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Effect of long term climate change on the vertebrate fauna of Mariepskop, South Africa

by

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Declaration

I, …….**Vonica Perold**……. declare that this thesis/dissertation, which I hereby submit for the degree …………**MSc Zoology**............ at the University of Pretoria, is my own work and has not previously been submitted by me for a degree at this or any other tertiary institution.

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SUMMARY

Climate change is leading to loss of global and local biodiversity through changes in the ecology of fauna and flora. Changes in environmental temperature influence species distributional ranges. They respond by either migrating along with the shift in ecological zones or adapting to the new environmental conditions within a habitat. If neither adaptation nor migration is possible, local extinction of the species can result. This study was performed at Mariepskop mountain which served as the ideal environment for quantifying species distribution along an altitudinal gradient within different vegetation types. The information collected was used to quantify the factors shaping species distribution and to predict the fate of these species at Mariepskop with future climate change scenarios.

In this study I identified vertebrate taxa with restricted distribution along the altitudinal gradient representing low, high and generalist species. Regional geographical distribution and temperature data were analysed to create geographical distribution and temperature profiles for each species. Local distribution data and temperature profiles created from data recorded at automated weather stations within the study area and long-term interpolated data were compared to the geographical profiles for each species. Habitat requirements at a geographical scale were investigated for each species and related to the local habitat selection rationale at Mariepskop. Quantifying vegetation types and land types in the study area I predicted the possible shifts in vegetation zones with future climate change. Using this rationale we predicted which species at Mariepskop were most likely to be affected by future temperature increases and to what extent.

A detailed study focussing on the factors shaping the local restricted altitudinal distribution of the Drakensberg crag lizard (*Pseudocordylus melanotus melanotus)* to the highest altitudinal site was also performed. Factors investigated were suitable shelter and prey availability, ambient temperature conditions and operative temperatures recorded with copper lizard models. A behaviour study on focal lizards at the highest altitudinal sites was also performed to create diurnal activity pattern profiles for crag lizards. Activity profiles were related to temperature data and diurnal activity time budgets were calculated. We established that the restriction provided by the upper thermal limit of this species is the factor most likely responsible for limiting it to the highest altitudinal site. A temperature simulation model based on laboratory experiments and field data was designed to simulate future increased temperature scenarios at Mariepskop. It revealed a reduction in the diurnal activity time budget for *P. m. melanotus* with increased temperature. In summation we predicted that future climate change could affect three vertebrate species at Mariepskop due to shifts in vegetation zones. The Drakensberg crag lizard is however unlikely to be affected by a future 2˚C increase in environmental temperature.

Key words: Climate change, altitudinal distribution, vertebrates, habitat selection, operative temperature, vegetation zones.

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DISCLAIMER

The research chapters within this dissertation were structured with scientific journal publication in mind. Chapters are concise and presented as to be able to stand alone as journal articles. I apologise for overlap and repetition between the chapters.

Chapter 1

General introduction

Climate change and vertebrates

During recent decades the scientific study of climate change has progressed significantly. New and advanced technologies allow for more accurate predictions about future impacts and the results indicate substantial biodiversity loss at multiple scales (Walther *et al.*, 2002; Wilson *et al*., 2005; Thuiller, 2007; Sinervo *et al.*, 2010; Hockey *et al.*, 2011; Monasterios *et al.*, 2013; Ceia-Hasse *et al.*, 2014). Locally, models have predicted that climate change will have profound impacts on terrestrial animal species in South Africa (Erasmus *et al*., 2002). Studies have found that species range-retractions are one of the responses to increases in environmental temperature. This response is rationalised by the following concepts: It is accepted that all species have a specific physiological threshold for survival regarding temperature and water availability (Penuelas & Boada, 2003). Other requirements like habitat type and food availability will also determine species survival within a particular area. In essence the fundamental niche requirements of a species, not the habitat, determine its ability to survive in a particular habitat (Kearney & Porter 2004). Climatic regimes are responsible for controlling the above factors and will thus ultimately shape the distribution and colonization of a species within a particular habitat (Walther *et al.*, 2002; Penuelas & Boada, 2003; Fei *et al.*, 2012). Alterations of these requirements by climate change have the potential to cause fundamental changes in species distribution and survival (Thuiller, 2007; Fei *et al.*, 2012; Scheffers *et al.*, 2014). This is because small changes in prevailing temperature are expected to shift the suitable climatic conditions up altitudinal gradients (Sinervo *et al.*, 2010; Fei *et al.*, 2012; Monasterios *et al.*, 2013; Scheffers *et al.*, 2014). Furthermore, specialist species that generally have smaller ranges are under greater threat for climate change induced range shifts than generalist species (Botts *et al.*, 2013).

Vertebrates generally have three possible responses to climate change. The first is migration whereby species expand their distributional ranges to track changing habitats. This is not possible for all vertebrates as some are specialist species (Wilson *et al.*, 2010) restricted by fixed features within a particular habitat e.g. lizards requiring large boulders for sunbasking. If restricted to a habitat by fixed habitat features, migration is unfeasible and the success of the species can be compromised. The second response is adjustment whereby species adapt to the new environmental conditions within the habitat instead of shifting their distributional ranges. However, adaptation is not possible for all species due to a large number of factors, an example being ectotherms that have designated temperature ranges allowing for efficient thermoregulation. Changes in ambient temperatures can influence the time allocated to thermoregulation, causing the species to compensate by reducing time spent on essential activities like feeding and breeding. If a species is neither capable of migration nor adjustment, local extinction may result (Erasmus *et al.*, 2002; Meynecke, 2004).

Why mountains are important in climate change studies

Mountains have the advantage of acting as natural laboratories (Thuiller, 2007). Distinct vegetation zones and ecotones, temperature gradients, and a high level of biodiversity within each zone allows for collection of both qualitative and quantitative data through space and time (Beniston, 2003; Thuiller, 2007; Elsen & Tingley, 2015). Mountains also provide a high degree of habitat diversity along several environmental gradients (e.g. moisture, temperature, wind) over a short distance. Changes in the above factors can be monitored along an altitudinal gradient by delineating study sites, establishing the distributional ranges of species within sites and performing surveys to detect any changes. Mariepskop Mountain has the advantage of comprising of four vegetation types and five land types (Mucina & Rutherford, 2006) and forms part of the privately owned Moholoholo Nature Reserve and Mariepskop State Forest (managed by the Department of Forestry and Fisheries). Therefore it is an excellent study site due to its high biodiversity and unlikely probability of being subjected to anthropogenic impacts like urbanisation and development in future years.

Monitoring for climate change

Vertebrate taxa can be selected to act as bio-indicators warning of changes in environmental conditions (Niemi & McDonald, 2004). The criteria used to select indicator species are: 1) stable taxonomy, 2) readily identifiable, 3) abundant, 4) habitat specific (Niemi & McDonald, 2004). Out of the 87 vertebrates we recorded at Mariepskop, 34 were selected for further analysis. Out of this 34, 30 species had limited altitudinal distributions and could serve as indicator species for monitoring future climate change. One species was selected for a detailed study, the Drakensberg crag lizard *Pseudocordylus melanotus melanotus*. The crag lizard is an ectotherm, critically dependent on the thermal environment to be active (McConnachie, 2006; Bickford *et al.*, 2010; Sinervo *et al.*, 2010; Ceia-Hasse *et al.*, 2014). Increases in environmental temperature can alter the microhabitats of lizards leading to changes in ecological and biological processes, negatively impacting the success of the species (Walther *et al.*, 2002; Fei *et al.*, 2012; Logan *et al.*, 2013). In South Africa, there is a dire need for climate change monitoring programs (Minter, 2011). Without the knowledge, information cannot be presented to decision makers regarding biodiversity conservation policies, strategies and planning. Therefore this study is a contribution to the foundation of a long-term monitoring program to quantify the effects of climate change on biodiversity at a localised scale.

The overall objective of this study was to:

1. Investigate the altitudinal ranges of vertebrates at Mariepskop and identify factors responsible for shaping the distribution.
2. Consider the effect future increase in environmental temperature will have on the survival of these species.

Specifically, this objective was addressed in two partly independent studies using the following approaches:

Chapter 2:

1. To quantify the altitudinal distribution and temperature profiles of vertebrates at Mariepskop and compare it to their regional geographical distribution and temperature profiles:
    a. Classifying species as low, high or generalist taxa based on abundance data collected along the gradient.
    b. Relating local distribution ranges (based on their altitudinal distribution) to regional geographical distribution ranges.

   c. Investigate the role of temperature in restricting vertebrate altitudinal distribution at Mariepskop:

2. To investigate the role of habitat requirements in shaping species distribution:
   a. Identifying vertebrates dependent on fixed physical habitat characteristic.
   b. Identifying the location of fixed habitat features along the altitudinal gradient.

3. To investigate the effect of future increases in environmental temperature on the success of these species:
   a. Investigate soil-rainfall gradients and the role it plays in the ability of vegetation zones to shift and encroach on other zones.
   b. To investigate the ability of vertebrates to track shifts in vegetation zones.

Chapter 3:

1. To investigate the role of temperature in restricting the altitudinal distribution of *P. m. melanotus* at Mariepskop:
   a. Comparing ambient, inside crevice, and microhabitat temperatures along the altitudinal gradient.
   b. Investigate the effect of operative temperature on restricting the altitudinal distribution of crag lizards (recorded with copper lizard models).
   c. Investigating how temperature influences the behaviour and activity budget of *P. m. melanotus*.

2. To investigate the role of habitat requirements in shaping the distribution of *P. m. melanotus*:
    a. Investigating the presence of suitable prey and shelter for *P. m. melanotus* along the altitudinal gradient.

3. To investigate the effect of future increases in environmental temperature on the success of crag lizards at Mariepskop:
    a. Simulating operative temperatures of *P. m. melanotus* with future temperature increases.

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Chapter 2

Is temperature increase an important driver of the geographical distribution ranges of vertebrates on mountains?

Vonica Perold and J. Willem H Ferguson

Abstract

Due to large environmental gradients within a relatively small area, altitudinal gradients on mountains represent exceptional sites for quantifying the effects of global warming on the geographical distributions of indigenous fauna and flora. It is well established that, with global warming, fauna and flora are expected to move further up the slopes of mountains as the physiological conditions under which they thrive are found at progressively higher altitudes. We recorded the altitudes at which birds, frogs, lizards and small mammals occurred on the altitudinal gradient of some 1500 metres (temperature gradient ~ 10 °C) at Mariepskop, within the Drakensberg centre of endemism in South Africa. Many species were restricted to particular sections of the gradient and could be characterised as low-elevation, high-elevation or generalist taxa. The temperature-dependent characteristics of these species were calculated for South Africa, based on the known geographical distributions reflected in existing databases. All the species investigated occurred within a significantly narrower temperature zone at Mariepskop than for the temperature ranges encountered at the regional level. The species with restricted altitudinal ranges at Mariepskop were dependent on particular physical characteristics of their habitats not found along the whole gradient. The effects of climate change on the fauna at Mariepskop is unlikely to be a smooth upslope movement as predicted on the basis of temperature alone, but is dependent on the occurrence of the major habitat characteristics for each species.

We argue that these habitat characteristics include both physical features and major vegetation zones that are not necessarily collectively mobile and that impede the expected smooth upslope movement of taxa. This hinders the simple prediction of animal distributions at Mariepskop, based on temperature change alone.

Key words: Vertebrates, altitudinal gradients, climate change, temperature, habitat requirements

Chapter 2

Introduction

Climate change has impacted biodiversity and geographical ranges of species at multiple scales (Hughes *et al.*, 2000; Erasmus *et al.*, 2002; Thuiller, 2005; Wilson *et al.*, 2005; Bickford *et al.*, 2010). Herpetofauna (reptiles and amphibians) are ectothermic and more dependent on the thermal conditions of their environment for survival than are endotherms (Gibbons *et al.*, 2002; Fischer & Lindenmayer, 2005; Bickford *et al.*, 2010) because of the need to bask to maintain body temperatures at the desired temperature to be physiologically active (Sinervo *et al.*, 2010). Increased temperature causes shifts in sex ratios of reptiles by favouring female hatchlings and also alters microhabitats, forcing reptiles to either adjust or migrate, resulting in changes in their geographical distribution (Meynecke, 2004; Bickford *et al.*, 2010; Sinervo *et al.*, 2010; Barrows, 2011). Amphibians are exceptionally dependant on a balanced temperature and precipitation range (Duellman & Trueb, 1986; Feder & Burggren, 1992; Bickford *et al.*, 2010). Timing of rainfall and availability of freestanding water sources are extremely important for reproduction and metamorphosis to occur (Botts *et al.*, 2015). As with reptiles, changes in these climatic variables influence the behaviour, distribution and breeding success of amphibians (Corn, 2005; Du Preez & Carruthers, 2009; Minter, 2011; Botts *et al.*, 2015).

Within the context of climate change, endotherms have not been studied as extensively as ectotherms because they are less dependent on the external environment and have the ability to thermoregulate via increasing or decreasing their metabolic rate (Boyles *et al.*, 2011; Brinkmann *et al.*, 2011). However, a robust relationship exists between the geographical distribution of birds and climate (Crick, 2004; Matthews *et al.*, 2004). Climate change affects the phenology and population dynamics of birds that in turn, influences their geographical distribution (McCarty, 2001; Both *et al.*, 2006). Studies on the effect of climate change on small mammals revealed that range contractions occurred for species living at high altitude, while range expansion resulted in response to past climate change for species living at low-altitude (Moritz *et al.*, 2008).

Several studies indicated a general upslope movement of plant vegetation in response to the global temperature increase (Lenoir *et al.*, 2008; Kelly & Goulden, 2008; Dullinger *et al.*, 2012). This predicts that the vertebrates inhabiting mountain slopes are likely to follow the upslope movement of the vegetation they inhabit. However, since many vertebrates dependent on specific plant taxa as food or shelter, their response to global warming may not exactly follow that of the major plant communities. However, McClure *et al.* (2012) showed that the geographical distributions of bird species in North America changed in a northerly direction as predicted for plants. To accurately predict the effects of changes in environmental temperature on species fitness, a mechanistic approach is needed (Kearney & Porter, 2004). This approach allows for an understanding of how these species' requirements interact with the physical environment and is the foundation for predicting the effects of climate change on species survival (Kearney & Porter, 2004; Kearney & Porter, 2009; Williams *et. al.*, 2008). The conceptual framework for assessing species vulnerability by Williams *et al.* (2008) provides important information on how individual factors will interact leading to different outcomes for species under climate change. The framework comprises of three key fundamentals: 1) Sensitivity, 2) exposure and 3) feedback and cascading impacts (Williams *et al.*, 2008). Sensitivity of a species is governed by intrinsic factors such as ecology, physiology and genetic diversity. Sensitivity is counteracted by resilience and adaptive capacity of species (Williams, *et al.* 2008; Huey *et al.*, 2012). Exposure will be determined by the degree of regional climate change and if a species is capable of surviving in a sheltered microhabitat, buffered from regional climate change (Williams *et al*., 2008). Finally, feedback and cascading events are inevitable with changes in community composition and predator-prey relationships, terminating mutualistic relationships and increasing parasitic infections. The exact magnitude of feedback and cascading events are perplexed and need to be monitored closely and timely (Williams *et al.*, 2008). This framework explains the fundamentals of species response to climate change. We applied these principles with information from additional literature to explain the impact and effect of climate change on vertebrate species:

A better understanding of the interaction between vertebrates and their environment will foster a better understanding of the effects of global warming on the geographical ranges of vertebrates (Kearney & Porter, 2004). This study reports on the local and regional temperature preferences of vertebrate animals at Mariepskop, South Africa and how these relate to other habitat characteristics and future climate change.

The objectives of this study were:

- To quantify the distribution ranges of vertebrates along the altitudinal gradient at Mariepskop.

- To compare the temperature characteristics of the regional geographical distribution of selected species at a quarter degree geographical resolution to that of their local distribution at Mariepskop.

- To identify habitat features determining the small scale distribution of vertebrate taxa at Mariepskop.

- To predict some of the effects of climate change on the altitudinal distribution of vertebrate taxa at Mariepskop.

Chapter 2

Materials and Methods

Study site

Mariepskop lies within the Wolkberg centre of endemism and boasts high floral and faunal biodiversity (Van Der Schijff & Schoonraad, 1971; Van Wyk & Smith, 2001; Mucina & Rutherford, 2006). It is locally the highest mountain reaching from around 600 metres above sea level (m a.s.l.) to 1 949 m, an altitudinal gradient of around 1 500 m corresponding to a temperature gradient of around 10 °C. The study was performed in Moholoholo Private Nature Reserve at 24° 31′ S, 30° 49′ E and Mariepskop mountain at 24° 30’ S, 30° 58’ E on the eastern edge of the Blyde River Canyon, South Africa. Moholoholo Private Nature Reserve is located at the foot of Mariepskop and experiences a warm subtropical climate while the top of Mariepskop experiences a cool climate. Seven study sites at 300 meter increments a.s.l. (Table 2.1) and, as far as possible, in close proximity to permanent automated weather stations along the altitudinal gradient (Fig. 2.1). Except for sites 3 and site 6 (Fig. 2.1), all sites were within 500 m horizontal distance of a weather station.

Local altitudinal distribution

Reptiles: Due to the difficulties in quantitatively assessing reptile abundance (McDiarmid *et al*., 2012), a preliminary survey was performed during 2010 and 2011 to choose taxa appropriate as focal species for this study. Five species were selected based on their high abundance and ease of detection: *Lygodactylus occelatus occelatus, Pseudocordylus melanotus melanotus, Lygodactylus capensis capensis,* *Trachylepis margaritifer* and *Platysaurus intermedius intermedius* (Appendix 1). Active searching was performed at each of the sites (Fig. 2.1) which included scanning an area with binoculars, turning over rocks, exploring rock crevices and examining other suitable habitats such as fallen logs (Lemos-Espinal *et al.*, 1998; Sutherland, 2006). Habitat disturbance was minimised by replacing all objects in their original position afterwards. Since temperature influences reptile activity (Wymann & Whiting, 2002; Effenberger & Mouton, 2007), surveys were only performed on warm sunny days, amounting to 200 hours of site-specific surveys.

Amphibians: A combination of active searching and acoustic surveys (males call to attract females) provided a comprehensive representation of the amphibian community along the altitudinal gradient (Doan, 2003; Sutherland, 2006). Surveys were performed during the breeding period on evenings following rain (Shoo & Williams, 2004). Four surveys were performed at each site (Fig. 2.1), comprising active searching along ponds, dams and streams for four consecutive hours (i.e. 16 h per site in total). Calls were recorded using an Olympus sound recorder (WS-760M; Cape Town South Africa) and species identified with existing sound recording collections (Du Preez & Carruthers, 2009).

Small mammals: Small mammals were trapped using Sherman live traps at the seven sites (Fig. 2.1). Traps were baited with a mixture of peanut butter, oats and sardines. At each site, 40 traps were deployed in two grids of 20 traps each. The two grids were separated by 150 - 200 m, determined by topography (Heaney, 2001). Each grid comprised traps separated by 10 m and arranged in a 30 x 40 m grid of four rows with five traps in each row (Heaney, 2001; Wilson *et al.*, 2010). The traps were checked daily in the morning and late afternoon and re-baited if necessary. Each captured animal was placed in a clear plastic bag, weighed, photographed, transferred to a plastic bucket, photographed again, identified and released within 3 m of the trap. Trapping was performed for five consecutive nights at each site during September – November 2011 and again during February – March 2012 amounting to 2 800 trap nights. The total number of small mammal species caught per night for each site was enumerated to determine whether the number of trapping nights were adequate to determine the species composition of the area. If no new species were caught after the third trap night, it could be accepted that five trapping nights were sufficient (Li *et al.*, 2003).

Avifauna: Line transects were used as it is an adaptable, cost- and time efficient method for assessing bird species community composition (Sutherland, 2006). Surveys comprised walking a predetermined 500 m long permanent line transect between 5:30 – 7:30 am and 16:00 – 18:00 pm at a constant slow pace so that the end of the transect was reached after an hour. Two parallel 500 m transects separated by 500 m apart were used per site and walked four times during the survey period, amounting to eight hours of surveying per site (Fig. 2.1). Birds observed on either side of a transect were recorded and identified visually using binoculars or from their calls. Bird calls were recorded and identified using existing sound collections (Gibbons, 1995).

Data analyses and climate profiling

Altitudinal distribution: A combined species inventory was created for the study area (Appendix 1). The mean altitudinal distributions including altitudinal range were calculated for species for which four or more observations were obtained during the above surveys (Table 2.2). Species were classified into altitudinal classes based on their range of altitudinal distribution: low altitude (mean altitudinal distribution < 1 300 m a.s.l.), high altitude (mean altitudinal distribution > 1300 m a.s.l.) and altitudinal generalists (species present along the entire altitudinal gradient).

Local climate data from automated weather stations: Local temperature data were extracted from seven newly-erected permanent weather stations at Mariepskop established by the University of Pretoria at 300 m increments along the altitudinal gradient (Fig. 2.1). The mean, minimum and maximum local temperature data for only summer (Dec - Feb; 2012/2013) were extracted from these stations and analysed for each study site to create a short term local altitudinal temperature profile for each species (Fig. 2.2). Only summer data were used for the comparison as incomplete data recording occurred during winter due to recent establishment and malfunctioning of the automated weather stations.

Local climate profile from historical temperature data: A long-term downscaled local altitudinal temperature profile for the different sites at Mariepskop was obtained at a resolution of 30 arc-seconds (~ 1km) using WorldClim data (1950 – 2005; Hijmans *et al.*, 2005**)** for summer (Dec - Feb). Temperature data from the local weather stations at Mariepskop (collected over a short period: Dec - Feb 2012/2013) were compared to the WorldClim data to assess the accuracy and consistency of the interpolated local WorldClim data (representing a much longer period of measurement).

Geographical temperature and distribution: Long-term historical climatic data consisting of annual mean temperature (calculated on a monthly basis at hourly intervals or from interpolated weather station data) at 5 arc-minutes resolution were obtained from WorldClim – Global Climate Data (Hijmans *et al.*, 2005**)**. The mean temperature within each quarter degree square (QDS) in South Africa was calculated by averaging the mean temperature of available data for all 5 arc-minute blocks within each QDS using ArcMapV10 (ESRI, Redlands CA). The result was a climate profile for mean annual temperature for each QDS in South Africa. To validate the accuracy and consistency of the interpolated WorldClim data: annual mean, maximum and minimum daily temperature data were obtained from South African Weather Services (SAWS) for seven weather stations located in the Drakensberg area. The seven stations were: Shaleburn (29˚46’49.45”S 29˚21’5.91”E; 1 603 m. a.s.l.), Giant’s Castle (29˚15’30.37”S 29˚31’35.70”; 1 719 m a.s.l.) Royal Natal (28˚39’58.53”S 28˚59’21.83”E; 1 461 m a.s.l.), Estcourt (29˚2’45.85”S 29˚54’39.64”E; 1 293 m. a.s.l.), Mooirivier 29˚11’39.49”S 30˚0’49.35”E; 1 392 m a.s.l.), Cedara (29˚32’32.23”S 30˚15’52.52”E; 1 070 m a.s.l.) and Pietermaritzburg (29˚38’28.95”S 30˚23’32.30”E; 697 m .a.s.l.). The mean daily maximum temperature, mean daily average temperature and mean daily minimum temperatures were calculated with data available between 1950 – 2005 and compared to the mean daily maximum, mean daily average and mean daily minimum temperature data obtained from the long term interpolated WorldClim data at 5 arc-minutes resolution (1950 – 2005; Hijmans *et al.*, 2005). The regional distribution data (at QDS level) of study species were obtained from several sources. Avifauna distributional data were obtained from SABAP1: Southern African Bird Atlas Project (Harrison *et al.*, 1997). The amphibian and reptile distribution data were obtained from Minter *et al.* (2004) and Bates *et al.* (2014)

respectively. The small mammal distribution data were obtained from the South African National Spatial Biodiversity Assessment (Rouget *et al.*, 2004) based on information obtained from various natural history museums in South Africa. The distributional data for small mammals were consolidated, evaluated, and updated by taxon experts and literature sources (Freitag & van Jaarsveld, 1995; Keith, 2005). Using ArcMapV10 and the WorldClim dataset a temperature profile applicable to the geographical distribution of each species was generated.

Analysing the geographical distribution of species in conjunction with the temperature profile at a QDS scale for South Africa provided predicted regional temperature characteristic for each species. The QDS temperature data were adapted by excluding the outlying 5 % of temperature values to exclude outlier temperature data caused by the effect of distributional boundaries (Fig. 2.3). The maximum mean and minimum mean regional temperature for each species was used to indicate individual regional temperature ranges for the focal species. The resulting four data sets, with terminology (in italics) were as follows: 1) *Local altitudinal distribution* of vertebrates at Mariepskop, based on the field surveys 2.) *Short term local temperature* data for Mariepskop, based on weather stations on the mountain. 3) *Long-term local temperature* characteristics at Mariepskop, based on WorldClim data. 4) *Regional geographical temperature data*, representing mean annual temperatures from WorldClim, applicable to the regional geographical distribution of each species at QDS resolution.

Chapter 2

Habitat requirements

Literature searches allowed us to describe the geographical distribution and the habitat requirements of each species. The local habitat requirements and the habitats (vegetation types) where they were met at Mariepskop were described (Appendix 1).

Results

Local altitudinal distribution at Mariepskop

Reptiles revealed a distinct separation between low and high altitude species for example the altitudinal distribution ranges of the Cape Dwarf Gecko *Lygodactylus c. capensis* and the Rainbow skink *Trachylepis margaritifer* were separated by ~ 400 m range in altitude from the Drakensberg Crag Lizard *Pseudocordylus m. melanotus* and the Occelated dwarf gecko *Lygodactylus o. occelatus* (Table 2.2). The amphibians revealed a separation between low and high altitude species based on their mean altitudinal distribution for example the altitudinal ranges of the Southern foam nest frog *Chiromantis xerampelina* and the Common river frog *Amietia quecketti* were separated by ~ 400 m in altitude (Table 2.2). Two altitudinal generalists (Painted reed frog *Hyperolius marmoratus taeniatus* and the Plaintive rain frog *Breviceps verrucosus*) were present at the highest and lower sites along the altitudinal gradient (Table 2.2). A distinction between the low and high altitude avifauna was apparent with the Mocking cliff chat *Thamnolaea cinnamomeiventris* only occurring at the highest altitudinal site and the Bushveld species (e.g. Black-backed puffback *Dryoscopus cubla*, Ashy fly-catcher *Muscicapa caerulescens* and Black-crowned tchagra *Tchagra senegalus*) residing in the lower altitudinal Legogote sour Bushveld (Table 2.2). Five trap nights were adequate to establish the small mammal community composition of the study area as after the third trap night no new species (however, some of the species already recorded were trapped again) were caught at any of the sites (Heaney, 2001; Li *et al.*, 2003; Wilson *et al.*, 2010). No small mammal species was restricted to the low altitudinal site and all species were present at the highest site.

The Namaqua rock rat *Micaelamys namaquensis* was present along the entire altitudinal gradient and is therefore an altitudinal generalist in the study area.

Temperature profiles and geographic distribution

Local temperature: Relatively small discrepancies between the WorldClim data set and the local weather station temperature data during summer were apparent (Fig. 2.2). The decrease in temperature with increasing altitude is close to the predicted lapse rate of −0.65°C / 100 m (Blandford *et al.*, 2008). The *short term local temperature* data for summer obtained from the local automated weather stations were consistent with the downscaled *long term local temperature* values derived from WorldClim.

Regional geographical temperature and vertebrate distribution:

The temperature data obtained from seven weather stations in the Drakensberg area were also consistent with the long term interpolated WorldClim data (Table 2.3). The mean difference in the temperature ranges between the weather station data and the WorldClim data were consistent at 0.65˚C for daily maximum, daily average and daily minimum temperatures (Table 2.3). Therefore the long term interpolated WorldClim data were used in the regional analyses instead of the short term local temperature data.

The exclusion of the outlying 5 % QDS temperature data points revealed that these data points were located at the boundaries of the geographical distribution of the species and had a high probability of presenting atypical habitat characteristics (Fig.

2.3). Therefore the outlying 5 % temperature data points were excluded in the analyses.

Reptile temperature profiles and geographic distributions: Three species (gecko *L. c. capensis*, the rainbow skink *T. margaritifer* and the common flat lizard *P. i. intermedius*) were present at lower altitudes locally (Table 2.2). These species also preferred lower lying altitudinal habitats throughout their geographical distribution (Fig. 2.3; Appendix 1). Local temperature ranges fell within the geographical temperature ranges for the low altitude species (Fig. 2.4a). The gecko *L. o. occelatus* and crag lizard *P. m. melanotus* occupied the higher altitudinal sites at Mariepskop (Table 2.2). They also preferred higher altitudinal habitats throughout their geographical distribution (Fig. 2.3; Appendix 1). The local temperature ranges for both species fell within the geographical temperature ranges but were towards the lower extreme (Fig. 2.4a).

Amphibian temperature profiles and geographic distributions: The Banded rubber frog *Phrynomantis bifasciatus* and the Southern foam nest frog *C. xerampelina* preferred low altitude sites locally (Table 2.2) and at a regional scale (Appendix 1). However some species that preferred lower altitudes locally like the Bubbling kassina *Kassina senegalensis*, Red toad *Schismaderma carens* and the Guttural toad *Amietophrynus gutturalis* (Table 2.2) occur at higher altitudes at a geographical scale (Fig. 2.4b; Appendix1). Similarly, two of the species present at higher altitudes locally, (Common river frog *Amietia quecketti* and Clicking stream frog *Strongylopus grayii*) also occur at lower altitudes at a geographical scale (Appendix 1). The habitat-specific Natal cascade frog *Hadromophryne natalensis* was found at mid – high altitudes in the study area locally, coinciding with the presence of *Podocarpus* escarpment forest and steep slopes (Boycott, 2004), but over a large range of regional temperatures (Fig. 2.4b). The altitudinal generalists (*B. verrucosus* and *H. m. taeniatus*) also exhibited a wide range of altitudinal distribution at a geographical scale (Appendix 1). Local maximum and minimum mean temperature ranges at Mariepskop for all amphibians were within the limits of their maximum and minimum mean geographical temperature range (Fig. 2.4b).

Avifauna temperature profiles and geographic distributions: Some of the birds at the lower altitudes at Mariepskop were also present at higher altitudes at a geographical scale and *vice versa* (Appendix 1). Locally, low altitude Bushveld species preferred the low altitude Legogote sour Bushveld vegetation (Table 2.2; Appendix 1). These species do however occur in areas with higher altitudinal Bushveld vegetation (Fig. 2.5a; Appendix 1). Locally, the Chorister Robin chat *Cossypha dichroa* was restricted to the high altitudinal evergreen forest but geographically occupies a wide range of altitudes (Appendix 1). Local maximum and minimum mean temperature ranges at Mariepskop for avifauna were consistent with their maximum and minimum mean geographical temperature ranges (Fig. 2.5a).

Small mammal temperature profiles and geographic distributions: Locally, Brant's climbing mouse *Dendromus mesomelas*, the Forest shrew *Myosorex varius* and the Striped mouse *Rhabdomys pumilio* occupied higher altitudinal sites (Table 2.2) but regionally have geographical distributions comprising a much wider range of altitudes (Appendix 1). The altitudinal generalist Namaqua rock-rat *M. namaquensis* had a wide-spread distribution locally (Table 2.2) as well as geographically at varying altitudes (Appendix 1). The local altitude temperature range for each small mammal fell within its geographical temperature range, except for *R. pumilio* where the minimum local temperature was slightly lower than the geographical temperature (Fig. 2.5b).

The results indicate that the majority of taxa occupy a much smaller part of their range on Mariepskop than predicted by geographical ranges. Therefore the local temperature ranges were substantially narrower that those predicted by regional temperatures.

Habitat requirements:

Identifying the habitat requirements pertinent to each species enabled us to explain some of the above restricted distributions observed at Mariepskop (Appendix 1). The species chose to occupy specific habitats or vegetation types that met their requirements, both geographically and locally at Mariepskop. Altitudinal generalists however, enabled by their catholic habitat requirements were capable of occupying a variety of habitats locally and geographically (Appendix 1). The habitat features at Mariepskop that led to certain species having restricted altitudinal distributions were permanent dams, rocky outcrops, suitable crevices and fast flowing clear streams. These features were not present along the entire altitudinal gradient and therefore we were able to compare restricted altitudinal distribution to presence of critical habitat features.

Discussion

Do regional geographical ranges and temperature profiles of species predict their altitudinal range at Mariepskop?

The altitudinal distributions of the species at Mariepskop represent only a fraction of their regional altitudinal distribution which is mostly quite wide (Fig. 2.3, 2.4, 2.5; Appendix 1). Of the 34 species studied here, 18 were classified locally as low altitude specialist taxa (Table 2.2). Some of the species i.e. the amphibians (*K. senegalensis, P. bifasciatus and C. xerampelina*) had their local temperature range defined as 20.3˚C (Fig. 2.4b), while collective geographical temperature ranges were much wider (~ 16 – 22˚C). The two reptiles (*L. capensis*, and *T. margaritifer*) classified as low altitude specialist had the same mean annual temperature range (17 - 20˚C) locally, whilst geographically showed wider ranges of temperatures (16 - 23˚C) (Fig. 2.4a). Ten of the low altitude bird species had local temperature ranges (~ 20˚C) also much narrower than their geographical temperature ranges (Fig. 2.5a). A total of 12 species were classified as high altitude specialist taxa (Table 2.2). Two of these were reptiles (*P. m. melanotus* and *L. o. occelatus*) with local mean temperature of 14.1 ˚C (Fig. 2.4a) although geographical temperature ranges were much wider (14 - 19˚C). Three small mammal high altitude specialists (*D. mesomelas*, *M. varius* and *R. pumilio*) had local temperature ranges that were much narrower than the geographical temperature ranges (Fig. 2.5b). The high altitude bird (*T. cinnamomeiventris*) had a mean local temperature range of ~14˚C but with geographical temperature ranges similar to those of the low altitude specialists (Fig. 2.5a). Examining the temperature ranges of the four altitudinal generalist taxa (*B. verrucosus*, *H. m. taeniatus*, *O morio* and *M.*

namaquensis) with large altitudinal ranges both locally and geographically answered some questions (Table 2.2). These generalists had geographical mean temperature ranges of 13 - 23˚C (Fig. 2.4b; 2.5a, b). Comparing these ranges to the geographical mean temperature ranges (13 – 22˚C) of high altitudinal specialist taxa (*H. natalensis, S. grayii* and *A. quecketti*) revealed similar ranges (Fig. 2.4b). The same can be said for low altitude specialist bird taxa (*D. cubla, D. adsimilis and L. torquatus*) with geographical temp ranges of 14 – 23 ˚C (Fig. 2.5a). The coarse resolution of the grids (QDS) used to calculate the regional temperature ranges of species consisted of various microhabitats and microclimates whereas the mean temperature was more homogenous (Botts, *et al.* 2013). This explains why local species had narrower temperature ranges compared to the regional geographical temperature ranges (Fig. 2.3, 2.4, 2.5). Therefore if local altitudinal distribution was solely based on regional temperature ranges, these high and low altitude specialist would have been able to occupy habitats along the entire altitudinal gradient. These examples indicate that the regional geographical distribution and temperature ranges do not predict the local altitudinal distribution of species at Mariepskop.

Is the altitudinal distribution of a species largely restricted by suitable habitat?

Classifying the species into low, generalist and high altitude specialist taxa we related their altitudinal distribution range to habitat characteristics (Table 2.2). Each vegetation type has specific habitat features which met the requirements of individual species. The low altitude site comprises of Legogoto Sour Bushveld vegetation with exposed granite boulders, trees, fallen logs and permanent dams. For the five low altitude specialist amphibians, this habitat met their habitat requirements (Table 2.2;

Appendix 1) e.g. the Southern foam nest frog *C. xerampelina*, which requires seasonal or permanent waterbodies with surrounding vegetation to suspend their foam nests during reproduction (Minter *et al.*, 2004; Du Preez & Carruthers, 2009) (Appendix 1). Open water bodies with suitable nest sites were not found at the higher altitudinal sites at Mariepskop. The three low altitude specialist reptiles required exposed granite boulders (*T. margaritifer and P. i. intermedius*) and trees (*L. c. capensis*) which were abundant at the lower altitudes (Table 2.2; Appendix 1). Ten of the low altitude specialist bird species required habitats with suitable broad-leaved trees which were only present in the Legogoto Sour Bushveld (Table 2.2; Appendix 1). The high altitudinal sites consisted of Northern Escarpment Quartzite Sourveld (Grassland), Northern Mistbelt Forest and Northern Escarpment Afromontane Fynbos (Fig. 2.1; Table 2.1). These habitats were characterised as follows: grassland with rocky outcrops; fynbos vegetation with shrubs and large boulders and suitable crevices; evergreen forests with clear fast flowing streams. The two high altitude specialist reptiles (*P. m. melanotus* and *L. o. occellatus*) are rupiculous and require rocky outcrops in mountainous terrain with suitable crevices for shelter (Appendix 1). These requirements were only met at the higher altitudinal sites. The three high altitude specialist bird species (Table 2.2) required rocky outcrops within grassland or fynbos vegetation (*C. aberrans* and *T. cinnamomeiventris)* and trees and shrubs in evergreen forests (*C. dichroa*), only present at the higher altitudinal sites (Appendix 1). Although, *C. dichroa* was locally restricted to the higher lying Northern Mistbelt Forest, this species occupies evergreen forests at lower altitudes (and higher temperatures) across Southern Africa and is classified as an altitudinal migrant (Harrison *et al.*, 1997) (Appendix 1). The high altitude amphibian (*H. natalensis*) required gulleys in forests with clear fast-flowing streams, only found higher up in the study area (Appendix 1). The three high altitude small mammal specialists (*R. pumilio, D. mesomelas* and *M. varius*) require dense grass covered habitats, found only at the higher altitudes (Table 2.2; Appendix 1). Three of the four altitudinal generalists in our study (*M. namaquensis, H. m. taeniatus* and *B. verrucosus*) present at both low and high altitudes have catholic habitat requirements (Table 2.2; Appendix 1). Altough *O. morio* was classified as an altitudinal generalist; it requires rocky cliffs. These requirements were however present at low (~1 100 m .asl) and high altitudes, justifying the classification as an altitudinal generalist. From these examples it is clear that immediate habitat characteristics constitute a much stronger limitation on the geographical distribution of vertebrate species than altitude or temperature themselves (Botts *et al.*, 2013). Species are being restricted by physical habitat characteristics, not by altitude and therefore temperature (Appendix 1). The following discussion will focus on the major vegetation or habitat zones (Fig. 2.1; Table 2.1) at Mariepskop because they control habitat characteristics. If habitat characteristics are altered, distributional ranges of species could also be potentially altered if the animals are unable to adjust or adapt to the new environmental conditions.

The impact of climate change on major vertebrate habitats at Mariepskop is complex.

Climate change in South Africa is predicted to cause slight changes in mean precipitation that will occur later in the year (Beniston, 2003; Dlamini, 2011). Temperature is predicted to increase by 2.5 to 3 ˚C in South Africa by 2050 (Shannon, 2000; Erasmus *et al.*, 2002; Hansen *et al.*, 2006; Dlamini, 2011) and 4 ˚C globally by 2100 (Thuiller, 2007). If incapable of adapting to these predicted warmer temperatures, vegetation is expected to shift to cooler climates at higher elevations (Hannah *et al*,, 2005; Hannah *et al*., 2007; Lenoir *et al*., 2008; Dlamini, 2011). Land type data (Fb182) for the northerly Legogoto Sour Bushveld (Fig. 2.1; Table 2.1) indicated that this vegetation has poorly drained, rocky shallow soil composed of (in decreasing proportion) glenrosa, cartref, mispah and hutton soil forms (Department of Agriculture & Water Supply 1989). With the Northern Escarpment Quartzite Sourveld (Grassland), land type data (Ic157) indicated shallow, rocky soil consisting of mostly rock and (in decreasing percentage) mispah, hutton and glenrosa soil forms. Due to shallow rocky soils present where these two vegetation types are found and that they are both on the northerly side of the rainfall gradient, it is predicted that the northerly Legogoto Sour Bushveld is likely to encroach on the Northern Escarpment Quartzite Sourveld (Grassland) slopes (Rutherford, 1999; Dlamini, 2011). Indeed, aerial photographs show rapid expansion of the Bushveld onto the grassy lower slopes of Mariepskop after 1970. This grassland that currently ranges from about 1 200 m a.s.l. to the top of the mountain is therefore likely to contract in altitudinal range due to encroachment from below by the Legogoto Sour Bushveld (Rutherford, 1999; Thuiller, 2007; Scheiter & Higgins, 2009; Dlamini, 2011). The Mistbelt Forest is on the cooler southerly side of the rainfall mountain where wetter conditions prevail, representing land types Ab32; and Ab41 with deep, apedal soil on dolomite/granite composed of (in decreasing percentage) hutton and glenrosa soil forms (Department of Agriculture & Water Supply 1989). This soil form is important for root establishment of forest trees and differs from the soil forms in the Bushveld vegetation. In the fynbos habitat, Land type data (Ib193) indicated shallow, rocky soil consisting mostly of rock and (in decreasing proportion) hutton, mispah and glenrosa soil forms. Shallow soil depth (<15 cm, too shallow for root establishment of forest trees (Laclau *et al*., 2013)) is likely to impede encroachment of the Mistbelt Forest in the higher elevation fynbos. Therefore it is possible that the forest habitat could just simply disappear, even though it is not found on the top of the mountain above 1700 m a.s.l. The grassland is on the drier northerly side of the rainfall gradient compared to the fynbos vegetation on the cooler southerly side. Thus the conditions in the fynbos vegetation is too cool and seasonally too marshy to allow for grassland encroachment. At Mariepskop we expect that the Northern Escarpment Afromontane Fynbos at Mariepskop will not be encroached by the Quartzite Sourveld (i.e. grassland). In conclusion the possibility of vegetation to move upslope is determined by moisture and soil type, not by temperature. Except for Bushveld vegetation, none of the vegetation zones appear to have soil-rainfall conditions that promote movement upslope.

The effect of climate change on vertebrate populations at Mariepskop is complex

Many species have specialised habitat requirements i.e. large exposed boulders, rocky outcrops with crevices and permanent waterbodies that are fixed along the altitudinal gradient. Specialist species therefore have smaller ranges than generalists (Botts *et al*., 2013). Small range size has been documented to be the most important single life history trait implicated in the decline of amphibians (Botts *et. al*¸ 2013). Out of the 34 species in our study, 15 species are restricted by these fixed habitat features. Examples include *T. margaritifer and P. i. intermedius* (large exposed granite boulders), *P. m. melanotus* and *L. o. occelatus* (suitable crevices), *T. cinnamomeiventris and T. melba* (rocky outcrops) and eight amphibians (permanent dams and streams). These features cannot move upwards with climate change induced vegetation shifts and the species dependent on these features may survive in the habitat even if surrounding vegetation changes. However, changes in the availability of food resources with shifts in vegetation could potentially affect these species. Several species are associated with vegetation zones that cannot move along the altitudinal gradient (The Northern Escarpment Afromontane Forest and the Northern Escarpment Quartzite Sourveld). Examples include *C. dichroa* and *H. natalensis* restricted to the forest and *C. aberrans* present in the grassland habitat. The three small mammals (*R. pumilio, M. varius* and *D. mesomelas*) were present in both the grassland and fynbos habitat in areas with dense grass and might therefore migrate to the fynbos site. The four altitudinal generalists with their catholic habitat requirements are not foreseen to be affected by vegetation change on Mariepskop (*B. verrucosus, H. m. taeniatus, O morio* and *M. namaquensis*). The Bushveld species which include the ten low altitude bird species and *L. c. capensis* would be able to move upslope with the vegetation shift as the habitat features they require (trees) are not fixed and capable of moving upslope during grassland encroachment.

A future increase of 4 ˚C, predicted globally by 2100 (Thuiller, 2007) is unlikely to cause the disappearance of vertebrate species due to increased temperature alone. The regional geographical temperature ranges of the species support this conclusion as species had wider temperature ranges at a regional scale than locally, indicating wide ranges of temperature tolerance (Fig. 2.4, 2.5). The indirect effect of increased temperature on the composition and distribution of vegetation that comprise the physical habitat for vertebrates could, however, fundamentally affect species that are unable to move along with vegetation range shifts. Locally at Mariepskop, the Northern Escarpment Quartzite Sourveld (grassland) species (Lazy cisticola *Cisticola aberrans*) and the Northern Mistbelt Forest species (Natal cascade frog *H. natalensis* and Chorister robin-chat *C. dichroa*) are likely to be strongly negatively affected by climate change.

Conclusion

An understanding of the long term effects of climate change on montane vertebrate populations is unlikely to only come from an understanding of the ecophysiology and temperature tolerances of vertebrates inhabiting the altitudinal gradient. Changes in phenology, shifts in abundance and behaviour of interacting species are likely to impact the biological synergy of a habitat (Thuiller, 2007; Williams, *et al.*, 2008; Buckley, 2013). The classical model of a gradual upward movement of vegetation zones (Lenoir *et al.*, 2008) is probably simplistic. The physical and chemical characteristics of soil, as well as other environmental attributes such as lateral (rainfall – rain shadow) rainfall gradients on the altitudinal gradient make this process much more complex (Kearney & Porter, 2009). It is more probable that some vegetation zones and their vertebrate inhabitants will simply disappear from a particular mountain slope. The ubiquitous approach of predicting effects of climate change by quantifying changes in distributional ranges of species lacks detail about the asymmetry in species responses to physical and to biological processes (Walther *et al.*, 2002; Thuiller, 2007; Buckley, 2013; Logan *et al.*, 2013; Moritz *et al.*, 2013)**.** Phenotypic plasticity further complicates assessing the vulnerability of species to climate change due to individual acclimation abilities (Seebacher *et al.*, 2012). The framework by Williams *et al.* (2008) provides important guidelines for fully assessing the vulnerability of species to climate change. A mechanistic approach and detailed understanding of their habitat requirements such as shelter, breeding sites, hibernation sites and food sources, together with an understanding of the factors affecting the distribution of their habitat, are more likely to yield fundamental insight about the potential susceptibility of these populations to the effects of climate change (Kearney & Porter, 2004; Thuiller, 2007; Williams *et al.*, 2008; Kearney & Porter, 2009; Ceia-Hasse *et al.*, 2014). Mountains allow us to quantify the rate of species migration along steep temperature gradients, sharp transition in vegetation zones and the limited extent of migration constrained by the altitudinal limit (Beniston, 2003; Thuiller, 2007; Loarie *et al.*, 2009; Elsen & Tingley, 2015). Therefore this study provides valuable information which could serve as a reference to monitor and quantify future changes in vertebrate distribution along an altitudinal gradient.

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Chapter 2: Tables

Table 2.1. The seven study sites along the altitudinal gradient at Mariepskop, showing altitude and vegetation type classified following Mucina & Rutherford (2006).

Site	**Altitude** (m a.s.l.)	**Vegetation type**
1	1 900	Northern Escarpment Afromontane Fynbos
2	1 600	Northern Mistbelt Forest
3	1 400	Northern Mistbelt Forest with Northern Escarpment Quartzite Sourveld patches
4	1 600	Northern Escarpment Quartzite Sourveld
5	1 300	Northern Escarpment Quartzite Sourveld
6	1 000	Legogote Sour Bushveld
7	700	Legogote Sour Bushveld

Table 2.2. The number of observations at the altitudinal sites with the mean altitudinal distribution (m a.s.l.), altitudinal distribution range and altitudinal class (Gen = Generalist) for the selected species.

Species	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**Mean altitude (m) and range (min - max)**	**Class**
Reptiles									
Lygodactylus c. capensis					6	7	25	843 (686 – 1 356)	Low
Trachylepis margaritifer					3	7	13	896 (660 – 1 262)	Low
Platysaurus i. intermedius					8	9	6	1002 (711 – 1 322)	Low
Lygodactylus o. occelatus	64			4				1889 (1 599 – 1 937)	High
Pseudocordylus m. melanotus	49							1901 (1 829 – 1 956)	High
Amphibians									
Chiromantis xerampelina							4	696 (634 – 862)	Low
Phrynomantis bifasciatus							4	662 (637 - 693)	Low
Schismaderma carens					2	2	6	910 (636 - 1 252)	Low
Hyperolius m. taeniatus	10						5	1662 (666 – 1918)	Gen
Amietophrynus gutturalis			3		1	1	5	975 (636 - 1403)	Low
Kassina senegalensis							7	662 (632 - 688)	Low
Amietia quecketti	2		2		2			1494 (1 272 – 1 918)	High
Hadromophryne natalensis		1	3					1356 (1 257 - 1602)	High
Breviceps verrucosus	6	1		1	4		1	1589 (809 – 1 933)	Gen
Strongylopus grayii	3	4	5		2	1		1437 (1 144 – 1 916)	High
Birds									
Muscicapa caerulescens							4	700	Low
Pogoniulus chrysoconus						3	1	925 (700 – 1 000)	Low
Malaconotus blanchoti						3	2	880 (700 – 1 000)	Low
Turtur chalcospilos						4	7	809 (700 – 1 000)	Low
Tchagra senegalus						5	8	815 (700 – 1000)	Low
Dryoscopus cubla							7	700	Low
Lybius torquatus						3	2	880 (700 – 1 000)	Low
Pycnonotus tricolor				2		16	1	1047 (700 – 1 600)	Low
Dicrurus adsimilis						2	2	850 (700 – 1 000)	Low
Cuculus solitarius						3	4	829 (700 – 1 000)	Low
Cossypha dichroa		4						1600	High
Onychognathus morio	27			8	8	25		1463 (1 000 – 1 900)	Gen
Tachymarptis melba	5					1		1750 (1 000 – 1 900)	High
Cisticola aberrans	5				5			1600 (1 300 – 1 900)	High
Thamnolaea cinnamomeiventris	4							1900	High
Small mammals									
Micaelamys namaquensis	10			2	5	3	48	960 (700 – 1 900)	Gen
Dendromys mesomelas	1		14					1433 (1 400 – 1 900)	High
Rhabdomys pumilio	53		7	7				1816 (1 400 – 1 900)	High
Myosorex varius	6		3	2				1709 (1 400 – 1 900)	High

Table 2.3. Temperature range differences between the annual temperatures measured at seven automated weather stations (spanning an altitude range from 700m to 1 700 m a.s.l.) in the Drakensberg area and the predicted temperatures within the respective quarter degree square (QDS) spatial units from WorldClim at 5 arc minutes resolution. The difference in range, mean and standard error of the mean (S. E. M.) for daily maximum, mean daily average and mean daily minimum were calculated. (S.E.M – Standard Error of the Mean).

Temperature difference variable	**Range (ºC)**	**Mean (ºC)**	**S.E.M. (ºC)**
Mean daily maximum temperature	-0.41 to 1.37	0.65	0.27
Mean daily average temperature	-0.09 to 1.52	0.65	0.27
Mean daily minimum temperature	-0.77 to 2.22	0.65	0.43

Chapter 2: Figures

Fig. 2.1 A topographical map indicating the study sites (1 – 7) and vegetation types (Table 2.1) with the location of the seven automated weather stations (⚑) along the altitudinal gradient at Mariepskop.

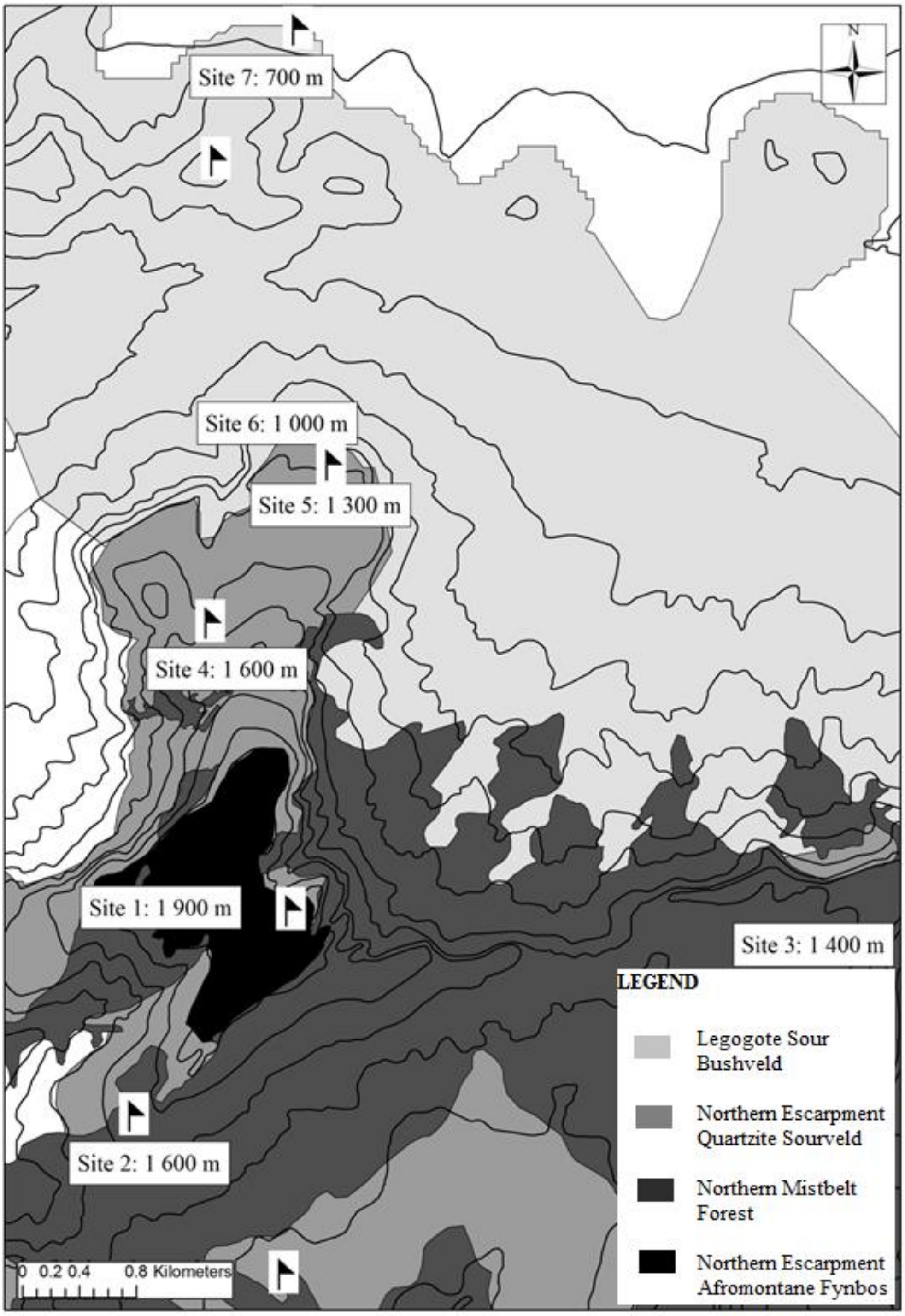
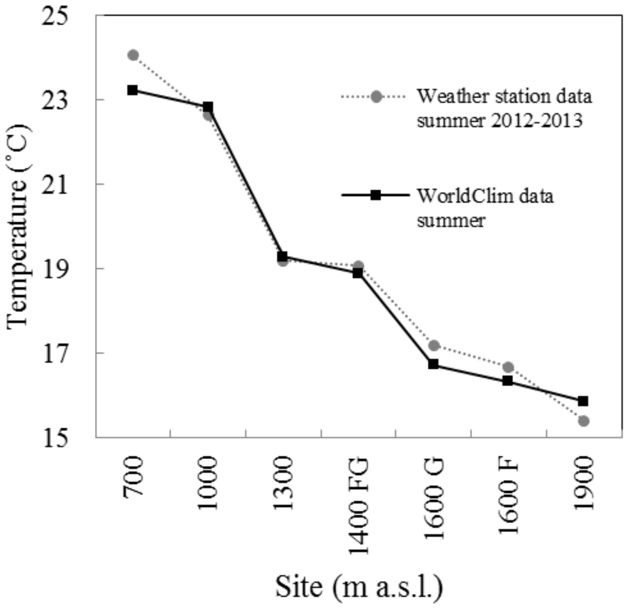
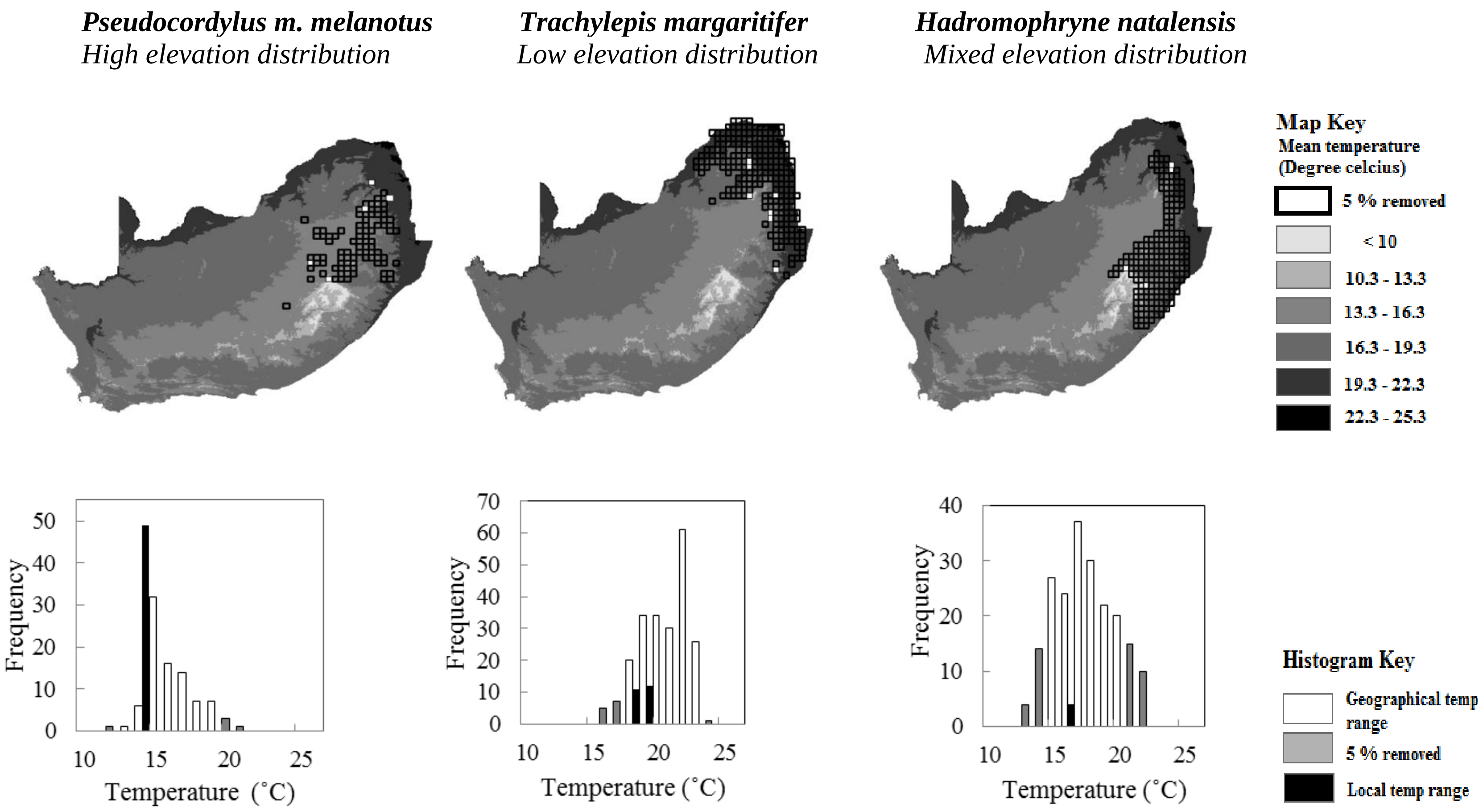


Fig. 2.2 The local mean temperature for summer obtained from WorldClim data (1950 - 2005) compared to the local weather station data for summer (Dec - Feb: 2012/2013) at each altitudinal site. (FG = Forest with Grassland patches; G = Grassland; F = Forest).



Chapter 2: Figures

Fig. 2.3 Map of the geographical QDS distribution of three species with 5 % of the QDS mean annual temperature range outliers removed. The histogram accompanying each map indicates the geographical mean annual temperature range values that were removed (5 %) and the temperature range at Mariepskop (local). The mean annual temperature data (geographically and locally) were obtained from WorldClim.



Pseudocordylus m. melanotus
High elevation distribution

Trachylepis margaritifer
Low elevation distribution

Hadromophryne natalensis
Mixed elevation distribution

Fig. 2.4 (a) Range of annual maximum and minimum mean geographical (5 % removed) and local temperature of reptiles with accompanying altitudinal class at Mariepskop (L = Low altitude species, H = High altitude species; G = altitudinal generalist). **(b)** Range of annual maximum and minimum mean geographical (5 % removed) and local temperature of amphibians with accompanying altitudinal class at Mariepskop. The mean annual temperature data (geographically and locally) were obtained from WorldClim.

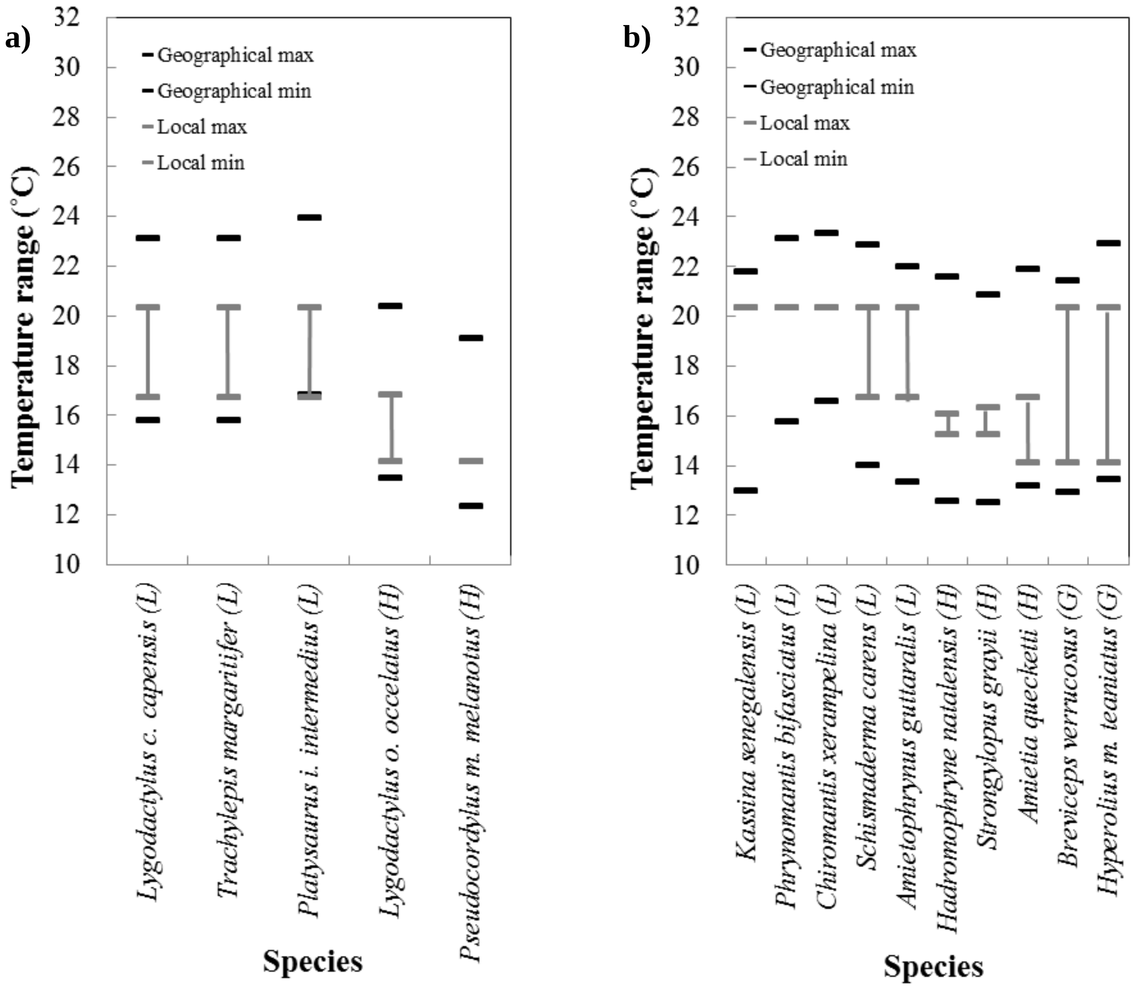
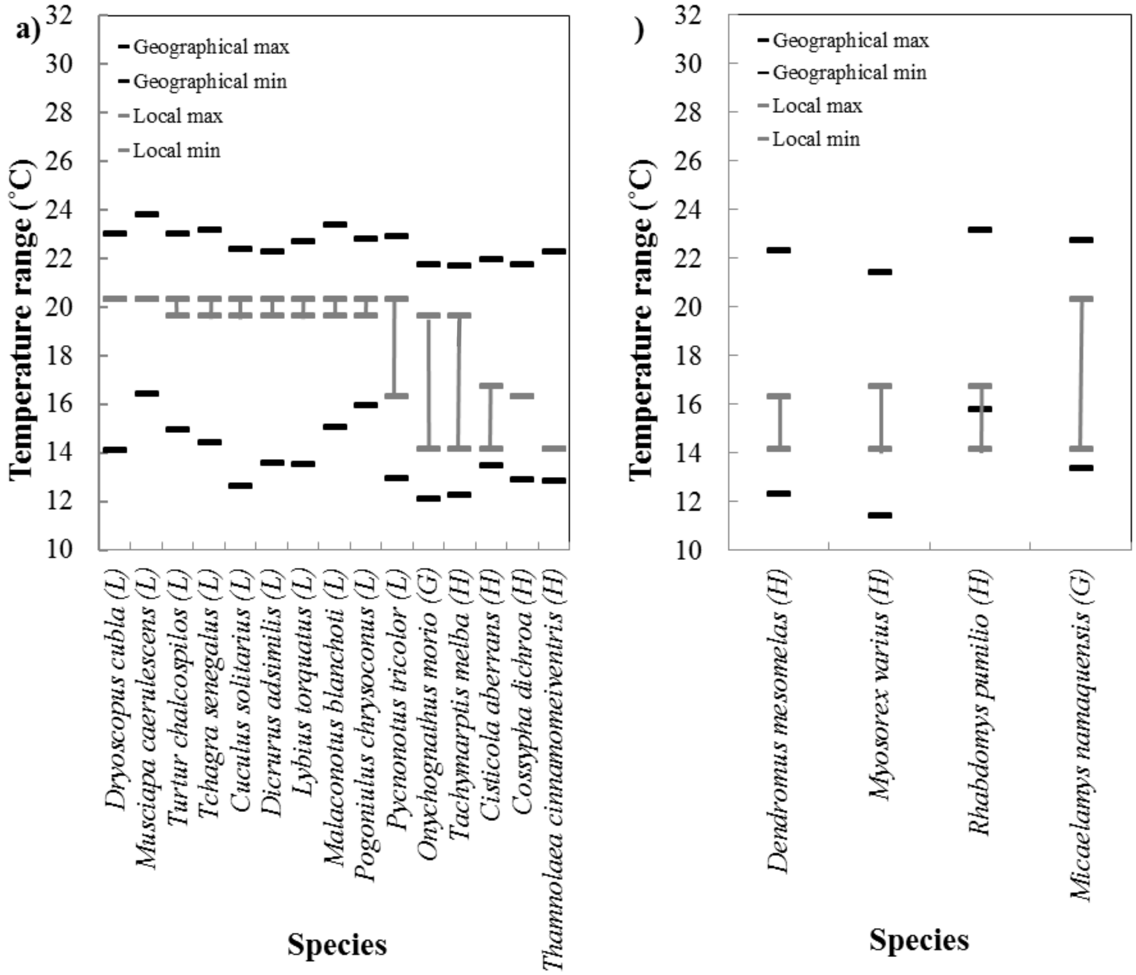


Fig. 2.5 (a) Range of annual maximum and minimum mean geographical (5 % removed) and local temperature of avifauna with accompanying altitudinal class at Mariepskop (L = Low altitude species, H = High altitude species; G = altitudinal generalist). **(b)** Range of annual maximum and minimum mean geographical (5 % removed) and local temperature of small mammals with accompanying altitudinal class at Mariepskop. The mean annual temperature data (geographically and locally) were obtained from WorldClim.



Appendix 1. First column: the common and scientific names of the species recorded in the study. Second column: the geographical distribution of the selected species (within South Africa) and their habitat requirements. Third column: local distribution (Mariepskop) and habitat selection rational based on habitat requirements. Fourth column: Number of time the species were observed.

Species	**Geographical distribution and habitat requirements**	**Distribution at Mariepskop and habitat selection rational**	**# Obs.**
Reptiles	References: Branch, 1998; Jacobsen, 2005; McConnachie, 2006.		
Cape dwarf gecko *Lygodactylus c. capensis*	North West, Limpopo, Mpumalanga and KwaZulu-Natal provinces at low altitudes. Requires trees and fallen logs in Bushveld vegetation.	Low altitudinal distribution in the Legogote sour Bushveld with ample tree cover to meet the arboreal needs of this species.	38
Rainbow skink *Trachylepis margaritifer*	Limpopo, KwaZulu-Natal and parts of Mpumalanga provinces. Requires large exposed granite boulders in Bushveld vegetation.	Low altitudinal distribution in the Legogote sour Bushveld where exposed granite boulders were abundant to meet the needs of this rupiculous species.	23
Common flat lizard *Platysaurus i. intermedius*	Limpopo, Mpumalanga and parts of KwaZulu-Natal Provinces. Requires exposed rock surfaces in mesic and arid Bushveld.	Low altitudinal distribution in the Legogote sour Bushveld where exposed granite boulders were abundant to meet the needs of this rupiculous species.	23
Occelated dwarf gecko *Lygodactylus o. occelatus*	Limpopo, North West, Gauteng and Mpumalanga Provinces at high altitudes. Requires rocky outcrops with boulders and crevices in Montane grassland.	High altitudinal distribution within the rocky outcrops of the Northern Escarpment Afromontane Fynbos and Northern Escarpment Quartzite Sourveld (Grassland) where suitable crevices and boulders were abundant for this rupiculous species.	68
Drakensberg crag lizard *Pseudocordylus m. melanotus*	Drakensberg Escarpment, Gauteng, Mpumalanga, and parts of Free State province at high altitudes. Requires rocky outcrops with suitable crevices in mountainous areas.	Highest altitudinal distribution within the rocky outcrops of the Northern Escarpment Afromontane Fynbos where suitable crevices were present for this rupiculous species.	49

Amphibians	References: Minter *et al.*, 2004; Du Preez & Carruthers, 2009.		
Southern foam nest frog *Chiromantis xerampelina*	Parts of North West, Limpopo, Mpumalanga and KwaZulu-Natal provinces. Requires seasonal or permanent open waterbodies with adjacent vegetation in Bushveld.	Low altitudinal distribution in Legogote sour Bushveld at the permanent dams and surrounding vegetation that this species requires.	4
Banded rubber frog *Phrynomantis bifasciatus*	Parts of North West, Limpopo, Mpumalanga, Gauteng and KwaZulu-Natal provinces. Adapted to live in hot, arid environments. Requires waterbodies in Woodland, grassland or Bushveld vegetation.	Low altitudinal distribution in Legogote sour Bushveld at the permanent dams that this species requires.	4
Red toad *Schismaderma carens*	Parts of North West, Limpopo, Mpumalanga, Gauteng and KwaZulu-Natal provinces. Requires waterbodies in Bushveld or grassland vegetation.	Low altitudinal distribution in Legogote sour Bushveld at the permanent dams and seasonal streams that this species requires.	10
Painted reed frog *Hyperolius m. taeniatus*	Limpopo, Mpumalanga, Kwazulu-Natal. Large altitudinal range. Requires waterbodies with reeds or surrounding vegetation in Savannah, grassland, Forest and Fynbos Biomes.	Altitudinal generalist found in highest Northern Escarpment Afromontane Fynbos and lowest Legogote sour Bushveld in reeds next to permanent waterbodies that this species requires.	15
Guttural toad *Amietophrynus gutturalis*	Throughout SA except for Western Cape and parts of Eastern and Northern Cape. Large altitudinal range. Requires semi-permanent or permanent waterbodies in Savannah, grassland and Thicket Biomes.	Low altitudinal distribution in the Legogote sour Bushveld and Northern Escarpment Quartzite Sourveld (Grassland) where the waterbodies were present that this species requires.	10
Bubbling kassina *Kassina senegalensis*	Throughout SA except for Western Cape and parts of Eastern and Northern Cape. Large altitudinal range. Temporary or permanent waterbodies in Savannah and grassland Biomes.	Low altitudinal distribution in Legogote sour Bushveld, found in the vegetation surrounding the waterbodies which is what this species requires.	7
Common river frog *Amietia quecketti*	Throughout SA except for most of Western Cape and parts of Northern Cape. Requires slow-flowing streams or permanent waterbodies in grassland, Savannah and Forest Biomes.	High altitudinal distribution in the Northern Escarpment Quartzite Sourveld (grassland) and Northern Escarpment Afromontane Fynbos close to streams that this species requires.	6

Natal cascade frog *Hadromophryne natalensis*	Along the Drakensberg Escarpment. Requires clear, fast-flowing streams in Forests, kloofs and grassland.	High altitudinal distribution in the Northern Mistbelt Forest and kloofs in the Northern Escarpment Quartzite Sourveld (Grassland) in fast-flowing streams that this species requires.	4
Plaintive rain frog *Breviceps verrucosus*	Along the Drakensberg Escarpment, parts of Eastern Cape, KwaZulu-Natal and Mpumalanga. Requires grassland, Afromontane Forest and Bushveld-grassland. Annual rainfall of > 700 mm and well-shaded soil.	Altitudinal generalist occupying Legogote sour Bushveld, Northern Escarpment Quartzite Sourveld (Grassland), Northern Mistbelt Forest and Northern Escarpment Afromontane Fynbos were it was found and heard calling amongst the vegetation. All of these habitats met the requirements of this species.	13
Clicking stream frog *Strongylopus grayii*	Widespread throughout SA except for North West, Northern Cape and parts of Free State provinces. Large altitudinal distribution. Capable of occupying most of the vegetation Biomes and breeding in poor water quality.	Preferred the higher altitudinal Legogote sour Bushveld, Northern Escarpment Quartzite Sourveld (Grassland), Northern Mistbelt Forest and Northern Escarpment Afromontane Fynbos, found close to streams which this species requires.	15
Avifauna	References: Hockey *et al.*, 2005; Sinclair & Ryan, 2009.		
Ashy fly-catcher *Muscicapa caerulescens*	Limpopo and Mpumalanga Provinces, lowlands of KwaZulu-Natal and coastal lowlands of Eastern Cape. Requires broad-leaved Woodland.	Low altitudes in the Legogote sour Bushveld where suitable broad-leaved trees were present which this species requires.	4
Yellow-fronted tinkerbird *Pogoniulus chrysoconus*	North West, Mpumalanga and Limpopo provinces. Requires broad-leaved Woodland and Savannah. Not present in moist evergreen Forests.	Low altitudes in the Legogote sour Bushveld where suitable broad-leaved trees were present which this species requires.	4
Grey-headed bushshrike *Malaconotus blanchoti*	Limpopo, Mpumalanga and lower lying areas of KwaZulu-Natal Provinces including Eastern Cape. Requires broad-leaved Woodland and Savannah or riverine Forests.	Low altitudes in the Legogote sour Bushveld where suitable broad-leaved trees were present which this species requires.	5
Emerald spotted wood dove *Turtur chalcospilos*	North-eastern parts of South Africa, south into Eastern Cape. Requires trees in Savannah, Sand Forests and Thickets.	Low altitudes in the Legogote sour Bushveld with suitable tree cover which this species requires.	11

Black-crowned tchagra *Tchagra senegalus*	North-eastern parts of South Africa, south into Eastern Cape. Requires Woodland or Savannah.	Low altitudes in the Legogote sour Bushveld with suitable tree cover which this species requires.	13
Black-backed puffback *Dryoscopus cubla*	North-eastern parts of South Africa, KwaZulu-Natal and along the coastal belt into the South-eastern Cape. Requires Woodland, Savannah and Forest habitats.	Low altitudes in the Legogote sour Bushveld where suitable broad-leaved trees were present which this species requires.	7
Black collared barbet *Lybius torquatus*	North-eastern parts of South Africa, KwaZulu-Natal and Eastern Cape. Requires Woodland, Savannah, riparian and coastal dune Forest. Absent from evergreen Forests.	Low altitudes in the Legogote sour Bushveld with suitable tree cover which this species requires.	5
Dark-capped bulbul *Pycnonotus tricolor*	North-eastern parts of South Africa, KwaZulu-Natal and Eastern Cape. Requires wooded habitat in Savannah, Forest edges and gardens with ample fruiting trees or shrubs.	Low altitudes in the Legogote sour Bushveld with suitable tree cover and availability of fruit which this species requires.	19
Fork-tailed drongo *Dicrurus adsimilis*	Throughout South Africa except for parts of the Karoo, Namaqualand and West coast. Requires Woodland, Savannah, and grassland with adequate perches.	Low altitudes in the Legogote sour Bushveld with suitable tree cover which this species requires.	4
Red-chested cuckoo *Cuculus solitarius*	North and Eastern parts stretching coastally into the Western Cape. Requires trees in Forests, Woodland and Thicket.	Low altitudes in the Legogote sour Bushveld with suitable tree cover which this species requires.	7
Chorister robin-chat *Cossypha dichroa*	Limpopo, Drakensberg Escarpment and parts of KwaZulu-Natal, Eastern Cape and Western Cape provinces. Wide altitudinal range. Requires trees and shrubs in evergreen Forests and thicket.	High altitudinal distribution in the Northern Mistbelt Forest with evergreen trees and shrubs which this species requires.	4
Red-winged starling *Onychognathus morio*	Throughout South Africa except for the arid Western regions. Requires rocky outcrops and cliffs (versatile and common in urban areas where it nests on buildings).	Altitudinal generalist except for the Northern Mistbelt Forest. Preferred areas with rock cover and trees.	68

Alpine swift *Tachymarptis melba*	Throughout SA except for patchy distribution in Northern cape. Requires mountainous areas for breeding and wide range of habitats for foraging.	Preferred a higher altitudinal distribution in the Northern Escarpment Afromontane Fynbos where ample rock cover was present which this species requires.	6
Lazy cisticola *Cisticola aberrans*	North-eastern parts of SA, KwaZulu-Natal, Gauteng, Free State and Eastern Cape. Requires rocky outcrops in Woodland or grassland.	High altitudinal distribution in the rocky outcrops of the Northern Escarpment Quartzite Sourveld (Grassland) and the Northern Escarpment Afromontane Fynbos which this species requires.	10
Mocking cliff chat *Thamnolaea cinnamomeiventris*	Eastern parts of SA from Limpopo to Eastern Cape. Requires well-wooded rocky outcrops, ravines and hillsides with large boulders.	High altitudinal distribution in the rocky outcrops of the Northern Escarpment Afromontane Fynbos which this species requires.	4
Small mammals	References: Skinner & Smithers, 1990.		
Namaqua rock rat *Micaelamys namaquensis*	Distributed throughout the country except for coastal KwaZulu-Natal and parts of central and northern Western Cape. Catholic requirements but prefer rocky outcrops.	Altitudinal generalist except for the Northern Mistbelt Forest. Preferred areas with rock cover.	68
Brant's climbing mouse *Dendromys mesomelas*	Distributed throughout the South-western Cape, east towards Kwazulu-Natal and in Mpumalanga and Limpopo provinces up to high altitudes. Requires tall, dense grass and scrubs.	High altitudinal distribution in the Northern Escarpment Quartzite Sourveld (Grassland) and the Northern Escarpment Afromontane Fynbos where it lives in the tall grass which this species requires.	15
Striped mouse *Rhabdomys Pumilio*	Distributed throughout the country with a large altitudinal range. Catholic requirements but prefer ample grass cover.	High altitudinal distribution in the Northern Escarpment Quartzite Sourveld (Grassland) and the Northern Escarpment Afromontane Fynbos where it lives in the tall grass which this species requires.	67
Forest shrew *Myosorex varius*	Distributed throughout the Eastern parts of the country including the Western Cape and stretching into the North-western coastal areas. Requires moist habitat with dense vegetation cover or drier mountainous areas with frequent mist.	High altitudinal distribution in the Northern Escarpment Quartzite Sourveld (Grassland) and the Northern Escarpment Afromontane Fynbos where it lives in the tall grass or rocky areas with frequent mist which this species requires.	11

Chapter 3

Will climate change induced temperature increase affect the survival of the Drakensberg crag lizard (*Pseudocordylus melanotus melanotus)*?

Vonica Perold and J. Willem H Ferguson

Abstract

Ectotherms like the Drakensberg crag lizard *Pseudocordylus melanotus melanotus* rely on the external thermal environment for thermoregulation. Habitat selection is based on suitable shelter, prey availability, and climatic conditions allowing for optimal thermoregulation. Locally at Mariepskop, this species is restricted to the highest altitudinal habitat on top of the mountain and thus an ideal subject to study the effects of increased temperature due to climate change. This study investigated the possible factors shaping the limited altitudinal distribution of crag lizards at Mariepskop. We quantified the altitudinal distribution and collective thermal environment at three sites along the altitudinal gradient. The availability of suitable shelter and prey were quantified at each altitudinal site along with the temperature data. A behavioural observation study established diurnal activity profiles during winter, spring and summer. We recorded operative temperature using copper models of the lizards at the three altitudinal sites, allowing us to calculate the availability of total diurnal activity time at each site. Quantifying the diurnal activity time (based on time available below the upper thermal limit of 35˚C) at the lower altitudinal sites revealed a reduction in available time as more time needs to be allocated to thermoregulation. Essential activities like feeding and breeding might have to be curtailed at the lower altitudinal sites due to the reduced diurnal activity time. Combining all the information gathered we were able to determine that the collective thermal environment at the lower altitudinal sites might be too high even though suitable prey and shelter is present. Simulating future climate change scenarios at the highest altitudinal site indicated that with a 1˚C increase, a 9 % reduction in total diurnal activity time (time $T_e < 35$˚C) and with 2˚ C increase, a 17 % reduction will occur. Quantifying the exact magnitude of the impact of future climate change on the survival of the Drakensberg crag lizard is difficult as there is a large pool of variables that need to be considered and quantified. Long-term ecological changes in vegetation and the effect of future climate change on effective insolation and wind speed needs to be investigated. However, using the information gathered in this study we can make tentative predictions regarding the fate of the Drakensberg crag lizard. A proposed future 2˚C increase in ambient temperature (T_a) should not affect the survival of the Drakensberg crag lizard at Mariepskop.

Key words: Ectotherm, altitudinal gradient, habitat selection, operative temperature, thermoregulation, climate change

Introduction

During the last 40 years climate change induced temperature increases influenced the distribution, phenology and dynamics of faunal and floral communities and triggered the extinction of several species (Sinervo *et al.*, 2010; Moreno-Reuda *et al.*, 2011; Moritz & Aguda, 2013). Sinervo *et al.* (2010) predicted that by the year 2080, 40 % of global lizard populations and 20 % of all lizard species may be extinct. Knowledge to determine, anticipate, monitor and alleviate the impacts of climate change on our ecosystems is vital (Ballesteros-Barrera *et al.*, 2007; Dunford & Berry, 2012).

Predicting the effects of climate change on species is best achieved by understanding a species fundamental niche using a mechanistic approach (Kearney & Porter, 2004; Huey *et al.*, 2012). The framework for assessing species vulnerability to climate change proposed by Williams *et al.* (2008) adheres to mechanistic principles allowing consideration of interacting factors responsible for species survival in a particular habitat (Huey *et al.*, 2012). The key fundamentals of this framework are: 1) Sensitivity, 2) exposure and 3) feedback and cascading impacts (Williams *et al.*, 2008). Sensitivity of a species is governed by intrinsic factors such as ecology, physiology and genetic diversity. Sensitivity is counteracted by resilience and adaptive capacity of species (Williams, *et al.* 2008; Huey *et al.*, 2012). Exposure will be determined by the degree of regional climate change and if a species is capable of surviving in a sheltered microhabitat, buffered from regional climate change (Williams *et al.*, 2008). Finally, feedback and cascading events are inevitable with changes in community composition and predator-prey relationships, terminating mutualistic relationships and increasing parasitic infections. The exact magnitude of feedback and cascading events are perplexed and need to be monitored closely and timely (Williams *et al.*, 2008). This framework explains the fundamentals of species response to climate change. We applied these principles with information from additional literature to explain the impact and effect of climate change on vertebrate species:

The ecology, physiology and behaviour of reptiles are highly influenced by body temperature and availability of microhabitats meeting their thermal requirements is essential for thermoregulation (Singh *et al.*, 2002; Angilletta *et al.*, 2006; McConnachie *et al.*, 2007; Fei *et al.*, 2012). This critical dependence on ambient temperature for thermoregulation exposes ectotherms to a greater degree to climate change (Bell *et al.*, 2007; Whitfield *et al.*, 2007; Boyles *et al.*, 2011). Other factors that contribute to habitat selection include suitable shelter and the availability of food resources (Diego-Rasilla & Pérez-Mellado, 2003; Seebacher & Shine, 2004; Goodman *et al.*, 2008). Since climate change either directly or indirectly affects the above factors it shapes the distribution of reptiles within a particular habitat (Walther *et al.*, 2002). Those species unable to migrate or adapt to the changes in environment due to climate change can become extinct (Holt, 1990; Meynecke, 2004). Reptiles are more likely to change their patterns of distribution by migration in response to climate change than by adaptation (Huey *et al.*, 2010; Ihlow *et al.*, 2012) because the rate of climate-change is rapid and their generation time is too long to allow for evolutionary adaptation to occur at the time scale of rapid climate change (Bradshaw & Holzapfel, 2006; Ihlow *et al.*, 2012). However, reptiles have limited regional dispersal capabilities and are therefore at a greater risk of extinction than other vertebrates (Gibbons *et al.*, 2000).

The Drakensberg crag lizard *Pseudocordylus melanotus melanotus* is limited to the higher altitudinal areas in South Africa (Branch, 1998; McConnachie, 2006;). The crag lizard is a diurnal, rupiculous, sit-and-wait forager living in rocky outcrops at high altitudes in mountainous areas suggesting that it is adapted to colder temperatures (Branch, 1998; McConnachie, 2006; McConnachie *et al.*, 2007). The diet of this lizard consists of invertebrates, mainly from the order Coleoptera as well as berries, millipedes, grasshoppers, termites, wasps, and bees (Branch, 1998; McConnachie, 2006; Alexander & Marais, 2007). The lizard thermoregulates by shuttling between exposed rock surfaces for sunbasking and sheltered rock crevices acting as buffers for cooling (McConnachie *et al.*, 2007; Fei *et al.*, 2012). If the ambient temperature is too high the lizard has to curtail feeding and breeding activities in order to thermoregulate, thus decreasing resource acquisition with potentially negative impacts on survival (Martin, 2001; Kearney & Porter, 2004; Hofmann & Todgham, 2010; Fei *et al.*, 2012). Therefore, since mountain-top restricted lizards are at the limit of their altitudinal distribution and migration to higher altitudes is impossible, they face a high risk of extinction due to climate change (Chamaillè-Jammes *et al.*, 2006; Raxworthy *et al.*, 2008). What are the effects of increased ambient temperature on crag lizard activity and how does this knowledge help us to understand both the likely effects of climate change and the altitudinal distribution of this species? These questions are addressed using the following approaches:

- Compare the regional distribution and mean annual temperature profile of *P. m melanotus* in southern Africa to the local altitudinal distribution and local mean annual temperature profile at Mariepskop based on long-term interpolated climate data.

- Quantify local temperature profiles for different altitudinal sites at Mariepskop based on data from automated weather stations and field recordings.

- Compare shelter and prey availability at different altitudes at Mariepskop

- Determine how the diurnal activity and behaviour of free-ranging crag lizards is affected by daily ambient temperature at Mariepskop.

- Predict the implications of current and future climate change on the body temperature and activity of crag lizards at Mariepskop using both field data and laboratory-based data.

Materials and methods

Study site:

The study was performed on the adjacent sites Moholoholo Private Nature Reserve and Mariepskop Mountain (24° 30’ S, 30° 58’ E) on the eastern edge of the Blyde River Canyon, South Africa. Moholoholo Private Nature Reserve is located at the foot of Mariepskop and experiences a warm subtropical climate while Mariepskop has a cooler climate allowing an altitudinal temperature gradient of ~10˚C. The rainy season is predominantly during summer with annual rainfall between 1 300 – 2 000 mm (Wilson *et al.*, 2010). The area has an altitudinal gradient from approximately 600 m to 1 945 meters above sea level (a.s.l.) with high floral and faunal biodiversity (Van Der Schijff & Schoonraad, 1971). Three different altitudinal sites (Fig. 3.1) representing rocky habitat potentially available for crag lizards were chosen and classified as follows: (Mucina & Rutherford, 2006).

- Site A: High altitude ~ 1 900 m a.s.l. (Northern Escarpment Afromontane Fynbos)
- Site B: Mid altitude ~ 1 700 m a.s.l. (Northern Escarpment Quartzite Sourveld)
- Site C: Low altitude ~ 1 300 m a.s.l. (Northern Escarpment Quartzite Sourveld)

Regional geographical distribution and mean annual temperature profile:

The geographical distribution of *P. m. melanotus* was obtained as quarter degree squares (QDS, i.e. geographical units of 15‘ by 15’) from Bates *et al.* (2014). Long-term historical climatic data consisting of annual mean temperature (calculated on a monthly basis based on hourly intervals from interpolated weather station data at 5 arc-minutes resolution) were obtained from WorldClim – Global Climate Data (Hijmans *et al.*, 2005**)**. The mean annual temperature within each QDS inhabited by *P. m. melanotus* was obtained from the WorldClim data set (using ArcMap 10; ESRI, Redlands CA) resulting in a regional mean annual temperature profile for the species. The outlier data (cold or hot extremes in annual temperature) largely represented QDS's near the boundary of the geographical distribution of the species. Consequently we excluded 5 % of the temperature values, representing outliers (Fig. 3.3a).

Local altitudinal distribution and mean annual temperature profile:

The local altitudinal range of the species was determined by active searching along the altitudinal gradient from 700 m a.s.l. continuing up to 1 945 m a.s.l. A total of 200 hours of active searching was performed along the altitudinal gradient. Reptile activity is influenced by temperature and therefore surveys were only performed on clear sunny days (Wymann & Whiting, 2002; Effenberger & Mouton, 2007). The location and altitude of each crag lizard along the altitudinal gradient was recorded using a GPS. The local mean annual temperature profile at 1 900 m a.s.l. was calculated using long-term historical climatic data consisting of annual mean temperature (calculated on a monthly basis based on hourly intervals or from interpolated weather station data at 5 arc-minutes resolution) obtained from WorldClim – Global Climate Data (Hijmans *et al.*, 2005**)**.

Suitability and availability of shelter and prey at different altitudes:

Availability of suitable shelter: We located and measured variables for 24 crevices occupied by *P. m. melanotus* at the high altitude site (1 900 m a.s.l.). Since crag lizards were only found in the high altitudinal area, this information was used as a reference for selecting crevices at the lower sites (1 300 m and 1 700 m a.s.l. where *P. m. melanotus* was absent). Twenty crevices where chosen at each of the 1 300 m and 1 700m sites, comprising a total of 64 crevices for which the following measurements were taken (Diaz *et al*., 2006; McConnachie, 2006):

- Height of crevice entrance (mm): Measured with callipers in the middle of the crevice opening
- Depth of crevice (mm): Measured from entrance of the crevice to the deepest point a wire could reach inside the crevice. The length of the inserted wire was measured with measuring tape. If a crevice was deeper than 1 000 mm or open all the way through it was recorded to have a depth of 1 000 mm.
- Aspect: using a compass the aspects were recorded and grouped into the closest cardinal point (North, East, South and West).

Prey availability: Pitfall trapping was used to collect invertebrates at the three altitudinal sites. During winter, spring and summer, 12 days of trapping per season were divided into three rounds. During each round, three crevices were chosen at each altitudinal site and a pitfall trap deployed within a distance of less than five metres from each crevice. Each round lasted 4 days after which the traps were removed and the samples collected, washed and preserved in 70 % ethanol. This method was repeated for the next two rounds until 9 samples per altitude and 27 samples in total were collected per season. The pitfall traps consisted of two litre plastic bottles with the top half removed, inverted and placed inside the bottom half to act as a funnel. They were sunk into the soil so that the top of the container was flush with the surface. The containers were filled a quarter full with propylene glycol (2:1). Three drift fences of 1.2 metres long and 10 cm in height were placed around the sunken trap to increase the efficacy of the pitfalls. Rain cover lids were placed over each trap to prevent flooding of the traps and washing out of the samples. Species were identified to order and family level where possible. Based on the published prey preferences of this species (Branch, 1998; McConnachie, 2006; Alexander & Marais, 2007) and on field observations (Table 3.3), five of the invertebrate orders were selected for data analysis. We compared the abundance of these orders (classified into families where possible) to the altitudinal sites and season of year to determine if there were significant differences in prey availability (Table 3.3). A two-way ANOSIM (Analysis of similarity) with altitude and season as factors, and NMDS was performed on the insect communities trapped, using PRIMER-E (Version 5.2.0, Plymouth Marine Laboratories, Plymouth UK).

Local temperature profiles based on automated weather station data and field recordings:

General climatic conditions: At each site (1 300 m, 1 700 m and 1 900 m a.s.l.) an automated weather station two metres above ground (Mike Cotton Systems or Campbell Instruments) recorded wind speed ($m.s^{-1}$), temperature (˚C) and insolation (W/m^2). This allowed us to compare baseline thermal conditions at the different altitudes. The mean, standard deviation and range of daily temperatures and insolation were calculated for each weather station. Due to technical problems with these remote weather stations, resulting in incomplete data for the summer of 2013, data for the summer of 2012 were used. The air temperature and insolation data for each season and each altitude were analysed using general mixed-effects ANOVA taking into account temporal autocorrelation (Pinheiro & Bates, 2000) using R V2.14.2 (R development core team, 2012).

Temperature inside crevices: We recorded the temperature within each crevice during winter, spring and summer using DS1922L Thermochron iButtons (Maxim Integrated, San Jose USA). These were calibrated in a temperature controlled water bath against a high precision mercury thermometer from 5 – 55 ˚C (Wilms *et al.*, 2011). At each altitudinal site we selected 12 crevices (i.e. a total of 36 crevices). The crevices used at the high altitudinal site were all occupied by *P. m. melanotus.* An iButton was placed inside each crevice at a standardised depth of 100 mm, recording temperature at 10 minute intervals and the data downloaded using ClimaStats Software (Fairbridge Technologies; Johannesburg South Africa). The temperatures inside the crevices were recorded for twelve days divided into three 4 day rounds as follows: Temperatures were recorded in four crevices per altitudinal site for 4 days, the data downloaded and iButtons moved to the next four crevices at each site. This resulted in 48 sampling days per season (winter, spring and summer) per altitudinal site. At each crevice, microhabitat ambient temperature was recorded using an iButton recording at 10 minute intervals inside an inverted polystyrene cup with eight ventilation holes, placed within 6 meters of and at a similar height above ground as the crevice.

Operative temperature: Operative temperature (T_e) (Wilms *et al.*, 2011) 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; Wilms *et al.*, 2011). To measure T_e, 12 copper lizard models were constructed following Bakken and Gates (1975). A replicate of a female *P. m. melanotus* was created by constructing a wax mould from a museum specimen. The mould was copper electroplated after which the wax was removed by melting. In order to match the lizard's absorptivity for insolation, the models were painted to match the colouration of an adult female lizard (Scheers & Van Damme, 2002). A small "L" shaped incision was made in the ventral surface of each model to create a flap that was used to insert an iButton (with 10 minute recording interval). The insertion point was then sealed with a small amount of clay. The models were positioned approximately 10 cm from the crevice entrance, horizontally on the rock surface in the sun. T_e was recorded simultaneously with crevice and ambient microhabitat recordings and followed the same 12 day recording protocol. In a study by McConnachie (2006) the lizards showed signs of heat stress at 35˚C to such an extent that ethical considerations terminated further exposure of the lizards to this temperature. This temperature was taken as the proposed upper thermal limit for the species in this study and will be expressed as T_{max}. This allowed measurement of the percentage of time T_e exceeded T_{max} (35˚C) (Fig. 3.5).

Diurnal activity and behaviour of free-ranging crag lizards

Ten focal lizard individuals were selected and their diurnal activity recorded during winter, spring and summer. The individuals were identified using either a coloured elastic band around their necks or with a small streak of non-toxic paint on the dorsal or lateral body surface. Since crag lizards have strict site fidelity, locating the focal individuals during the different seasons was simple (McConnachie, 2006). Observations were only performed on cloudless sunny days and data recording started at 7:30 and continued until 17:30. Recordings were terminated if the weather became unfavourable. An adjustment period of one day after marking and 15 minutes before each observation period minimised the effect of observer on lizard behaviour. Observations were made at a distance of 5 – 10 meters from the focal animal. Observation periods lasted 60 minutes and a minimum of ten observation hours per daily hour was performed per season. Behaviour of the focal lizard was classified as sunbasking (animal outside crevice in sun) or inside crevice. The time spent in minutes per hourly observation period on these two activities was recorded and analysed for all three seasons. Successful and unsuccessful feeding events were recorded and the prey identified using binoculars if possible.

Laboratory temperature measurements for modeling lizard body temperatures at different altitudes and climate change scenarios:

Experimental design: The same copper lizard models used in the field observations were used in laboratory experiments. The copper lizard models were mounted on the flat surface of a large rock, similar to the rocks found at Mariepskop. The surface area of the rock measured at the widest part was 55 x 25 x 15 cm. Temperatures were recorded with MT630 Digital thermometers (Major Tech; Johannesburg South Africa) using thermocouples. These instruments were calibrated in a temperature controlled waterbath at 22 and 60 ˚C for 30 minutes at a time using a precision mercury thermometer G3THE017Z (Lasec; Cape Town South Africa).

To record the temperature of the copper lizard models, thermocouples were placed inside the models at the ventral “L” incision, sealed with clay. Temperatures were recorded every minute during consecutive heating and cooling cycles. A 500 W halogen floodlight FS18B (Eurolux; Johannesburg South Africa) was used as the artificial heat source at insolation intensities of 50, 100, 200, 400, 600, 800 and 1000 W/m^2. Insolation was recorded (W/m^2) using a LI-200 Pyranometer (Li-Cor; Nebraska USA). The insolation was manipulated by adjusting either the height or the voltage supplied to the light and verified placing the pyranometer in the positions of the models.

Two electric fans were used to generate wind at two speeds (0.5m.s^{-1} and 1m.s^{-1}), manipulated by controlling their voltage supply with one fan positioned 60 cm in front of the rock and the second one 20 cm behind to create a flow of air across the models. Wind speed was measured with a Kestrel pocket weather tracker 4000 (Nielsen-Kellerman; Pennsylvania USA). The wind speed indicated by the Kestrel meter was calibrated (1.0 – 2.0 m.s-^{1} at 0.1m.s^{-1} increments) using the Wind Sentry model 03002 (Young; Michigan USA) meteorological anemometer ($r^2 = 1.000$).

Four experiments were performed:

1. *Cardboard no wind*

The models were mounted on a sheet of double-riffled cardboard. The heat source was mounted vertically above the models at a height required to achieve the desired insolation. Two lizard models at a time were spaced 10 cm apart on the cardboard and heated at the desired insolation intensity until the operative temperature stabilised, starting with 50 W/m^2. The heat source was then switched off, allowing cooling to ambient temperature (T_a). This was repeated at the different insolation intensities and temperatures for the models were recorded every minute. Each experiment was repeated for a different pair of models following the same protocol, totalling data for four models at each of the insolation intensities.

2. *Rock no wind*

The same design and protocol was followed as in experiment 1 except the models were placed directly on the rock surface. Since the rock used in the laboratory was much smaller than the rocks used by live animals in the field, the exposed rock areas around the models were covered with double-riffled cardboard to minimise the heating of the rock except for the surface directly underneath and around the model. The models were allowed to heat and cool to ambient temperature (T_a) at all the different insolation intensities and temperature readings were recorded every minute.

3. *Rock with 0.5m.s^{-1} wind*

The same design and protocol was followed as in experiment 2 but with a constant air movement of 0.5m.s^{-1} over the models from the start of heating until the models cooled down to ambient temperature.

4. Rock with 1m.s^{-1} wind

The same design and protocol was followed as in experiment 3 but a with constant air movement of 1m.s^{-1} over the models from the start of heating until the models cooled down to ambient temperature.

Data analyses: Results were analysed using Newton's Law of Cooling (Vollmer, 2009) assuming a cooling rate that is directly proportional to the difference between the model temperature and the ambient (equilibrium) temperature (Tipler, 1982). Newtons's Law of Cooling is an empirical law that largely takes into account convective cooling: radiation and conduction are additional heat exchange processes (Vollmer, 2009). Preliminary experiments with our copper models showed that they did not satisfy Newton's Law over the whole range of temperatures encountered during cooling. However, they did satisfy this law for temperatures within 7-15 ºC of the ambient (equilibrium) temperature where the following formula was used for cooling:

$$\frac{dT}{dt} = -K(T - T_a) \qquad (1)$$

where t is the time, K a constant dependent on the overall heat exchange characteristics of the body and T_a the ambient (equilibrium) temperature of its surroundings. This is a reasonable assumption if the body is much smaller than its surroundings, i.e. the surrounding can absorb the relatively small amount of heat emitted by the relatively small body without increasing its temperature significantly.

With this assumption, the solution to the differential equation (1) taken with its natural logarithm produced a straight line equation as a function of time:

$$Kt = \ln(T_0 - T_a) - \ln(T - T_a) \tag{2}$$

where T_0 is the initial temperature (i.e. at time $t = 0$) of the body. The slope of the straight line is used to estimate the constant K.

For the heating, a similar approach was used.

$$\frac{dT}{dt} = +k(T_a - T) \tag{3}$$

Where T_a is the equilibrium temperature during heating where heat gain from the heat source is balanced by heat loss to the environment. This is therefore a more complex process than cooling and not merely an inverse process. There is no reason to automatically expect the relationship in (3) to hold during heating since this is dependent on the characteristics of the object being heated. However, this relationship did hold approximately for the copper lizards for T within 5 ºC of T_a. Taking the natural logarithm of this equation resulted in a similar equation as (2) and a similar linear curve with a positive slope. These equations allowed estimation of the constants K and k for cooling and heating of the copper lizard models for the different experiments. The ambient (equilibrium) temperatures (T_a) for each experiment at each insolation indicated a linear relationship between insolation and T_a (Fig. 3.2a) and intercept and slope of T_a for each experiment was included in the temperature simulations (Table 3.1). The values for K cooling and k heating were plotted against the different insolation intensities and although not precisely linear, the discrepancies were small enough to use the data to assume a linear relationship (Fig. 3.2b, c). The intercepts and slopes of K cooling and *k* heating calculated for each experiment were used in the body temperature simulation (Table 3.1). Within a particular cooling experiment, a constant value of *K* applies independent of initial temperature of model. For heating, the value of *k* was insolation-dependent (Fig. 3.2b, c).

Simulating lizard body temperatures at different altitudes and climate change scenarios:

Assuming that our copper models have similar thermal characteristics to those of a live lizard (Bakken & Gates, 1975; Dzialowski, 2005; Wilms *et al.*, 2011), we estimated the thermal profile of a basking lizard on a large horizontal rock. Our calculations took into account the azimuth and elevation of the sun, based on a series of photographs of the lizard models from many angles, estimating the effective surface of the model directly exposed to the sun. Three scenarios were used:

a) To simulate thermal conditions at the lower 1 700 m and 1 300 m a.s.l. sites, data from the temporary weather stations 2 m above ground at each site (Fig. 3.1) were extracted. Hourly temperature and insolation data for 1 600 m a.s.l. (up to 21˚C and 890 W/m^2) and 1 300 m a.s.l (up to 24˚C and 900 W/m^2) for a typical cloudless summer day (recorded simultaneously at each site), were included in the simulation to compare the thermal conditions present at the lower altitudinal sites to that of the high altitudinal site. Three insolation intensity scenarios were used with 0.5m.s-^{1} wind

- ○ 1 100 W/m^2 insolation at all three sites simulating the maximum insolation that could be encountered
- ○ 660 W/m^2 insolation at all three sites simulating the typical insolation intensities that could be encountered
- ○ 660 W/m^2 (1 900 m), 558 W/m^2 (1 700 m) and 510 W/m^2 (1 300 m) insolation simulating the effect of cloud cover often accumulating just beneath the peak of Mariepskop below 1 900 m a.s.l. Cloud cover decreases the intensity of solar insolation reaching the lower sites by 7 % at 1 600 m and 15% at 1 300 m a.s.l. (Calculated using mean insolation intensities recorded during summer at the three sites (Table 3.4)).

b) Temperatures and insolation data (up to 1150 W/m^2) for a typical cloudless summer day at 1 900 m a.s.l. obtained from the permanent automated meteorological station at this site. This represents the hottest extremes likely to be encountered by crag lizards.

c) Mean hourly temperature, insolation and wind values from a temporary weather station placed 2 m above ground in the core habitat of the crag lizards from December 2012 until March 2013 and representing the thermal environment during the summer (December, January, February), including cloudy conditions.

At 05h00 before sunrise the temperature of the model is at ambient. At 1-minute intervals, the ambient temperature and insolation data were used to predict the temperature of the model, given the position of the sun. The process was iterated for each minute of the day until 19h00 when the sun sets. During heating, the equilibrium temperature of the model was determined by wind, effective insolation and ambient temperature, measured in the laboratory (Fig. 3.2a). The difference between ambient temperature and the operative temperature (T_e) was always less than 2˚C, i.e. far inside the linear zone of easily-predictable increase in T_e, i.e. a scenario with heat exchange characteristics compatible with Newton's Law. When the predicted T_e of the model was higher than the predicted equilibrium temperature (Fig. 3.2a), then a cooling scenario was used with the predicted equilibrium operative value being used as the effective ambient temperature. For cooling, the cooling constant was independent of insolation but dependent on wind speed (Fig. 3.2b). For heating, the heating constant was dependent on both insolation and wind speed (Fig. 3.2c). A typical summer day at Mariepskop provides a total of 660 minutes of diurnal activity time (7am -6pm) for the lizard. The number of daily minutes with $T_e < T_{max}$ indicate the degree to which a lizard can be active outside of the shelter, foraging and mating (time where T_e exceeds T_{max} would be lost to thermoregulation). If the ambient temperature increases by a fixed amount (as with climate change, and assuming insolation and wind are not affected) one can estimate the degree to which the activity of a lizard is likely to be reduced. Using the simulations we calculated the percentage of diurnal activity time available ($T_e < 35$˚C) (assuming 11 h of total daily time available) at different altitudes to quantify the constraints of T_e on the altitudinal distribution of the species. Likely implications for future climate change scenarios (1 – 2 ˚C increase in temperature) were simulated in a similar way.

Results

Regional geographical distribution and mean annual temperature profile.

Crag lizards occur along the higher lying areas of the Drakensberg escarpment, southern Africa (Fig. 3.3a). The geographical distribution of outlier mean annual temperatures comprising 5% of the total QDS units were on the boundaries of the crag lizard geographical distributional range (Fig. 3.3a). The mean annual regional temperature range for this species (all QDS units, 5% outliers removed) was 12.29 - 19.05 with a mean of 15.68 ˚C (Fig. 3.3b), based on WorldClim.

Local altitudinal distribution and mean annual temperature profile:

The geographical distribution of the Drakensberg crag lizard was restricted to altitudes higher than 1 829 m, in the Northern Escarpment Afromontane Fynbos vegetation on top of Mariepskop (Fig. 3.1). The mean annual temperature at Mariepskop, based on the interpolation of WorldClim data, (14.1˚C) is well within the regional temperature range and near the mode of the distribution of regional mean annual temperatures (Fig. 3.3b).

Suitability and availability of shelter and prey at different altitudes:

Availability of suitable shelter: There were no significant differences in the heights or the depths of crevices between the three different altitudes (Table 3.2). In addition, a

Chi-square test indicated that there was no significant difference in the orientation of these crevices at the three altitudes ($X^2 = 2.69$; df = 6; $p > 0.05$).

Prey availability: The trapping data indicated that the percentage of Coleoptera in the samples at the three sites increased from 6 % in winter and 7 % in spring to 13 % in summer. The occurrence of Diptera increased from 1 % in winter and 5 % in spring to 19 % in summer. Millipedes comprised a total of 0.4 % in winter and 1 % in spring and summer. Formicidae (ants) decreased from 91 % in winter to 84 % in spring and 61 % in summer. Orthoptera increased from 1 % in winter to 3 % in spring and to 6 % in summer (Table 3.3). The Global *R* statistic revealed that between the three altitudes there was no significant difference in invertebrate community composition (Global $R_{altitude} = -0.095$, $p = 0.65$). Between seasons however, there was a significant difference (Global $R_{season} = 0.67$, $p = 0.01$). A NMDS visualisation indicated little dissimilarity between the sites for the three seasons (Fig. 3.4). Comparing season to altitude revealed dissimilarities (Fig. 3.4). For focal animal observations ants were the most frequent prey caught by the lizards with 23 % in spring and 38 % in summer. The selection of Diptera increased from 15 % in spring to 23 % in summer and Coleoptera increased from 4 % in spring to 23 % in summer.

Local temperature profiles based on automated weather station data and field recordings:

Climatic conditions: The 1 900 m site had lower minimum, maximum and mean temperatures than the two lower weather stations (Table 3.4). The results of the ANOVA taking into account temporal autocorrelation for temperature and insolation at the different altitudinal sites during winter, spring and summer all revealed a significant difference in ambient temperature (data from automated weather stations) between the altitudes (Table 3.4).

Temperature inside crevices: The 1 900 m site had lower mean temperatures inside the crevices than the lower altitudinal sites except during summer (Table 3.4). This site also had lower maximum and minimum temperatures compared to the lower altitudinal sites except for the minimum temperature recorded during summer. The temperatures recorded inside the crevices at the three altitudinal sites differed significantly (Mixed-effects ANOVA Table 3.4). The 1 900 m site had lower means and ranges of microhabitat ambient temperatures recorded at the crevices during each season than that at the lower altitudinal sites (Table 3.4). Mixed-effects ANOVA revealed a significant difference in the microhabitat temperatures (recorded at each crevice) between the three altitudinal zones during all three seasons (Table 3.4).

Operative temperature (T_e)*:* Mixed-effects ANOVA indicated that mean T_e at 1 600 and 1 300 m a.s.l were higher than at 1 900 m a.s.l. during both spring and summer (Table 3.4). However, maximum T_e at 1 900 m during summer was higher than the lower sites, explained by the presence of clouds. The clouds often accumulate just beneath the peak of the mountain, leaving the lower altitudinal zones covered and subjected to lower intensities of insolation. This does not occur every day as the mean T_e indicates (Table 3.4) Comparing the percentage of time $T_e > 35$ ˚C (T_{max}) for summer in four timeslots between sites, revealed that T_e was the highest at 1 300 m, second highest at 1 700 m and the lowest at 1 900 m a.s.l. (Fig. 3.5).

No feeding activity was recorded during winter (118 observation hours). Spring had the highest number of feeding attempts with 26 successful and 3 unsuccessful attempts, an 89.65 % success rate (116 observation hours). During summer the number of feeding attempts decreased to 13 successful captures and zero unsuccessful attempts providing a 100% success rate (114 observation hours). Feeding activity started between 8:30 – 9:30 am and reached a maximum between 9:30 – 11:30 am (Fig. 3.6a). Feeding activity was not recorded during the mid-day period and it commenced again after 13:30. No feeding activity was recorded after 15:30 (Fig. 3.6a). During winter lizards only emerged from their crevices between 8:30 - 9:30 (Fig. 3.6b). The maximum number of minutes spent sunbasking during winter was observed during the mid-day period (12:30 – 13:30) when the ambient temperature and insolation reached the daily maximum. T_e was not recorded during winter. During spring the lizards emerged earlier, from 7:30 am (Fig. 3.6c). The lizards spent less time sunbasking during mid-day in spring than during winter and increased the time spent sunbasking after the warmest mid-day period. The time spent sunbasking gradually decreased while T*e* increased and reached a minimum during the hottest part of the day. During summer the lizards were actively sunbasking before the start of the first observation hour (Fig. 3.6d). They spent the first four hours of the day sunbasking and then retreated into their crevices when T_e reached a maximum during the mid-day period, emerging from their crevices when the temperature decreased in the afternoon (Fig. 3.6d).

Laboratory measurements to simulate ambient temperature scenarios at Mariepskop:

Experimental design: Creating different scenarios in the laboratory experiments illustrated the effects of convection and conduction on heating and cooling of the model. Comparing cardboard no wind (1) with the other experiments revealed that ambient equilibrium temperature (T_a) was higher at each increasing insolation intensity (Fig. 3.2a). The insulation provided by the cardboard surface prevented heat conduction between the model and the rock while the absence of wind prevented increased heat loss via convection. Comparing this to the experiment on rock with no wind (2), T_a was lower (Fig. 3.2a). This is explained by the conductive heat transfer between the model and the rock surface. With 0.5m.s^{-1} wind on rock (3), T_a was lower than the previous scenarios (Fig. 3.2a), explained by conduction as well as convective heat loss due to the air movement across the models. Increasing the wind speed to 1m.s^{-1} further reduced T_a, again explained by conduction and convective heat loss (Fig. 3.2a). The scenario of lizard on rock with 0.5m.s^{-1} wind (3) was used in the simulation as it depicts a typical summer day at Mariepskop and takes into account the effect of conductive and convective heat loss the lizard would experience in the field (Fig. 3.8a, 3.9). Different insolation intensities were used in the simulation (1 100, 600, 558 and 510 W/m^2) to compare the effect of insolation on T_e for each of the scenarios (Fig. 3.8b).

Simulations at different altitudes:

High altitude: The ambient conditions at 1 900 m a.s.l. during a summer day (6am - 6pm) at the high altitude site is characterised by a mean insolation of 600 W/m^2, temperature 14 – ~19 ˚C and wind speed of 1.0 – 1.9 m.s^{-1} (Fig. 3.7, 3.8a). During these simulations, T_e was always within 0.2 ˚C of ambient, i.e. far within the linear zone of the logarithmic graphs allowing direct estimates of cooling or heating constants. The simulation indicated that T_e exceeded T_{max} between 9h30 - 15h30 allowing only 44.6 % of diurnal activity time of 11 h (Fig. 3.8a). Mornings had a higher percentage of diurnal activity time available ($T_e < T_{max}$) than afternoons (Fig. 3.8b). At 1 100 W/m^2 insolation, only 28.3 % of diurnal activity time ($T_e < T_{max}$) was available, a fraction of 0.3 less time than for 600 W/m^2 insolation (Fig. 3.8b). The lizards retreated to their crevices during the hottest mid-day timeslot when $T_e > T_{max}$ (Fig. 3.8b).

Mid-altitude: Simulating mean temperature data for a typical summer’s day at 1 700 m a.s.l. with 600 W/m^2 insolation indicated that T_e exceeded T_{max} between 09:00 and 16:30 with a 2.1˚C increase in mid-day temperature compared to 1 900 m a.s.l. (Fig. 3.8a). At 600 W/m^2 insolation, activity time was reduced by a fraction of 0.24, and when simulating with 1 100 W/m^2 insolation, it was reduced by a fraction of 0.3 compared to activity time available at 1 900 m a.s.l. (Fig. 3.8b). At 558 W/m^2 (representing the insolation intensity when cloud cover forms below the peak) a 0.10 reduction in the fraction of diurnal activity time available compared to 1 900 m a.s.l was calculated (Fig. 3.8b). More diurnal activity time was present during the mornings than afternoons (Fig. 3.8b).

Low altitude: Simulating mean temperature data for a typical summer’s day at 1 300 m a.s.l. with 600 W/m^2 insolation indicated that T_e exceeded T_{max} between 08:30 and 17:00 with a 4.7˚C increase in mid-day temperature compared to 1 900 m a.s.l. (Fig.

3.8a). At 600 W/m^2 insolation, diurnal activity time was reduced by a fraction of 0.54 of time available compared to 1 900 m a.s.l. and at 1 100 W/m^2 insolation, it was reduced by a fraction of 0.65 (Fig. 3.8b). At 510 W/m^2 (representing the insolation present at this site during cloudy conditions) a reduction in fraction of available diurnal activity time (0.4) compared to 1 900 m a.s.l (with 600W/m^2 insolation) was also apparent (Fig. 3.8b). Once again, more diurnal activity time was available in the mornings than afternoons (Fig. 3.8b).

Modeling for climate change scenarios at high altitude:

Ambient condition of 1 100 W/m^2 insolation and 0.5 m.s^{-1} wind allows for 28.3 % (where $T_e < T_{max}$) diurnal activity time (Fig. 3.9a). With a 1˚C increase in ambient temperature (T_a), T_e will exceeded T_{max} between 08:30 – 16:30 (Fig. 3.9a) resulting in reduction of a fraction of 0.01 in available activity time (Fig. 3.10). A 2˚C increase will lead to a larger reduction (0.19) in fraction of available activity time (Fig. 3.10). Ambient conditions of 600 W/m^2 insolation and 0.5m.s^{-1} wind allows for 44.6 % diurnal activity time. With 1˚C increase in ambient temperature (T_a), $T_e > T_{max}$ later in the morning (09:00 am) and decrease earlier in the afternoon (16:00) resulting in a reduction (0.09) of the fraction of available activity time available (Fig. 3.9b, 3.10). A 2˚C increase will reduce the activity time by a fraction of 0.17 (Fig. 3.10). Simulating conditions of 1m.s^{-1} wind at 1 100 W/m^2 insolation with a 1˚C increase, will cause a smaller reduction (0.07) in the fraction of time available below T_{max} (Fig. 3.10). With a 2˚C increase, crag lizards will lose a fraction of 0.14 of total diurnal activity time (Fig. 3.10). At 1m.s^{-1} wind and 600 W/m^2 insolation, a future 1˚C increase will have a

0.09 reduction in fraction of time available below T_{max} (Fig. 3.10). With a 2˚C increase, crag lizards will lose even more (0.17) total diurnal activity time (Fig. 3.10).

Discussion

Do the regional geographical distributions and temperature profiles relate to the local scale distribution at Mariepskop?

The local distribution of *P. melanotus* coincides with the regional geographical distribution as it prefers higher lying rocky habitats both locally and geographically (Fig. 3.3). The geographical temperature range was between 14 - 19˚C (Fig. 3.3b) and if local altitudinal distribution was solely based on geographical temperature ranges, crag lizards would have been able to occupy habitats from as low as 1 300 m asl. up to 1 900 m a.s.l. at Mariepskop. The coarse resolution of the grids (QDS) used to calculate the regional temperature ranges of species consisted of various microhabitats and microclimates whereas the mean temperature was more homogenous (Botts, *et al.* 2013). This explains why locally, narrower temperature ranges were present compared to the regional geographical temperature ranges. Therefore the regional geographical distribution and temperature range do not predict the local altitudinal distribution of crag lizards at Mariepskop. Other factors are responsible for shaping the distribution at Mariepskop.

What determines the altitudinal distribution of crag lizards at Mariepskop?

Crevice availability: The similarity in measurements and orientation (Table 3.2) between the crevices along the altitudinal gradient from 1300m to 1900 m infers that morphologically suitable refugia exist along most of the altitudinal gradient, albeit that the crevices were less abundant and spaced further apart at the lower altitudinal sites. Therefore, an absence of morphologically suitable shelter along the lower slopes is not the factor directly responsible for the limited altitudinal distribution of crag lizards at Mariepskop.

Prey availability: Altitudinal similarity in prey availability between the sites indicates the presence of suitable prey in sufficient abundance at the lower altitudes (Fig. 3.4). The difference in prey availability between seasons (Fig. 3.4) could be attributed to the phenology of invertebrates (Jamieson, *et al.* 2012). Therefore the absence of availability of suitable prey at the lower sites is not the factor directly limiting the distribution of crag lizards at Mariepskop.

Operative temperature: The increased frequency of T_e exceeding the upper thermal limit T_{max} (35 ˚C) at the lower altitudes (Fig. 3.5) infers that less diurnal activity time would be available for feeding and breeding activities. Simulating the climatic conditions at the three altitudinal sites (Fig. 3.8a) indicated that the fraction of daily activity time available where $T_e < T_{max}$ decreases with altitude (Fig. 3.8b). The typical climatic conditions of 600 W/m^2 insolation and 0.5m.s-^{1} wind indicated that with 0.24 reduction in fraction of activity time available at 1 700 m and 0.54 at 1 300 m a.s.l. (compared to time available at 1 900 m a.s.l.) the lizard would have to compromise essential activities such as feeding and breeding (Fig. 3.8b). Crag lizards are unlikely to function at the lower attitudinal sites due to the thermal constraints imposed by T_{max} (Fig. 3.8a, b). Other studies measuring operative temperatures of lizards agree that with higher temperatures; activity time of lizards decrease (McConnachie, 2006; Wilms *et al.*, 2011; Logan *et al.*, 2013).

To what degree is crag lizard activity shaped by ambient temperature?

Behavioural adjustments are a key component to successful thermoregulation, as changes in orientation, duration of exposure to the sun and activity highly influences body temperature of an ectotherm (Bauwens *et al.*, 1999; Ibargüengoytia *et al.*, 2008; McConnachie *et al.*, 2007; McConnachie *et al.*, 2009; Wilms *et al.*, 2011). Changing location by moving between shaded crevices and sun exposed areas and minimising activity during times of high temperature and insolation (Fig. 3.6d) allows the lizard to control duration and intensity of heat exposure (Adolph, 1990; McConnachie *et al.*, 2009; Fei *et al.*, 2012). The contrasting, unimodal diurnal activity behaviour during winter compared with summer (Fig. 3.6b, d) shows that temperature and insolation are critical factors bringing about behavioural thermoregulation (Adolph, 1990; McConnachie *et al.*, 2009). The higher means and ranges of temperatures recorded at the lower sites during each season for the weather stations, inside crevices and microhabitats (Table 3.4) confirm that the lower altitudinal sites are warmer habitats than present at 1 900 m a.s.l. 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 during the time when temperatures and insolation reached a maximum (Fig. 3.6c, d) to maintain body temperature at the optimum level for physiological processes (Carrasscal *et al.*, 1992; McConnachie, 2006; Kiefer *et al.*, 2007; Fei *et al.*, 2012). The higher temperatures at the lower altitudinal sites limits available diurnal activity time and therefore occupation by lizards appear to be prevented by the thermal unsuitability of the habitat (Ibargüengoytia *et al.*, 2008). In a study by Sinervo *et al.* (2010) on heliothermic *Sceloporus* lizards, operative temperatures were recorded at two extinct and two persistent habitats of *S. serrifer*. Quantifying the availability of activity time between the sites revealed that it was significantly decreased in the extinct habitat when compared to the persistent habitat (Sinervo *et al.*, 2010). The restraint of the lizard’s upper thermal limit reducing diurnal activity time is therefore the factor most likely to shape its limited altitudinal distribution at Mariepskop.

Could climate change affect the future of the Drakensberg Crag lizard at Mariepskop?

With the future 2 ˚C increase in mean annual temperature predicted for South Africa, the increased ambient temperature (T_a) should still fall within its mean regional temperature range and thermal limits for crag lizards (Fig. 3.3b). The simulation predicted ($600 W/m^2$ and $0.5 m.s^{-1}$ wind) that with a 1˚C increase, total diurnal activity time $< T_{max}$ would decrease by a fraction of 0.09, while with 2˚C increase, it will decrease by 0.17 (Fig. 3.10). This is a modest decrease in available activity time compared to the altitudinal effects discussed above.

Other potentially significant variables that we did not consider are the effect of future climate change on wind speed and effective insolation at the different altitudinal sites. The heating and cooling rates are dependent on insolation intensity and wind speed, higher wind speed increases heat loss due to convection (Fig. 3.2a) and lower equilibrium temperatures (T_a). With lower wind speed, T_a is higher. This will affect the time available below T_{max}, once again leading to changes in the diurnal activity time budget. The framework followed in this study allowed us to assess all of the information we collected in a mechanistic manner before predicting the potential impact of climate change on the species (Williams *et al.*, 2008). We predict that a future 2˚C increase will lead to a modest reduction in diurnal activity time. Therefore we assume that the future of the Drakensberg crag lizard at Mariepskop is theoretically secure with a 2˚C increase in ambient temperature.

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Table 3.1 The intercept and slope values used in the temperature simulation.

	CB no wind	**Rock no wind**	**Rock 0.5m.s^{-1}**	**Rock 1m.s^{-1}**
T_a – heating				
Intercept	8.400	6.150	4.050	1.30
Slope	0.053	0.039	0.023	0.025
***k* – heating**				
Intercept	0.203	0.198	0.190	0.163
Slope	0.00007966	0.00003548	0.00004373	0.00006833
***K* – cooling**				
Intercept	0.064	0.052	0.163	0.100

Table 3.2 Measurements (crevice height and depth) at each of 64 crevices at three altitudes, including the frequencies of their different aspects (North, East, South and West). Results indicate mean ± standard deviation (range). Last column indicates probability from a single classification ANOVA comparing the three altitudes (df=2,61).

Altitude	**1900 m**	**1700 m**	**1300 m**	**ANOVA**
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)	$p > 0.05$
Crevice depth (mm)	647±267 (280-1000)	584±276 (200-1000)	495±217 (240-1000)	$p > 0.05$
North	10	6	9	-
East	6	6	7	-
South	4	3	2	-
West	4	5	2	-

Table 3.3 Invertebrates trapped using pitfalls during each season at each altitude. Taxa we selected for analysis (published studies; our field observations on lizard feeding) are presented, not all taxa trapped.

Season	**Winter**			**Spring**			**Summer**		
Altitude	**1900**	**1700**	**1300**	**1900**	**1700**	**1300**	**1900**	**1700**	**1300**
COLEOPTERA									
Carabidae	0	8	1	2	1	1	2	19	20
Staphylinidae	2	1	0	3	4	0	6	0	0
Scarabaeidae	2	0	0	0	2	2	0	1	0
Elateridae	0	0	0	2	3	3	2	4	2
Tenebrionidae	2	4	3	0	0	3	1	4	3
Curculionidae	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									
Formicidae	132	144	198	63	246	253	127	113	125
ORTHOPTERA									
Anostostomatidae	2	2	0	4	1	2	9	6	4
Gryllidae	0	0	1	1	7	1	2	8	5
Acrididae	0	0	0	0	0	2	0	0	1
Pamphagidae	1	0	1	0	0	0	0	0	0

Table 3.4 The daily (6am -6pm) mean weather station air temperature, insolation, inside crevice temperature, microhabitat ambient temperature and operative temperatures (T_e) at each altitude for the three seasons. Results indicate mean ± standard deviation (range) and the ANOVA results for the three seasons taking into account temporal autocorrelation.

	Winter				**Spring**				**Summer**			
Altitude	**1900**	**1700**	**1300**	**Anova**	**1900**	**1700**	**1300**	**Anova**	**1900**	**1700**	**1300**	**Anova**
Weather station air temp	11.2±1.64 (5.6-17.2)	14.91±2.83 (7.8-22.8)	16.6±2.52 (9.3-24.8)	$F_{2,1254} = 255.87$ $p < 0.001$	13.00±1.82 (2.9-24.7)	18.11±2.32 (7.8-30.9)	15.94±2.26 (6.3-28.9)	$F_{2,1110} = 9.59$ $p < 0.001$	16.94±2.42 (9.9-21.5)	18.29±2.64 (13.0-34.0)	21.15±3.7 (5.5-43.3)	$F_{2,771} = 30.86$ $p < 0.001$
Insolation	245.91±205 (0-635.6)	275.30±212 (0-603.3)	268.88±195 (0-608.8)	$F_{2,1254} = 50.03$ $p < 0.001$	408.96±231 (0-988.0)	389.65±245 (2.8-967.4)	339.26±22 (2.7-839.6)	$F_{2,804} = 24.96$ $p < 0.001$	463.69±313 (21.2-1032.0)	324.89±266 (1.3-936.0)	391.98±298 (0-950.8)	$F_{2,492} = 96.99$ $p < 0.001$
Inside crevice temp	11.92±3.06 (7.1-20.4)	14.30±2.53 (9.6-22.3)	17.26±2.9 (11.8-24.8)	$F_{2,711} = 63.13$ $p < 0.001$	13.90±3.96 (7.7-25.3)	15.56±4.51 (9.3-30.8)	13.90±3.96 (7.7-25.3)	$F_{2,903} = 156.77$ $p < 0.001$	22.14±0.93 (20.2-25.5)	20.25±3.47 (14.1-32.3)	22.99±3.3 (15.8-36.5)	$F_{2,747} = 39.13$ $p < 0.001$
Micro-habitat ambient temp	10.03±2.98 (5.4-20.5)	12.17±4.20 (7.5-26.7)	14.81±3.8 (6.7-23.8)	$F_{2,456} = 17.07$ $p < 0.001$	13.01±5.87 (3.0-30.1)	14.33±5.03 (7.1-31.1)	17.42±5.68 (5.6-35.9)	$F_{2,894} = 33.47$ $p < 0.001$	17.28±4.43 (10.8-33.9)	18.52±5.49 (12.3-40.2)	21.45±5.06 (14.7-44.5)	$F_{2,783} = 9.58$ $p < 0.001$
Operative temp (T_e)	-	-	-	-	14.98±7.54 (4.3-41.8)	16.31±6.40 (7.0-36.3)	19.76±7.27 (8.9-47.9)	$F_{2,1053} = 5.02$ $p = 0.0068$	19.73±7.25 (11.2-50.2)	21.41±7.01 (13.1-46.4)	23.92±6.08 (15.2-45.0)	$F_{2,720} = 4.18$ $p = 0.0156$

Fig. 3.1 Topographical map of part of Mariepskop. The three altitudinal sites are marked as High (1 900 m), Mid (1 700 m) and Low (1 300 m) a.s.l. with the locations of the automated weather stations : ⚑

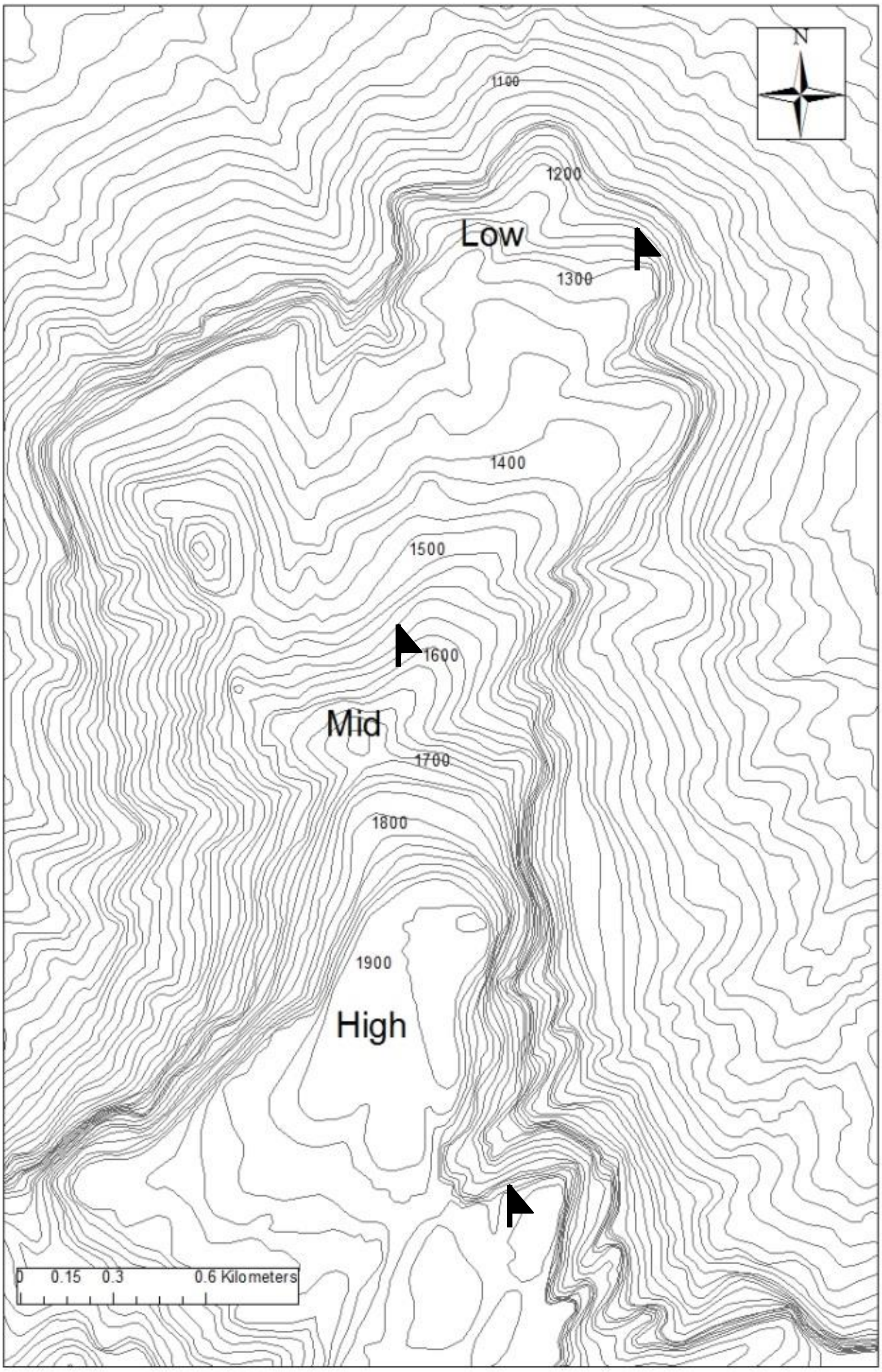


Fig. 3.2 (a) The ambient (equilibrium) temperature T$_a$ for each heating experiment at the different insolation values (CB = cardboard). The constant *k* for heating **(b)** and *K* for cooling **(c)** are plotted against the different insolation values.

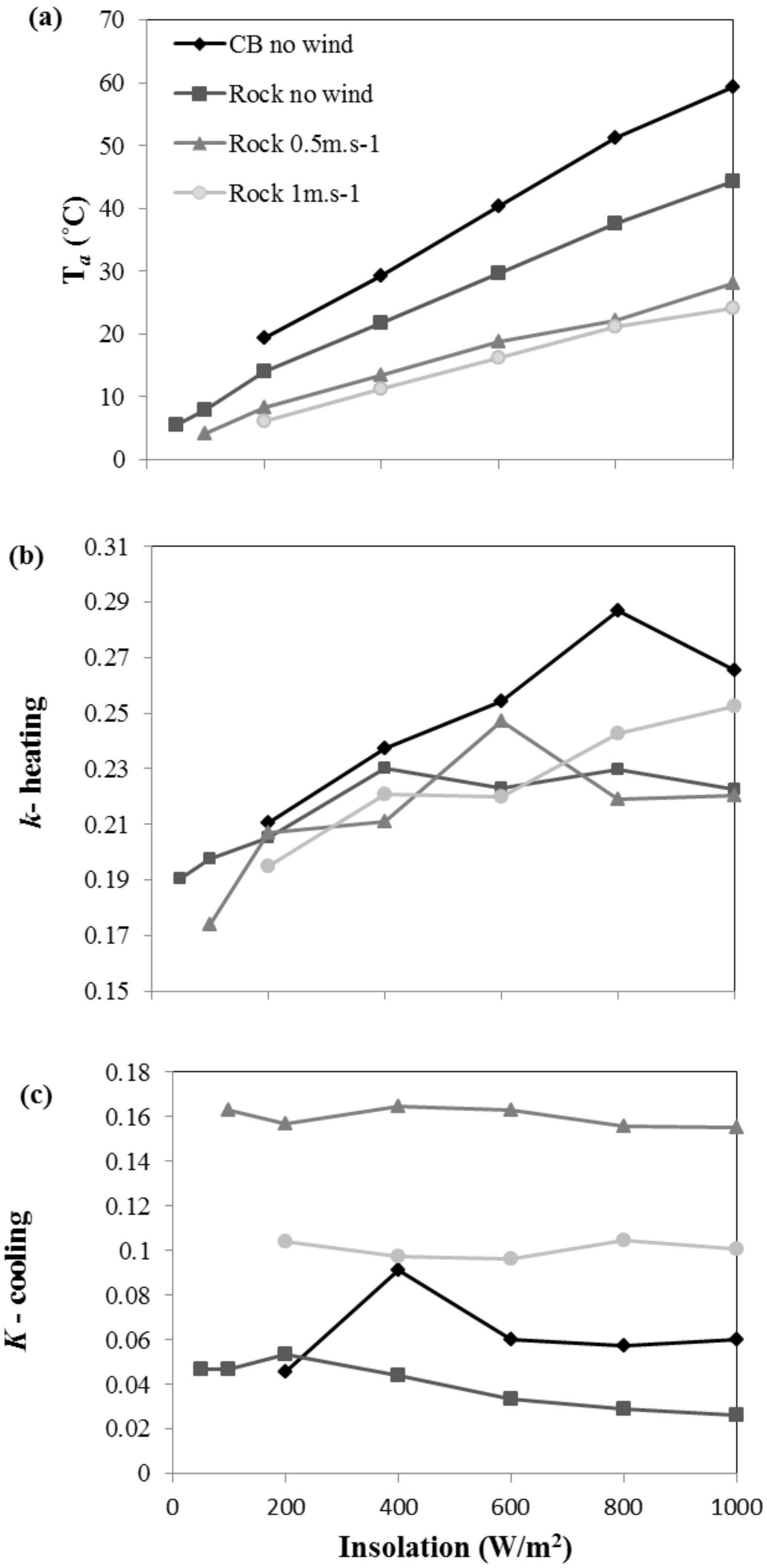


Fig. 3.3 (a) Map of geographical QDS distribution with outliers (5 % white blocks) accompanied by a histogram **(b)** indicating the regional temperature values that were removed (5 % removed grey blocks in histogram) and the mean annual temperature of local distribution (calculated from long term interpolated WorldClim data) at Mariepskop (Black bars on Histogram).

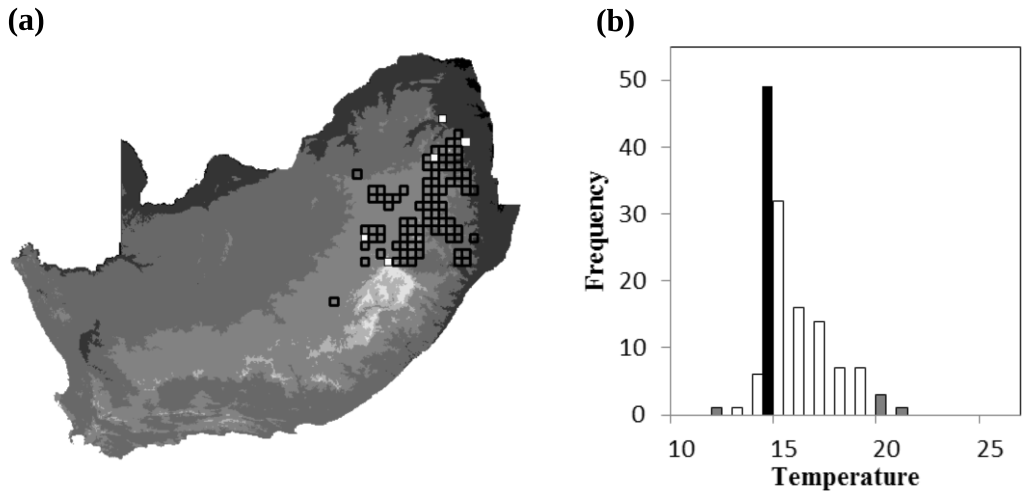


Fig. 3.4 NMDS plots (Square-root transformed Bray-Curtis dissimilarity; 10 repeats) indicating the relationship between invertebrates collected at different sample sites during winter, spring and summer and between season and altitude (H = high altitude, M = mid altitude, L = low altitude). (1 = winter, 2 = spring, 3 = summer).

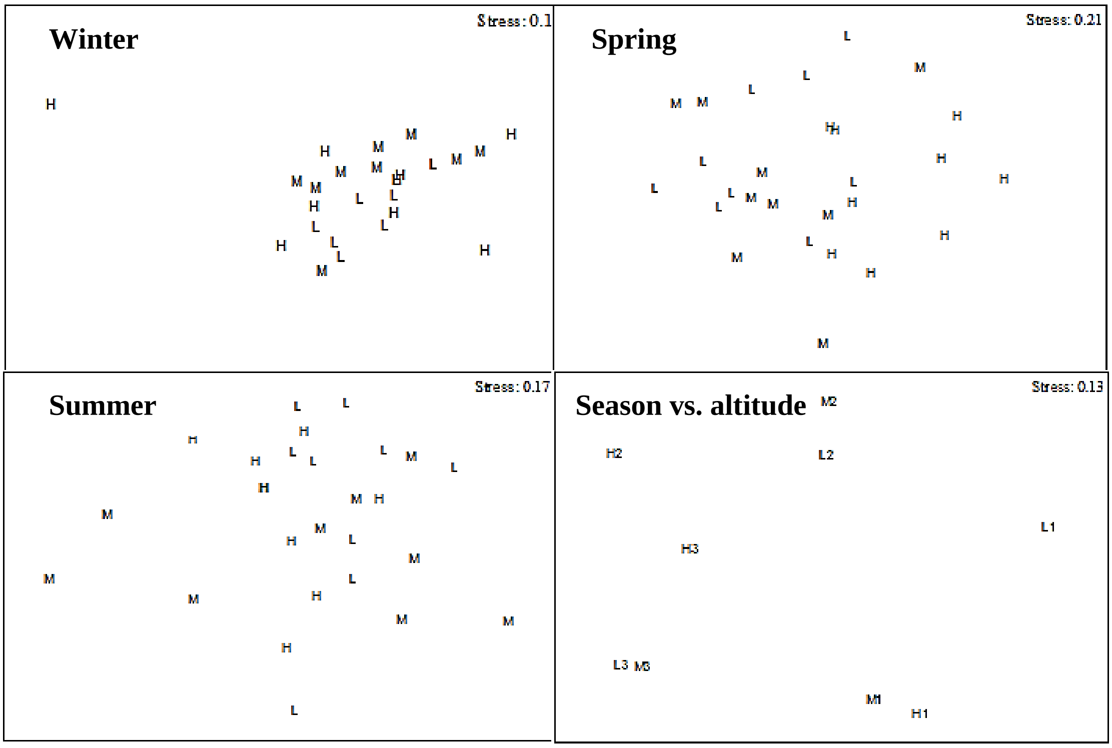


Fig. 3.5 The percentage of times T_e recorded in the field was > 35 ˚C in four activity timeslots during summer at the three altitudinal sites.

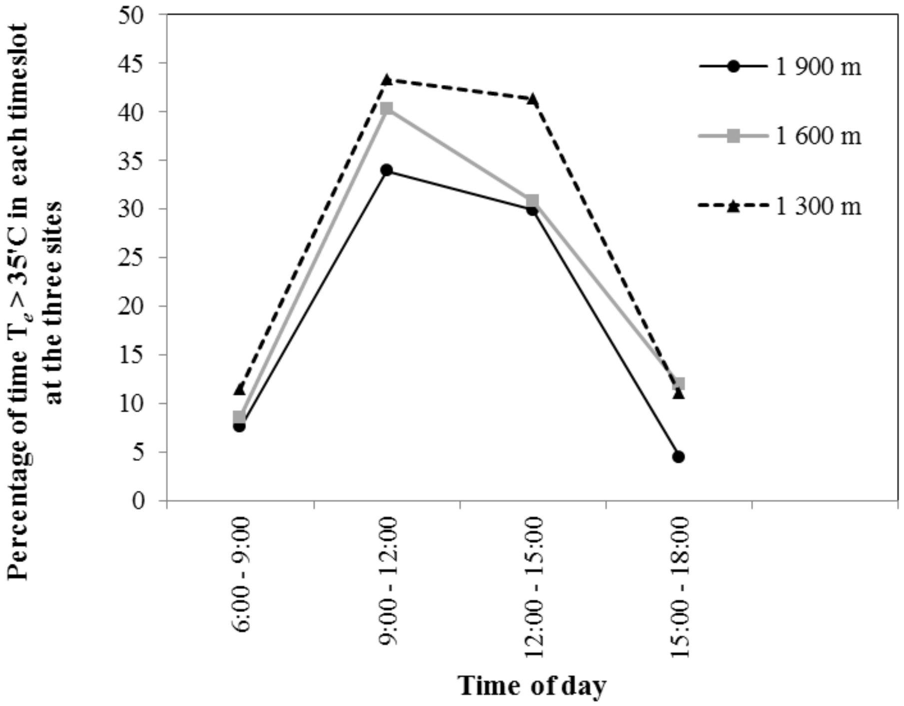


Fig. 3.6 (a) Foraging success of crag lizards within hourly periods during spring and summer. (**b): ** The mean number of minutes per hour spent sunbasking during winter compared to air temperature, inside crevice temperature (left Y-axis) and insolation (right Y-axis). **(c):** The mean number of minutes per hour spent sunbasking during spring compared to operative temperature (T_e), air temperature, inside crevice temperature, upper thermal limit (T_{max}) (left Y-axis) and insolation (right Y-axis). **(d):** The same layout as for spring, however representing summer**.**

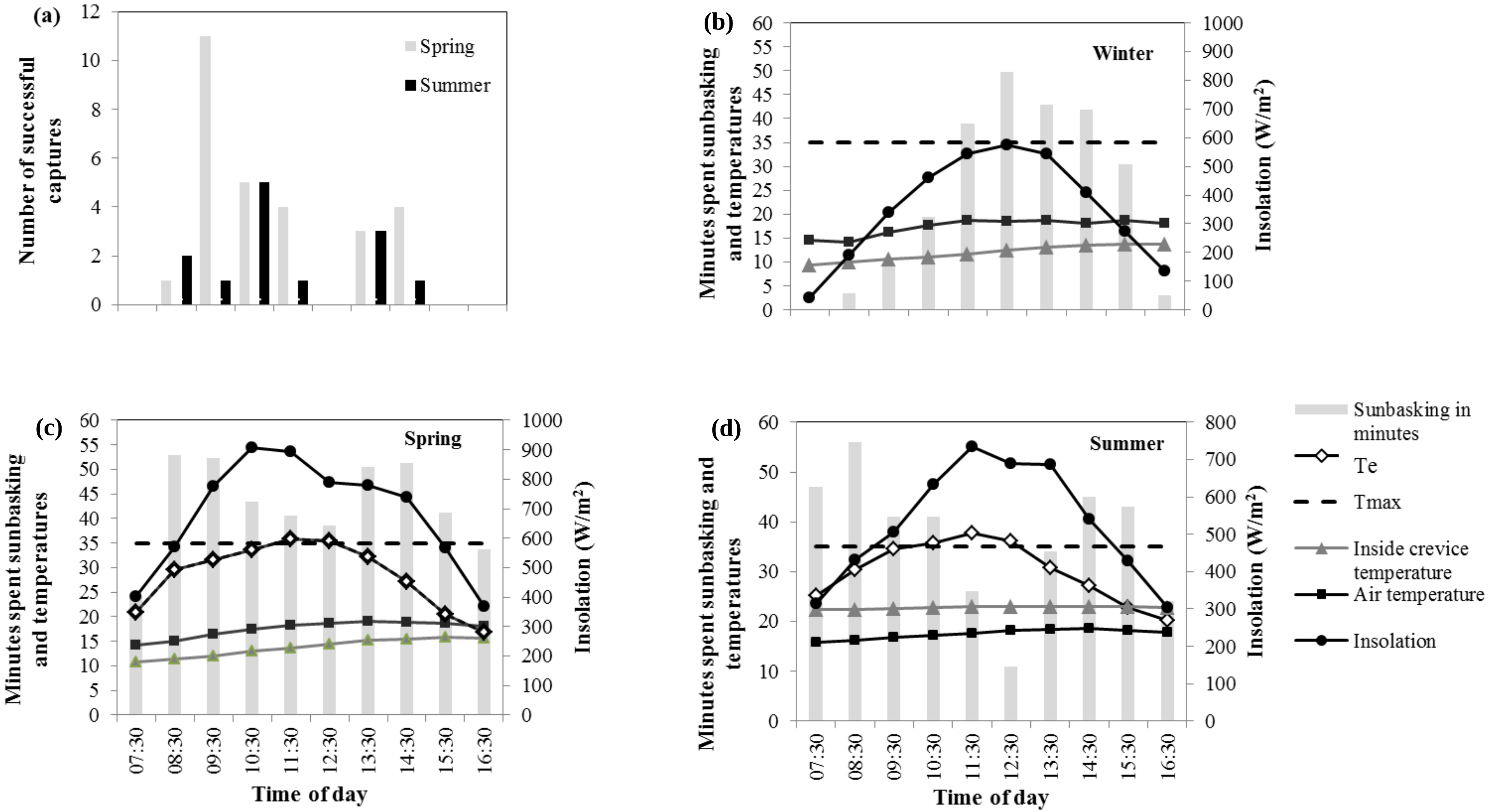


Fig. 3.7 (a) Mean hourly insolation (W/m^2), **(b)** temperature (˚C) and **(c)** wind speed (m.s^{-1}) for a typical summers day at Mariepskop, obtained from a temporary automated weather station 2m above ground within the area where crag lizards were common. These values were used in the temperature simulations. Range and standard deviation are included for **(a)** and **(b)**.

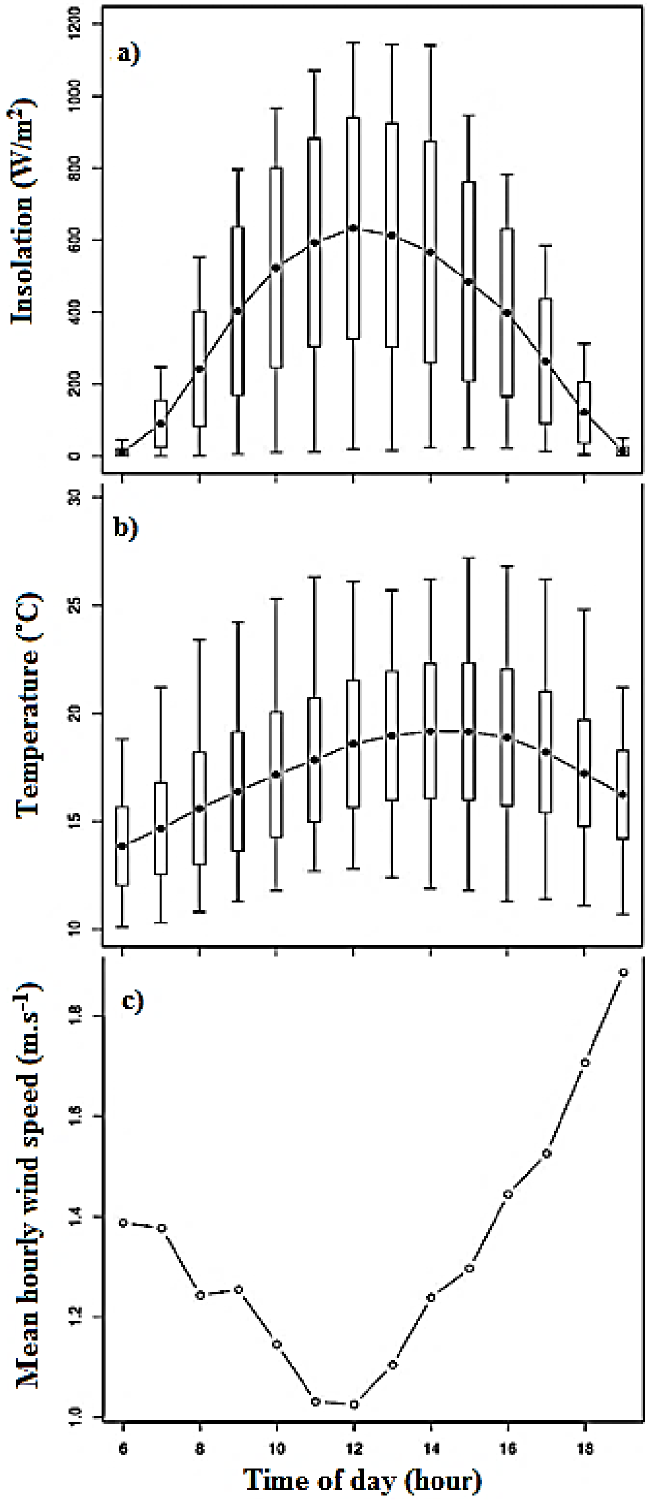


Fig. 3.8 (a) Temperature simulation for a typical summer day (rock with 0.5 m.s^{-1} wind, 600W/m^2) comparing T_e of lizard models between the three attitudinal sites, the mean number of minutes per hour spent sunbasking during summer at 1 900 m a.s.l and T_{max} (35˚C). **(b)** Comparing the percentage of time in minutes between7 am – 6 pm (total 660 min) where T is < 35˚C during morning and afternoon at each altitudinal site (rock with 0.5 m.s^{-1} wind) and different insolation intensities. The reduction in fraction of time T_e < 35˚C (compared to 1 900 m) is indicated above each bar for 1 700 m and 1 300 m sites.

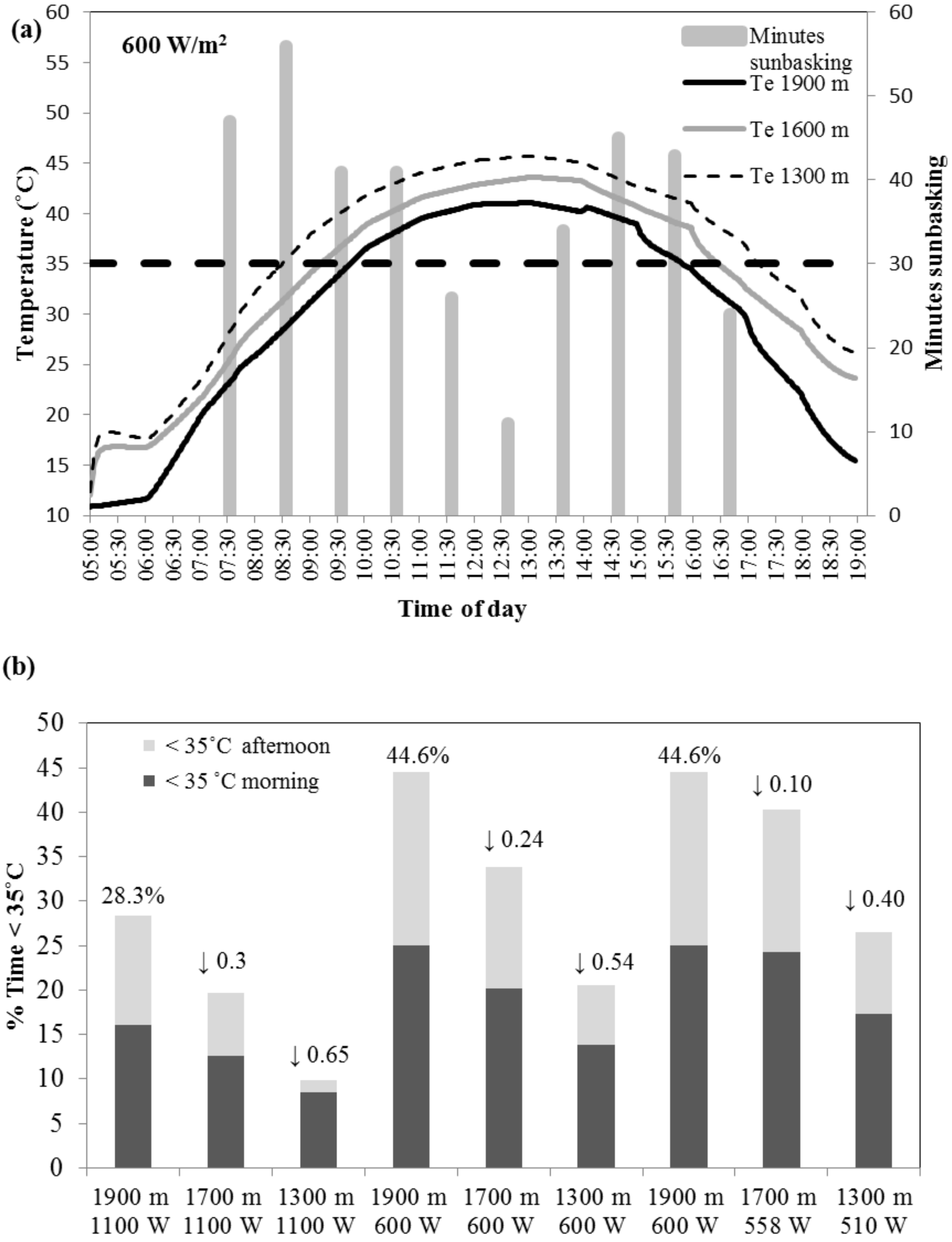


Fig. 3.9 (a) Simulating T$_e$ on rock at 1900 m a.s.l with 1100 W/m^2 insolation and at **(b):** 600 W/m^2 isolation with 0.5m.s^{-1} wind. Simulated future climate change scenario of 1 and 2˚C temperature increase are included along with ambient temperature and T$_{max}$ (upper thermal limit = 35˚C). Diurnal activity during field observations, represented in minutes spent sunbasking per hourly observation, is included (right Y-axis).

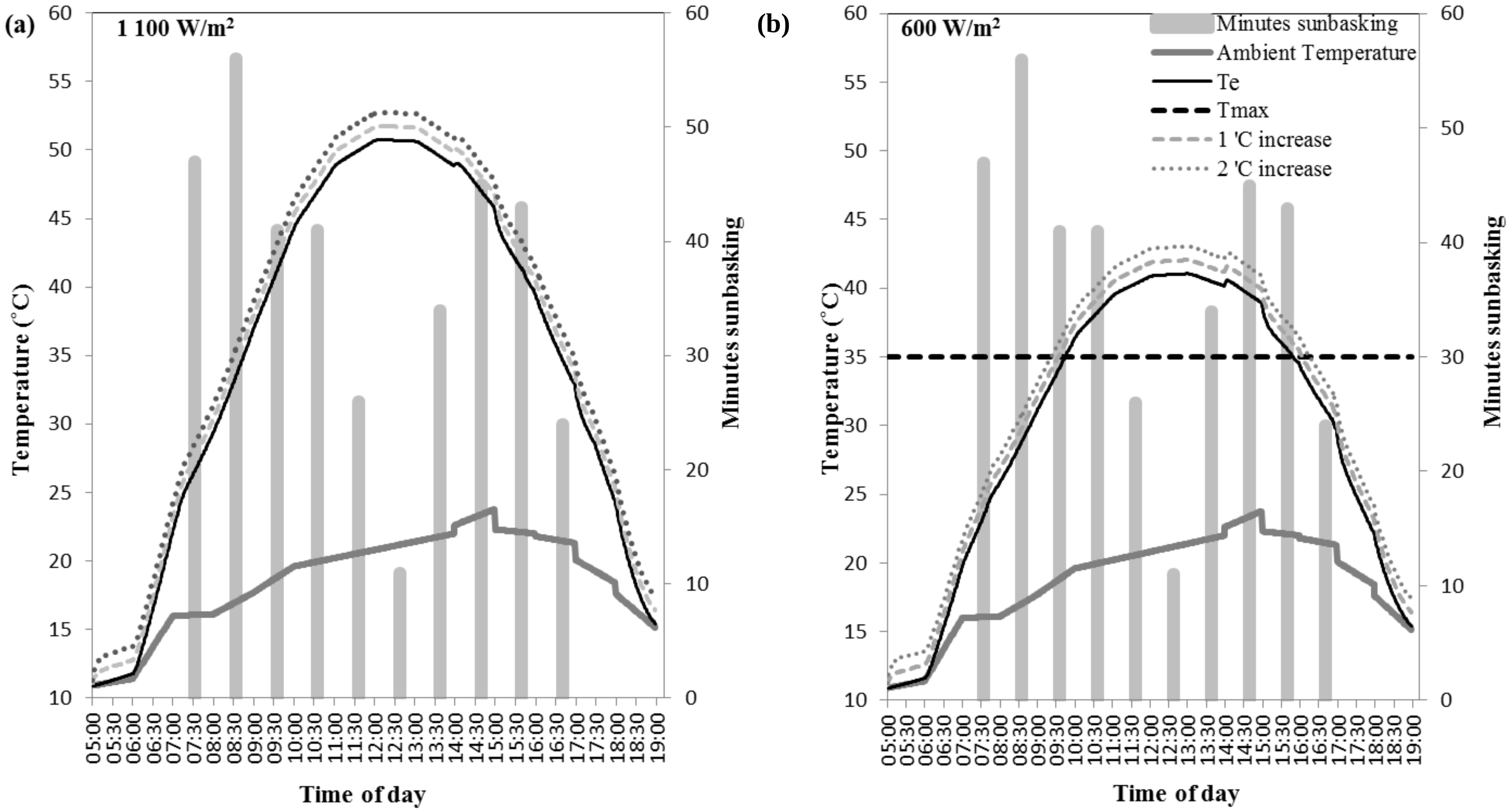
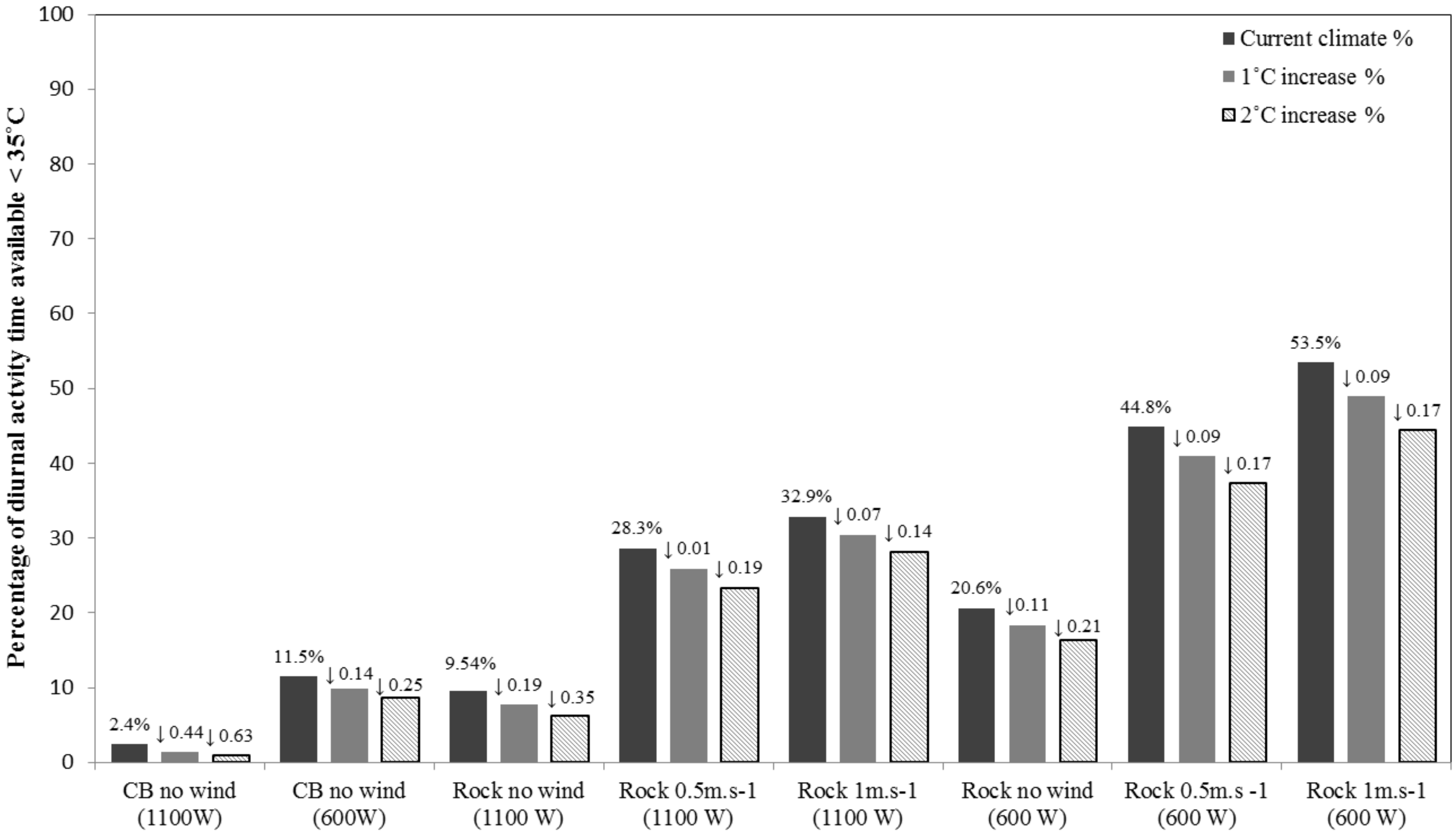


Fig. 3.10 Comparing the diurnal activity time (minutes) available where $T_e < 35$˚C for the different experimental designs with the total time (660 minutes) indicated how much diurnal activity time is actually available at current, 1˚C and 2˚C future temperature increases. The reduction in fraction of activity time (minutes) $< T_{max}$ between current and future scenarios indicated on top of each bar for 1 and 2˚C increases.



Chapter 4

General conclusion

Synthesis

Most studies only use ambient temperature data recorded with weather stations globally (Logan *et al.*, 2013) to predict the impact of climate change on species. Uncertainty and inconsistency in future climate projections regarding temperature and precipitation changes complicates the prediction process (Loarie *et al.*, 2009; Monasterio, 2013). Furthermore, predictions generally focus on the direct effects on increased ambient temperature, not considering the indirect effects such as shifts in phenology, behaviour and interspecific competition of species (Thomas *et al.*, 2004; Thuiller, 2007; Buckley, 2013). The framework proposed by Williams *et al.* (2008) takes this into consideration when assessing the vulnerability of species to climate change. This mechanistic approach is a great framework of how to approach climate change studies (Kearney & Porter, 2004; Kearney & Porter, 2009; Williams, *et al.* 2008). An example to better understand the potential impact of climate change on vertebrates is quantifying habitat suitability within vegetation zones. This is especially significant for montane species (Huang *et al.*, 2014) as they reside at the extremes of the altitudinal gradient.

Fortunately, the trend in global climate change forecasting has started to adapt to include these indirect factors (Kearney & Porter, 2004; Williams, *et al.* 2008; Kearney & Porter, 2009; Scheiter & Higgins, 2009; Buckley, 2013; Logan *et al.*, 2013). Our study included indirect factors such as changes in vegetation zones and availability of habitat requirements along the altitudinal gradient (Chapter 2). Since the interaction between ectotherms and the environment is a multidimensional physical relationship including three modes of heat exchange namely, convection, conduction and radiation (Bakken & Gates, 1975, Logan *et al.*, 2013), we included operative temperature measurements in our study for *Pseudocordylus m. melanotus* (Chapter 3).

The study revealed five findings: 1) Geographical distribution temperature ranges of vertebrates do not reliably predict local altitudinal distribution. 2) Altitudinal distribution ranges of species are largely shaped by suitable habitat. 3) The effect of climate change is a dynamic process and predictions cannot be made solely on simple ambient temperature increases. 4) The upper thermal limit of *Pseudocordylus melanotus melanotus* is the factor most likely restricting its altitudinal distribution. 5) Three species at Mariepskop are likely to be negatively impacted by future climate change.

Although the altitudinal distribution of vertebrates at Mariepskop presented only a fraction of their regional geographical distribution ranges, certain species showed clear restricted altitudinal ranges locally (Chapter 2). Mariepskop Mountain has clear transitions in vegetation zones. Quantifying altitudinal distribution of vertebrates within these zones allowed creating a reference to monitor future changes in species distributional ranges, taking into effect fixed and mobile habitat requirements. The future of three vertebrate species Lazy cisticola *C. aberrans*, Natal cascade frog *H. natalensis* and Chorister robin-chat *C. dichroa* are likely to be strongly negatively affected by climate change (Chapter 2) not because of temperature change in itself, but because of the potential for large scale changes in their habitat. These species rely on fixed habitat requirements and are restricted to immobile vegetation zones unlikely to move upslope with climate change.

Quantifying daily activity time available for crag lizards based on the restrictions provided by the upper thermal limit (T_{max}) between altitudes revealed that the lower sites provided less daily activity time (Chapter 3). The lower altitudinal sites have sufficient prey availability and suitable shelter and therefore we concluded that the lizard is restricted to the highest sites due to the reduced activity-time budget present at the lower sites. Using this information we predicted the effects of future temperature increases on the success of this species at Mariepskop. A fairly modest reduction in diurnal activity time was the result with no strong evidence that this species is likely to be catastrophically affected by a rise in ambient temperature of up to 2 ºC. This is contrasting to some of the predictions of other authors (Bickford *et al.*, 2010; Sinervo *et al.*, 2010) that forecast catastrophic effects of increased temperature on reptile survival. We are unable to rule out the possibility that earlier activity times (mornings could become warmer, earlier in the day) for the species could possibly counteract the activity time lost during the midday. The above results allow us to conclude that the prediction of the vulnerability of vertebrate taxa to climate change is much more complex than could be predicted on the basis of temperature change alone. In order to predict the effects of climate change one needs an intimate knowledge of the ecology and habitat preference of each of the species being considered.

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Ethical clearance

The University of Pretoria Animal Ethics Committee had no ethical concerns with this study (EC038-16).