The importance of body posture and orientation in the thermoregulation of *Smaug giganteus*, the Sungazer

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Abstract

Body temperature (T_b) is the most influential factor affecting physiological processes in ectothermic animals. Reptiles use behavioural adjustments, i.e. shuttling behaviour and postural and orientation adjustments, such that a target T_b (T_{target}) can be attained. T_{target} is attained so that various physiological functions can occur within their respective thermal optima. The Sungazer, *Smaug giganteus,* is unique amongst the Cordylidae in that individuals inhabit self-excavated burrows in open grasslands, where conductive heating is restricted. Therefore, their T_bs are more likely influenced by postural and orientation adjustments than by conductive mechanisms. The purpose of this study was to measure the T_{target} of Sungazers and to assess the impact of body posture and orientation on thermoregulation in Sungazers. Thermocron® iButtons were modified to function as cloacal probes, set to record temperatures every minute and were inserted in the cloacas of 18 adult Sungazers. Sungazers were released at their respective burrows where camera traps recorded photographs every minute of the diurnal cycle to record behaviour. Copper models recorded the range of operative temperatures; an exposed model set up in "sungazing" posture, and a model inserted 0.5 m into an active Sungazer burrow. Data were successfully recorded from nine Sungazers. Sungazers achieved a T_{target} of 30.17 ± 1.35 ˚C (Mean ± SD) and remained at this range for 332.56 ± 180.60 minutes (Mean ± SD). There was a significant effect of the anterior body-up (high) and anterior body-up (low) posture on T_b, which were significantly different to all other postures. An anterior body-up (high) posture was the only posture that enabled Sungazers to achieve their T_{target}, with a heating rate of 2.57 ºC ± 3.62 ºC per 15 minutes. A significant difference in the time spent at each posture was apparent and a limited time (25.11 ± 44.01 min) was spent at the anterior body-up (high) posture. Orientation of basking Sungazers showed no statistically significant effect on $T_{b,}$ however lizards heated up faster facing when away from the sun (2.66 ºC ± 2.50 ºC per 15 min) and spent proportionally more time facing this orientation in the morning when T_bs were lower than T_{target}. This study suggests that changes in climatic conditions will result in basking Sungazers either increasing or reducing the time spent in an anterior body-up (high) posture while orientated away from the sun in order to achieve thermal demands.

Keywords

behavioural thermoregulation, body posture, orientation, *Smaug giganteus*, target temperature, thermal profile

1. Introduction

1.1 Thermoregulation

Body temperature (T_b) is the most influential factor of ecophysiology in ectothermic animals (Angilleta Jr. *et al.*, 2002), and has a significant impact on growth, digestion and locomotion and metabolic processes (Seebacher and Franklin, 2005; Truter, 2011). While most endothermic animals typically regulate their T_bs within a narrow range and are considered to be thermal specialists (Ivanov, 2006; Truter, 2011), reptiles (ectotherms) have a wider selected thermal range (Truter, 2011), in which a target T_b (T_{target}) is achieved (Alexander, 2007). Reptiles primarily rely on behavioural mechanisms (e.g. site selection, postural and orientation adjustments and shuttling behaviour) in an attempt to reach T_{target}, the temperature at which many physiological functions occur within their respective thermal optima (Truter, 2011). Behavioural adjustments in the form of postural and orientation adjustments are often used to modify the rates of thermal exchange (Alexander, 1996). These behaviours aid the animal in its ability to control T_b at levels that are conducive to its performance. Should temperature extremes occur within the environment, the animal's physiological and behavioural components regulate their T_bs to a narrow range in comparison to environmental temperatures (Angilleta Jr. *et al.*, 2002).

Behavioural thermoregulation in reptiles was first investigated in desert-dwelling lizards by Cowles and Bogert (1944). Since this seminal work, behaviour has been regarded as the principal mechanism of reptile thermoregulation (Avery et al. 1982; van Wyk, 1992; Truter, 2011). Reptiles thermoregulate by modifying rates of heat gain and loss to the environment, and temporal variation within the environment accounts for variation in diel and seasonal activity patterns and T_b variations (van Wyk, 1992; Diaz and Cabezas-Diaz, 2004). Since the primary mechanism for thermoregulation in reptiles is through behaviour, aspects such as shuttling, postural and orientation adjustments as well as regulated activity periods are vitally important in achieving T_{target} (Huey, 1962; Muth, 1977; Bohorquez-Alonso *et al.*, 2011; Truter, 2011).

Muth (1977) associated different postures and orientations with T_b of *Callisaurus draconoides*, an American Phrynosomatid lizard. The study also highlighted the role of posture in rates of heat exchange and found significant differences in heating rates for different postures (Muth, 1977). A more recent study on *Gallotia galloti*, a Lacertid lizard, highlighted the importance of posture and orientation in relation to the position of the sun

(Bohorquez-Alonso *et al.*, 2011). The study found that postural and orientation adjustments not only directly impact an ectotherm's ability to thermoregulate, but also contribute to efficient social signalling (Bohorquez-Alonso *et al.*, 2011). Typical postures range from a body-down posture to an anterior body-up high posture (van Wyk, 1992; Fig. 1), with subtle adjustments (Greenberg, 1977). These postures were explored through Greenberg's (1977) work on *Sceloporus cyanogenys*, a Phrynosomatid lizard, in which lizards adjusted postures based on thermal requirements. Van Wyk (1992) expanded the work on body postures through research on *Smaug giganteus*, a South African Cordylid, in which he assigned body postures to several different categories (Fig. 1). He found that Sungazers spend most of their activity period in anterior body-up postures, maximising the exposure of the dorsal parts of the body to the sun (van Wyk, 1992). Additionally, orientation changes accordingly based on the position of the sun as lizards attempted to regulate heat gain from the environment (van Wyk, 1992).

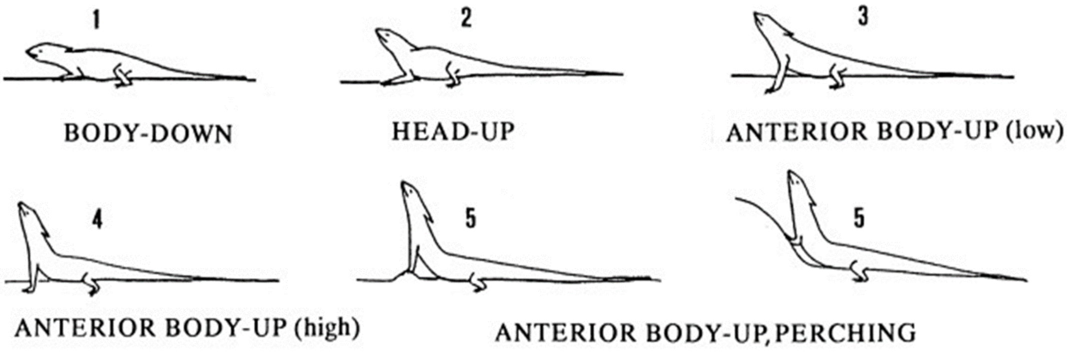

Figure 1: Typical body postures adopted by *S. giganteus* (van Wyk, 1992).

1.2 Family: Cordylidae

The Cordylidae is the only lizard family endemic to mainland Africa (Bates *et al.*, 2014). Cordylids occupy an array of habitats but the majority of species are strictly rupicolous (Tolley, 2010; Bates *et al.*, 2014). However, there are species that are not rupicolous: three species of *Chamaesura*, two species of *Cordylus* (*Cordylus macropholis* and *Cordylus ukingensis*), and *Smaug giganteus* are considered terrestrial, while two *Cordylus* species, *Cordylus jonesi* and *Cordylus tropidosternum*, are considered arboreal (Bates *et al.*, 2014). Cordylids are diurnal, mostly insectivorous and generally ambush foragers, with many species showing well developed territoriality (Bates *et al.*, 2014). Rupicolous Cordylids live in habitats that are mostly not impacted from human transformation (Bates *et al.*, 2014).

However, terrestrial Cordylids such as *S. giganteus* are threatened by land transformation and illegal harvesting (Parusnath, 2014).

Rupicolous Cordylids use rocks to facilitate basking. Due to the nature of the substrate, rocks heat rapidly, due to insolation, and cool convectively allowing them to make a suitable substrate for basking lizards (Tolley, 2010). Sungazers inhabit open grasslands, a habitat that tends to be devoid of rocks, and hence conductive heating in Sungazers, when they are out their burrows and in the surrounding grass patches, is limited. Although postural and orientation adjustments are largely understudied in the Cordylidae, it is possible that since conductive heating is limited among Sungazers because of their habitat, postural and orientation adjustments are likely more commonplace behavioural mechanisms that are employed in comparison to most rupicolous Cordylids, where conductive heating is frequent (Truter, 2011). While rocks are important basking sites for rupiculous species, terrestrial and arboreal Cordylids bask using other vantage sites, if available (Muth, 1977; Clusella-Trullas *et al.*, 2009).

Despite the Cordylidae being a unique and diverse family, the thermoregulatory characteristics of species within this family have received little research attention (Truter, 2011) and T_bs of few Cordylids have been measured. For species where measures have been made, T_bs tend to range from 28.9 °C (*Cordylus macropholis*; a thermoconformer; Bauwens *et al.*, 1999) to 30.8 °C, 32.3 °C, 33.8 °C and 33.4 °C in *Cordylus cordylus*, *Cordylus niger*, *Cordylus polyzonus* and *Cordylus oelofseni* respectively (Clusella-Trullas *et al.*, 2007), but measures are likely also partially dependent on methods employed. These species showed clear evidence for thermally-motivated decisions as they shuttled between the shade and sun as needed (Bowker, 1984). Van Wyk (1992) recorded the range of T_bs (27 ºC-40 ºC) in a single individual *S. giganteus*. However, to date, there is no measure of T_{target} for this species.

1.3 Measuring T_b

Thermocron® iButtons are widely used in biological studies on thermal physiology (Robert and Thompson, 2003; Lovegrove, 2009). However, they present a challenge when working with small animals, where the iButtons are too large to be implanted internally/sub-cutaneously. Veterinary assistance is also needed if iButtons are surgically implanted and this can be a logistical impediment when working in the field. However, modification of Thermocron® iButtons to reduce the weight and size by de-housing and trimming the circuit board has proven to be successful when working with smaller animals (Robert and Thompson, 2003; Lovegrove, 2009; Truter, 2011).

Truter (2011), modified iButtons which were then glued to the dorsal region of individuals of *Cordylus cataphractus* such that indirect measures of T_b could be made. To show that modified iButtons would be accurate tools for measuring T_b, Truter (2011) measured the relationship between the mounted iButton and cloacal temperature. The results showed a positive correlation ($R^2 = 0.93$) between the two devices suggesting that modified iButtons are effective tools when performing thermal studies on small animal species such as small lizards (Truter, 2011).

1.4 Assessing T_{target}

Alexander (2007) performed research on the thermal biology of Southern African Pythons (*Python natalensis*) in which criteria were introduced to identify whether or not a python was at its T_{target} (see Alexander, 2007). Since these criteria can be applied to all reptiles that employ basking, they can used to assess whether or not the T_{target} of Sungazers falls within environmental temperatures (T_e) (Fig. 2). Furthermore, evidence for behavioural thermoregulation (thermally-induced decisions) needs to exist so that an assessment of a lizards T_{target} can be made (Fig. 2).

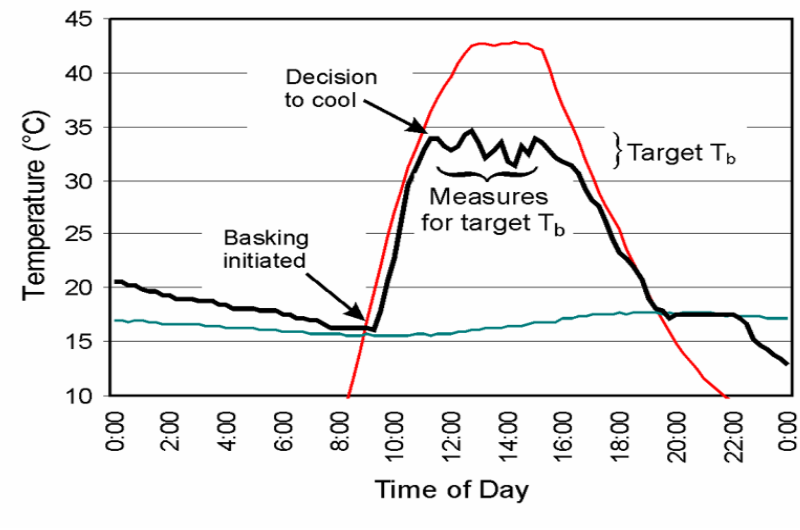

Figure 2: Thermal profile over a 24 hour period. Red line represents measures of maximum environmental temperatures, blue line represents minimum environmental temperatures and the solid black line represents T_b of a reptile. Figure adapted from Alexander (2007).

1.5 Study Purpose and Aims

Previous research has attempted to measure the range of T_bs of Sungazers, as well as the postures and orientations that are selected during basking (van Wyk, 1992). However, the range of T_bs were lightly investigated since the study only recorded T_bs of a single lizard. The previous research also assessed how behavioural mechanisms vary seasonally (van Wyk, 1992). However, these behavioural factors have not been investigated as mechanisms behind Sungazer thermoregulation, as no link has been made with the postures and orientation, and T_b. This leaves a gap in our understanding of how posture and orientation affect heat exchange rates in the Sungazer in an environment lacking in structural heterogeneity. Understanding this information will form the next step in assessing whether or not limits in Sungazer thermoregulation implicate their range limitation. The aims of this study are to: 1) measure T_{target} in *Smaug giganteus*, 2) assess the effect of body postures and orientations on thermoregulation in *S. giganteus* and 3) assess the effect of body postures and orientations on the rates of heating in *S. giganteus*.

2. Methods

2.1 Study site

Sungazers were monitored at their burrows on two farms in the Volksrust district of Mpumalanga – both of which had high densities (more than the mean of 11.24 ± 7.27 individuals/ha; Parusnath, 2014) of Sungazers. During January 2015, Sungazers were monitored on a farm approximately 30 km North of Volksrust and during May 2015, another colony was monitored on a farm approximately 25 km North West of Volksrust. These farms occur in the *Themeda triandra* dominated Highveld grasslands with an open landscape with few rock outcrops or trees (Bates *et al.*, 2014). Termite mounds (*Trinervitermes trinervoides*) are dispersed in the habitat. Temperatures are generally described as temperate to cool where summers are relatively warm and winters cold (van Wyk, 1992). Most rainfall (approximately 70%) occurs during the summer months (November to March) and annual means are between 600 mm and 700 mm (van Wyk, 1992). However, leading into the winter months (June to August), when Sungazers are inactive, rainfall is reduced, accounting for approximately 5% of the annual precipitation (van Wyk, 1992).

2.2 Study species

Smaug giganteus is a heavily-armoured, Threatened (V) Cordylid lizard, endemic to the Highveld grasslands of South Africa, in the north-eastern Free State and southern

Mpumalanga provinces (Branch and Patterson, 1975; De Waal, 1978; Jacobson, 1989; Parusnath, 2014). Sungazers live in self-excavated burrows in gently sloping *Themeda trianda* grasslands (Bates *et al.*, 2014; Parusnath; 2014). These diurnal lizards make frequent use of their burrows throughout the day and activity is generally within a one-metre radius of the burrow mouth. A total of 18 Sungazers were monitored across the two study sites; 10 in January 2015 and eight in May 2015.

2.3 Experimental design and protocol

2.3.1 iButton Modification

Fifteen Thermocron® iButtons (DS1922L) were modified for cloacal insertion in Sungazers. They were de-housed and deconstructed following the methodology by Lovegrove (2009). The circuit board was completely removed from the battery, and three flat wires, each 30 mm in length, were attached to the battery and circuit board terminals and secured with heat shrink. Insulated wires were then soldered to the input/output (I/O) terminal of the circuit board and ground tab of the battery, respectively, so that the iButtons could be set to record a mission (Lovegrove 2009). The entire probe was dipped in wax to seal the circuitry against moisture (Fig. 3). Modified iButtons were programmed to record temperatures every minute using the software program, 1-Wire version 1.0.0.1 (Maxim Integrated).

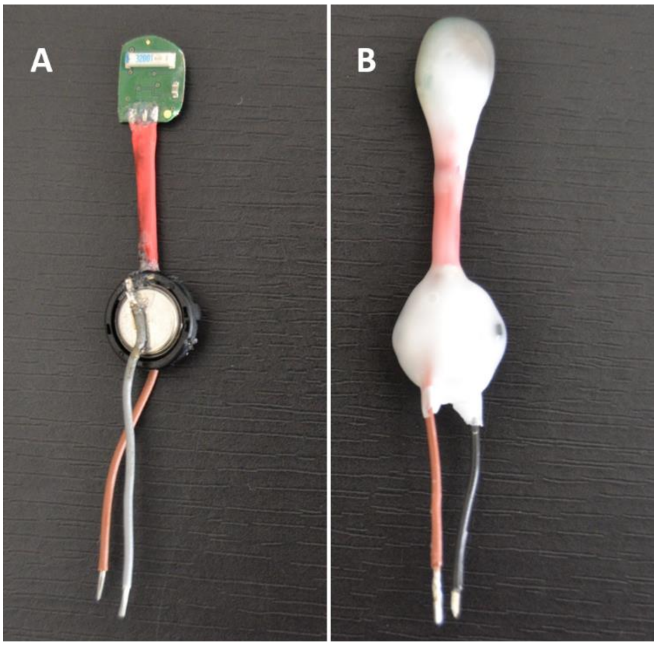

Figure 3: Modification of iButtons. A – Modified iButton showing the wires attached to the circuit board and battery. B – Modified iButton after wax coating.

2.3.2 Sungazer capture and release

Noose traps (van Wyk, 1992) were placed at burrow entrances using standardised noosing techniques. Once secured, the traps were deployed and checked at 10-minute intervals. Noosed lizards were carefully removed from their burrows so as to prevent their occipital spines from anchoring to the roof of the burrow (van Wyk, 1992).

Longitude/latitude coordinates of the burrows of captured lizards were recorded. iButtons were disinfected using F10 disinfectant spray and lizards' cloacas were cleaned and disinfected using the same substance. Following this, a waxed circuit board was inserted into each lizard's cloaca, facilitated with KY gel lubrication. The exposed battery and wires were secured to the ventral scales of the tail with superglue and micropore tape wedged between the tail spines. The lizards were then released into their home burrows.

Bushnell Trophy Cam HD 119577 camera traps were programmed to take a photograph every minute between 05h00 and 18h30 so as to include the full range of Sungazer activity period. Cameras were secured to tripods setup at an appropriate position to photograph the burrow entrance of each released Sungazer. All cameras were set to face north to facilitate orientation analysis.

Modified iButtons and camera traps were left to record over a period that included at least one full diel cycle. Data recorded on the day following iButton and camera deployment allowed for lizards to habituate to the scientific apparatus. Lizards were recaptured on the third day using the same methodology, so that iButtons could be removed; their cloacas were cleaned using F10 and they were released back into their burrows.

2.3.3 Model Sungazers

Copper models similar in shape, size (150 mm X 30 mm copper tubing filled with silicon with inserted iButton) and posture of the study species were used to record operative temperatures (T_e) (Shine and Kearney, 2001; Diaz and Cabezas-Diaz, 2004; Truter, 2011) in order to assess the thermal range available to the lizards. Two models were programmed to record temperature every minute and were set up at the central burrow within the colony that was being monitored to record T_e; one was positioned in a "sungazing" posture, while the other was placed 0.5 m inside a burrow. Models provided measures of the temperatures available to the lizard throughout the day and the sun-gazing model gave temperature readings that a Sungazer could reach if it remained at an anterior body up high posture the entire day. These models allowed me to assess the climatic patterns throughout a day. Before the models were positioned, they were programmed to record temperatures every minute and were setup during both data collection periods for the Sungazers.

2.4 Data analysis

2.4.1 Temperatures

Operative temperatures and measures of lizard T_b were downloaded and graphed showing the thermal profile of Sungazers as well as the environmental temperatures from the models (Fig. 2). The T_{target} was calculated for each lizard using the method described in Alexander (2007). The behaviours (thermally-motivated decisions) that Sungazers performed were inferred from the different body T_bs.

2.4.2 Posture and orientation

Photographs from the cameras were downloaded and the orientation of each Sungazer was scored as one of eight compass points for each photograph. A body posture was also assigned to the lizard in each photograph following the standard Sungazer thermoregulatory postures defined by van Wyk (1992) (Fig. 1). Since photographs were captured every minute, each posture and orientation was linked to a T_b measurement from the iButtons.

Delta T_b was calculated for each lizard at each posture and orientation. For this, a change in T_b, for both posture and orientation, was calculated at 15 minute intervals. This allowed for an assessment of the rates of heating between postures and orientations. I also introduced a second category of orientation; facing the sun and facing away from the sun. For this category, I used the same method to calculate the rates of heating in the lizards.

The percentage of each hour during the day (between 06:00 a.m. and 19:00 p.m.), at an East, West, North and South orientation was recorded for each lizard and an average for all nine lizards was calculated for the respective orientations. Following this methodology, I was able to assess Sungazer orientation patterns relative to the position of the sun.

2.4.3 Statistical analysis

Mean T_b for each posture and orientation was calculated for each lizard and an average for all nine lizards at the different postures and orientations was calculated. Data were tested for normality and necessary transformations were made. A single-factor analysis of variance (ANOVA) was used to compare the link between these T_bs and respective postures and orientations. I assessed whether a lag effect between each postural and orientation adjustment existed. To assess this, I assigned a five minute T_b delay to each respective posture and orientation, performed a single-factor ANOVA and graphed the results. Furthermore, the average time that the lizards spent at each posture and orientation was calculated and a single-factor ANOVA was performed for each category (posture and orientation) to test for significant differences. An independent t-test was used to test for a significant difference between the rates of heating facing the sun and facing away from the sun. A single-factor ANOVA was performed to test for significant differences for heating against different postures and orientations. Lastly, the data showing the percentage of time spent, per hour, at a particular orientation was arcsine transformed in Microsoft Excel 2013 and a repeated-measures ANOVA followed to test for significant differences. Post-hoc Tukey HSD tests were conducted for all ANOVA and repeated-measures ANOVA tests to identify where significant differences between the groups exist. All statistical analyses were conducted using statistical software, Statistica version 8.

3. Results

3.1 ***Thermal Profile***

Data were successfully captured and analysed for nine lizards; four from the January 2015 collection period and five from the May 2015 collection period. Data from the remaining nine lizards could not be analysed due to battery failures in the iButtons that resulted from water damage in moist Sungazer burrows. A representative figure showing the thermal profile of one lizard is shown below (Fig. 4). In general, T_b follows the trend of the Sungazing model (external operative temperatures (T_e). At approximately 08:45 a.m. T_es begin to rise above burrow temperatures (T_{burrow}) which remains fairly constant at approximately 20 ºC (Fig. 4). Basking is initiated at approximately 10:15 a.m. and T_b begins to rise (Fig. 4). Before reaching T_{target}, T_e shows a decrease which is paralleled with the Sungazer's T_b decrease. Coupled with the decrease in T_e during this time, darkened photographic images suggest the presence of cloud cover. Thereafter, temperatures begin to rise and between 13:05 p.m. and 17:47 p.m. this lizard is at its T_{target} which is 29.75 ºC ± 0.70 ºC (Mean ± SD) (Fig. 4; Table 1.). This representative spends approximately 283 minutes at its T_{target} (Table 1).

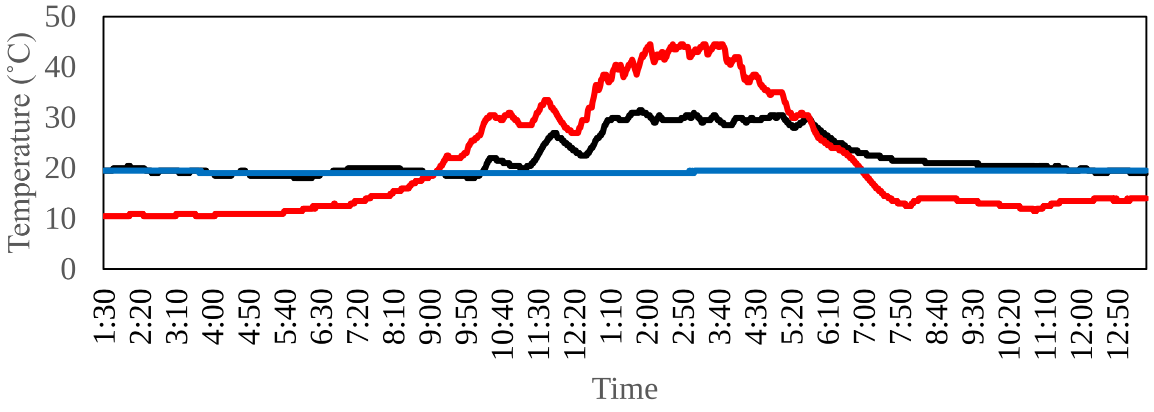

Figure 4: Thermal profile of lizard 1006A over a 24 hour cycle. The red line represents T_e recorded the sun-gazing model, the blue line represents T_e within burrows and the black line is representative of T_b of Sungazer 1006A.

On average, Sungazers achieved an average T_{target} of 30.17 ºC ± 1.35 ºC (Mean ± SD) (Table 1). Furthermore, an average of 332.56 ± 180.60 minutes (Mean ± SD) are spent within the T_{target} range, with the shortest time being from lizard 1030A at only 95 minutes (Table 1). The greatest time spent at T_{target} was from lizard 1008B at 594 minutes (Table 1).

Table 1. The T_{target} and time spent at T_{target} for each lizard. Data are shown with standard error from each individual.

Lizard Reference Number	Target Body Temperature ± Standard Deviation (ºC)	Time Spent at Target T_b (Min)
1005A	30.76 ± 1.18	215
1006A	29.75 ± 0.70	283
1008B	29.27 ± 1.86	594
1030A	31.80 ± 1.07	95
1033A	32.49 ± 1.08	108
1038A	29.26 ± 1.38	347
1052A	30.49 ± 0.98	586
1075A	27.74 ± 1.97	383
1102A	29.98 ± 1.90	382
Mean:	30.17 ± 1.35	332.56 ± 180.60

3.2 Effects of Posture

Body posture influenced the mean T_b (ANOVA, $F_{4,36} = 8.51$, $P < 0.05$; Fig. 5.1). The anterior body-up (high) posture had the greatest impact on T_b relative to the rest of the postures, except for the anterior body-up (low) posture (Tukey HSD, $P > 0.05$). Moreover, at an anterior body-up (high) posture, Sungazers achieved their T_{target} ($\bar{x} = 30.17$ ˚C ± 1.35 ºC; Fig. 5.1). The rest of the body postures resulted in the Sungazers being able to achieve T_bs below T_{target} but within T_e and T_{burrow} (Fig. 5.1).

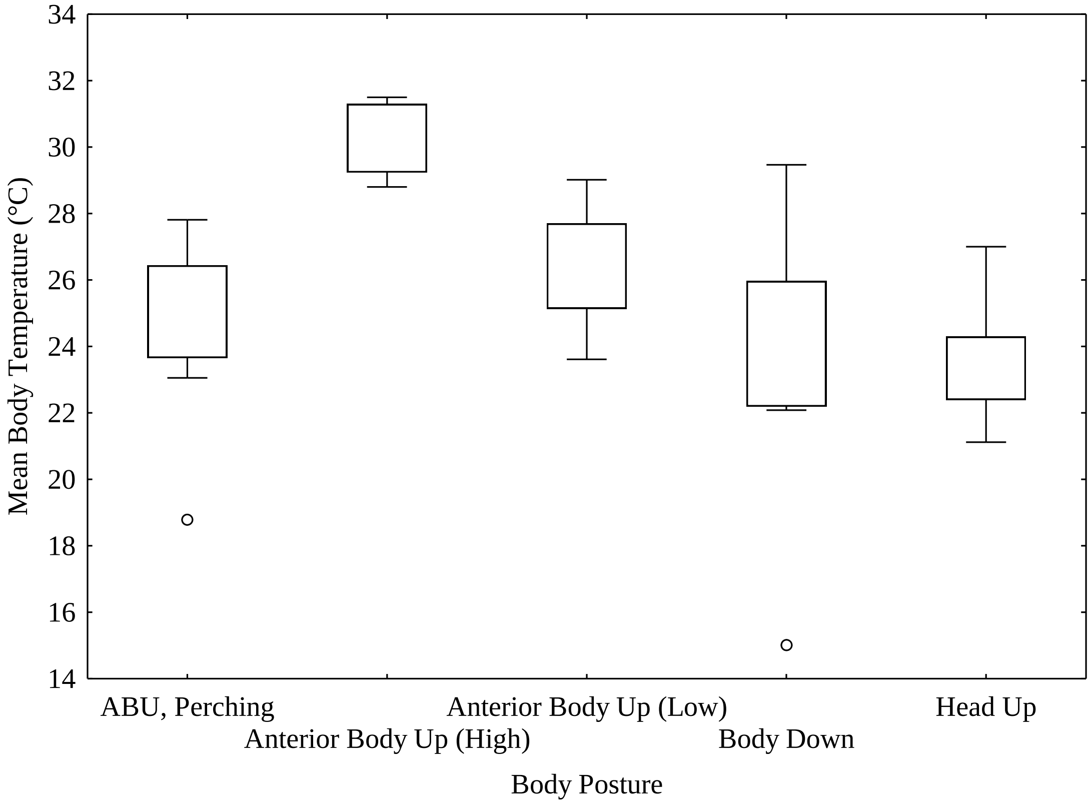

Figure 5.1: The effects of body posture on the mean T_b that the lizards were able to achieve. ANOVA, $F_{4,36} = 8.51$, $P = 0.00006$, significant differences exist among the postures. Open circles are representative of outliers.

Similarly, Sungazers spend, on average, a different amount of time at each body posture diurnally (ANOVA, $F_{4,40} = 9.52$, $P < 0.05$). A preference for the anterior body-up (low) posture ($\bar{x} = 146 \pm 47.98$ min) is shown while a preference for an anterior body-up (high) and body down posture with $\bar{x} = 25.11 \pm 44.01$ min and $\bar{x} = 16.22 \pm 21.06$ min, respectively, is limited (Fig. 5.2).

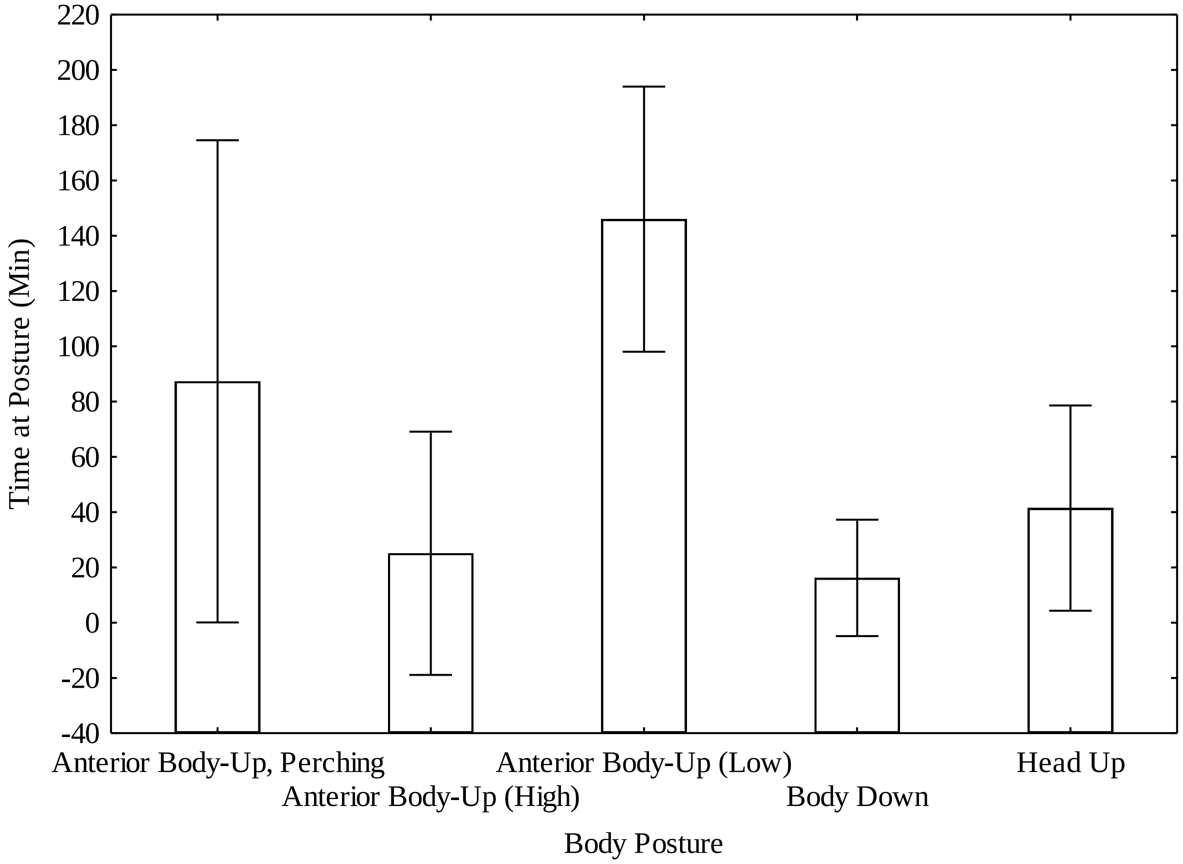

Figure 5.2: The mean time spent at each posture during a day. Results are representative of x̄ ± SD from the individuals at each body posture (n = 9 for each posture). ANOVA, $F_{4,40}$ = 9.51, P = 0.00002, significant differences exist among the postures.

3.2 Effects of Orientation

The mean T_b that the lizards were able to achieve was not influenced by orientation (ANOVA, $F_{7,64}$ = 0.81, P > 0.05; Fig. 6.1). Mean T_bs remained with in the 20 ºC-30 ºC interval with no orientation resulting in the lizards T_{target} (Fig. 6.1). Similarly, lizards showed no preference for a particular orientation throughout the day (ANOVA, $F_{7,64}$ = 1.22, P > 0.05; Fig. 6.2). The lizards spent the shortest amount of time (x̄ = 20.56 ± 19.36 min) in a North orientation (Fig. 6.2).

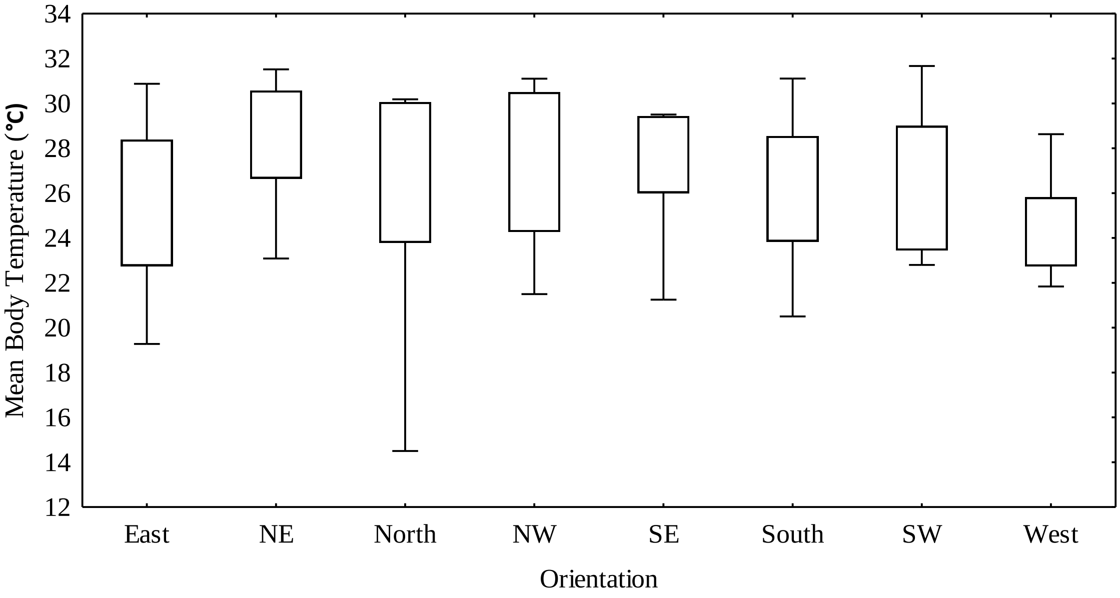

Figure 6.1: The effects of body orientation on the mean T_b that the lizards were able to achieve. ANOVA, $F_{7,64} = 0.81$, $P = 0.58$, no significant differences exist among the orientations.

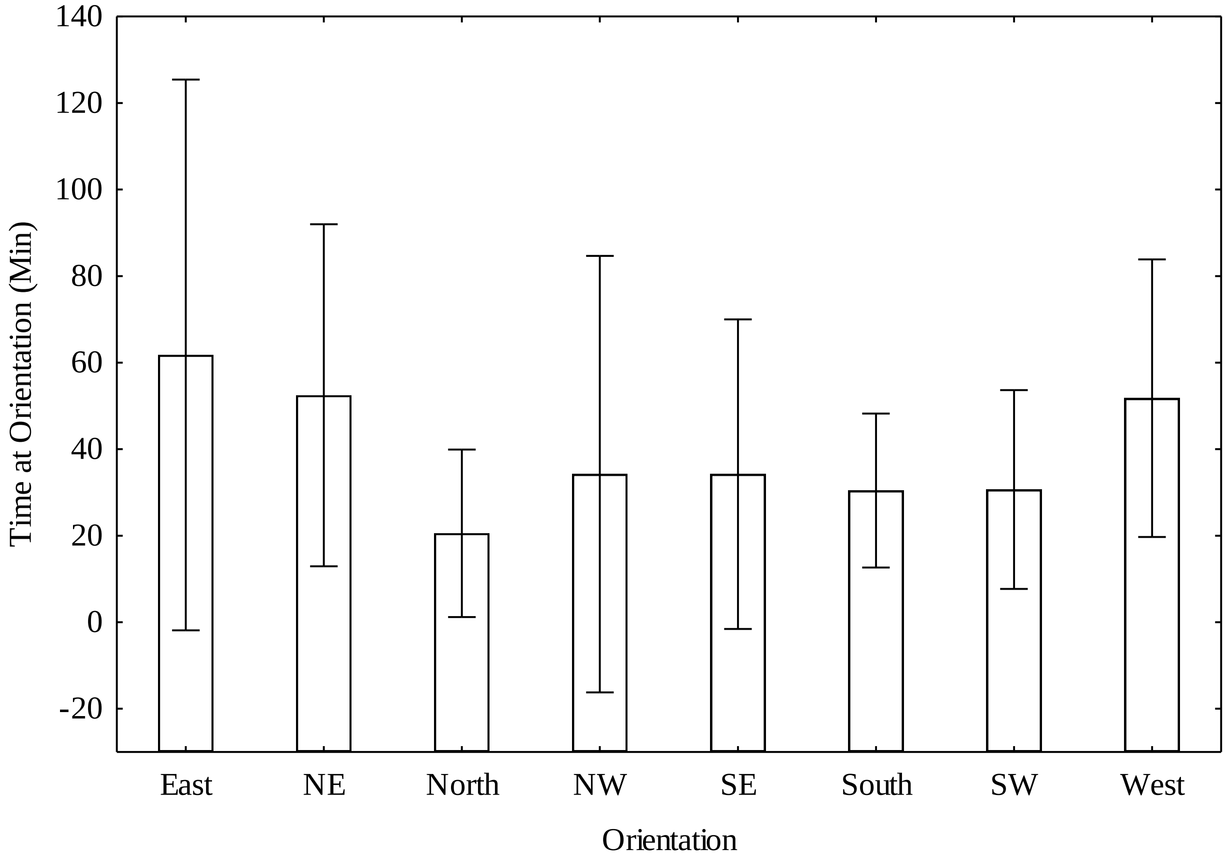

Figure 6.2: The mean time spent at each orientation during a day. Results are representative of x̄ ± SD from the individuals at each orientation (n = 9 for each orientation). ANOVA, $F_{7,64} = 1.22$, $P = 0.30$, no significant differences exist among the orientations.

3.3 Rates of Heating

On average, changing body postures varies the rates of heating significantly (ANOVA, $F_{4,32} = 2.79$, $P < 0.05$; Fig. 7.1). Lizards heat faster ($\bar{x} = 2.57$ °C ± 3.62 ºC per 15 min) in an anterior body-up (high) posture (ANOVA, $F_{4,32} = 2.79$, $P < 0.05$; Fig. 7.1). No differences exist among the rates of heating at the rest of the four postures (Post hoc Tukey HSD, $P > 0.05$). However, the trend is that a head up posture results in a loss, rather than a gain of heat ($\bar{x} = -0.48$ ºC ± 1.05 ºC per 15 min; Fig 7.1).

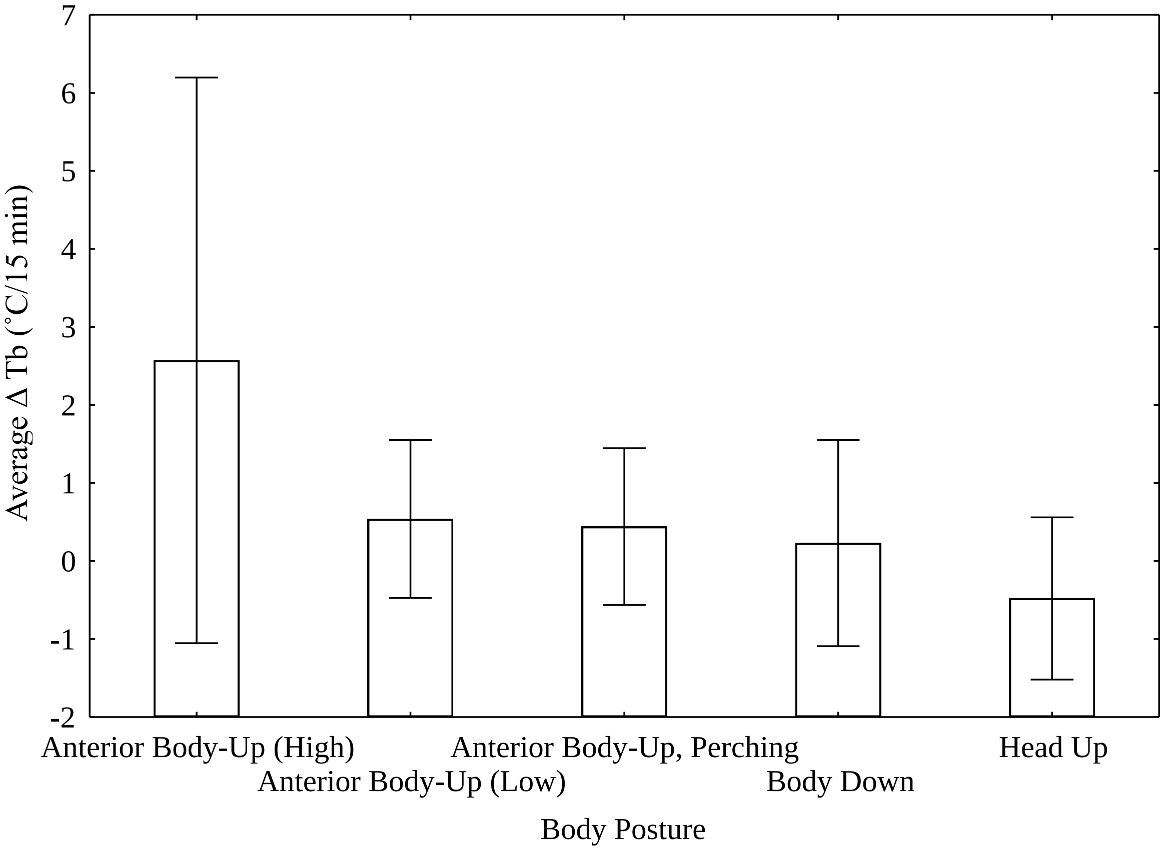

Figure 7.1: The mean change in T_b per 15 minutes at each body posture. Results are representative of $\bar{x}$ ± SD from the individuals at an anterior body-up (high) posture (n = 5), anterior body-up (low) posture (n = 9), anterior body-up, perching posture (n = 9), a body-down posture (n = 6) and a head-up posture (n = 8). ANOVA, $F_{4,32} = 2.78$, $P = 0.04$, significant differences exist among the postures.

Changing orientations did not change rates of heating significantly (ANOVA, $F_{7,63} = 0.70$, $P > 0.05$; Fig 7.2). The mean rate of heating for individuals was never more than 1.82 ºC ± 0.69 ºC per 15 minutes (Fig. 7.2). However, the rates of heating across orientations were similar (Fig. 7.2).

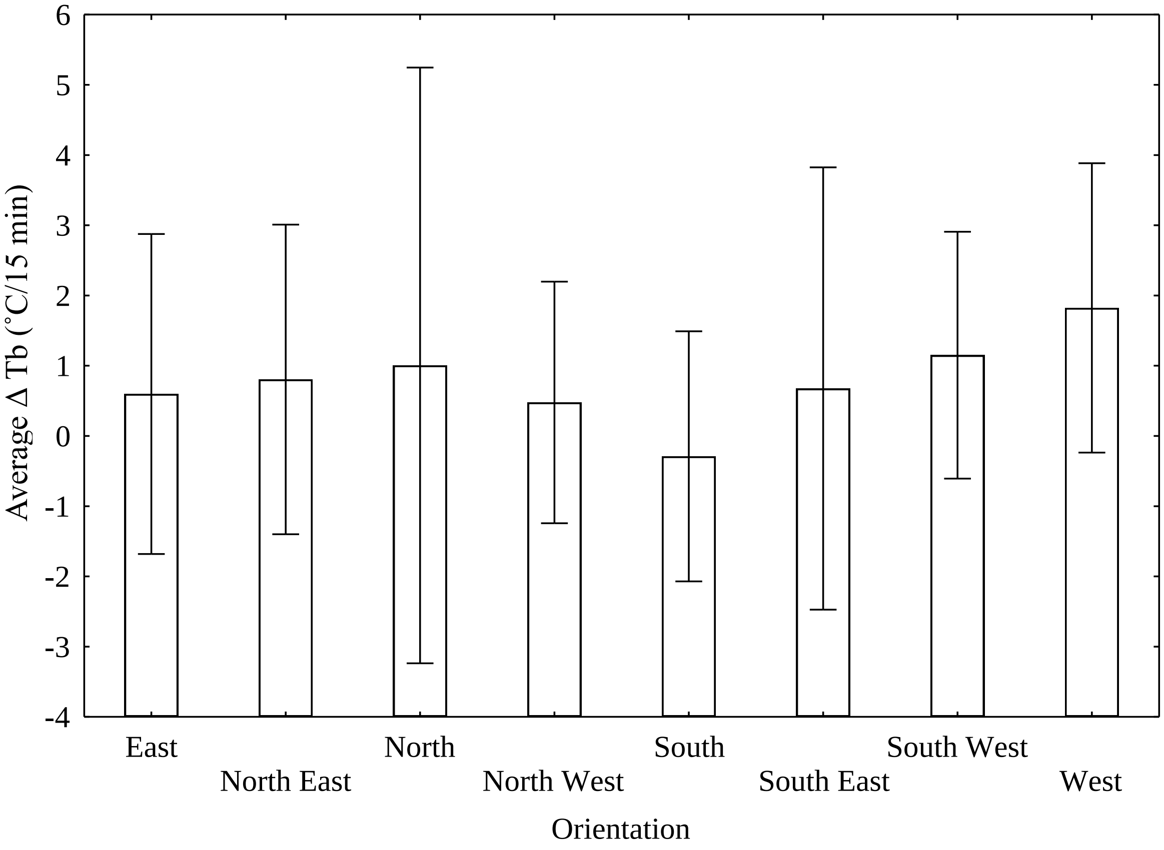

Figure 7.2: The mean change in T_b per 15 minutes at each orientation. Results are representative of x̄ ± SD from the individuals an east (n = 9), north east (n =8), north (n = 6), north west (n = 6), south (n = 8), south east (n = 4), south west (n = 8) and west (n = 9) orientation. ANOVA, $F_{7,63} = 0.70$, $P = 0.67$, no significant differences exist among the orientations.

When facing away from the sun, in the morning between 08:00 a.m. and 10:00 a.m., Sungazers heat at an average rate of 2.66 ºC ± 2.50 ºC per 15 minutes in comparison to facing the sun (x̄ = 0.02 ºC ± 2.10 ºC per 15 minutes) (Fig. 7.3). However, the data did not vary significantly (t-test, $t = -1.91$, $P > 0.05$).

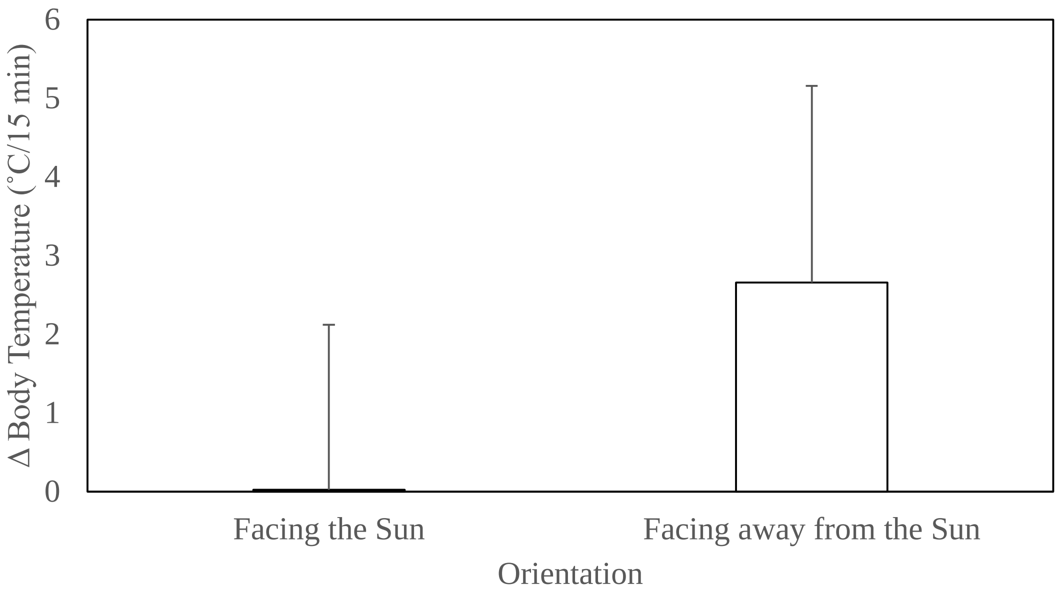

Figure 7.3: The mean change in T_b per 15 minutes at each orientation. Results are representative of $\bar{x}$ + SD from the individuals facing the sun (n = 6) and those facing away from the sun (n = 6). T-test, t = -1.91, P = 0.08, no significant differences exist among the orientations.

3.4 Proportion of Time Spent at Orientations

There was no significant variation between orientations (East, West, North, South) when the proportion of time that the lizards spent at each orientation throughout the daily activity period are considered (Repeated-measures ANOVA, $F_{3,32} = 2.83$, $P > 0.05$). However, a significant difference in the proportion of time spent at different time intervals throughout the day occurred (Repeated-measures ANOVA, $F_{12,384} = 3.16$, $P < 0.05$) and there was a significant difference when the interaction of time intervals and orientation is considered (Repeated-measures ANOVA, $F_{36,384} = 1.72$, $P < 0.05$).

In general, lizards spent proportionally more time facing an orientation between 08:01 a.m. and 11:00 a.m. which was significantly different to the proportion of time spent facing those orientations in the late afternoon, early evening; between 17:01 p.m. and 19:00 p.m. (Post-hoc Tukey HSD, $P < 0.05$; Fig. 8). In the morning time intervals, the lizards spent at least 10% of the time in either an East or West orientation while the remainder of their time was generally spent in their burrows (Fig. 8). Although there was no significant difference ($P > 0.05$), lizards spent proportionally more time in a North orientation during the midday time intervals than the rest of the day (Fig. 8). There were also no significant differences in the proportion of time that the lizards spent in a South orientation throughout the day (Post-hoc Tukey HSD, P > 0.05; Fig. 8).

The proportion of time spent when the lizards were facing West at the 09:01 a.m. to 10:00 a.m. time interval varied significantly against the East, North and South orientations in the early morning and late afternoon time intervals (Post-hoc Tukey HSD, P < 0.05; Fig. 8). Lizards spent significantly more time facing West than North and South for the same morning time interval (Post-hoc Tukey HSD, P < 0.05; Fig. 8). However, no significant difference occurred between the East and West orientations at the same morning time interval (Post-hoc Tukey HSD, P > 0.05; Fig.8).

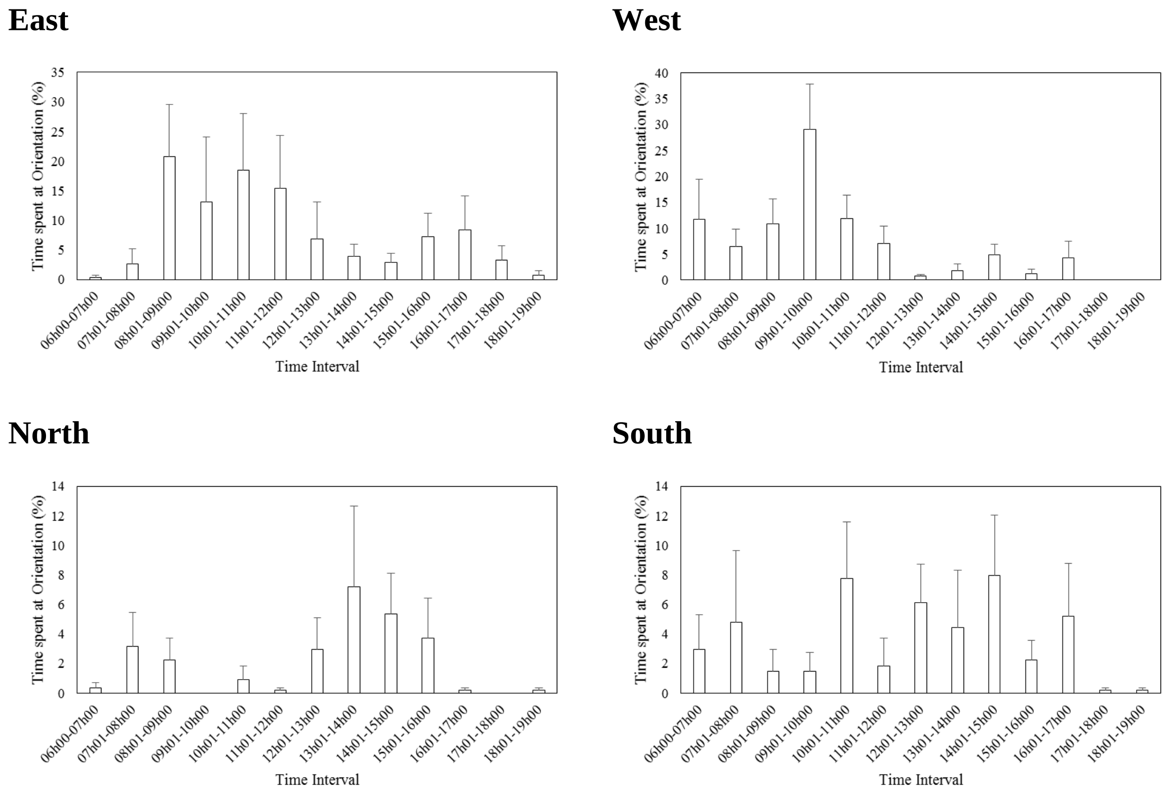

Figure 8: The percentage of time that lizards spend per hour of the day at a particular orientation. Data are representative of x̄ + SD from the individuals at each time interval.

4. Discussion

Sungazers monitored in this study were capable of maintaining a T_{target} of 30.17 ºC ± 1.35 ºC for a large portion of the day (332.56 ± 180.60 min) through behavioural adjustments while basking; shuttling in and out of burrows, and postural and orientation adjustments. The assessment of photographs against the thermal profiles provided evidence that Sungazers were making thermally-motivated decisions and that T_bs were not constrained by environmental temperatures during the daily activity period. Thus the thermal profiles that were generated allowed me to classify Sungazers at their target T_bs (see Alexander, 2007 for a detailed description on T_{target} criteria). Upon emergence from burrows, Sungazers used behaviours that facilitated a rapid increase in T_bs, a common observation amongst reptiles (van Wyk, 1992; Muth, 1977; Truter, 2011). In the morning (09:01-10:00 a.m. time interval), when T_e was relatively low, lizards, on average, spent proportionally more time facing west/away from the sun than other orientations, suggesting that the lizards employed this orientation to maximise rates of heating. Since the sun remains in an easterly orientation until approximately 11:00 a.m. (Fig. 9, Brackenridge, 2015), lizards facing away from the sun show maximum utilization of insolation during this time period.

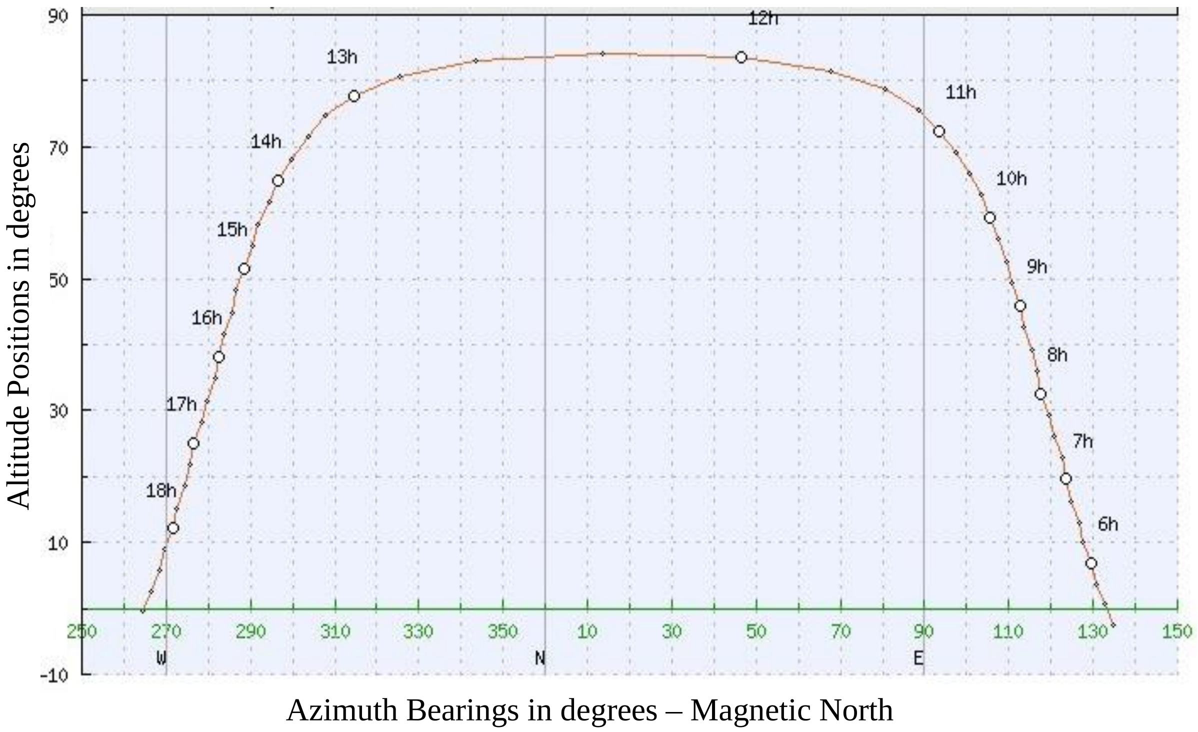

Figure 9: A representative figure of the orientation movements exhibited by the sun during a typical summer's day in Mpumalanga province, South Africa (Brackenridge. 2015). The sun rises in an east orientation and remains easterly until 11:00 a.m. Thereafter a north orientation is observed during the midday hours and a westerly orientation succeeds this in the late afternoon hours. Open circles represent the sun.

Moreover, Sungazers were able to maximize the rates of heating and were able to achieve T_{target} in a short time frame (25.11 ± 14.67 min) when they employed an anterior body-up (high) posture facing away from the sun as this posture allowed Sungazers to maximise exposure of their dark, dorsal surfaces to the sun. These results suggest that should operative temperatures increase or decrease below the norm, Sungazers are able to respond accordingly; reducing or increasing the time spent at an anterior body-up (high) posture while orientated away from the sun. Further, it suggests that should climate change become increasingly influential in southern Africa, as is happening throughout the world (Aubret and Shine, 2010), these lizards will be able to shift their behaviours to meet their thermoregulatory requirements (Aubret and Shine, 2010).

Body posture had a significant effect on the average T_bs that Sungazers were able to achieve and the rates of heating associated with the different postures suggesting that posture is a critical factor for thermoregulation in this species. However, when the orientation of Sungazers was considered with no reference to the position of the sun, T_bs were not affected. It is possible that a limited sample size (n = 9) was the reason no significant effect occurred. However, the results suggest that the position of the sun while Sungazers are at an orientation, accompanied with a posture, is important as to manipulate the amount of solar radiation that gets absorbed by the body (van Wyk, 1992). On days when ambient temperatures are colder, it is reasonable to suggest that Sungazers will spend proportionally more time at orientations that face away from the sun (van Wyk, 1992) so that T_{target} can be achieved.

The average time spent at each posture throughout the day varied significantly, suggesting that the different postures result in different rates of thermal exchange. The average time spent at the different orientations did not vary significantly, although, this was a measure of the average time spent at each orientation throughout the day. The most time was spent at anterior body-up postures, particularly at an anterior body-up (low) posture, suggesting that not only do these postures facilitate temperature maintenance but may also be important for other behavioural traits such as scouting the grassland landscape for potential predators or for prey items (van Wyk, 1992). Postural and orientation adjustments are often linked to site selection which may also positively contribute to thermal demands. However, site selection has a broader ecological context and may therefore also be attributed to the acquisition of resources and mate and prey availability (Bohóquez-Alonso *et al.*, 2011).

Sungazers spent a small proportion of time at orientations during midday suggesting that the lizards increase shuttling behaviour in and out of burrows which ultimately influences basking time. Shuttling in and out of burrows during the midday heat extremes would allow lizards to efficiently thermoregulate to remain at target level which would ensure physiological processes occur within their thermal optima. This also implies that despite midday temperatures, Sungazers are able to thermoregulate efficiently to remain at target level. Despite this observed shuttling behaviour, postural and orientation adjustments are more relevant.

Burrow temperatures remained relatively constant (~20 ˚C), which was predicted since burrows are well insulated (van Wyk, 1992). Furthermore, T_{burrow} consistency was similar to the mid-burrow temperatures (~20 ˚C) from van Wyk (1992). Recording measures of deep burrow and burrow-entrance temperatures could prove useful in providing baseline measures that will allow us to discover if there is a relationship between Sungazer emergence and burrow-entrance temperatures. However, lighting conditions co-vary with burrow-entrance temperatures which could limit the ability to infer a relationship between burrow-entrance temperatures and the emergence of Sungazers. Moreover, an examination of head temperatures, rather than cloacal temperatures could also provide vital information regarding the emergence of Sungazers, however, such data can only be recorded through extensive telemetry studies (King, 1980; van Wyk, 1992).

Van Wyk (1992) reported that the single Sungazer in his study was able to rapidly achieve a T_b close to 30 ˚C during the month of September 1987, which is a similar finding to the results achieved in this study. Although, shuttling behaviour and through orientation and postural adjustments, the T_b of the single lizard remained stable at 27 ˚C. Van Wyk (1992) also reported that the Sungazer was able to achieve a maximum of 40 ˚C during the month of October 1987, however, upon reaching that temperature, the Sungazer rapidly retreated down the burrow suggesting that the lizard was approaching its maximum thermal limit (although this is yet to be studied). Since van Wyk (1992) did not quantify T_{target}, my results of T_{target} are not comparable to van Wyk's (1992) but are comparable to measures made of other members of the Cordylidae (Table 2).

T_{target} among reptile genera is generally variable (Truter, 2011), but constrained amongst closely related species (Licht *et al.*, 1966; Huey, 1982; Kohlsdorf and Navas, 2006; Truter, 2011). However, the Cordylidae family could be considered an exception since T_{target} among the species are considerably variable, with a maximum difference of 3.6 ºC (Table 2). It is likely that the methods used to calculate T_{target} differ which could influence the respective results. Furthermore, since the species are considerably different, their respective T_{target}s differ which could also be due to the different habitats that these species inhabit. The T_{target} of *S. giganteus* falls within the lower limit of T_{target}s recorded among the Cordylidae family, sharing a T_{target} similar to *Ouroborous cataphractus* (T_{target} = 30.0 ºC ± 2.5 ºC) and *Pseudocordylus capensis* (T_{target} = 30.4 ºC ± 1.3 ºC) during the warmer months of the year. The low T_{target}s among these species can be attributed to their life histories; solitary versus group/colonial living (Truter, 2011). Although research regarding the social complexity of Sungazers remains limited, numerous individuals often inhabit a single burrow; and adult with juveniles (van Wyk, 1992; Parusnath, 2014). Truter (2011) was the first to report a T_{target} for a group-living species, *O. cataphractus*, and the T_{target} results for *S. giganteus* are the most similar to *O. cataphractus* further suggesting that the T_{target}s can be attributed to life history strategies (Clusella-Trullas *et al.*, 2009; Truter, 2011).

Table 2. The mean target body temperatures reported for members of the Cordylidae family.

Species	T_{target} ± SD (ºC)	Reference
Smaug giganteus	30.2 ± 1.35	Current study
Ouroborous cataphractus	30.0 ± 2.1	Truter, 2011
Pseudocordylus capensis	30.4 ± 1.3	Janse van Rensburg, 2009
Pseudocordylus melanotus melanotus	31.0 ± 0.1*	McConnachie *et al.*, 2009
Platysaurus intermedius wilhelmi	31.5 ± 1.7	Lailvaux *et al.*, 2003
Cordylus cordylus	32.1 ± 0.7	Clusella-Trullas *et al.*, 2007
Cordylus vittifer	32.1 ± 1.8	Skinner, 1991
Cordylus niger	32.6 ± 0.3	Clusella-Trullas *et al.*, 2007
Cordylus jonsei	33.5 ± 0.3	Wheeler, 1986
Cordylus polyzonus	33.6 ± 0.3	Clusella-Trullas *et al.*, 2007
Cordylus oelofseni	33.6 ± 0.3	Clusella-Trullas *et al.*, 2007

* ± Standard Error

The literature suggests that elevated postures are employed to increase convective cooling in small lizards (van Wyk, 1992; Clusella-Trullas *et al.*, 2007). However, the phenomenon in larger lizards, such as Sungazers, does not hold since larger lizards have a larger volume to surface area ratio and are therefore not constrained by the convective environment (Muth, 1977; Waldshmidt, 1979; Tracey, 1982). It is possible that other factors, e.g. wind speed, could be important in determining the net thermal exchange (Adolph, 1990), which would ultimately influence the time that lizards spend in a posture or at an orientation. However, research has suggested that there is a decrease in wind speed near the ground (Geiger, 1965; Stevenson, 1985), thereby reducing the convective effects of wind on terrestrial lizards such as Sungazers.

The elevated postures that Sungazers adopt result in an increase in T_b. Muth (1977) reported a similar find in that an elevated posture resulted in high rates of heating and a higher T_b in *Callisaurus draconoides*, the Zebra-tailed lizard. *Pseudocordylus melanotus melanotus*, a rupicolous Cordylid, performed head-up or body-up postures more frequently in summer, while body-down postures were more frequently observed in winter (McConnachie *et al.*, 2009). The body-down postures in the winter can be attributed to the thermal transfer, conductive heating, between the rocks and the lizards. However, since Sungazers are grassland Cordylids, they are unable to achieve the same thermal gradient that exists between rupicolous Cordylids and their rocky habitat.

Orientation relative to the sun appears to be an important factor affecting T_bs in Sungazers and other lizards. In the morning, when T_e is relatively low, Sungazers spent proportionally more time facing away from the sun than they do facing the sun, suggesting that this behaviour is important in maximising external heat gain. The importance of orientation relative to the sun is supported by Muth (1977) who reported that T_bs in *C. draconoides* are influenced by their orientation relative to the sun. Although, Muth (1977) also suggested that body postures are more important in determining T_bs than orientations relative to the sun and this prediction is supported by my study. Rupicolous lizards and those inhabiting semi-arid habitats with limited grass cover are more susceptible to heat gain via conduction than grassland species (Truter, 2011). Therefore, it is reasonable to suggest that grassland species are more susceptible to the impact of orientation relative to the sun than most other rupicolous or semi-arid dwelling lizards. Since the burrow entrances of Sungazers and the surrounding bare patches get hot (van Wyk, 1992), it may contribute to conductive heating which could be the reason why orientation relative to the sun is not as influential as body postures in this species. However, there is a large difference in the rates of heating when Sungazers are facing the sun and when they facing away from the sun. It is possible that orientation relative to the sun is more influential during the morning (low T_e) than in the afternoon, when T_e generally exceeds the target range of Sungazers. Sungazers are partially able to overcome conductive heating through shuttling in and out of burrows and by sitting on short, nearby grass (van Wyk, 1992).

Spending a small proportion of time at any orientation during midday is not uncommon among lizards (Burrage, 1974, Huey, 1974; Cronje and Mouton, unpublished data). It implies that the lizards increase shuttling behaviour in and out of burrows or rock crevices which ultimately influences basking time and thus they are able remain at target level despite the midday heat. A similar finding to my results was observed by van Wyk (1992) and in *Cordylus cordylus* (Burrage, 1974), *Cordylus niger* and *Cordylus oelofseni* (Cronje and Mouton, unpublished data). Furthermore, *Anolis cristatellus*, typically a forest-dwelling lizard, tends to avoid perches that are exposed to the sun during the midday as to avoid the midday temperature extremes (Huey, 1974).

The major limitation of this study was a relatively small sample size. Due to time constraints, I was unable to achieve a large sample size ($n > 15$). This study is the first to use iButtons modified as cloacal probes. The technique proved to be effective for recording T_bs over short period of time (24-48 hours). However, several of the probes failed during deployment, probably due to water entering the circuitry or due to battery failures. Thus it is important that the entire circuitry of the modified probe is protected against water-damage and that wires are securely attached so that the probe is versatile in the environment. Sungazers showed no apparent change in behaviour after the insertion of the cloacal probe. For the purposes of this research, the modification of iButtons into cloacal probes was highly effective when they did not fail.

As T_b measures were successfully recorded, the next important aspect to consider was the analysis of postural and orientation adjustments. The body postures assigned by van Wyk (1992) for Sungazers were useful in understanding diel behavioural patterns. Muth (1977) reported two postural adjustments; a flat versus elevated posture. While general analyses can be performed using just two postures, the five used in this study, adopted from van Wyk (1992), allowed for better resolution regarding intraspecific patterns. Moreover, few studies, such as Muth (1977), record lizard orientation in terms of relative angle to the sun. While this method is effective, simple compass point analyses are equally efficient and can be interpreted in a similar fashion. Although, an understanding of the sun's diel orientation patterns for the study site are required to buffer the interpretation of lizard orientations.

The use of camera traps to capture photographs of the Sungazers and their immediate surroundings was highly effective. This method was more effective than the telescope method used by van Wyk (1992) since it meant that data for more lizards could be recorded at the same time. The only limitation regarding the camera traps was the threat of theft (although none were stolen during the study) and cattle on the land. Cattle contributed to limiting my sample size since four cameras were tampered with, rendering the data unusable for these lizards. However, once lizard T_bs were linked to the data from the photographs, trends were shown and conclusive findings could be made, at least with regard to body posture influences. Overall, the methodology employed in this study was sufficient to meet the aims.

Understanding how ectotherms thermoregulate has been a topic of discussion for decades (Muth, 1977; Greenberg, 1977; van Wyk, 1992; Alexander, 2007; McConnachie *et al.,* 2009; Truter, 2011). Recent advances in technology has allowed researchers to improve their accuracy when recording data. The modification of iButtons has led to its uses in smaller animals and this study has shown that through further modification, it is possible to create a cloacal probe that can be used to record T_bs over shorter time frames.

This study measured the T_{target} of Sungazers that occur along the eastern-edge of their distribution. A worthwhile comparison would be to investigate whether this target level differs to that of populations near the central and western regions of the distribution. However, it is reasonable to suggest that because populations that occur in the western regions of Sungazer distribution experience warmer temperatures (van Wyk, 1992), they will spend less time at an anterior body-up (high) posture in an attempt to achieve target level. Fitting a climate envelope model to the distribution of Sungazers against their T_bs will provide evidence regarding the implications of climate change on the distribution of Sungazers.

Sungazers differ from most other Cordylids in that they inhabit flat grasslands where vantage points for basking are limited. However, this study empirically showed that Sungazers are able to modify their behaviour, through postural and orientation adjustments, to meet their thermal demands. Anterior body-up postures are important in allowing the lizards to achieve thermal demands but are also important for other ecological behaviours. Simply recording orientations for lizards is irrelevant and thus orientations relative to the sun need to be considered. Finally, my study has shown that Sungazers are capable of attaining a T_{target} of 30.17 ºC ± 1.35 ºC and therefore should climatic conditions change, simply increasing or reducing the time spent at an anterior body-up (high) posture or facing away from the sun would enable these lizards to meet their thermal requirements.

Acknowledgements

I thank my supervisor, Prof Graham Alexander, and Shivan Parusnath for their assistance in designing this research project. Their assistance and guidance throughout this research was invaluable. I thank Shivan Parusnath and Andrew Robson for their assistance in the field. Their help in setting up field equipment is much appreciated. I thank my father, Keith Stanton-Jones, for helping me modify iButtons into cloacal probes. Furthermore, I thank my colleagues, family and friends for guiding and supporting me throughout the year; both academically and personally. I would also like to thank the Rufford Foundation (Second Grant #13956-2, granted to Shivan Parusnath), National Geographic and The Alexander Herp Lab for financing all the field work and equipment relating to this project. I thank Hendrik Van Der Merwe and Hennie Louw for allowing me onto their farms to work with their Sungazers. This study was cleared by the ethics committee at the University of the Witwatersrand's Animal Ethics Screening Committee, ethics number: 2014/56/B.

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