temperature were biggest, followed by respectively the ceiling temperature and the ambient temperature. In this model, the soil temperature reflects the conduction. The ceiling temperature reflects the radiation and the ambient temperature can function as a parameter for the convection of heat transfer (Fei et al., 2012).

Recommendations

When measuring the cloacal temperature with a calibrated thermocouple, there could be some inaccuracy. To optimise the measuring, it is necessary to record temperatures in a standardised way. This could be realised by determining how far and how long the thermometer will be placed in the tortoise and by performing controlling measurements.

For more continual measurements during the day, for an exact determination of the carapace temperature and for preventing inaccuracies while measuring the temperature of a tortoise, the carapace temperatures can be measured with iButtons (Mcmaster, 2007). Because of the small body size of *C. boulengeri,* it was now choosen not to use iButtons, but maybe this will be an option in future studies.

We had a limited number of measurements of active tortoises, so drawing conclusions about the specific behaviours was unreliable. Emphasising on the active tortoises by measuring them multiple times on a day could result in more data on these active tortoises.

Furthermore, the crevices seems to be very important for the thermoregulation and conservation of the tortoises. More specific information about the climate and behaviour in the crevices could explain the typical hiding-behaviour. This information could also give opportunities for the conservation of *C. boulengeri*. For example by supporting the preservation of the crevices in their habitat.

In this research an overview of the thermoregulatory factors in *C. boulengeri* is given which may help to clarify the lifestyle of this tortoise. Because of the proposed Endangered status on the IUCN red list, the importance of research on the thermoregulation, for conservation measures is even more important.

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