



# The impact of posture and basking orientation on thermoregulation in the Sungazer (*Smaug giganteus*)



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## ABSTRACT

Body temperature ( $T_b$ ) is one of the most influential factors affecting physiological processes in ectothermic animals. Reptiles use behaviours such as shuttling, and postural and orientation adjustments to ensure that  $T_b$  remains close to a target. It is thought that target body temperature ( $T_{target}$ ) is aligned to the physiological and behavioural thermal optima of the animal. The Sungazer (*Smaug giganteus*), a Threatened lizard species, is unique amongst the Cordylidae in that lizards inhabit self-excavated burrows in open grasslands, a habitat in which there are few exposed rock basking sites. In this situation,  $T_b$ s are likely to be greatly influenced by postural and orientation adjustments during basking. We measured  $T_b$ s using modified iButtons, and calculated  $T_{target}$  of free-ranging Sungazers in order to assess the impact of body posture and orientation in the thermoregulation of the species. We used camera traps to record lizard behaviour at burrow entrances and aligned these measures to measures of  $T_b$ .  $T_{target}$  was  $30 \pm 1.4$  °C, and  $T_b$ s remained within this range for  $371 \pm 162$  min per day. The anterior body-up postures resulted in faster heating and higher  $T_b$ s. Lizards heated faster when facing away from the sun and spent proportionally more time in this orientation in the morning when  $T_b$ s were lower than  $T_{target}$ . Our findings suggest that their wide behavioural repertoire allows Sungazers to thermoregulate effectively over a broad range of environmental conditions and may thus be able to effectively respond to changing climatic conditions.

## 1. Introduction

Body temperature ( $T_b$ ) is one of the most fundamental components in the ecophysiology of ectothermic animals (Angilleta Jr. et al., 2002), and has significant impacts on growth, locomotion, digestion, metabolic processes and most performance traits (Seebacher and Franklin, 2005). While endothermic animals regulate their  $T_b$ s within a narrow range (Ivanov, 2006; Truter et al., 2014), ectotherms such as reptiles typically regulate their  $T_b$ s over a wider range (Truter et al., 2014). Reptiles thermoregulate primarily by modifying rates of heat gain and loss to the environment, and temporal fluctuations of thermal conditions in the environment account for much of the range in  $T_b$  variation, and consequently, diel and seasonal activity patterns (Diaz and Caberzas-Dias, 2004). The thermal physiology of ectotherms is therefore an important factor in their energy balance and life histories since variations in rates of thermal exchange lead to changes in the costs of thermoregulation (Huey et al., 2012; Buckley et al., 2015).

Reptiles employ thermally-motivated behaviours (e.g. site selection, postural and orientation adjustments, activity periods and shuttling behaviour) to modify rates of heat gain and loss to enable them to reach a

target body temperature ( $T_{target}$ ; *sensu* Alexander, 2007).  $T_{target}$  is considered to be generally aligned to physiological thermal optima of field-active ectothermic animals (Alexander, 2007). An assessment of thermoregulation in field-active ectothermic animals can be made as long as individuals are not constrained by the thermal environment – the difference in measures of  $T_b$  and environmental temperatures ( $T_e$ ; Wills and Beaupre, 2000). In addition, how closely  $T_{target}$  matches  $T_e$ , provides an indication of the thermal quality of a habitat; a large difference suggests a low thermal quality and individuals have to thermoregulate to achieve  $T_b$ s close to  $T_{target}$  (Hertz et al., 1993). Different protocols to assess thermoregulation, and most measures of reptile  $T_b$ s (presented as  $T_{target}$ ,  $T_{set}$ ,  $T_{sel}$ ,  $T_{opt}$  and  $T_{pref}$ ; see Hertz et al., 1993, Currin and Alexander, 1999, Alexander and Currin, 1999, and Clusella-Trullas and Chown, 2014 for a review and discussion on the definition of these concepts) have been conducted under laboratory conditions, with some important exceptions (e.g. Hertz et al., 1993; Wills and Beaupre, 2000; Alexander, 2007), and often neglects physical or biotic constraints found in the natural environment (Hertz et al., 1993; Clusella-Trullas et al., 2007).

The Sungazer (*Smaug giganteus*) is a Threatened lizard that exists within a well-defined climatic niche (Parusnath et al., 2017). Yet

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despite being named after its characteristic basking posture, the  $T_{\text{target}}$  or how the species employs posture and orientation to maintain  $T_{\text{target}}$  has not been explicitly measured. Although it has been shown that through the manipulation of posture and orientation, Sungazers are able to manipulate solar radiation absorption through the darker, dorsal surface of their bodies (Van Wyk, 1992), the surface areas of exposed surfaces of their bodies (both dorsal and ventral) when above ground has also not been measured. We used modified iButtons to record  $T_b$  and used the method described by Alexander (2007) to assess the  $T_{\text{target}}$  of free-ranging Sungazers, and deduced when field-active lizards were making thermally-motivated decisions to remain at a  $T_{\text{target}}$  range that falls within the limits of  $T_e$ . The measures of  $T_b$  combined with camera trap data was used to test the hypothesis that different orientations and anterior body-up postures of Sungazers aid in their ability to achieve and maintain their  $T_{\text{target}}$ . Additionally, we hypothesized that the darker, dorsal surfaces has a greater area of exposure to the sun compared to the lighter, ventral surfaces when the lizards are above ground, further contributing to thermoregulation in the species.

## 2. Methods

### 2.1. Study sites

We studied Sungazers on three privately-owned farms; two near the town of Volksrust (27° 22' S, 29° 53' E) in the Mpumalanga Province, and the other near the town of Heilbron (27° 17' S, 27° 58' E) in the Free State Province, South Africa. Sungazers are relatively inactive during winter and typically do not often emerge from their burrows between June and August (De Waal, 1978; Van Wyk, 1988), and research was therefore conducted during summer months – January 2015 and January 2016, and autumn – May 2015. Summer (November to March) temperatures average 24 °C, and 70% of the rain falls over this period.

### 2.2. Study species

*Smaug giganteus* is restricted to the Highveld grasslands in the north-eastern Free State and southern Mpumalanga provinces of South Africa (Branch and Patterson, 1975; De Waal, 1978; Jacobsen, 1989; Van Wyk, 1992; Parusnath, 2014). Although most other cordylids are rupicolous (Tolley, 2010; Bates et al., 2014), Sungazers live in self-excavated burrows in gently sloping *Themeda triandra* dominated grasslands (Van Wyk, 1992; Bates et al., 2014; Parusnath, 2014) that are naturally devoid of trees and rock outcrops. They make frequent use of their burrows throughout the day and rarely stray more than a meter from the burrow mouth (Van Wyk, 1992; Ruddock, 2000). *Smaug giganteus* is classified as Vulnerable (IUCN, 2017) due to habitat transformation and illegal harvesting for both the pet trade and traditional medicine (Parusnath et al., 2017).

### 2.3. Experimental design and protocol

#### 2.3.1. iButton Modification

We modified Thermocron iButtons (Maxim Integrated) to make cloacal probes for measuring  $T_b$  of Sungazers. iButtons were de-housed and deconstructed following a similar methodology to Lovegrove (2009). Briefly, the circuit board was detached from the battery, and three flat wires, each 30 mm in length were attached to the battery and circuit board terminals, and secured by heat-shrink. Insulated wires were then soldered to the input/output (I/O) terminal of the circuit board and ground tab of the battery so that the iButtons could be programmed to record a mission (Lovegrove, 2009). The entire probe was dipped in surgical wax to seal the circuitry from moisture. Modified iButtons (average mass of 2.8 g) were programmed to record

temperatures every minute using 1-WIRE version 1.0.0.1 (Maxim Integrated). Temperature measures were calibrated to within 1 °C of a Hotbed Thermometer.

#### 2.3.2. Sungazer capture and release

We monitored 17 Sungazers across the three study sites (7♂; 10♀), and included only sub-adults and adults in our sample because immature lizards (< 5 years) were too small to easily accommodate the cloacal probe. We captured Sungazers using standard techniques (Van Wyk, 1992) and recorded the coordinates of the burrows of captured lizards on a hand-held GPS (Garmin GPSmap 78s; datum WGS1984). F10 disinfectant spray was used to disinfect the probes and cloacas of captured lizards, and insertion of the probes into the lizards' cloacas was facilitated with the use of KY gel lubricant. The exposed battery and wires were wedged between the tail spines and secured to the ventral scales of the tail with superglue and micropore tape. We returned lizards to their burrows at 6 p.m. on the day of capture. A camera trap (Bushnell Trophy Cam HD 119577) was installed near the burrow entrance and set to record a photograph of the burrow entrance and surroundings every minute. All cameras were set north-facing to facilitate analysis of lizard orientation. The day following the release of the Sungazers was used as the data collection period. On the day following a complete day of recordings, we recaptured lizards, removed cloacal probes, and downloaded data from the camera trap. Lizards' cloacas were disinfected using F10 and the lizards were released into their burrows of capture. We did not observe any impacts on Sungazer behaviour due to the deployment of the probes.

#### 2.3.3. Operative temperature measures

We made models to measure operative temperatures ( $T_e$ ) within Sungazer habitat, using copper tubing (150 mm long × 28 mm diameter) filled with silicon and a modified iButton (after Alexander, 2007; McConnachie et al., 2009). The silicon-filled copper tube has proven to be a successful method of recording operative temperatures and models the  $T_b$  of a large-bodied cordylid well (McConnachie et al., 2009). Operative temperatures were recorded every minute (calibrated to within 1 °C of a Hotbed Thermometer), and models were set up at a central burrow within the aggregation of burrows being monitored. One model was positioned in the anterior body-up position, with the use of attached wire arms, 300 mm from the burrow mouth. The other was placed 0.5 m down the burrow.

## 2.4. Data analysis

### 2.4.1. Temperatures

We graphed  $T_b$ s collected from lizards, and the simultaneously-collected  $T_e$ s to visualise the thermal profiles of each lizard (Fig. A.1). Sungazers are ambush foragers (Van Wyk, 1992; Ruddock, 2000), and have similar thermal profiles to ambush-foraging snakes. Thus, we used the protocol described by Alexander (2007) to calculate the  $T_{\text{target}}$  for each lizard. Briefly, the protocol involves the identification of the plateau-phase of  $T_b$  (see Fig. A.1) during the active period (defined by the first and last peaks in  $T_b$ ). Measures of  $T_b$  over this period were averaged to calculate  $T_{\text{target}}$ .

### 2.4.2. Posture and orientation

We scored the orientation and posture of each Sungazer for each camera trap photograph throughout the day, assigned orientations of each Sungazer in each photograph to one of eight standard compass points and recorded whether basking lizards were facing towards or away from the sun. Postures were assigned based on Van Wyk's (1992) designation of typical Sungazer thermoregulatory postures (Fig. A.2). The percentage of each hour during the diel cycle was recorded for each

orientation and posture for each lizard, and an average for all 17 lizards was calculated. The postures and orientations for each Sungazer were linked for each minute of the diel cycle to the simultaneous  $T_b$  measurements from iButtons. We calculated the rate of  $T_b$  change ( $\Delta T_b$ ) of posture and orientation for each lizard over 15-min periods.

We also assessed the impact of orientation on basking behaviour by using photographs of seven Sungazers each basking while facing the sun and facing away from the sun. From each photograph of each lizard we measured the total surface areas of both dorsal (lizard facing away from the sun) and ventral surfaces (lizard facing the sun) directly exposed to sunlight, using the computer software ImageJ version 1.51, and calculated the average of the seven Sungazers for each of the exposed surfaces.

### 2.4.3. Statistical analysis

We calculated the mean  $T_b$  for each posture and orientation for each lizard and calculated the average for all 17 lizards.  $T_b$  data were tested for normality, and because  $T_b$  data were not normal, we log-transformed the data for analysis of posture and orientation. A five-minute  $T_b$  delay was assigned to each respective posture and orientation to account for any potential lag effect that may have existed while these large-bodied lizards adjusted posture and orientation (Seebacher and Shine, 2004). We used repeated-measures analyses of variances (ANOVAs) to compare the relationship between  $T_b$ s and respective postures and orientations, and included sex as a co-factor in our analyses. Single-factor ANOVAs were used to assess the average time that the lizards spent at each respective posture and orientation, and to test for differences in heating rates at different postures and orientations. An independent *t*-test was used to test for difference between the rates of heating facing the sun and facing away from the sun, and to test for differences in the surface areas of the dorsal and ventral profiles. Lastly, the percentage of time spent per hour, at a particular orientation, was logit-transformed and a repeated-measures ANOVA was conducted to test for significant differences. Because the assumptions of sphericity had been violated for this assessment ( $X^2(77) = 179.9$ ,  $P < 0.05$ ), we applied the Greenhouse-Geisser (G-G) correction to our repeated-measures ANOVA. We conducted post-hoc Tukey HSD tests for all ANOVA and repeated-measures ANOVA tests to identify where significant differences between the groups exist. All statistical analyses were conducted in STATISTICA version 8.0 (StatSoft Inc, 2007).

## 3. Results

### 3.1. Thermal profile

#### 3.1.1. Operative temperatures

Operative temperatures within burrows remained  $\sim 20^\circ\text{C}$  throughout the 24-h cycle (Fig. A.1). The  $T_e$ s recorded from the exposed model were lower than burrow  $T_e$ s during the night (20h00–05h00), but exceeded burrow  $T_e$ s from  $\sim 08\text{h}15$ , often exceeding  $40^\circ\text{C}$ , for the duration of the day, declining only after sunset.

#### 3.1.2. Sungazer thermal profiles

Sungazers initiated basking behaviour outside of the burrow as early as 06h50 (with an average basking initiation time of  $07\text{h}40 \pm 54\text{ min}$  (Mean  $\pm$  SD)), shortly after sunrise, and spent a total of  $321.2 \pm 116.2\text{ min}$  (Mean  $\pm$  SD) out of their burrows throughout a diel cycle. When  $T_e$ s were below  $T_{\text{target}}$ ,  $T_b$  fluctuations followed fluctuations in  $T_e$  (Fig. A.1). Average  $T_{\text{target}}$  was  $30 \pm 1.4^\circ\text{C}$  (Mean  $\pm$  SD) (Table A.1) and lizards remained within the  $T_{\text{target}}$  range  $371 \pm 162\text{ min}$  (Mean  $\pm$  SD) per diel cycle. The lizards were also able to remain at target level for  $\sim 50\text{ min}$  once in their burrows. No

significant differences existed among  $T_{\text{target}}$  (*t*-test,  $t = 0.9$ ,  $P = 0.4$ ) or time spent at  $T_{\text{target}}$  (*t*-test,  $t = 0.8$ ,  $P = 0.8$ ) between sexes.

### 3.2. Effects of Posture on $T_b$

Body posture influenced the mean  $T_b$  of basking Sungazers (Sphericity assumed:  $X^2(9) = 16.8$ ;  $P = 0.06$ ;  $F_{4,32} = 4.2$ ;  $P < 0.05$ ; Fig. A.3), and there were no differences between male and female lizards ( $F_{1,32} = 0.001$ ;  $P = 0.97$ ). The anterior body-up (high) posture had the greatest impact on  $T_b$  (Tukey HSD,  $P < 0.05$ ), and Sungazers were able to effectively achieve their  $T_{\text{target}}$  (Mean  $\pm$  SD =  $30 \pm 1.4^\circ\text{C}$ ), which was maintained through the anterior body-up (low) posture (Tukey HSD,  $P > 0.05$ , Fig. A.3). The other body postures resulted in  $T_b$ s falling below  $T_{\text{target}}$ .

The time Sungazers spent at each body posture was significantly different ( $F_{4,80} = 25.0$ ;  $P < 0.001$ ). There is a clear preference for the anterior body-up (low) posture ( $171.2 \pm 68.6\text{ min}$ ; Mean  $\pm$  SD) throughout the day (Tukey HSD,  $P < 0.001$ ). There was no significant difference between time spent in the anterior body-up (high) ( $27.4 \pm 35.6\text{ min}$ ; Mean  $\pm$  SD) and body down postures ( $14.6 \pm 17.5\text{ min}$ ; Mean  $\pm$  SD; Fig. A.4).

Sungazers heated up faster (Mean  $\pm$  SD =  $1.8 \pm 2.7^\circ\text{C}$  per 15 min) in an anterior body-up (high) posture ( $F_{4,64} = 4.8$ ,  $P < 0.05$ ; Fig. A.5) than in any other basking posture. There were no significant differences in the rates of heating for the other four postures (Post hoc Tukey HSD,  $P > 0.05$ ). On average, a head-up posture resulted in a loss, rather than a gain (Mean  $\pm$  SD =  $-0.5 \pm 1.1^\circ\text{C}$  per 15 min; Fig. A.5).

### 3.3. Effects of orientation on $T_b$

No significant differences existed in the rates of heating when body orientations, based on compass points, were considered ( $F_{7,105} = 0.7$ ;  $P = 0.6$ ; Fig. A.6). However, there was a significant difference in heating rates between Sungazers facing towards and away from the sun. The average rate of heating while facing away from the sun was  $1.9 \pm 2.1^\circ\text{C}$  per 15 min, and  $0.3 \pm 2.1^\circ\text{C}$  when facing towards the sun (*t*-test,  $t = -2.2$ ,  $P < 0.05$ ). Similarly, when facing away from the sun, the dorsal surfaces of basking Sungazers receive significantly more exposure to sunlight than ventral surfaces in a ABU (high) posture (Dorsal:  $\bar{x} = 5733.1\text{ mm}^2$ , Ventral:  $\bar{x} = 2330.2\text{ mm}^2$ ; *t*-test,  $t = 12.1$ ,  $P < 0.001$ ).

The mean  $T_b$  achieved by Sungazers was not influenced by orientation based on compass points (Sphericity assumed:  $X^2(27) = 36.1$ ;  $P = 0.1$ ;  $F_{7,91} = 0.9$ ,  $P = 0.5$ ; Fig. A.7), nor did it differ between sexes ( $F_{1,91} = 0.04$ ,  $P = 0.9$ ). Mean  $T_b$ s remained within  $20\text{--}30^\circ\text{C}$  with no specific orientation resulting in lizards reaching  $T_{\text{target}}$  faster (Fig. A.7). Similarly, above-ground active lizards showed no overall preference for a particular orientation, when compass points were considered ( $F_{7,128} = 1.9$ ;  $P = 0.1$ ; Fig. A.8).

The proportion of time per hour that Sungazers spent at different orientations (East, West, North and South) at different times of the day differed significantly (G-G correction:  $\epsilon = 0.64$ ;  $F_{22.9,489.1} = 1.6$ ;  $P < 0.05$ ). Sungazers spent proportionally more time (at least 10%) out of their burrows in either an East or a West orientation in the morning (Fig. A.9). However, during the 09h00–09h59 time interval, Sungazers spent proportionally more time in a West orientation (Post Hoc Tukey HSD,  $P < 0.05$ ). Following this, there were no discernible differences in the other time intervals. The later afternoon time intervals showed no observable pattern (Fig. A.9). Lastly, Sungazers spent less than 5% of their total time out of their burrows during midday (Fig. A.9).

#### 4. Discussion

Our measure of Sungazer  $T_{\text{target}}$  ( $30 \pm 1.4^\circ\text{C}$ ) is relatively low in comparison to  $T_{\text{b}}$ s selected by lizards in general (average =  $32.4 \pm 3.8^\circ\text{C}$ ; Clusella-Trullas and Chown, 2014). Sungazers were able to rapidly raise  $T_{\text{b}}$  to  $T_{\text{target}}$  while basking in the anterior body-up (high) posture, and on average,  $T_{\text{b}}$  rose  $1.8^\circ\text{C}$  per 15 min while they were in this posture. However, our measures indicate that heating rates can approach a maximum of  $8.5^\circ\text{C}$  per 15 min on occasion. The high rate of heat gain in this posture is augmented when Sungazers are facing directly away from the sun, especially in the morning time intervals, as this orientation exposes more than twice the surface area of the lizard to direct solar radiation in comparison to when the lizard is facing towards the sun. This finding is supported by Van Wyk (1992), who found that the darker coloration of the dorsal surface results in higher absorptivity of solar radiation and further increases heating rates when facing away from the sun. From the later morning time intervals (10h00 onwards) there was no observable pattern in orientation, therefore, there was insufficient evidence to suggest that Sungazers face the sun once  $T_{\text{target}}$  has been reached. However, orienting directly away from the sun in the anterior body-up (high) posture maximises heating rates and Sungazers were able to remain at  $T_{\text{target}}$  for a large portion of the day through behavioural adjustments, shuttling in and out of burrows, and postural and orientation adjustments.

The use of photography in conjunction with  $T_{\text{b}}$  thermal profiles and  $T_{\text{e}}$ s provided direct evidence that Sungazers were making thermally-motivated decisions and that  $T_{\text{b}}$ s were not constrained by environmental temperatures during most of the day. Upon emergence, Sungazers behaved in ways that facilitated a rapid increase in  $T_{\text{b}}$ . Since  $T_{\text{e}}$  reached a peak at midday, Sungazers required less time basking above ground to remain at  $T_{\text{target}}$ . Photographic evidence showed that Sungazers displayed reduced basking activity at midday by increasing shuttling behaviours or remaining within their burrows to avoid midday highs, which is a similar finding to Van Wyk (1992). Burrow temperatures remained relatively constant throughout the day ( $\sim 20^\circ\text{C}$ ) and our results show that Sungazers were able to remain at target level for  $\sim 50$  min when in their burrows. Although the use of photography has numerous advantages and can provide direct evidence for thermally-motivated behaviours, the use of the technology can be costly following the deployment of multiple cameras. However, for low-budget studies, a single camera monitoring a single burrow for a 24-h data collection period could be used and re-used to monitor a different burrow following the same data collection period, which would provide the same result as the present study. We therefore advocate the use of photography in behavioural studies.

Our study is the first to use iButtons modified into cloacal probes to record  $T_{\text{b}}$ s of free ranging animals. Although our bio-logging system functioned effectively, probes did fail on occasion, primarily as a result of water seeping into the probe circuitry, and it is thus vital that the entire circuitry be sealed carefully before use. Our method proved to be effective for recording internal  $T_{\text{b}}$ s over short time periods (24–48 h) for field-active lizards, without the need for the implantation of recording devices or the use of body surface temperature as a proxy for  $T_{\text{b}}$  (e.g. Truter et al., 2014). However Truter et al. (2014) modified iButtons for surface use and showed that the use of modified iButtons can be used to measure  $T_{\text{b}}$ s of field-active lizards. Our method differed to Truter et al. (2014), as our modified iButtons were used for cloacal insertion, to record internal  $T_{\text{b}}$ s, and modified iButtons for internal implantation have proven to be successful, even in small animals (Lovegrove, 2009). Our technique showed no observable impact on the lizard's natural behaviours, as Sungazers were observed the following day performing regular basking behaviours shortly after sunrise, which allowed for an assessment of internal  $T_{\text{b}}$ s. Additionally, since all the lizards defecated

upon initial capture, and that the iButtons were only within the lizards' cloacas for a short time period, it was unlikely that the lizards were impacted by the presence of the cloacal probes. We recommend this technique for short-term temperature measurements.

Using the combined temperature records from the model Sungazer, burrow model and  $T_{\text{b}}$ s of the Sungazers, we were able to generate thermal profiles from which measures of the  $T_{\text{target}}$  of Sungazers could be calculated. Our method to calculate  $T_{\text{target}}$  was based on free-ranging pythons (Alexander, 2007), and differs from most other studies whereby the laboratory gradient method is used (e.g. Truter, 2011). The method was appropriate as free-ranging Sungazers produced thermal profiles similar to those of free-ranging, ambush foraging snakes, and the method overcomes limitations of the gradient method in which individuals may not be motivated to thermoregulate (Alexander, 2007). We were able to record environmental temperatures available to Sungazers both above ground and within burrows to assess the range of temperatures available to the lizards at any given time. This allowed us to assess if  $T_{\text{e}}$ s restricted their ability to thermoregulate at any given time. From the thermal profiles we were able to assess that the  $T_{\text{b}}$ s of the lizards were generally not constrained by  $T_{\text{e}}$ s during most of the day, suggesting that the lizards had the choice of selecting lower or higher  $T_{\text{b}}$ s within the limits of  $T_{\text{e}}$ . Additionally, it showed that the lizards were making thermally-motivated decisions during the plateau-phase (Alexander, 2007). Our data collection protocol was especially effective when we combined it with the use of camera traps which recorded the behaviour of the lizards at the same frequency as  $T_{\text{b}}$  recordings and provided further evidence for the individuals making thermally-motivated decisions. Thus, we advocate this protocol for free-ranging lizards that have high site fidelity, as is the case for Sungazers (Ruddock, 2000).

$T_{\text{target}}$  tends to be similar amongst closely related reptile species and conserved among families (Licht et al., 1966; Huey, 1982; Pianka and Vitt, 2003; Kohlsdorf and Navas, 2006; Truter et al., 2014; Clusella-Trullas and Chown, 2014). Our measure of  $T_{\text{target}}$  for *S. giganteus* falls near the lower edge of range and is significantly lower ( $P < 0.001$ ; difference tests STATISTICA version 8.0) than preferred and selected  $T_{\text{b}}$ s recorded for other cordylids (ranging from  $29.8$  to  $33.6^\circ\text{C}$ ; Truter et al., 2014, with an average of  $32.7 \pm 0.9^\circ\text{C}$ ; Clusella-Trullas and Chown, 2014). Additionally, our measure of  $T_{\text{target}}$  cannot be directly compared to Van Wyk (1992) as in the latter study,  $T_{\text{target}}$  was not explicitly measured but did show that the single lizard for which  $T_{\text{b}}$ s were recorded had a  $T_{\text{b}}$  that remained stable at  $\sim 27^\circ\text{C}$  and showed a range of  $T_{\text{b}}$ s from  $20$  to  $35^\circ\text{C}$ . However, limited  $T_{\text{b}}$  data were available to Van Wyk (1992) and variation between individuals were not shown. Lower preferred  $T_{\text{b}}$ s in comparison to the average within the cordylidae have been shown in the largest members of the family;  $\sim 30^\circ\text{C}$  in *Ouroboros cataphractus* (Truter et al., 2014), *Pseudocordylus capensis* (Janse van Rensburg, 2009) and *S. giganteus* (present study). Since *S. giganteus*, *O. cataphractus* and *P. capensis* are amongst the largest members of the family,  $T_{\text{target}}$  may be related to body size in the family – a topic that has received little attention in the literature.

Rupicolous lizards and those inhabiting semi-arid habitats with limited grass cover are able to heat via conduction, particularly later in the day when rocks have become warmer (Muth, 1977). Conductive heating is also often used in conjunction with postural adjustments. *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 thermal transfer through conductive heating between the rocks and the lizards, as body down postures result in an increase in the surface area of the body in contact to the ground further facilitating heating via conduction (O'Connor and Spotila, 1992). However, for grassland

species, where there are few rocks to facilitate conductive heating, postural adjustments and orientation relative to the sun are more important than it is for rupicolous lizards. In addition, postural and orientation adjustments provide an ecological advantage in assisting the lizards with a better vantage to visually scout for prey items and potential predators.

Thermoregulatory studies on lizard species from other families have also found higher rates of heating and high  $T_b$  when in an elevated posture. For example, Muth (1977) reports higher rates of heating and a higher  $T_b$  in *Callisaurus draconoides*. Bohorquez-Alonso et al. (2011), highlighted the importance of posture and orientation of lizards in relation to the position of the sun for *Gallotia galloti*. It is possible that orientation relative to the sun is more influential during the morning when  $T_e$  is lower. During the afternoon,  $T_e$  generally exceeds the target range of Sungazers (Pianka and Vitt, 2003). Spending a small proportion of time at any orientation during midday is not uncommon among lizards (Burrage, 1974; Huey, 1974). It suggests that the lizards increase shuttling behaviour in and out of burrows or rock crevices, affecting basking time and thus they are able remain at target level despite the midday heat.

Our study estimated the  $T_{target}$  for a population of Sungazers that occurred near the eastern, cool edge of the distribution. An informative comparison would be to investigate whether this  $T_{target}$  differs from that of populations near the central and warmer 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, they will exhibit behavioural adjustments and spend less time at an anterior body-up postures in an attempt to achieve and maintain  $T_{target}$ . This scenario would be relevant in the

consideration of the impact of climate change: Sungazers could simply modify postures and orientations to align with changes in climatic conditions.

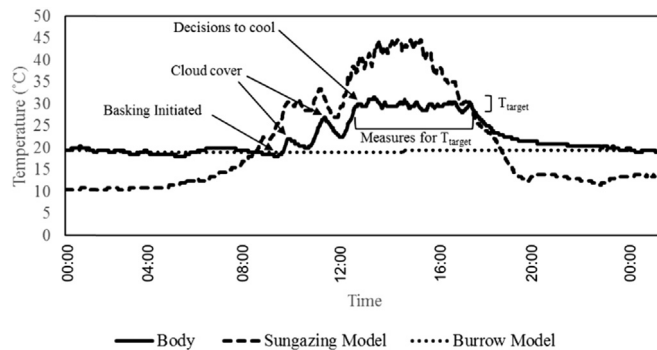
Sungazers differ from most other cordylids in that they inhabit flat grasslands where vantage sites for basking are limited. However, this study confirmed our hypothesis that they modify their behaviour, through postural and orientation adjustments, to meet their thermal requirements, confirming the initial observations of Van Wyk (1992). The anterior body-up postures, and increased area of exposure of dorsal surfaces are important in allowing the lizards to raise  $T_b$  to  $T_{target}$ , and raised postures also account for other ecological behaviours. Finally, our study has revealed that Sungazers have a low  $T_{target}$  and they appear to easily raise  $T_b$  to target by postural and orientation adjustments. This suggests that they would be able to cope with changing climatic conditions change, simply by modifying behaviour.

### Acknowledgements

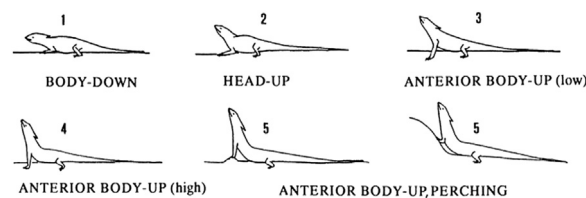
Financial support was provided by The Rufford Foundation Booster Grant (18728-B) to Shivan Parusnath, National Geographic Society Young Explorer Grant (C288-14) to Shivan Parusnath, and the Alexander Herp Lab. We thank Hendrik Van Der Merwe, Hennie Louw and Peter Wales for allowing us access to Sungazers on their land and for assisting with accommodation. Alex Bass and Keith Stanton-Jones provided assistance with the modification of iButtons. We thank Andrew Robson and Nicole Cornelius for their assistance in the field. This study was cleared by the University of the Witwatersrand's Animal Ethics Screening Committee, ethics number: 2014/56/B.

### Appendix A

See Figs. A.1–A.9.



**Fig. A.1.** Representative thermal profile of a single Sungazer over a 24-h period during January 2016. The dotted lines are representative of environmental temperatures within the burrow (Burrow model) and above ground (Sungazer model). Average  $T_b$  over the plateau-phase (Measures for  $T_{target}$ ) was used to calculate  $T_{target}$ . Although this thermal profile is for a single lizard, the thermal profiles for the other lizards were similar to this representative.



**Fig. A.2.** Typical body postures adopted by *Smaug giganteus* (after van Wyk, 1992).

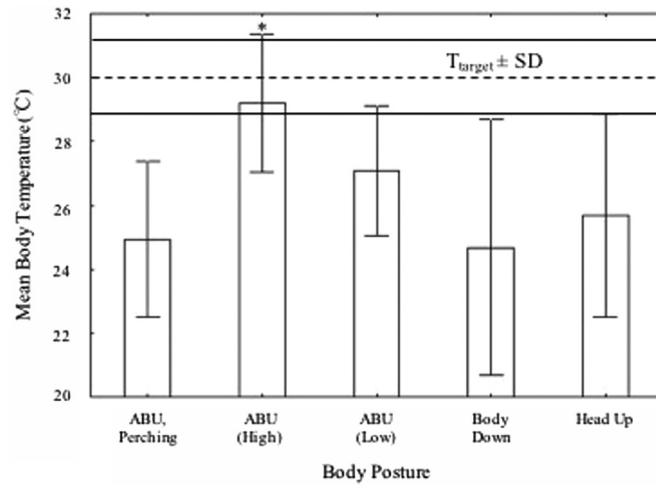


Fig. A.3. Effects of body posture on mean  $T_b$  achieved. The dotted line represents  $T_{target}$ , and the solid lines, standard deviation (SD). Significant differences are represented by an asterisk. ABU represents anterior body-up.

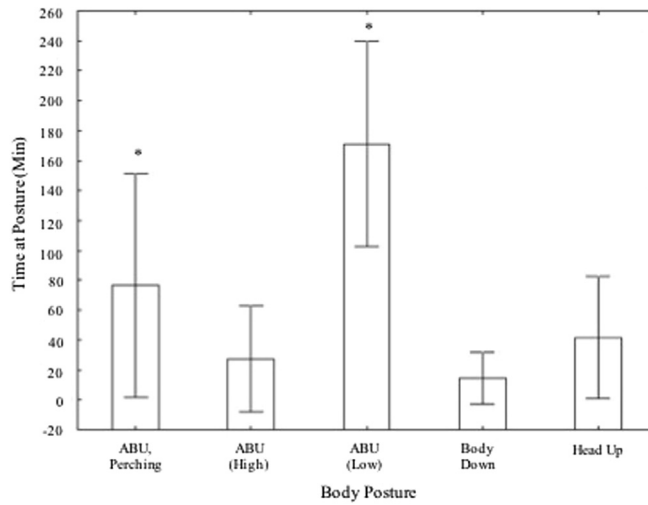


Fig. A.4. Mean time spent at each posture during a diel cycle. Results are representative of Mean  $\pm$  SD from the individuals at each body posture ( $n = 17$  for each posture). ABU: Anterior Body-Up. Significant differences are represented by an asterisk.

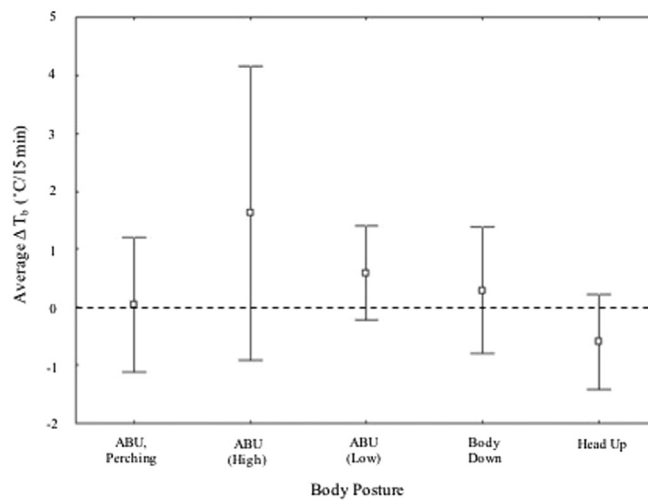


Fig. A.5. Mean rate of  $T_b$  change per 15 min at each body posture. Results are representative of Mean  $\pm$  SD from the individuals at an anterior body-up (high) posture ( $n = 9$ ), anterior body-up (low) posture ( $n = 17$ ), anterior body-up, perching posture ( $n = 17$ ), a body-down posture ( $n = 10$ ) and a head-up posture ( $n = 14$ ). ABU represents Anterior body-up. Zero is represented by the dotted line.

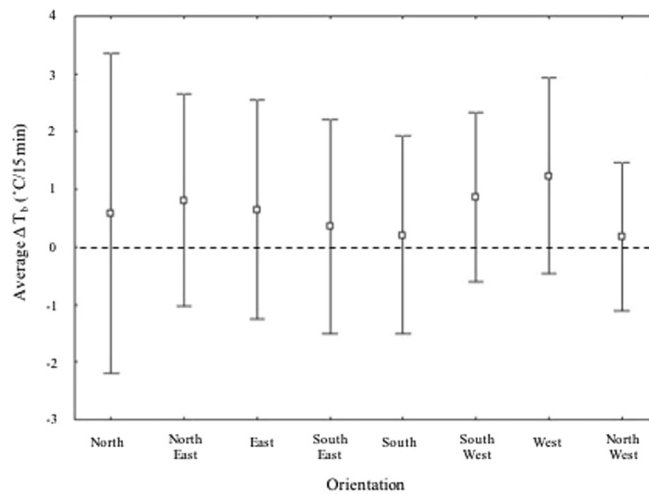


Fig. A.6. Mean change in  $T_b$  per 15 min, at each orientation. Results are representative of Mean  $\pm$  SD from the individuals an east ( $n = 16$ ), north east ( $n = 16$ ), north ( $n = 14$ ), north west ( $n = 14$ ), south ( $n = 13$ ), south east ( $n = 10$ ), south west ( $n = 13$ ) and west ( $n = 17$ ) orientation. Zero is represented by the dotted line.

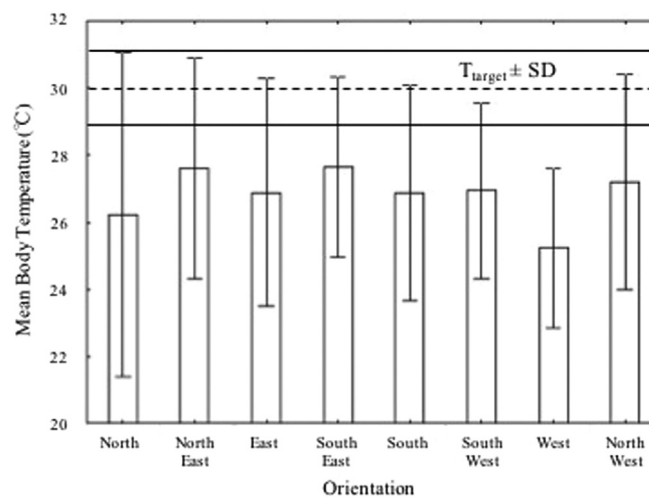


Fig. A.7. Effects of body orientation on mean  $T_b$ . The dotted line is representative of  $T_{target}$ , and the solid lines show standard deviation.

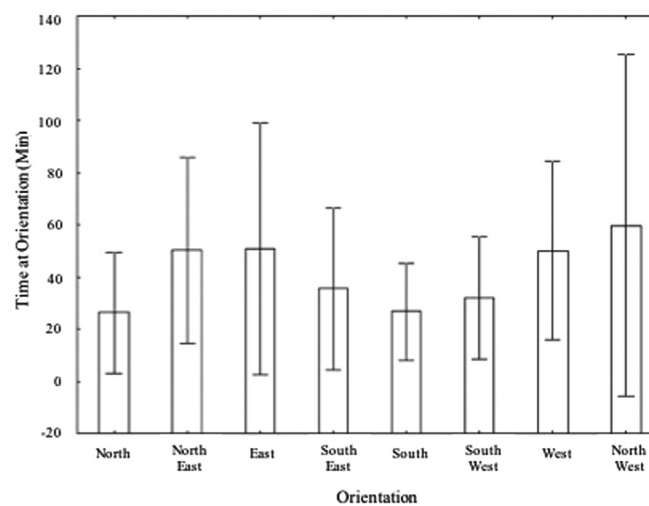
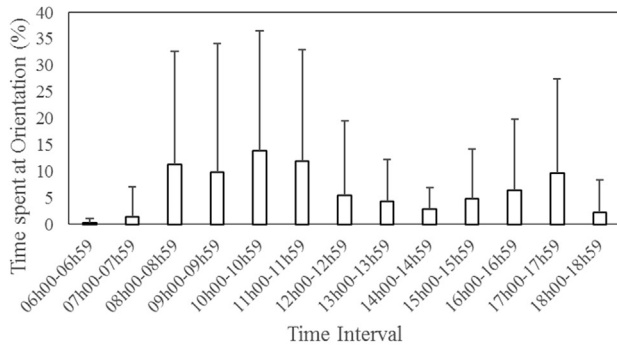
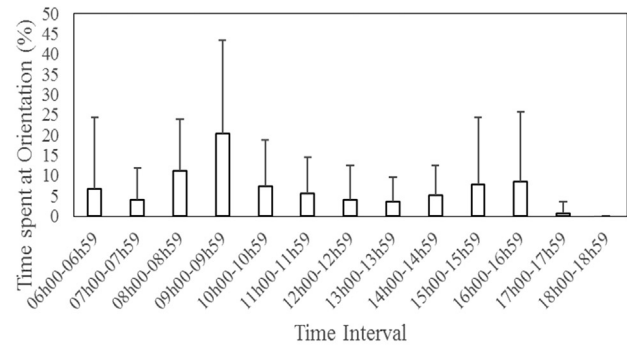


Fig. A.8. Mean duration at each orientation during a day. Results are representative of Mean  $\pm$  SD from the individuals at each orientation ( $n = 17$  for each orientation).

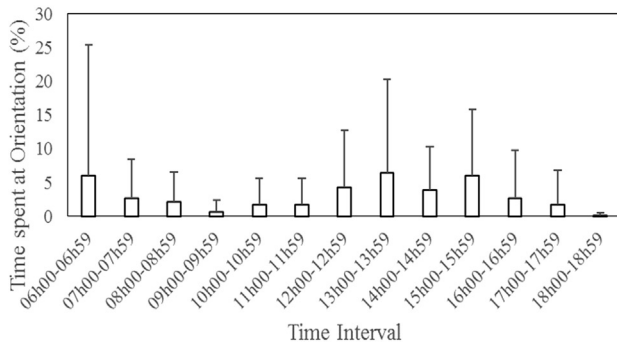
### East



### West



### North



### South

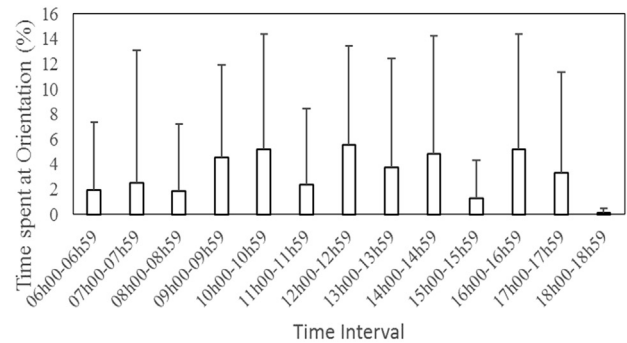


Fig. A.9. Proportion of time spent by lizards per hour of the day at each of the primary compass points.

See Table A.1

Table A.1

T<sub>target</sub> and time spent at T<sub>target</sub> for each lizard.

| Sex    | Target Body Temperature (Mean ± SD) (°C) | Time Spent at Target T <sub>b</sub> (Min) |
|--------|--|---|
| Male   | 30.8 ± 1.2                               | 215                                       |
| Male   | 31.8 ± 1.1                               | 95  |
| Male   | 29.3 ± 1.4                               | 347                                       |
| Male   | 27.2 ± 2.0                               | 383                                       |
| Male   | 30.6 ± 1.0                               | 472                                       |
| Male   | 28.4 ± 1.6                               | 473                                       |
| Male   | 29.3 ± 1.6                               | 530                                       |
| Female | 29.8 ± 0.7                               | 283                                       |
| Female | 29.2 ± 1.9                               | 594                                       |
| Female | 32.5 ± 1.1                               | 108                                       |
| Female | 30.5 ± 1.0                               | 586                                       |
| Female | 30.0 ± 1.9                               | 382                                       |
| Female | 31.0 ± 1.2                               | 395                                       |
| Female | 30.0 ± 1.1                               | 522                                       |
| Female | 30.2 ± 0.5                               | 104                                       |
| Female | 30.4 ± 1.8                               | 389                                       |
| Female | 28.8 ± 3.5                               | 432                                       |
| Mean:  | 30.0 ± 1.4                               | 371 ± 161                                 |

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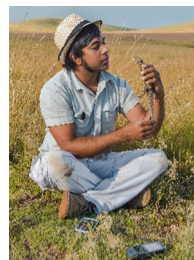
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