

Are high elevation crag lizards sensitive to climate change?

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Abstract

Crag lizards are restricted to montane areas where biota are strongly exposed to the effects of climate change. We investigated the factors shaping the distribution of Drakensberg crag lizards (*Pseudocordylus melanotus melanotus*; Cordylidae) by quantifying their elevational ranges, availability of shelter and prey as well as the thermal environment at three elevations. We recorded expected body temperatures using copper models of the lizards at each elevation in the field and in the laboratory, estimating the duration for which lizards must shelter from high temperatures. This correlated strongly with field observations of lizard activity during winter, spring and summer. Our models predicted that at lower elevations, lizards would shelter for longer periods each day, resulting in a marked reduction in time available for essential activities such as feeding and breeding, possibly explaining why these animals do not occur at lower elevations. The distribution and survival of these animals therefore appear to be impacted by the degree to which daytime temperatures limit their activity. Modelling future climate change scenarios at the high elevation site indicates that crag lizards would be resilient against small to moderate warming reflected by RCP4.5 climate change predictions, but populations are unlikely to persist under conditions predicted in the RCP8.5 scenario. This study is important as, unlike broader-scope studies that cannot quantify climate change impacts on individual species, we combine detailed field data with laboratory measurements and modelling of a single species to assess the ecological constraints to which crag lizards are exposed.

Keywords: climate change, ectotherm, elevational range, habitat selection, operative temperature, thermoregulation.

Introduction

Climate change-induced temperature increases influence the distribution, phenology and dynamics of biological communities and have triggered the extinction of several species (Moreno-Rueda *et al.* 2011; Moritz & Aguda 2013). Sinervo *et al.* (2010) predict that by the year 2080, 39% of lizard populations globally and 20% of all lizard species will be extinct. Böhm *et al.* (2016) performed a global trait-based analysis of climate change vulnerability in 1498 reptile species and found that 80.5% were highly sensitive to the effects of climate change. Considering temperature in isolation limits our ability to predict the effects of

climate change on a species and therefore, it is necessary to try assess the habitat requirements of a species (Huey *et al.* 2010, 2012).

For reptiles, the availability of microhabitats meeting their thermal requirements is essential (Stanton-Jones *et al.* 2018), and shelter and food resources are vital characteristics of these microhabitats (Goodman *et al.* 2008). Furthermore, the critical dependence on ambient temperature for thermoregulation by reptiles makes them more susceptible to the effects of climate change compared to other vertebrates (Berriozabal-Islas *et al.* 2018). Small lizards have limited dispersal abilities and are therefore at a greater risk of extinction due to increased insolation and temperatures associated with climate change than most other vertebrates (Gibbons *et al.* 2000; Berriozabal-Islas *et al.* 2018).

The Drakensberg crag lizard (*Pseudocordylus melanotus melanotus*; Cordylidae) is a heliothermic, rupicolous, sit-and-wait insectivore found on rocky outcrops. It weighs between 40 and 50 g (McConnachie 2014), and adult snout–vent length ranges between 80 and 136 mm (Branch 1998; McConnachie 2014).

The geographical distribution of this species is limited to montane areas in the eastern and northern parts of South Africa, 1100–2300 m.a.s.l. (Branch 1998; Bates 2005; McConnachie *et al.* 2007). It is adapted to cold temperatures, and thermoregulation is achieved by shuttling between exposed rock surfaces for basking and shaded areas for cooling (McConnachie *et al.* 2007; Fei *et al.* 2012). Since lizards restricted to mountaintops are at the limit of their elevational range (migration to higher, cooler, elevations is not possible), they face a high risk of extinction from increased ambient temperatures (Ortega *et al.* 2016; Vicenzi *et al.* 2017). The elevation-specific distribution of *P. m. melanotus* was investigated by quantifying and evaluating their habitat requirements within the context of climate change. We investigate three explanations for the elevational distribution of the lizards: food availability, shelter availability and temperature limitations. Our objectives were to: (i) Use field data on climate, shelter and prey availability at different elevations to evaluate why these lizards are elevation-specific. (ii) Use behavioural and temperature observations to assess how the behaviour of free-ranging crag lizards was constrained by ambient temperature and insolation. This included providing a link between ambient temperature and feeding which is critical for survival. (iii) Use non-invasive field and laboratory measurements to model lizard body temperature profiles to quantify the daily duration during which field temperatures are too high for normal lizard activity. This was done for three elevations. (iv) Using the same approach, model the implications of climate change on lizard activity and extrapolate these to the survival probability of crag lizards under different climate change scenarios.

Materials and methods

Study site

Field work was performed at Mariepskop Mountain (24°30'S, 30°58'E) South Africa. The foot of Mariepskop experiences a warm subtropical climate, while the mountain is cooler with a temperature gradient of ~10°C from 600 m.a.s.l. to 1945 m.a.s.l. Three study sites at different elevations (Fig. 1) with rocky habitat potentially available for crag lizards were

chosen: (i) 1900 m site: High elevation 1866–1900 m.a.s.l.; (ii) 1700 m site: Mid-elevation 1696–1832 m.a.s.l.; and (iii) 1300 m site: Low elevation 1256–1333 m.a.s.l.

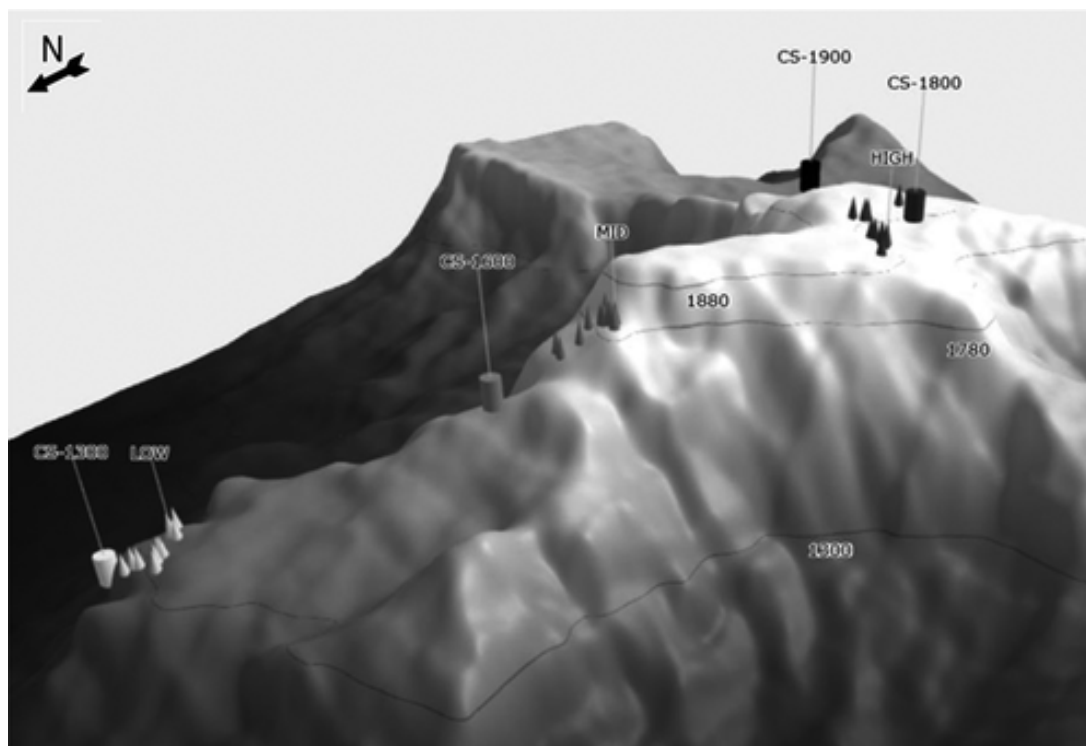


Fig. 1. Digital elevation model of study sites on part of Mariepskop. Each sample crevice at sites ‘HIGH’ (1900 m.a.s.l.), ‘MID’ (1700 m.a.s.l.) and ‘LOW’ (1300 m.a.s.l.) is indicated with a cone. Automated weather stations are shown as tall cylinders labelled as ‘CS’ and their elevation.

Elevational range of crag lizards at Mariepskop

The elevational range of crag lizards at Mariepskop was assessed by active searching (200 h) from 700 m.a.s.l. to 1945 m.a.s.l, only on sunny days (Effenberger & Mouton 2007). The location and elevation of each observed crag lizard was recorded using a GPS (Garmin eTrex 10; <15 m accuracy).

Availability of suitable shelter

We measured the physical features of 24 randomly selected crevices occupied by *P. m. melanotus* at the 1900 m site. A further 40 crevices were randomly chosen at the 1300 m ($n = 20$) and 1700 m ($n = 20$) sites (unoccupied by *P. m. melanotus* as the lizards have not been recorded at these lower elevations), for which the following were measured (Diaz *et al.* 2006): (i) Height of entrance (mm) using callipers in the middle of the crevice opening; (ii) Depth (mm) from entrance to the deepest point using wire strand (5 mm diameter) with low flexibility (1 mm resolution; depth > 1 m was scored as 1 m); (iii) Aspect of opening (nearest cardinal direction) using a compass. Dimension variables were analysed using a single-factor anova and aspect using a chi-square goodness of fit test.

Prey availability

During winter, spring and summer, pitfall traps were deployed at all three elevational sites within 5 m of nine crevices for four days. Traps comprised 2-L plastic bottles with the top half removed, inverted and placed inside the bottom half to act as a funnel. Traps were sunk into the soil with the top of the container flush with the soil surface, covered with rain cover lids and filled with ~350 mL of 2:1 water: propylene glycol. Three drift fences 1.2 m long and 10 cm high were placed around the trap radiating outwards, to increase trapping efficiency. Trapped invertebrates were washed and preserved in 70% ethanol and identified to order and family. Invertebrates, of the taxa Coleoptera, Diptera, Diplopoda, Orthoptera and Hymenoptera, were analysed based on the published prey preferences of *P. m. melanotus* (Branch 1998; McConnachie 2006; Alexander & Marais 2007) and on our own field observations. We compared the insect communities between elevational sites and seasons using a two-way ANOSIM (analysis of similarities) using square-root transformation of Bray–Curtis dissimilarity indices and elevation and season as factors (PRIMER-E V5.2.0; Plymouth Marine Laboratories, Plymouth, UK).

Diurnal activity and behaviour of free-ranging crag lizards

The diurnal activity of ten focal lizards was recorded during winter, spring and summer. Individuals were identified using a coloured elastic band around the neck (Ribeiro *et al.* 2009) or with a small streak of non-toxic paint on the dorsal or lateral body surface (Simon & Bissinger 1983). Since crag lizards are philopatric, locating the focal individuals during different seasons was simple. Observations were only performed on cloudless sunny days from 07h30 until 17h30. A habituation period of one day after marking as well as 15 min before each observation period reduced the effect of the observer on lizard behaviour. Observations were made at a distance of 5–10 m, lasted 60 min, and a minimum of ten observation hours per hourly period (from 07h30 to 17h30 = 10 hourly periods) in the day was performed per season (100 h per season). Lizard behaviour was categorised as basking (outside crevice in sun) or lying inside crevice. Successful and unsuccessful feeding events were catalogued and where possible, the prey item was identified.

General climatic conditions

At each elevation site, an automated weather station positioned two metres above ground (Mike Cotton Systems or Campbell Instruments) recorded wind speed ($\text{m}\cdot\text{s}^{-1}$), temperature ($^{\circ}\text{C}$) and insolation ($\text{W}\cdot\text{m}^{-2}$) at 10 min intervals. We compared difference in diurnal temperature and insolation between elevations using generalised least-squares anova (function `gls()`; Pinheiro & Bates 2000) with R V2.14.2 (R Development Core Team 2012), taking into account temporal autocorrelation in time series of environmental measurements.

Temperature inside crevices

Temperature was recorded in each of 12 crevices per site during winter, spring and summer using DS1922L Thermochron iButtons (Maxim Integrated, San Jose, CA, USA) calibrated in a temperature-controlled water bath against a high precision mercury thermometer

(G3THE017Z Lasec; Cape Town, South Africa) at 5 and 55°C. An iButton was placed inside each crevice at a depth of 10 cm in the shade, logging temperature every 10 min. At 1900 m, these crevices were all occupied by lizards. Additionally, at each crevice, the microhabitat ambient temperature (T_a) was recorded every 10 min using an iButton inside an inverted polystyrene cup with eight ventilation holes, placed within 6 m of the crevice at a height of 1 m above the ground.

Field-measured operative temperature

Operative temperature (T_e) is the temperature of an inanimate object with zero heat capacity where the object shares the same size, shape and colouration of the experimental animal exposed to the same microclimate (Bakken & Gates 1975; Shine & Kearney 2001). Twelve copper lizard models were constructed following Bakken and Gates (1975), offering a non-invasive approach to study the thermal dynamics of small animals. A female crag lizard museum specimen was moulded using wax and electroplated with copper after which the mould was removed by melting and the model oxidised using potassium sulphide until colouration matched that of an adult female lizard (Scheers & Van Damme 2002). A small incision was made in the ventral surface of each model allowing insertion of an iButton with a 10-min recording interval. Models were positioned horizontally on a rock surface in direct sunshine approximately 100 mm from the focal crevice entrance. T_e was recorded simultaneously with crevice temperature and T_a for 4 days at each of 12 crevices at each elevation during spring and summer. McConnachie (2006) found that crag lizards in the laboratory showed heat stress at >35°C ambient temperature. We used this temperature as the upper thermal limit (T_{max}) for the species, allowing calculation of the proportion of time that T_e exceeded T_{max} .

Estimation of lizard operative temperatures using copper models

Newton's Law of Cooling (Vollmer 2009) assumes a cooling rate directly proportional to the temperature difference between the model and the ambient (equilibrium) temperature (Tipler & Llewellyn 2012). This is an empirical law largely taking into account convective cooling (Vollmer 2009). Our copper models satisfied this law for temperatures within 15°C of T_a where the following formula was used for cooling:

$$\frac{\Delta T_e}{\Delta t} = -K(T_e - T_a) \quad (1)$$

where t is time, K a constant dependent on the overall heat exchange characteristics of the body, T_e operative temperature (lizard body temperature) and T_a the ambient (equilibrium) temperature. This equation can be rearranged, allowing calculation of the cooling constant K and providing a predictive tool for estimating lizard operative temperature for a specific cooling scenario. For the heating, a similar approach was used.

$$\frac{\Delta T_e}{\Delta t} = +k(T_{eq} - T_e) \quad (2)$$

where T_{eq} is the final equilibrium temperature during heating where heat gain from the heat source is balanced by heat loss from the lizard model to the environment. There is no reason to expect the relationship (2) to hold during heating since this is dependent on the characteristics of the object being heated. However, it did hold approximately for the lizard models for T within 5°C of T_{eq} , allowing calculation of the heating constant k and providing a predictive tool for estimating the operative temperatures of lizard models heated by the sun. For cooling, K was not affected by the initial temperature of the copper model. For heating, the value of k was linearly insolation-dependent as was the case for T_{eq} . These relationships were quantified through laboratory measurements using the models (Table 1).

Table 1. Intercept and slope values of T_e as a function of insolation (seven isolation levels) obtained from heating and cooling curves of lizard models in the laboratory, taking into account substrate and wind conditions

	CB no wind	Rock no wind	Rock 0.5 m.s ⁻¹	Rock 1 m.s ⁻¹
<i>T_a – heating</i>				
Intercept	8.400	6.150	4.050	1.30
Slope	0.053	0.039	0.023	0.025
<i>k – heating</i>				
Intercept	0.203	0.198	0.190	0.163
Slope	0.00007966	0.00003548	0.00004373	0.00006833
<i>K – cooling</i>				
Intercept	0.064	0.052	0.163	0.100

Laboratory measurements of lizard copper model temperatures to estimate k and K

The models were mounted on a flat rock surface (dimensions 55 × 25 cm) with similar geology to the rocks found at Mariepskop. Temperature inside models was recorded each minute using thermocouples (MT630 Digital thermometers; Major Tech, Johannesburg, South Africa), calibrated at 22 and 60°C in a temperature-controlled water bath using a precision mercury thermometer. A 500 W halogen floodlight FS18B (Eurolux, Johannesburg, South Africa) was used as an artificial heating source at insolation intensities of 50, 100, 200, 400, 600, 800 and 1000 W m⁻². Insolation was manipulated by adjusting the voltage to the light and verified at the positions of the models using a LI-200 pyranometer (Li-Cor, Lincoln, NE, USA). Two electric fans generated wind at 0.5 and 1 m.s⁻¹, adjusted by controlling their power supply. Wind speed was measured with a Kestrel pocket weather tracker 4000 (Nielsen-Kellerman, Boothwyn, PA, USA) and calibrated (1.0–2.0 m.s⁻¹ at 0.1 m.s⁻¹ increments) using a Wind Sentry model 03002 (Young, Traverse City, MI, USA) meteorological anemometer ($r^2 = 1.000$).

Four experiments were performed to estimate the effect of environmental conditions on the cooling and heating characteristics of the models:

Cardboard no wind

Models were mounted on a sheet of double-walled cardboard to eliminate heat conduction to the underlying rock. Two lizard models were spaced 10 cm apart and heated until the operative temperature stabilised. The heat source was then switched off, allowing cooling to ambient temperature (T_a). This was repeated at the seven different insolation intensities. Each experiment was repeated for another pair of models, yielding data for four models at each of the insolation intensities. Temperature of the rock surface under the cardboard was measured using a thermocouple.

Rock no wind

The procedure followed experiment 1 except models was placed directly on the rock surface, allowing heat conduction from the copper model to the rock. Waples and Waples (2004) measured that, at 25°C, granitic rocks have a substantial heat capacity of around $1.1 \text{ kJ kg}^{-1} \text{ }^\circ\text{C}^{-1}$. Given the large size of rockfaces on the mountain (several tonnes) and the relatively small surfaces instantaneously perpendicular to the sun, the temperature of these rocks would therefore be largely affected by mean daily temperature (around 15°C) and relatively little affected by solar radiation. This was consistent with field temperature measurements of rocks used for basking. Since the rock used in the laboratory was much smaller (8.5 kg) than those used by lizards in the field, the exposed rock around the models was covered with double-rifled cardboard to minimise the heating of the rock except for the surface directly underneath the model.

Rock with 0.5 m.s⁻¹ wind

The procedure followed experiment 2 but with a constant air movement of 0.5 m.s^{-1} over the models during the whole experiment, allowing increased convective heat loss due to wind in addition to heat loss to the underlying rock.

Rock with 1 m.s⁻¹ wind

The procedure followed experiment 3 but with air movement of 1 m.s^{-1} over the models, allowing even more convective heat loss due to wind, in addition to heat loss to the underlying rock.

Modelling lizard body temperatures at different elevations and for climate change scenarios

Four sources of information allowed estimating the operative temperature of a copper lizard model: (i) diurnal temperature (T_a) obtained from automated weather stations at each of the three elevations, (ii) responses of copper model temperatures to different insolation intensities obtained from the laboratory measurements, (iii) diurnal insolation profiles obtained from the weather stations and (iv) the cooling and heating constants obtained from the laboratory measurements. Using Eqns (1) and (2), we modelled the diurnal thermal profile of a basking lizard on a horizontal rock. Our calculations took into account the azimuth and elevation of the sun, based on a series of photographs of the models from

many angles, measuring the effective surface of the model directly exposed to the sun. Three sources of field information were used in the modelling:

1. To model thermal conditions at the 1700 and 1300 m sites, respectively, hourly temperature and insolation data from the weather stations at 1700 m.a.s.l. (up to 21°C and 890 W m⁻²) and 1300 m.a.s.l. (up to 24°C and 900 W m⁻²) for a typical cloudless summer day were used to compare the thermal conditions at the lower elevations to that of the high altitudinal site. Three insolation intensity scenarios were used with 0.5 m.s⁻¹ wind:
 - A. 1100 W m⁻² insolation at all three elevational sites, simulating the maximum insolation encountered;
 - B. 660 W m⁻² insolation at all three sites modelling directly comparable elevational effects at realistic mean insolation intensities;
 - C. 660 W m⁻² (1900 m) or 558 W m⁻² (1700 m) or 510 W m⁻² (1300 m), representing mean summer insolation values (December–February) from each of the automated meteorological stations, reflecting mean hourly insolation due to cloud cover beneath the peak of Mariepskop.
2. Temperatures and insolation data (up to 1150 W m⁻²) for a typical cloudless summer day at 1900 m.a.s.l. recorded at 10-min intervals from the permanent automated meteorological station 10 m above ground at this site. This represents the hottest extremes likely to be encountered by crag lizards.
3. A more restricted data set of mean hourly temperature, insolation and wind values from a temporary automated weather station placed 2 m above ground in the core habitat of the crag lizards from December until March and representing the thermal environment during the summer (December, January, February) including cloudy conditions.

From 05h00 until 19h00 and at 1-min intervals, the ambient temperature, wind, position of the sun and insolation data were used to predict the temperature of the model. When the T_e of the model was higher than the predicted equilibrium temperature, then a cooling scenario was used, else a heating scenario was used. During heating, the equilibrium temperature of the model was determined by wind, insolation and ambient temperature. The difference between ambient temperature and the operative temperature (T_e) was always <2°C, that is heat exchange characteristics consistent with Newton's Law. A typical summer day at Mariepskop provides 660 min of diurnal lizard activity time (07h00 to 18h00). The number of minutes with $T_e < T_{max}$ is an estimate of the time duration a lizard can be active outside its crevice. Likely implications for future climate change scenarios were simulated in this way (1–4°C increase in mean ambient temperature) in line with scenarios RCP4.5 and RCP8.5 of the IPCC 5th Assessment Report (Stocker *et al.* 2013).

Results

Elevational limits of lizards

Crag lizards were restricted to elevations above 1 829 m.a.s.l.

Availability of suitable shelter

There were no significant differences in the dimensions of crevices (height: $F_{2,61} = 1.96$, $P = 0.15$, width: $F_{2,61} = 0.07$, $P = 0.93$) or their orientation ($\chi^2 = 2.69$; d.f. = 6; $P = 0.55$) between the three elevations (Table 2). Although more locally distributed at 1700 m, many crevices were found at each elevation.

Table 2. Crevice height and depth ($n = 64$) at three elevations, including the frequencies of their different aspects (North, East, South and West)

Elevation	1900 m	1700 m	1300 m
Number of crevices	24	20	20
Crevice height (mm)	17.87 ± 5.4 (8.1–30.5)	18.46 ± 5.81 (11.8–30.2)	18.15 ± 3.93 (12.1–28.1)
Crevice depth (mm)	647 ± 267 (280–1000)	584 ± 276 (200–1000)	495 ± 217 (240–1000)
North	10	6	9
East	6	6	7
South	4	3	2
West	4	5	2

Results are mean ± standard deviation (range). No significant difference was found between crevice height [$F_{2,61} = 1.96$, $P > 0.05$] or width [$F_{2,61} = 0.07$, $P > 0.05$] between elevations. A chi-square test revealed no difference in the directional orientation of crevices ($P > 0.05$).

Prey availability

Table 3 indicates that the number of food insects trapped during each season tended to be inversely proportional to the elevation of a site. However, there were no significant differences in prey community composition (Global $R_{\text{elevation}} = -0.095$, $P = 0.65$) between the three elevations (Table 3). There were significant seasonal differences among prey items trapped (Global $R_{\text{season}} = 0.67$, $P = 0.01$) reflecting the seasonal turnover of the invertebrate taxa (Table 3). During focal observations (300 observation hours), only 30 prey capture events were observed. Ants were the most abundant prey captured comprising 62% of all insects in spring ($n = 16$) and 38% in summer ($n = 5$). Diptera captures increased from 8% in spring ($n = 2$) to 23% in summer ($n = 3$), and Coleoptera captures increased from 4% ($n = 1$) in spring to 23% in summer ($n = 3$).

Table 3. Invertebrates (no. of individuals) trapped using pitfalls during each season at each elevation

Class/order/family	Winter			Spring			Summer		
	1900	1700	1300	1900	1700	1300	1900	1700	1300
Coleoptera	6	16	5	14	11	22	13	36	29
<i>Carabidae</i>	0	8	1	2	1	1	2	19	20
<i>Staphylinidae</i>	2	1	0	3	4	0	6	0	0
<i>Scarabaeidae</i>	2	0	0	0	2	2	0	1	0
<i>Elateridae</i>	0	0	0	2	3	3	2	4	2
<i>Tenebrionidae</i>	2	4	3	0	0	3	1	4	3
<i>Curculionidae</i>	0	3	1	7	1	13	2	8	4
Diplopoda	1	1	0	1	0	3	0	5	3
Diptera	3	1	1	10	13	12	32	16	66
Hymenoptera									
<i>Formicidae</i>	132	144	198	63	246	253	127	113	125
Orthoptera	3	2	2	5	8	5	11	14	10
<i>Anostostomatidae</i>	2	2	0	4	1	2	9	6	4
<i>Gryllidae</i>	0	0	1	1	7	1	2	8	5
<i>Acrididae</i>	0	0	0	0	0	2	0	0	1
<i>Pamphagidae</i>	1	0	1	0	0	0	0	0	0
Total no.	149	180	213	112	297	310	207	244	272

Climatic conditions

The two lower weather stations had higher minimum, maximum and mean temperatures than the 1900 m station (Table 4). Taking into account temporal autocorrelation for temperature and insolation at the different elevations during winter, spring and summer, there were significant differences in ambient temperature, with lower sites being warmer (Table 4).

Table 4. Summary diurnal (6 am–6 pm) values (mean \pm standard deviation (range)) of mean weather station air temperature, insolation, within-crevice temperature, microhabitat ambient temperature and operative temperatures (T_e) at each elevation for three seasons

Elevation	Winter				Spring	
	1900	1700	1300	ANOVA	1900	1700
Weather station air temp (°C)	11.2 \pm 1.64 (5.6–17.2)	14.91 \pm 2.83 (7.8–22.8)	16.6 \pm 2.52 (9.3–24.8)	$F_{2,1254} = 255.87$ $P < 0.001$	13.00 \pm 1.82 (2.9–24.7)	18.11 \pm 2.32 (7.8–30.9)
Insolation (W m ⁻²)	245.91 \pm 205 (0–635.6)	275.30 \pm 212 (0–603.3)	268.88 \pm 195 (0–608.8)	$F_{2,1254} = 50.03$ $P < 0.001$	408.96 \pm 231 (0–988.0)	389.65 \pm 245 (2.8–967.4)
Inside crevice temp (°C)	11.92 \pm 3.06 (7.1–20.4)	14.30 \pm 2.53 (9.6–22.3)	17.26 \pm 2.9 (11.8–24.8)	$F_{2,711} = 63.13$ $P < 0.001$	13.90 \pm 3.96 (7.7–25.3)	5.56 \pm 4.51 (9.3–30.8)
Micro-habitat ambient temp (°C)	10.03 \pm 2.98 (5.4–20.5)	12.17 \pm 4.20 (7.5–26.7)	14.81 \pm 3.8 (6.7–23.8)	$F_{2,456} = 17.07$ $P < 0.001$	13.01 \pm 5.87 (3.0–30.1)	14.33 \pm 5.03 (7.1–31.1)
Operative temp (T_e ; °C)	–	–	–	–	14.98 \pm 7.54 (4.3–41.8)	16.31 \pm 6.40 (7.0–36.3)

Temperatures within and around crevices

The 1900 m site had lower mean temperatures inside the crevices than the lower altitudinal sites except during summer when crevice temperatures were higher at 1900 m (Table 3). These temperatures differed significantly between the three sites, even after applying Holm’s sequential Bonferroni correction for multiple comparisons (Holm 1979; Table 4). Generalised least-squares anova revealed a significant difference in the microhabitat temperatures (recorded near each crevice) between the three sites during all three seasons with the 1900 m site having lower means and ranges of ambient temperatures during each season than at the lower altitudinal sites (Table 3).

Field measurements of operative temperature (T_e)

Generalised least-squares anova indicated that mean field-recorded T_e at 1700 m and 1300 m was higher than at 1900 m during both spring and summer (Table 4). However, maximum T_e at 1900 m during summer was higher than for the lower elevational sites, explained by clouds beneath the peak of the mountain.

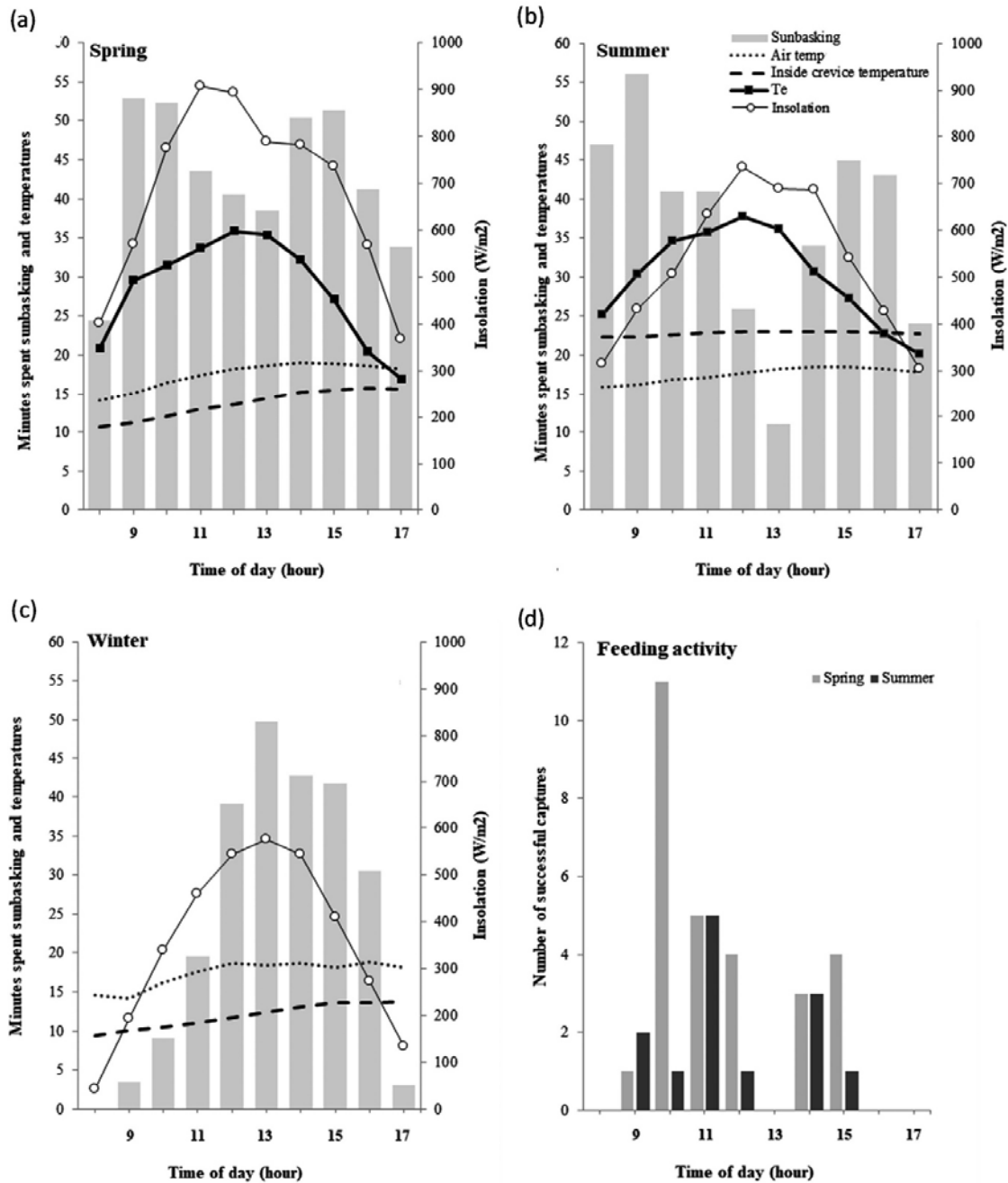


Fig. 2. Mean number of minutes per hour spent sunbasking during spring compared to operative temperature (T_e), air temperature, inside crevice temperature (left Y-axis) and insolation (right Y-axis). (b) The same layout for summer. (c) The mean number of minutes per hour spent sunbasking during winter compared to air temperature, inside crevice temperature (left Y-axis) and insolation (right Y-axis). (d) Foraging success of crag lizards during spring and summer.

Diurnal activity and behaviour of free-ranging crag lizards

During spring, the lizards emerged from 7:30 am (Fig. 2a), spent little time basking during mid-day, followed by increased basking after the warmest mid-day period (~14:00). During summer, they spent the first four hours of the day basking, then retreated into their crevices when T_e reached a maximum during the mid-day period, emerging again from their crevices when the temperature decreased in the afternoon (Fig. 2b). During winter, lizards emerged from their crevices between 8:30 and 9:30 (Fig. 2c) and the maximum fraction of time spent basking was during the mid-day period (12:30–13:30). Table 5 shows the time in the early morning that lizards became active as well as the times in the late afternoon when lizards retired to their shelters. These data result from a small number of measurements during the period July until February, indicating that morning activity in winter starts about 100 min later than during summer and ends about 60 min earlier in the afternoon. Analysing the onset and cessation of activity in response to excessive heat, one needs to exclude the winter observations as the temperatures were too low, after which a 1-way anova did not reveal any differences in the times of onset or cessation of activity during different months ($P = 0.39$). Moreover, an ancova did not reveal any trend within a month for an earlier onset or later cessation of activity when the ambient temperature was higher ($P = 0.22$). During the period November until February, there is therefore no clear indication that activity starts earlier in the morning during the hot months of January and February when temperature constraints on activity during mid-day are greatest. However, performing statistics on such a small set of observations makes conclusions tentative.

Table 5. Times of crag lizard emergence (onset) in early morning and sheltering in late afternoon (cessation) during mid 2012–early 2013

Month	Onset time	T_a (°C)	n	Cessation time	T_a (°C)	n
July	10h13	8.8	4	15h59	9.7	5
	<i>09h50–11h14</i>	<i>6.2– 9.9</i>		<i>15h20–16h22</i>	<i>7.4– 11.4</i>	
October	08h06	15.7	2	16h49	15.9	4
	<i>07h43–08h30</i>	<i>15.2– 16.2</i>		<i>15h50–17h16</i>	<i>14.9– 18.8</i>	
November	08h30	14.0	9	16h57	18.2	7
	<i>07h38–09h24</i>	<i>6.4– 19.3</i>		<i>16h34–17h10</i>	<i>9.2–24.2</i>	
January	08h28	18.1	5	16h42	18.3	4
	<i>07h38–09h36</i>	<i>14.2– 25.1</i>		<i>16h20–17h15</i>	<i>15.2– 20.9</i>	
February	08h22	15.6	4	17h07	16.0	2
	<i>08h04–09h00</i>	<i>14.5– 16.7</i>		<i>17h05–17h10</i>	<i>15.9– 16.1</i>	

Data represent mean values, range of observations (in italics) and sample size.

No feeding activity was recorded during winter (118 observation hours). Spring had the highest number of observed feeding attempts with 28 successful and three unsuccessful attempts (116 observation hours; Fig. 2d). During summer, the number of observed feeding attempts decreased to 13 successful captures and no unsuccessful attempts (114 observation hours). In both spring and summer, feeding activity started between 8:30 and 9:30, reached a maximum between 9:30 and 11:30 am, ceased during the mid-day period and commenced again after 13:30 (Fig. 2d).

Modelling lizard activity at different elevations and for different insolation levels

From laboratory measurements, the scenario of a lizard on rock with 0.5 m.s^{-1} wind (experiment 3) was used for modelling different climate change scenarios at different elevations, because it depicts a typical summer day at Mariepskop, taking into account conductive and convective heat loss a lizard would experience in the field (Figs 3,4a). Different insolation intensities were used in the models (1100, 600, 558 and 510 W m^{-2}) to compare the effect of insolation on T_e for each of the scenarios (Figs 4,5).

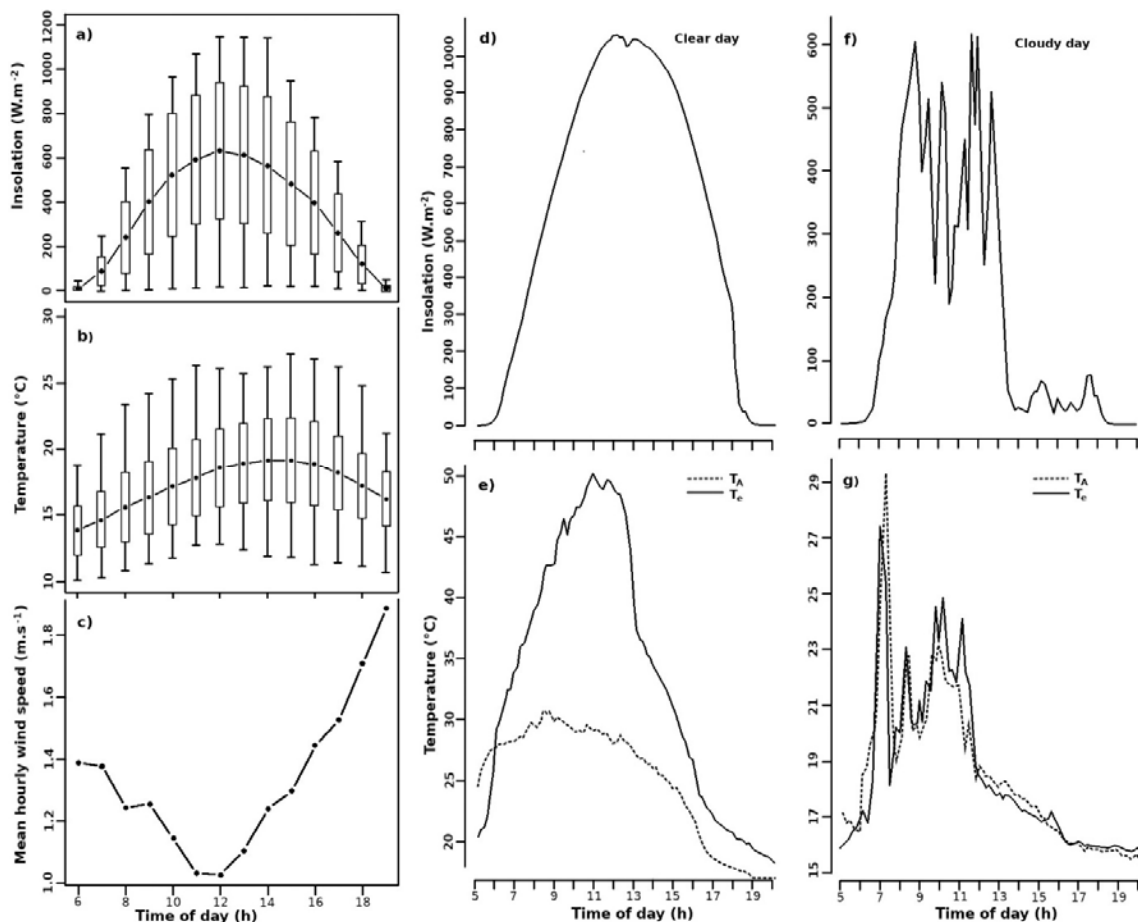


Fig. 3. Variation in summer (December–February) microclimate at Mariepskop and its effect on field-measured operative temperature (T_e). (a) Mean hourly insolation (W m^{-2}), (b) temperature ($^{\circ}\text{C}$) and (c) Wind speed (m.s^{-1}). Range and standard deviation are included for (a) and (b). Figures (d) and (e) indicate insolation, ambient temperature (T_a) and field-measured T_e on a cloudless day, while (f) and (g) represent T_e on a cloudy day with low T_a and insolation.

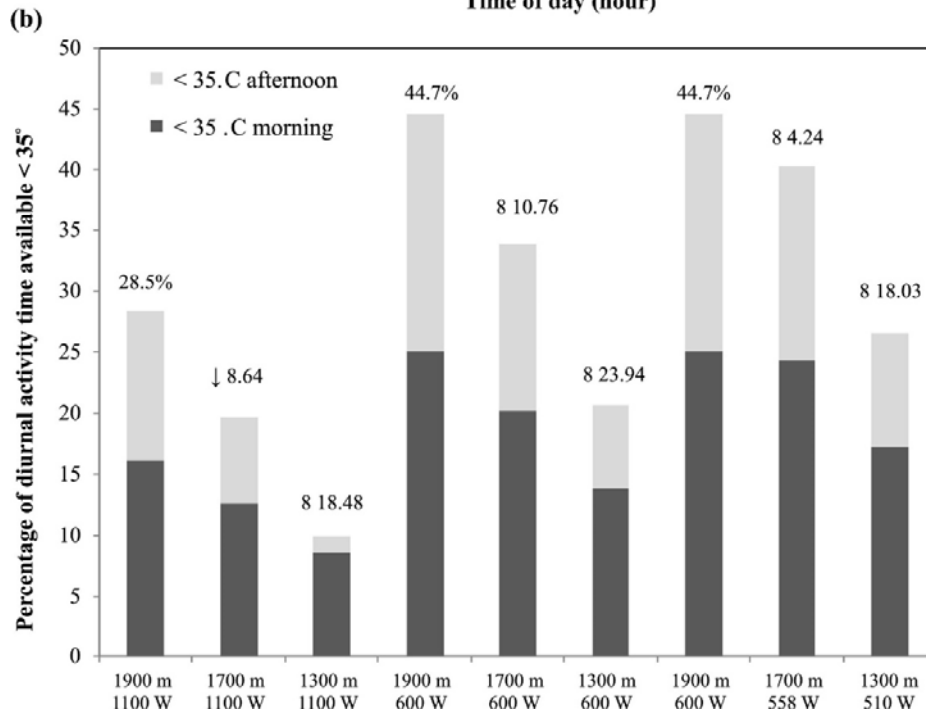
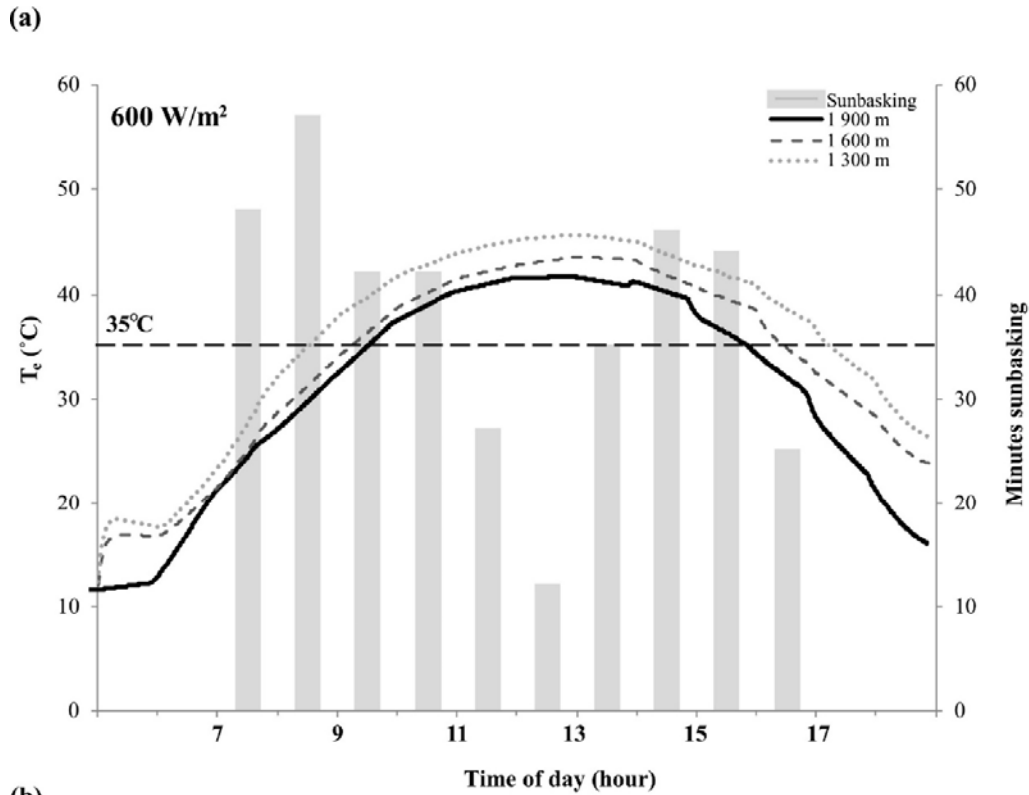


Fig. 4. (a) Effect of elevation on lizard T_e (rock with 0.5 m.s^{-1} wind) comparing the three altitudinal sites at 600 W m^{-2} , mean number of minutes per hour spent basking during summer at 1900 m.a.s.l. being indicated on the right Y-axis. (b) Proportion of time between 7 am and 6 pm where $T_e < 35^\circ\text{C}$ during morning and afternoon at each altitudinal site (rock with 0.5 m.s^{-1} wind) and different insolation intensities. The rightmost three bars are based on the mean diurnal insolation measured by weather stations at each of the elevations. The reduction in percentage of time $T_e < 35^\circ\text{C}$ (compared to 1900 m) is indicated above each bar for 1700 and 1300 m sites.

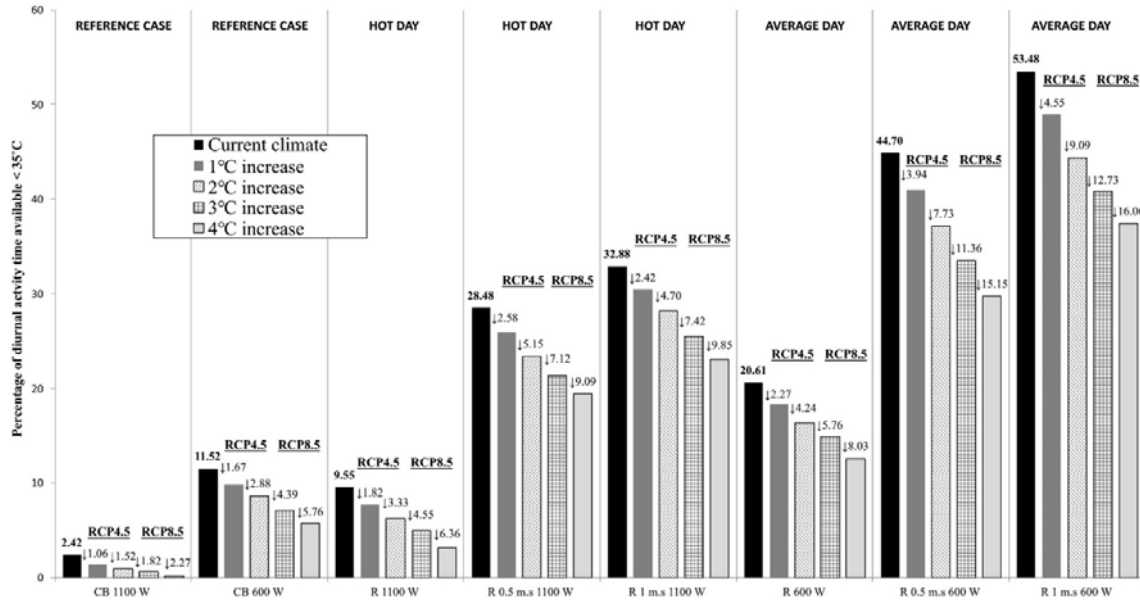


Fig. 5. Diurnal activity time (%) with $T_e < 35^\circ\text{C}$ at maximal and mean insolation values and different experimental designs (CB = cardboard; R = Rock; W = Watts; m.s = $\text{m}\cdot\text{s}^{-1}$ wind speed) and for increased ambient temperatures (1–4°C) reflecting IPCC scenarios RCP4.5 and RCP8.5. Bold numbers above black bars indicate value on y-axis. Numbers above other bars indicate the reduction in percentage of activity compared to current time conditions (i.e. black bars).

High elevation

Ambient conditions at 1900 m during a summer day (6:00–18:00) are characterised by a mean insolation of 600 W m^{-2} , T_a of 14 to $\sim 19^\circ\text{C}$ and wind speeds of $1.0\text{--}1.9 \text{ m}\cdot\text{s}^{-1}$ (Fig. 3a–c). In these models, T_e was always within 0.2°C of T_a . T_e exceeded T_{max} (35°C) in summer between 09h30 and 15h30 allowing only 44.7% (294 min) of diurnal activity time, in excellent agreement with field measurements of copper lizard models (Fig. 4a). Mornings comprised more activity time ($T_e < T_{\text{max}}$) than afternoons ($F_{1,16} = 4.68$, $P < 0.05$; Fig. 4b). At 1100 W m^{-2} maximum diurnal insolation (the maximal instantaneous insolation), only 28.5% (188 min) of diurnal activity time ($T_e < T_{\text{max}}$) was available (Fig. 5).

Mid-elevation

T_e exceeds T_{max} between 09:00 and 16:30 for a typical summer's day at 1700 m with 600 W m^{-2} insolation, with an associated 2.1°C increase in mid-day temperature compared to that for 1900 m. Only 34% of diurnal time (224 min) is available for lizard activity, which is a reduction of 10.8% (71 min) compared to 1900 m (294 min) at the same insolation (Fig. 4). At 558 W m^{-2} (the mean insolation intensity also including periods when cloud cover forms below the peak), a 4.2% (28 min) reduction in available diurnal activity time resulted compared to 1900 m (Fig. 4).

Low elevation

For a typical summer's day at 1300 m with 600 W m^{-2} insolation, T_e exceeded T_{max} between 08:30 and 17:00 with a 4.7°C increase in mid-day temperature compared to 1900 m (Fig. 4).

Diurnal activity time was 24% (158 min) less than at 1900 m. At 1100 W m⁻² insolation, diurnal activity time was further reduced by 18.5% (122 min) compared to 1900 m (294 min) at the same insolation (Fig. 4a). At 510 W m⁻² (i.e. the mean observed insolation at this site during cloudy conditions), an 18% (119 min) reduction in available diurnal activity time was observed compared to that at 1900 m (with 600 W m⁻² insolation; Fig. 4a).

Modelling for climate change scenarios at high elevation

During a hot day at 1900 m with 1100 W m⁻² insolation and 0.5 m.s⁻¹ wind, 28.5% (188 min) of diurnal activity time ($T_e < T_{max}$) is expected (Fig. 5). With a 1°C increase in ambient temperature (T_a), T_e exceeds T_{max} between 08:30 and 16:30 resulting in a 2.6% (17 min) reduction in available activity time (Fig. 5 – R 0.5 m.s⁻¹ 1100 W). Activity time is reduced by up to 9.1% (60 min) at an ambient temperature (T_a) increase of 4°C (Fig. 5). Ambient conditions of 600 W m⁻² insolation and 0.5 m.s⁻¹ wind at 1900 m.a.s.l., considered to be an ‘average day’, currently allow *P. melanotus* to be active 44.7% of the diurnal time. At 600 W m⁻² insolation and with a 1°C increase in T_a , $T_e > T_{max}$ later in the morning (09:00 am) and $T_e < T_{max}$ earlier in the afternoon (16:00) compared to the equivalent values for 1100 W m⁻², resulting in a further 3.9% (26 min) reduction of available diurnal activity time (Fig. 5). Increases of 4°C in T_a produce more pronounced reductions in diurnal activity time of 15.1% (100 min; Fig. 5). Conditions of 1 m.s⁻¹ wind at 1100 and 600 W m⁻² insolation produce similar reductions of activity time as in the cases discussed above (Fig. 5). In all of the scenarios in Fig. 5, an increase in T_a of 2°C reduces the activity time by approximately 9% (59 min), and an increase in T_a of 4°C reduces the activity time by approximately 13.4% (88 min), compared to the equivalent values with no warming (Fig. 5).

Discussion

We assessed the factors shaping the limited elevational ranges and the likely effects of climate change on the crag lizards. Many studies use only globally recorded ambient temperature data to predict the impact of climate change on species. Consideration of the broader ecological context is a more holistic approach when assessing the vulnerability of species to climate change (Kearney & Porter 2004). Although we used global temperature data with respect to macroclimate, we relied extensively on locally recorded data both from automated weather stations on site, copper models of lizards in the field as well as their feeding and basking behaviour. Our work has four caveats. Firstly, interpretations for predicting responses of plants and animals to Global Mean Temperatures (GMT; e.g. predictions by IPCC scenarios) should be treated with care because GMT does not necessarily reflect changes in the local temperatures. Secondly, the use of temperature alone in modelling the persistence of animals or plants (a substantial literature including this study) has limitations, since the long-term effects of GMT on clouds, rain and wind are much more difficult to predict. This is especially important in mountains where these phenomena are important environmental factors that interact with ambient temperature. Thirdly, there are caveats surrounding the use of copper replicate models in estimating operative temperature of animals. Mainly, different attributes may influence the operative temperature recordings, for example size, colour, degree of contact of model with the surface and local weather conditions (Shine & Kearney 2001). Seebacher and Shine (2004) concluded that size is the most important limiting factor, whereby the larger the animal, the

greater the risk of overestimating operative temperature ranges may be. Larger copper models require more metal, deviating from the assumption that the model has zero heat capacity. We minimised the mass of copper used by electroplating the models. In addition, crag lizards are small (mean mass approximately 45 g; McConnachie 2014) and therefore the size effect is minimal. Our results are consistent with the contexts for reliable use of copper models, proposed by Shine and Kearney (2001). Fourthly, the study was performed over a single year to include austral winter, spring and summer seasons. Since no climate extremes were observed during this period, we have no evidence that an equivalent multi-year study including all our different categories of field measurements would provide fundamentally different conclusions.

The similarity in the dimensions and orientation of crevices at the 1700 and 1300 m sites to the 1900 m site indicated that the limited elevational range observed for crag lizards at Mariepskop is not due to low availability of suitable crevices at the lower elevations. The similarity in prey abundance (as measured by trapping success) and community composition of prey at the lower elevations, compared to those at 1900 m, indicate that lack of suitable prey is unlikely to explain the elevational ranges of crag lizards. The difference in prey community composition between seasons was similar between elevations and is attributed to invertebrate phenology (Jamieson *et al.* 2012). Therefore, it is highly unlikely that refugia or prey availability are main factors limiting the elevational occurrence of this species.

Crag lizards' upper thermal limit constrains diurnal activity during the middle portion of the day. The fraction of available daily activity time, assuming a standardised start time of 07h00, correlates directly with elevation. Although the insolation decreased at lower elevations due to cloud cover, the increase in ambient temperature at lower elevations more than compensated for the insolation effect (Table 4). The typical climatic conditions of 600 W m^{-2} insolation and 0.5 m.s^{-1} results in a 10.8% (71 min) reduction in activity time available at 1700 m and 23.9% (158 min) at 1300 m.a.s.l. (compared to time available at 1900 m.a.s.l.) and lizards would have to reduce essential activities such as feeding and breeding (Fig. 4).

Lizards may adapt to the thermal constraints during the mid-day period by starting to forage earlier in the morning when it is very hot. Our very limited data are not consistent with this hypothesis, either when comparing hot summer months with cooler months in spring, or when comparing hot days within a month with cooler days. Consequently, ignoring other factors besides ambient temperature constraining the emergence time of these lizards, emergence time would have to be approximately 05h49 at 1700 m and 04h22 at 1300 m to compensate for the lost activity time during mid-day. Given that sunrise during the hottest part of the year (January/February) is between 05h22 and 05h44, this does not give sufficient time for lizards and prey insects to become hot enough to become active. Therefore, crag lizards are unlikely to persist at the lower altitudinal sites due to the thermal constraints imposed by T_{max} . Our results are consistent with those of Heath (1962) and Winne and Keck (2004) who did not find any dynamic adaptation of times of emergence of the lizards in their studies. Bishop and Echternacht (2004) found that, in cold-dominated activity patterns of *Anolis* lizards, variation in emergence time correlated with individual identity rather than to environmental attributes. Obviously, the topic of emergence times of

lizards with reduced opportunity of finding food requires in-depth study and our results within this context are tentative.

The behavioural observation data corroborate our conclusions based on T_e measurements as during summer there is an obvious reduction in basking when $T_e > T_{max}$ (Fig. 2b). Other studies, where operative temperatures of lizards were measured following similar methods, agree that with higher ambient temperatures, activity time of lizards decreases (McConnachie 2006; Logan *et al.* 2013; Stanton-Jones *et al.* 2018). Changing location by moving between shaded crevices and sun exposed areas and minimising activity during times of high temperature and insolation (Fig. 2) allows the lizard to control duration and intensity of heat exposure (Adolph 1990; Bauwens *et al.* 1999; Vidal *et al.* 2010; Fei *et al.* 2012). The contrasting, unimodal diurnal activity behaviour during winter compared with summer (Fig. 2) shows that temperature and insolation are critical factors influencing behavioural thermoregulation (Adolph 1990; McConnachie *et al.* 2009). Diurnal activity patterns during spring and summer are consistent with other behavioural studies on this species (McConnachie *et al.* 2009) where the lizard retreated into crevices to maintain body temperature during the time when temperatures reached a maximum (McConnachie 2006; Kiefer *et al.* 2007; Fei *et al.* 2012). The higher means and ranges of crevice and microhabitat temperatures recorded at the lower sites during each season, combined with weather station records (Table 4), confirm that the lower sites are warmer than at 1900 m.a.s.l. The higher temperatures at the lower altitudinal sites where $T_e > T_{max}$ for extended periods lead to reduced activity time and probably affect crag lizard survival because of the constraint on opportunity to feed and perform other critical activities. Similarly, Sinervo *et al.* (2010) found that the heliothermic *Sceloporus* lizard's modelled activity was significantly reduced in the habitat where they are now extinct (where $T_e > T_{max}$ for extended periods due to warmer climatic conditions) compared to the habitat where they still persist.

Seebacher and Shine (2004) indicate that for lizards with a mass of about 45 g (e.g. crag lizards), the amount of time that they can be exposed to high body temperatures can be reduced by 25% due to the finite period required for the body to heat up to 35°C. Our laboratory derived heating and cooling constants indicate that it takes a copper model about 9 min to heat up from 20°C in the crevice (Table 4) to within 2°C of T_{max} and that it takes about 11 min to cool down from T_{max} to within 2°C of the crevice temperature of 20°C. If they shuttled every 10 min, there would be very low exposure to T_{max} due to the lag in body temperature after shuttling between shelter and basking sites. The magnitude of this effect is determined by the following main factors: (i) the time duration between shuttling events; (ii) the time period at T_{max} that the lizards can tolerate; (iii) the final temperature to which they need to cool down to (do they need to cool down all the way to crevice temperature?) and (iv) the time period of cooling required after body temperature has reached T_{max} . Our field observations showed that shuttling was not common and that the lizards were mostly either in their shelter or at their basking spot for the majority of an hour-long observation period. Better understanding of the above factors can only be obtained from temperature measurements of live lizards in the field, an aspect requiring further investigation.

With respect to the global circulation models, our calculations covered ambient temperature increases up to 4°C, corresponding to the IPCC scenarios RCP4.5 and RCP8.5

that differ by the increase in insolation (RCP4.5 = 4.5 W m⁻², RCP8.5 = 8.5 W m⁻²) by 2100, corresponding to differences in human mitigation intensity of climate change. RCP4.5 predicts a temperature increase between 1.1 and 2.6°C by 2100, while RCP8.5 proposes an increase of 2.6 and 4.8°C. Assuming a standardised starting time, our model (600 W m⁻² and 0.5 m.s⁻¹ wind) predicted that with a 1 °C increase, total diurnal activity time decreases by 3.9% (26 min) based on the time for which $T_e < T_{max}$, while with 2°C increase, it decreases by 7.7% (51 min; Fig. 5). These are modest decreases in activity compared to the elevation effects and, within the framework of RCP4.5, there is therefore no strong evidence that crag lizards are likely to become extinct due to global increases in temperature. However, if the global temperatures increase by 4°C as in RCP8.5, the picture changes, because crag lizard activity would be expected to decrease by approximately 15% (100 min; Fig. 5). Climate models for the region of the Drakensberg around Mariepskop following a low-mitigation scenario yielded a projected temperature increase of 4°C by 2100 (Taylor *et al.* 2017), consistent with the RCP8.5 scenario. The current reduction in modelled activity for the lizards at 1700 and 1300 m at Mariepskop is around 10.8% and 23.9% compared to 1900 m. A reduction of 15% in activity time due to climate change would therefore appear to negatively affect the survival of this species as they do not currently inhabit the lower altitudinal habitats, even though suitable shelter and prey are available. Vicenzi *et al.* (2017) modelled the geographical distribution of herbivorous high-Andean lizards *Phymaturus palluma* and found that, under RCP4.5, the geographical range of this lizard is relatively unaffected, compared to RCP8.5. It appears that both herbivores and predators (like crag lizards) are subjected to similar ecological constraints with respect to global warming. Since mountains often have some of the most environmentally sensitive taxa with respect to global warming (Ortega *et al.* 2016), the degree of that sensitivity requires quantification. Differing from our initial expectations, our results suggest that crag lizards are robust against small to moderate degrees of temperature effects on diurnal activity associated with global warming, reflected by RCP4.5, consistent with the conclusions of Vicenzi *et al.* (2017) and that they will only be strongly affected by more intense warming (i.e. warming approaching 4°C). A study such as this cannot consider all environmental factors affecting lizard activity, for example interspecific competition, predation risk (e.g. more potential competitors and predators at lower altitudes that are not cold-adapted) or reproductive limitations. This leaves scope for studies that promote a more comprehensive understanding of the broader effects of environmental change on reptile survival.

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Author contributions

Vonica Perold: Conceptualization (equal); Data curation (equal); Formal analysis (equal); Investigation (equal); Methodology (equal); Project administration (equal); Writing-original draft (equal). **Jan Willem H. Ferguson:** Conceptualization (equal); Formal analysis (equal);

Funding acquisition (equal); Investigation (equal); Methodology (equal); Resources (equal); Software (equal); Supervision (equal); Writing-review & editing (equal). **Luke Verburgt:** Conceptualization (equal); Investigation (equal); Methodology (equal); Supervision (equal); Writing-review & editing (equal). **Johan B. Malherbe:** Investigation (equal); Methodology (equal); Validation (equal).

Conflict of interest

The authors declare no conflict of interest with respect to the interpretation and publication of this work.

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