

**Living on the Edge: Physiological and Behavioural Plasticity of African
Antelopes along a Climatic Gradient**

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**Living on the Edge: Physiological and Behavioural Plasticity of African
Antelopes along a Climatic Gradient**

Anil Kumar Shrestha

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Chapter 1

General Introduction

Anil Kumar Shrestha

“A lack of behavioural and physiological insight is the primary impediment to the successful prediction of the ecological effects of climatic change (modified from Piersma, T. and van Gils, J. A. 2010)”. Therefore, the role of phenotypic plasticity of behaviour and physiology in allowing populations to track changing environmental condition warrants further investigation.

General Introduction

Climate change, habitat loss and fragmentation are the primary threats to biodiversity conservation in the world (Opdam & Wascher 2004; Joubert & Bijlsma 2010; Mantyka-pringle et al. 2011). Over the next 50-100 years, not only the mean global temperature is predicted to increase further by 2-7°C but erratic rainfall, drought, flooding and other extreme climatic events are also predicted to increase (IPCC 2007). Likewise, anthropogenic habitat loss and fragmentation has been reported to increase at an alarming rate all over the world. Therefore, it is most likely that the synergetic effect of climate change, habitat loss and fragmentation may pose a greater threat to species survival and fitness than climate change or habitat loss and fragmentation by itself (Mantyka-pringle et al. 2011). Indeed, species in fragmented habitats are suggested to more vulnerable to climatic change than those in unfragmented habitat (Travis 2003; Opdam & Wascher 2004). Both changing climate and habitat loss and fragmentation individually or synergistically force species to live in sub-optimal condition in terms of climate and resource and therefore, pose threat to their survival and fitness. Consequently, a very crucial issue in the 21st century for biodiversity conservation is to understand the response of species to these changes more in particular if the ability of species to adapt can keep pace with a rapid changing environment.

To persist in a rapidly changing environment, species show adaptive responses, either by microevolution over a few generations or by employing phenotypic plasticity of behaviour, physiology and morphology within their life span (Gienapp et al. 2007; Visser 2008; Fuller et

al. 2010). Species with shorter generation times are expected to evolve faster than the species with longer generation times (Gienapp et al. 2008). Therefore, for long-lived endothermic species with longer generation times, phenotypic plasticity may be the most likely response to adapt to a changing environment (Hofmann & Todgham 2009; Fuller et al. 2010). Phenotypic plasticity of behaviour and physiology are expected to enable species to track their suitable climatic envelope or enable them to tolerate the changing environment (Feder 2010; Huey & Tewksbury 2009; Berg et al. 2010). Since behavioural and physiological plasticity is the ability of a single genotype to express different phenotypes in different environmental conditions (Schlichting & Smith 2002), populations of a conspecifics or range of species should demonstrate distinct behavioural and physiological response across various temporal and spatial scales (Komers 1997). Understanding behavioural and physiological traits within and between species along temporal and spatial scales will enhance our knowledge on the adaptive capacity of a species and therefore is essential to comprehend the ecological impact of changing environment on animal populations.

The adaptive capacity and, therefore, the sensitivity of a species for a changing environmental condition might vary depending on species characteristics and traits such as body size (small vs. large), niche width (specialist vs. generalist) and feeding type (grazer vs. browser). For example, it has been suggested that the larger species will become more sensitive to increased temperature than the smaller species because dissipating body heat become more problematic to larger individuals due to their lower surface area to volume ratio (Phillips & Heath 1995). Therefore, it is expected that becoming smaller could be a universal response to the warming climate (Sheridan & Bickford 2011; Gardner et al. 2011). Likewise, temperature specialist species because of their specialized thermal niche are expected to suffer more than the temperature generalist due to climate change and therefore, the specialists have higher risk of extinction (Huey & Kingsolver 1993). Despite the fact that these characteristics and traits of species might have implications for the persistence of

species, yet to date, only a few studies have been carried out, specially long-lived endotherms in their natural habitat (Fuller et al. 2010).

To adapt in a rapidly changing environments, species are expanding their range by shifting their distribution (longitude and altitude) to track their climatic envelope (Parmesan & Yohe 2003). While expanding their range now and in the future, many species are expected to live at or near their range margin, which might not be only sub-optimal in terms of resource and climate but these species will also expose to unknown biotic interactions (Feder 2010). Likewise, populations of species living at or near their range margin are expected to be more physiologically stressed than the populations living at or near the centre of their distribution because habitats at the range margins are considered to be sub-optimal in terms of resources and climate (Parsons 1991; Spicer & Gaston 1999; Gaston et al. 2009; Busch et al. 2011). Hence, understanding behaviour and physiology of populations of species living at or near the range margin at present will enhance our knowledge on the adaptive capacity of species in relation to environmental changes in the future.

For endothermic homeotherms such as antelopes, maintaining a narrow range of body temperatures is of utmost important for their optimal performance, survival and fitness (McNab 2002a; Angilletta 2009). When these species are exposed to sub-optimal environmental conditions (climate and resources), behavioural mechanisms such as adjustment in activity pattern, microhabitat selection and adjustment in home range size are considered to be the first line of defense in maintaining homeothermy (Bartholomew 1964; Willmer et al. 2005; Romeo et al. 2010; Coleman & Downs 2010). This is because behavioural adjustment is the most efficient response as it requires lower energetic demands and can be sustained longer than the physiological response to maintain homeothermy (Cabanac 1996; Maloney et al. 2005). Furthermore, behavioural adjustment also involves

reversible adaptive responses distributed along a continuum as a function of variation in the environment (Westerberhard 1989).

However, where behavioural responses are inadequate to cope with inhospitable environments, animals also employ physiological mechanisms such as adjustments in body temperature and metabolic rate, sweating, tachypnea (rapid breathing), shivering and non-shivering thermogenesis, and adjustments in circulatory convection (Schmidt-Nielsen 1997). Animals may employ these physiological mechanisms independently or in combination with behaviour. However, these autonomic responses can be costly for homoeothermic animals. For example, additional water for evaporative cooling or additional energy for elevated heat production is required (Willmer et al. 2005) and these may be scarce or difficult to access.

Understanding phenotypic responses of behaviour and physiology of long-lived animals to daily and seasonal variation of climate and resources may provide the first principles which we can use to predict the adaptive capacity of a species. However, it is likely that such studies do not necessarily characterize the climate change scenario in the future. Therefore, understanding the phenotypic response of species to extreme events of the current climate which will be a common feature in future (Rahmstorf & Coumou 2011), may characterize the future climate change and hence contributes to understand the effect of climate change. Most importantly, understanding patterns of phenotypic diversity of behaviour and physiology among a range of species in response to spatio-temporal variation in climate and habitats will likely provide a new or lack of phenotypic responses of species to changing environmental conditions. Therefore, studies on phenotypic differentiation within and between species give insight in the adaptive capacity and sensitivity of species to changing environmental condition.

Within this framework (Fig. 1), this thesis focuses on the first study of phenotypic plasticity of behaviour and physiology across various spatio-temporal scales of three species of

antelopes occurring in two climatically contrasting environments in the northern and southern part of South Africa. We selected South Africa and African antelopes because the biodiversity of South Africa is experiencing great threats due to rapid loss and fragmentation of habitat and a significant drying and warming trend in the last few decades which is predicted to increase even further in future (Erasmus et al. 2002; IPCC 2007). In South Africa, going from the South to North of the tropic of Capricorn, the climate becomes less seasonal with hot summers and mild winters (O'Connor & Kiker 2004; Mucina & Rutherford 2006) whereas the more southern part, at higher altitudes the climate is more seasonal with long and cold winters during which ambient temperatures frequently drop below zero and with occasional snow in the mountains (Mucina & Rutherford 2006; Lindsay et al. 2009). Such climatic variation along with the diverse topographic and soil conditions result range of vegetation types in South Africa. In the northern part of South Africa, savanna and *Mopane* vegetation are dominant whereas in the South in the Eastern Cape region, thickets and Karoo vegetation are the major vegetation types (Mucina & Rutherford 2006). This South African scenario provides a range of climatic gradients (hot vs. cold) and habitats (Mopane vs. Karoo) which offer an excellent situation to compare ranges of behavioural and physiological responses within and between species along spatial-temporal gradients to understand adaptive capacity of African antelopes to changing environmental condition. This is because tropical species are suggested to be already at or near their maximum thermal tolerance limits, therefore, they may be more vulnerable to increasing temperature (Tewksbury et al. 2008). But on the other hand, these tropical species are sensitive to cold stress because of their higher lower critical temperature, narrow zone of thermo-neutrality and thinner pelage compare to their arctic and temperate counter parts (Scholander 1955; Taylor & Lyman 1967; Hofmeyr 1981).

I selected Mapungubwe National Park, situated in the north of South Africa, with a hot and less seasonal climate (taken as 'core habitat') and Asante Sana Game Reserve situated in the

‘elevated’ southern part of South Africa with a more seasonal climate (taken as ‘edge habitat’). I selected three antelope species which differ in their body size and are also of two feeding types, namely eland *Taurotragus oryx* (~ 420 kg; mixed feeder), blue wildebeest *Connochaetes taurinus* (~ 180 kg; grazer) and impala *Aepycerus melampus* (~ 50 kg; mixed feeder).

With an aim to understand the behavioural plasticity of these different species of antelope, in Chapter 2, I investigate the influence of heat stress on the diurnal activity pattern across seasons, and extreme climatic condition as indicated by the 10 hottest days. Animals, when exposed to inhospitable environment, not only adjust their activity patterns but also select optimal habitats to maintain thermal balance. Therefore, in Chapter 3, I investigate the daily and seasonal selection of microhabitats based on altitude and microclimate of the eland in the Southern, more cooler, site. It will provide a better understanding of how antelopes in the range margin use topography and microhabitats as thermal refuge, a prominent behavioural mechanism to cope with climatic stress. In Chapter 4, I investigate the variation in seasonal home range size of the three species of antelope in the two climatically contrasting areas. In this comparative study I ask if the home range size of antelopes are larger in resource-poor seasons such as winter (cold, dry season) and spring (hot, dry season) than in the resource-rich summer (hot, wet season) within a study area (and thus I test the so-called ‘habitat productivity hypothesis’). Then, I investigate if the home range size of antelopes from populations at the edge of their distribution (Asante Sana with long, cold winters) will be larger than the home range size of their conspecifics within their core distribution range (Mapungubwe with short, mild winters) (the ‘core vs. edge hypothesis’). In Chapter 5, to understand physiological plasticity within a spatio-temporal context, I compare intraspecific variation of body temperature, as measured by amplitude, of the three species in the two climatically contrasting areas (the core vs. edge habitat). Further, this chapter also focusses on factors influencing variation in body temperature. Finally, in Chapter 6, I synthesize the

conclusion that can be drawn from the preceding chapters and discuss how animals in the past used phenotypic plasticity of behaviour to cope with a changing climate, which may have implication to understand how important is behaviour to cope with changing climate, habitat loss and fragmentation at present. Further, based on my findings of the adaptive capacity of behaviour and physiology of the studied antelopes, I extend the discussion by focussing on the implication of a certain feeding type (grazer or mixed feeder/browser) when condition change.

To record behavioural and physiological traits across spatial and temporal scale, I used GPS collars with mini-black globe temperature measuring devices, and telemetric activity and body temperature data loggers, which enable me to monitor behaviour and physiology of antelopes for nine months in their natural habitat without disturbing them. Studies of antelopes in their natural habitat for longer period of time are crucial to investigate adaptive capacity of antelopes in relation to climate change (Fuller et al. 2010; Boyles et al. 2011). To record environmental conditions of study areas, I installed portable weather station at respective sites which records ambient temperature, black globe temperature and mini-globe temperature. All experimental procedures were approved by the Animal Ethics Screening Committee of the University of the Witwatersrand (protocol no. 2007/60/4) and South African National Parks.

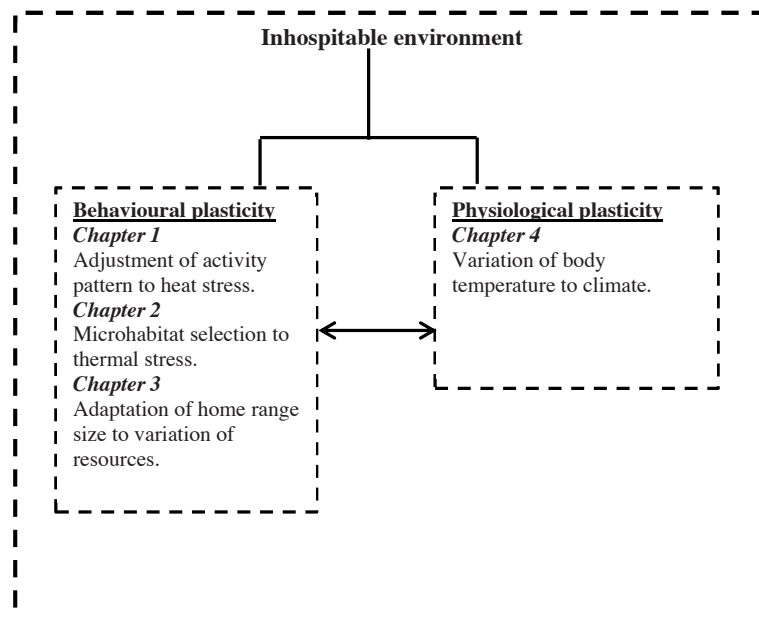


Figure 1. Conceptual framework of this thesis to study adaptation of animals exposed to inhospitable environment.

Chapter 2

Larger antelopes suffer more from heat
stress than smaller antelope in African
semi-arid environment

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Abstract

Heat stress can limit activity time budget of ungulates due to hyperthermia, which is relevant for African antelopes in ecosystems where temperature routinely increases above 40°C. Body size influences this thermal sensitivity as large bodied ungulates have a lower surface area to volume ratio than smaller ungulates, and therefore a reduced heat dissipation capacity. We tested if the diurnal activity of three antelope species of different body size, eland, blue wildebeest and impala, is negatively correlated with black globe temperature (BGT) during the hottest days and seasons in a South African semi-arid ecosystem. Furthermore, we tested whether larger bodied eland and wildebeest are less active than smaller impala during the hottest days and seasons. Our results show that indeed BGT was negatively correlated with the diurnal activity of eland, wildebeest and impala, particularly during summer. During spring, only the larger bodied eland and wildebeest were negatively influenced by BGT, but not the smallest impala. We argue that spring with its high heat stress, coupled with poor forage and water availability, could be critical for survival of these large African antelopes. Our study contributes to understanding how endothermic animals can cope with extreme climatic conditions, which are expected to occur more frequently due to climate change.

Key words: activity pattern, body size, heat stress, diurnal, nocturnal, thermoregulation

Introduction

A timely organization of the daily and seasonal activity pattern by ungulates is important for the optimization of their energy balance, especially in a dynamic environment with varying levels of stress and resource availability (Dunbar et al. 2009). Although biotic factors such as predation and resource availability are known to affect the activity time budget of ungulates (Lima & Dill 1990; Lima & Zollner 1996; Brown 1999), the combination of air temperature, solar radiation, wind speed, and relative humidity also have an impact because ungulates as endotherms have very confined thermal niches that influence their fitness (Porter & Kearney 2009). More extreme ambient conditions such as a combination of high air temperature, high solar radiation levels, low wind speed and high vapour pressure beyond the thermal limits of an ungulate pose a threat because dissipation of heat becomes more difficult (Schmidt-Nielsen 1975; Owen-Smith 1998; Speakman & Król 2010). Alternatively, conditions such as a combination of freezing temperature, snow and high wind speed enhance heat loss of ungulates. These adverse stresses of hot and cold environments limit the ungulate's activity time budget by an increasing risk of hyperthermia or hypothermia and pose a threat to its survival.

To cope with inhospitable environments of hot or cold conditions, behavioural thermoregulation, e.g., adjustments in the activity time budget, is considered to be the first line of defence by animals (Bartholomew 1964; Willmer et al. 2005) because it requires low energetic demands, which can be sustained longer than the energetically expensive autonomic responses (Cabanac 1996; Maloney et al. 2005).

Body size and shape of ungulates also have implications for the susceptibility to thermal stress due to the surface area to volume ratio (Porter & Kearney 2009). Indeed, smaller ungulates have a greater surface area to volume ratio than large bodied ungulates, and therefore higher rates of thermal conductance and lower thermal inertia (Calder 1984;

Schmidt-Nielsen 1984; Peters 1986; Haim & Skinner 1991). It is thus thought that under mild ambient temperatures, smaller ungulates can dissipate and gain heat relatively quickly. However, when ambient temperature is higher or lower than their body temperature, these smaller ungulates can quickly reach their limits of thermal tolerance. The smaller surface area to volume ratio of large ungulates reduces the rate of heat dissipation to the environment, which is disadvantageous in hot weather but may be beneficial in a cold climate (Bradley & Deavers 1980; Phillips & Heath 1995; McNab 2002b).

Many studies on the activity time budget of ungulates only focus on the energy acquisition capacity without considering the capacity to dissipate energy. According to the heat dissipation limitation hypothesis, the capacity to dissipate energy could be more important for the survival of most of the large endothermic animals than energy acquisition (Speakman & Król 2010). Understanding heat stress and thermoregulatory behaviour could be particularly relevant for African antelopes which inhabit arid and semi-arid ecosystems where ambient temperature routinely increases above 40°C (Kinahan et al. 2007). These antelopes are expected to adjust their activity budget according to daily and seasonal fluctuations in ambient conditions. Though many aspects of that behaviour are well studied, only a handful of studies include heat stress and thermoregulatory aspects (Owen-Smith 1998; Maloney et al. 2005). At the present context of climate change, it is highly relevant to understand the thermal sensitivity and the thermal limits of a species because heat dissipation and hyperthermia could become major issues for these large antelopes as current temperature trends over the 20th century (Warburton et al. 2005) and also predictive models (IPCC 2007) show significant warming in the southern part of Africa. Therefore, understanding an animal's behaviour in response to changing environmental conditions is crucial as behaviour affects and is affected by the animal's development, physiology and evolution (Sih et al. 2010).

We investigated how three commonly distributed antelopes of different body size, eland *Taurotragus oryx* (≈ 420 kg), blue wildebeest *Connochaetes taurinus* (≈ 180 kg) and impala *Aepycerus melampus* (≈ 50 kg), adjust their diurnal activity in relation to heat load patterns in a South African semi-arid ecosystem. We used black globe temperature (BGT), which is an index of heat load integrating the effects of ambient temperature, solar radiation and wind speed (Huey 1991; Fuller et al. 1999; Hetem et al. 2007). With this BGT, we tested the hypotheses that (1) the diurnal activity of these antelopes is negatively correlated with high BGTs during the hottest days and seasons, and (2) the larger bodied eland and wildebeest are less active than the smaller impala during the hottest days and seasons.

Materials and Methods

Study area

The study was conducted in Mapungubwe National Park (19,788 ha) in the northern part of South Africa (29°12'-29°23'E; 22°15'-22°30'S) from May 2008 to April 2009. The area is situated in the GMT +2 hours' time zone, so solar zenith occurs around 12:45 AM local time. The climate is semi-arid with mean rainfall ranging from 350-400 mm, most of which occurs from November to February. However, in 2008, rainfall started to peak only from late December. Drought of up to 3 years can occur in this area (O'Connor & Kiker 2004). The mean annual evaporation rate is 2200 mm (Midgley et al. 1994), which is six fold greater than that of the mean annual rainfall (O'Connor & Kiker 2004). The winter is mild with an average temperature of 20°C; however, summer temperatures can go up to 45°C.

The vegetation has been classified as Mopani Veld (Acocks 1988). More than 80% of the area is covered by *Colophospermum mopane* woodland (O'Connor & Kiker 2004). Riverine and flood plain vegetation includes *Acacia xanthophloea*, *Hyphaene petersiana*, and *Salvadora australis*, whereas *Acacia stuhlmanni* communities are found in old abandoned agricultural lands.

Common ungulates found in the park are elephant *Loxodonta africana*, giraffe *Giraffa camelopardalis*, eland, kudu *Tragelaphus strepsiceros*, blue wildebeest, zebra *Equus burchelli*, red hartebeest *Alcelaphus buselaphus*, gemsbok *Oryx gazella*, water buck *Kobus ellipsiprymnus*, impala, bushbuck *Tragelaphus scriptus*, and warthog *Phacochoerus aethiopicus*.

Data collection

We captured, collared and implanted a waxed miniature activity data logger (50X30X20 mm; African Wildlife Tracking, South Africa) into the retroperitoneal in the right side lateral aspect of the abdomen of five eland, five wildebeest and five impala (late-April 2008). The surgical procedure was similar to that used previously (Fuller et al. 1999; Hetem et al. 2009; Hetem et al. 2010). The waxed tag was equipped with a radio-transmitter with omnidirectional activity sensor, which transmitted activity data to the collar attached to the neck of the animals. We recorded activity data at an interval of 5 minutes for eland and wildebeest (N/day = 288) but of 10 minutes for impala (N/day = 144) due to limitation of the smaller battery for that smaller species. The data recorded per interval represents “0” for absolute resting and increasing number with increasing locomotor activity such as walking and running. All experimental procedures were approved by the Animal Ethics Screening Committee of the University of Witwatersrand (protocol no. 2007/60/4) and South African National Park.

We collected weather data from a portable weather station (Hobo micro station data logger, onset, USA) installed approximately 1 m above the ground on a mown lawn in the middle of Mapungubwe National Park (29°24'37.49" E; 22°12'49.54"S). Black globe temperature (accuracy $\pm 0.2^{\circ}\text{C}$, onset, USA) and ambient temperature (accuracy $\pm 0.2^{\circ}\text{C}$, onset, USA) were recorded from June 2008 to April 2009 with an interval of 5 minutes (N/day = 288). We also obtained daily rainfall data from the study area during the study period.

Data analysis

We defined three seasons: summer (December-February), spring (September-November) and winter (June-August) based on prevailing climatic conditions. Since the time interval for recording activity data was different between the species, we first calculated the mean activity for each two hours (i.e. the mean for 0:00 h includes activity data from 00:00 to 13:55, and so on) for each day. Then, we calculated the mean monthly activity and its variance for each two hours as a percentage of the maximum reading each logger recorded to correct for the sensitivity of individual activity data loggers (Hetem et al. 2008).

We compared the mean 24-hour (daily) seasonal activity between the three seasons for each species using a general linear model (GLM). Further, we compared mean diurnal (06:00-18:00h; local times) and nocturnal (20:00-4:00h) activity between the three seasons separately for each species using a GLM. Then, the diurnal activity (06:00-18:00h) of each species was regressed with the corresponding BGT (06:00-18:00h) for each season to test hypothesis 1, followed by a Bonferroni multiple comparison to test the differences between the slopes of the regression lines. To test hypothesis 2, we compared the slope of the regression lines describing the effect of BGT on activity (here after called β) between the three species over the three seasons separately. We also compared the slope of regression lines between the three species for the 10 hottest days based on black globe temperature to test hypothesis 2 under the hottest condition. We arcsine transformed the proportions of maximum activity before any statistical analysis (Zar 2009). We reported means and variance expressions (95% upper and lower bound) calculated from the original data throughout the paper. Out of the five individuals of each species, we were only able to retrieve data from two impala, two eland and four wildebeest during the nine month study period: two impala were killed by predators and the loggers got lost, whereas the data loggers of the other individuals from which we do not have the data could not be retrieved due to earlier battery and signal failure.

Results

Daily and seasonal black globe temperature (BGT) and rainfall patterns

The daily pattern of the BGT followed the general trend of a sinusoid curve with minima at dawn, dusk and night while BGT was always highest at midday (between 12:00 and 14:00 h) (Fig. 2). Summer exhibited the highest mean BGT ($31^{\circ}\text{C} \pm 11.5$), followed by spring ($29^{\circ}\text{C} \pm 11.2$) and winter ($21^{\circ}\text{C} \pm 13.2$). The total rainfall during the study period was 268 mm of which about 83% occurred during summer, whereas there was no rain in winter followed by only two days of rain in spring. During our study, winter was cool and dry, spring was hot and dry followed by a hot and wet summer.

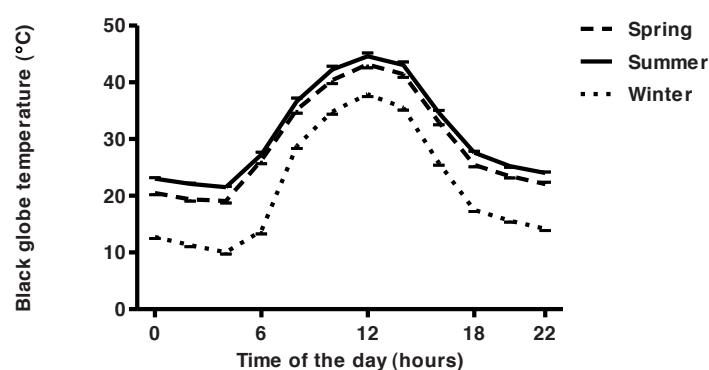


Figure 2. The mean two hourly black globe temperature (mean, 95% upper and lower bound) over the day during spring, summer and winter in Mapungubwe National Park (2008-2009).

Daily and seasonal activity rhythm

All species exhibited a typical bimodal activity pattern at dawn and dusk in all seasons, but they differed in their timing of peak activity particularly during dusk. In summer, the activity at dusk peaked at 18:00h (i.e. 18:00-19:55) whereas in winter it was at 16:00h (16:00-17:55). In line with this, the activity at dusk in spring peaked between 16:00 and 18:00h (Fig. 3).

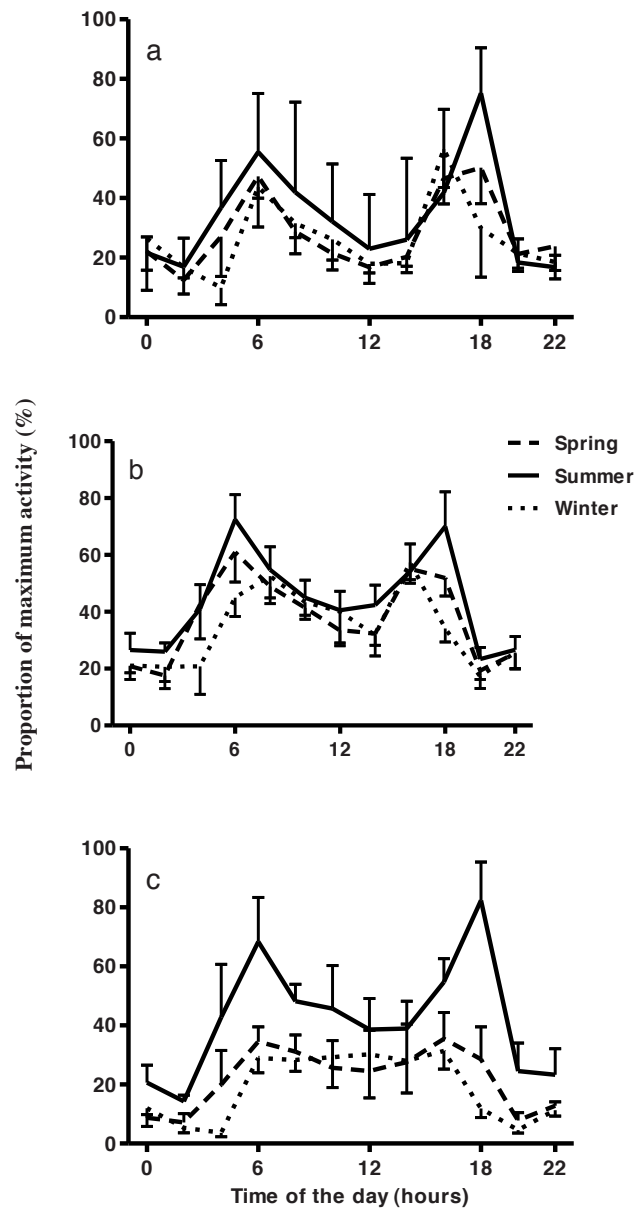


Figure 3. Daily activity pattern (mean, 95% upper and lower bound) during spring, summer and winter as proportion of the maximum activity of (a) eland (N=2), (b) wildebeest (N=4) and (c) impala (N=2).

Mean 24-hour activity of eland was significantly different between the seasons ($F_{2,189}=3.59$, $P=0.029$) (Fig. 4a). Mean 24-hour activity in summer was significantly higher than that in

winter ($P=0.032$), whereas it did not differ from spring ($P=0.106$). The activity in winter and spring was not significantly different ($P=1.00$). Diurnal activity (06:00-18:00) of eland differed significantly between the three seasons ($F_{2,109} = 3.838$; $P=0.025$) (Fig. 4b), whereas nocturnal activity (20:00-4:00) of eland did not differ between the seasons ($F_{2,77} = 0.952$; $P=0.391$) (Fig. 4c). Diurnal activity in summer was significantly higher than that in winter ($P=0.035$), but it was not significantly different between summer and spring ($P=0.057$) and between spring and winter ($P=0.786$).

Mean 24-hour activity of wildebeest differed between the three seasons ($F_{2,429} = 10.318$; $P<0.001$) (Fig. 4a). The mean 24-hour activity in summer was significantly higher than that in spring ($P=0.011$) and winter ($P<0.001$). Diurnal activity of wildebeest was also significantly different between the seasons ($F_{2,249} = 10.703$; $P<0.001$) (Fig. 4b). Summer diurnal activity was significantly higher than that of spring ($P=0.003$) and winter ($P<0.001$), but spring and winter did not differ ($P=0.760$). Nocturnal activity of wildebeest also differed between the seasons ($F_{2,177}=5.822$; $P=0.004$) (Fig. 4c). Summer nocturnal activity was significantly higher than that of winter ($P=0.002$), but not than that of spring ($P=0.429$). Spring and winter nocturnal activity were not significantly different as well ($P=0.165$).

Also for impala, mean 24-hour activity differed between the seasons ($F_{2,213}=37.87$; $P<0.001$) (Fig. 4a). Summer activity was higher than in spring ($P<0.001$) and winter ($P<0.001$), spring and winter did not differ ($P=0.977$). Diurnal activity of impala was significantly different between the three seasons ($F_{2,123}=38.462$; $P<0.001$) (Fig. 4b). Summer activity was higher than that of spring ($P<0.001$) and winter ($P<0.001$), but spring and winter were not different ($P=1.00$). Impala also exhibited significantly different nocturnal activity between the seasons ($F_{2,87}=30.573$; $P<0.001$) (Fig. 4c). Nocturnal activity in summer was significantly higher than that of spring ($P<0.001$) and winter ($P<0.001$), however, spring and winter did not differ ($P=0.335$).

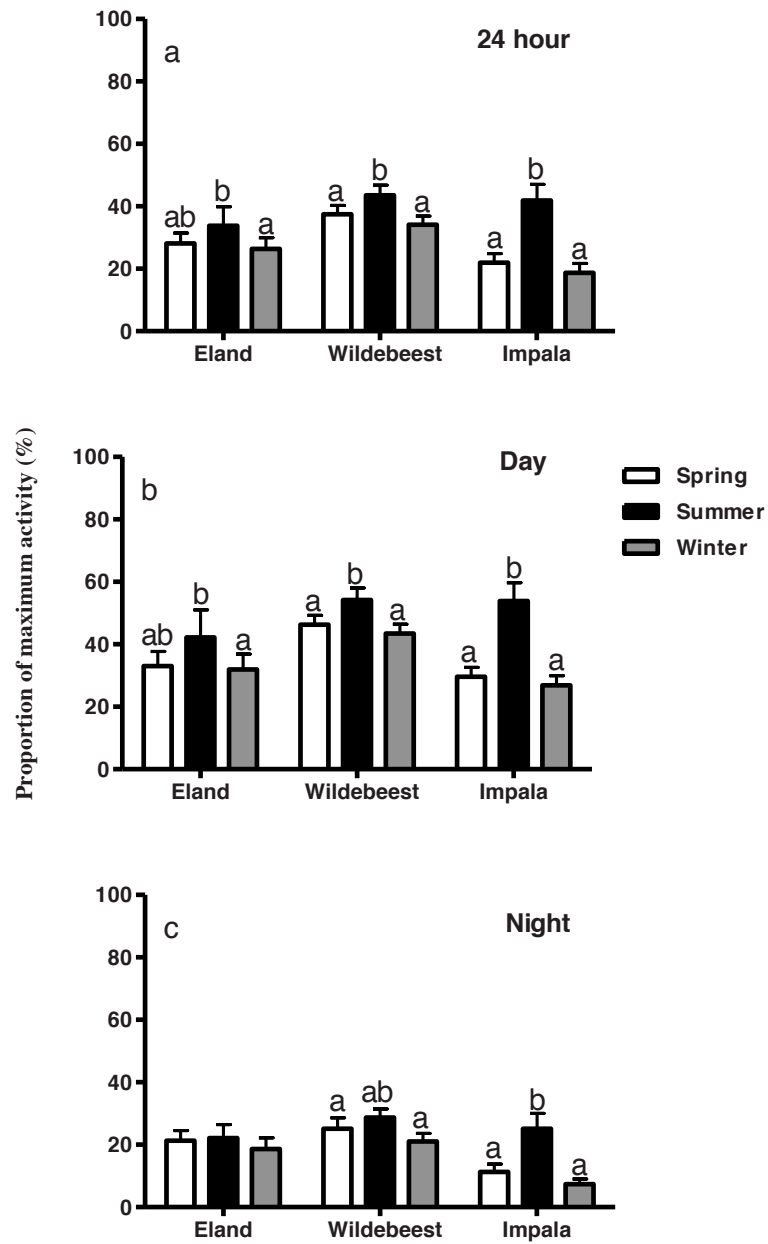


Figure 4. Seasonal mean activity levels as proportion of the maximum activity (mean, 95% upper and lower bound) for eland (N=2), wildebeest (N=4) and impala (N=2) during the 24-hour period (a), the day light period (b) and the night (c). Letters indicate significant different activity levels between season for each species after post-hoc test ($P < 0.05$).

Heat stress and diurnal activity

The diurnal activity of eland was negatively related with BGT for spring ($B_1=-1.92$, $P<0.001$, $R^2=0.80$), summer ($B_1=-2.34$, $P=0.001$, $R^2=0.60$) and winter ($B_1=-0.928$, $P=0.028$, $R^2=0.34$) (Fig. 5a). The slope of the regression lines describing the effect of BGT on activity (β) were significantly different between the seasons ($F_{2,36}=3.312$, $P=0.047$): β in summer was significantly larger than in winter ($P=0.039$), whereas β was not significantly different between winter and spring ($P=0.172$) and between spring and summer ($P=0.773$). This indicates that the effect of heat on diurnal activity of eland was pronounced in summer.

The diurnal activity of wildebeest was only negatively related with BGT during spring ($B_1=-1.359$, $P<0.0001$, $R^2=0.60$) and summer ($B_1=-1.359$, $P<0.0001$, $R^2=0.60$), but not in winter ($B_1=-0.267$, $P=0.65$, $R^2=0.008$) (Fig. 5b). The β s were significantly different between the seasons ($F_{2,78}=12.43$, $P<0.0001$). β in summer ($P<0.0001$) and spring ($P=0.011$) was significantly larger than in winter, however, it was not different between summer and spring ($P=0.589$). Apparently, the higher heat in summer and spring negatively affected the diurnal activity of wildebeest.

For impala, the diurnal activity was only negatively related with BGT in summer ($B_1=-2.106$, $P<0.0001$, $R^2=0.79$). However, the activity patterns in spring ($B_1=-0.387$, $P=0.228$, $R^2=0.11$) and winter ($B_1=0.340$, $P=0.205$, $R^2=0.13$) were not significantly related to BGT (Fig. 5c). In line with this, the β s were significantly different between the seasons ($F_{2,36}=16.99$, $P<0.0001$). β in summer was significantly larger than in spring ($P=0.001$) and winter ($P<0.0001$). Therefore, the diurnal activity of impala was negatively affected only in summer when the heat was at its highest.

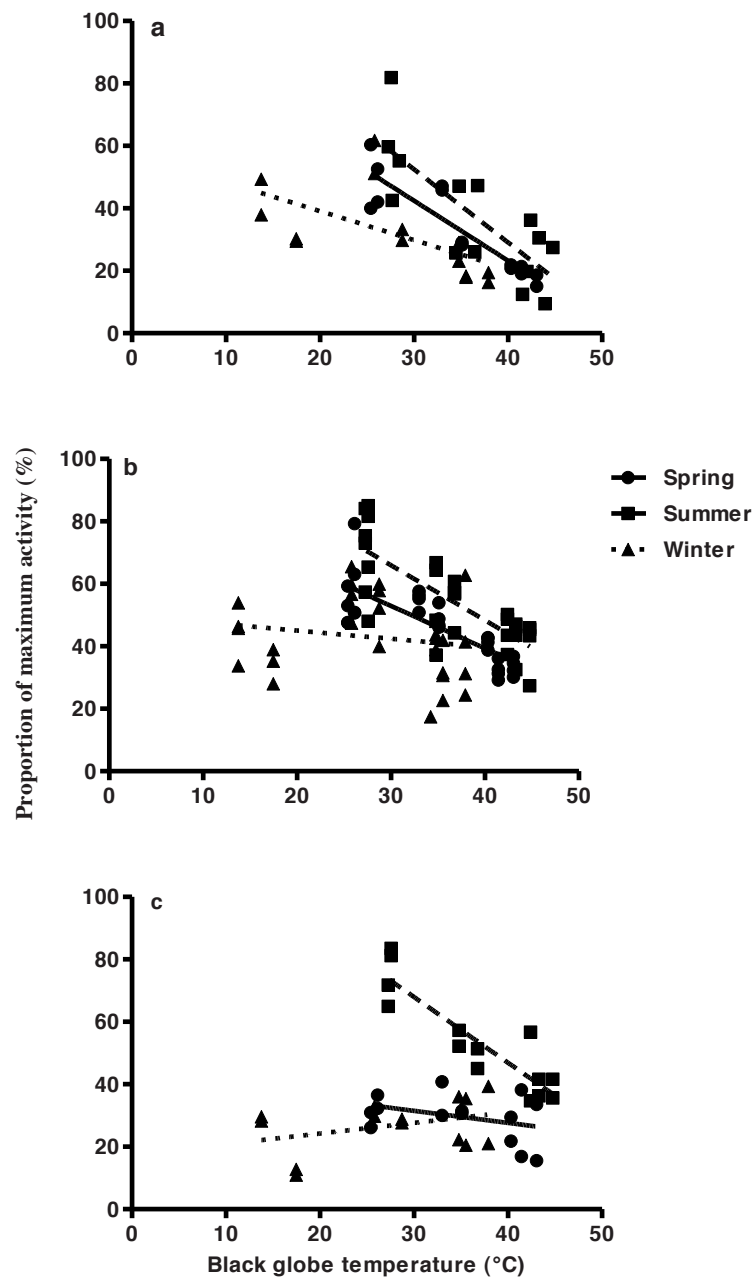


Figure 5. Relationship between black globe temperature (°C) and activity as proportion of the maximum activity (%) in spring, summer and winter for (a) eland (N=2), (b) wildebeest (N=4) and (c) impala.

Comparing the β s between the three species at each season showed that β in spring was significantly different between eland, wildebeest and impala ($F_{2,50}=6.9$, $P=0.002$). β for impala was significantly smaller than that of eland ($P=0.001$) and wildebeest ($P=0.019$), however, eland and wildebeest were not different ($P=0.247$). In contrast, β in summer ($F_{2,50}=0.318$, $P=0.728$) and winter ($F_{2,50}=1.675$, $P=0.197$) were not significantly different between the three species. Therefore, all the three antelopes exhibited a similar negative response to high BGT during summer when BGT was at its highest, while BGT was not influencing diurnal activity during winter. During spring, only the larger bodied antelopes were negatively influenced by BGT.

For the 10 hottest days, the diurnal activity of eland ($B_1=-1.501$, $P<0.0001$, $R^2=0.83$) and wildebeest ($B_1=-0.502$, $P=0.004$, $R^2=0.27$) was negatively correlated with BGT, while the diurnal activity of impala was not significantly related with BGT ($B_1=-0.577$, $P=0.164$, $R^2=0.15$). This confirms that the activity pattern of the larger bodied antelopes is largely affected by BGT, but not that of the smallest antelope, the impala.

Discussion

We investigated how the activity pattern of three antelopes species of different body size is affected by heat stress in a semi-arid system in South Africa. The results of our study confirm that the diurnal activity of these antelopes is negatively correlated with heat stress as measured by black globes (BGT) during the hottest days and seasons. The diurnal activity of the three species demonstrated a different sensitivity to the thermal regimes. The diurnal activity of the largest antelope, the eland, was negatively influenced by BGT throughout all three seasons. In contrast, the activity of the small impala only showed a strong negative relationship with BGT in summer. The activity of the intermediately sized wildebeest was negatively correlated with BGT in summer and spring but not in winter. Although these findings were consistent with previous studies on tropical African ungulates (Lewis 1977;

Klein & Fairall 1986; Owen-Smith 1998; Du Toit & Yetman 2005), the novelty of our study was to demonstrate the effect of heat stress on the fine temporal scale activity pattern of sympatric African ungulates taking into account a combination of potential heat stress factors like ambient temperature, solar radiation and wind speed. All the previous studies only took into account ambient temperature as heat stressor, while it is well known that solar radiation and wind speed also play a role in the thermal balance of ungulates (Chappell & Bartholomew 1981; Porter & Kearney 2009). For example, hartebeest exhibited a 5.4 times higher cutaneous water loss when exposed to the same ambient temperature (30°C) with solar radiation than without solar radiation (Maloiy & Hopcraft 1971). In addition, we have covered the higher temporal resolution by distinguishing the three different seasons, spring, summer and winter, which have their own ambient conditions. This was only possible by using telemetric activity data loggers without posing disturbance to the animals.

We have shown that during summer, when the potential for thermal stress is at its highest, all three species exhibited a similar response to heat with a larger effect of BGT (i.e., steeper negative slope of BGT regressed on activity) indicating that the higher thermal stress during summer negatively influences their diurnal activity (hypothesis 1). The explanation might be given by the heat dissipation limit hypothesis, which states that the maximum capacity to dissipate heat and therefore to avoid detrimental effects of hyperthermia is important for survival of endothermic animals (Speakman & Król 2010). This is particularly true for the antelopes we studied that live in a semi-arid system with high ambient temperature and solar radiation coupled with erratic rainfall and scarce water resources. However, the daily mean activity was the highest in summer for all the three species, in contrast to what we hypothesized. Indeed, we had expected a reduced activity among the three antelopes in summer if the heat stress actually influenced their activity negatively. The most likely explanation for this discrepancy is that increased rainfall during summer enhanced forage

availability both qualitatively and quantitatively since our semi-arid study area was situated under the summer rainfall belt (O'Connor & Kiker 2004). We suggest that despite the high ambient temperatures the higher forage availability leads these ungulates to maximize their energy/forage intake resulting in a better condition before the food scarcity in the dry season (winter and spring). A similar pattern was observed for other African ungulates which are found in resource limited systems in Africa (Beekman & Prins 1989; Owen-Smith 1994; Mduma et al. 1999; Ogutu et al. 2008). Further support for this explanation can be found when looking at the diurnal and nocturnal activity pattern. In summer, these antelopes exhibited higher activity either in the early morning or late in the evening or both suggesting to acquire more available forage and to avoid heat stress (Fig. 3). Our field observation also confirmed higher activity early in the morning and late in the evening and a long resting bout during midday when the heat stress was at its highest.

The differential effect of heat stress on the diurnal activity of the three differently sized antelopes was only evident in spring. During spring, the activity of the largest antelope (eland) and that of the intermediately sized antelope (wildebeest) exhibited a significant, negative relationship with BGT, but the activity of the smallest antelope (impala) was not related to ambient heat stress (hypothesis 2), which is confirmed by the results from the 10 hottest days. This can be explained by the idea that the ability to dissipate heat depends on body size due to the different surface area to volume ratios (Calder 1984; Peters 1986; Owen-Smith 1988). We thus argue that these large species are less active during periods of high heat stress so as to avoid the risk of hyperthermia. Further, pelage characteristics such as thickness and colour also influence the ability to gain or loose heat (Lewis 1977; Hofmeyr 1981; Hetem et al. 2009; Maloney et al. 2009). Our large species had a thinner mean pelage depth (eland: 1.0mm, wildebeest: 2.7mm, impala: 3.9mm) (Hofmeyr 1981). Therefore, we suggest that a thinner pelage of larger antelopes is an adaptation to overcome the negative

effect on potential heat stress of the smaller surface area to volume ratio of larger antelopes as compared to smaller ones.

We further put forward that the low availability of high quality forage and water also may play a critical role in the reduced activity level of the larger antelopes during spring. Spring is a hot, dry season with mean black globe readings as high as in summer, but there was a scarcity of forage and water resources. We argue that such elevated heat stress and water scarcity caused the large antelopes to reduce their activity and thereby reducing their metabolic heat production. Being less active at the time of maximum ambient temperature and solar radiation perhaps decreases the thermal load generated from muscular activity and the direct and indirect exposure to the solar radiation. Active behaviour such as grazing and travelling can increase heat production by fivefold and threefold respectively when compared to standing idle, as has been found in cattle (Malechek & Benton 1976). We consider that being less active serves to conserve water and energy in the harsh spring season. If this is not possible, the animals have to dissipate accumulated heat through evaporation, which could be very costly especially during times of reduced water availability. It has been shown that African antelopes reduced their food intake when they were exposed to acute heat stress coupled with dehydration (Maloiy et al. 2008). A low metabolic rate also reduces the maintenance requirement when food is in short supply (Taylor 1974; Choshniak et al. 1995; Wang et al. 2006), which might be the case for our species.

Many field studies have demonstrated a similar reduction in active behaviour for a range of African ungulates apparently due to heat stress (Lewis 1977; Leuthold & Leuthold 1978; Klein & Fairall 1986; Owen-Smith 1998; Du Toit & Yetman 2005; Maloney et al. 2005). Large bodied ungulates can afford this reduced activity because they have lower energy demands (per kg) and can tolerate lower quality forage because of their increased gut capacity and longer retention time (Bell 1971; Jarman 1974; Demment & Van Soest 1985;

Illius & Gordon 1987; Owen-Smith 1988). A small animal like impala might not have this advantage because of its higher energy demand (per kg) and thus, it must select relatively rare and widely distributed higher quality forage during the scarce season resulting in higher activity levels in impala than in the larger bodied ungulates. During heat stress periods, we can expect that impala due to their small size effectively select locations to forage with relatively cool microclimate to avoid this heat stress. Our anecdotal field observation confirms this hypothesis that impala confined themselves to riverine forest with a full canopy even during the dry period while the larger antelopes mainly occur in deciduous Mopane veld and open savannah woodland with few scattered Acacia trees, which stands without leaves during spring.

We have demonstrated that heat stress indeed negatively influenced the diurnal activity of eland, wildebeest and impala, particularly in summer and spring. In summer, the diurnal activity of all the three antelopes was negatively related with BGT, and they exhibited more activity at dawn, dusk and night when heat stress was at its lowest. In spring, only eland and wildebeest were negatively influenced by heat stress. We argue that the spring season with high heat stress coupled with poor forage and water availability could be critical for the survival of these large African antelopes in this semi-arid system. Our study contributes to understanding how these endothermic animals can cope with extreme climatic conditions. This could be further exacerbated by current climate change, which is predicted to increase frequencies of drought, erratic rainfall and temperature in this region (IPCC 2007; Lyon 2009). Therefore, abilities to cope with future climate change by these species will primarily depend on their ability to track resources during resource scarce season and shifting their activity pattern to the cooler part of the day.

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Chapter 3

Living on the edge: Daily and seasonal microhabitat selection based on altitude and microclimate of eland *Taurotragus oryx* in Asante Sana Game Reserve, South Africa

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Abstract

Within the present context of climate change, understanding microhabitat selection of ungulates in relation to their thermal constraints will increase knowledge on their adaptive capacity to find habitats that can act as thermal refuges. This is particularly relevant for African ungulates as their behaviour and physiology has been shown to largely depend on climatic conditions. We investigated if the largest African antelope, the eland, selects habitats with suitable microclimates (thermal refuge) to avoid hot or cold environmental conditions at the southern edge of its distribution in South Africa. We used GPS locations and the mini-globe temperatures from collared animals and a Digital Elevation Model (DEM) to quantify microhabitat selection of five individuals. The results show that eland selected lower altitudes when it was cold in the winter, presumably to prevent hypothermia. This was supported by the daily and seasonal selection of warmer microclimates when ambient conditions were below the thermal neutral zone. In contrast, eland did not select higher altitudes when it was warm in the summer. Selection of cooler habitats was only evident when heat stress was close to the upper end of the thermal neutral zone. The eland thus showed a behavioural adaptation in the daily and seasonal selection of altitude and microclimate to cope with both extreme cold and hot conditions. This microhabitat selection can help individuals to find thermal refuges from the predicted increase in extreme events due to climate change.

Keywords: behaviour; thermoregulation; microhabitat; microclimate; climate change

Introduction

Habitat selection patterns are typically the outcome of a series of habitat choices that maximize ecological benefits relative to costs (McLoughlin et al. 2005; Pettorelli et al. 2005). For ungulates, field studies have emphasized food availability (Stephens & Krebs 1986; Pretorius et al. 2011; Bjørneraas et al. 2012) and predation risk (Lima & Dill 1990; Latham et al. 2011; Thaker et al. 2011) as major factors determining habitat choice. Thermal costs and benefits have received less attention, even though the heat balance has a large influence on animal energetics (Dejours 1981) and therefore on survival and fitness. Habitats with more extreme ambient conditions such as a combination of high air temperature, high solar radiation levels, low wind speeds and high vapour pressures pose a threat because dissipation of heat becomes more difficult which may result in hyperthermia (Schmidt-Nielsen 1975; Speakman & Król 2010). On the other hand, habitats with a combination of freezing temperatures, snow, high wind speeds and very dry air enhance heat loss of animals which may result in hypothermia.

To cope with inhospitable environments of hot or cold conditions, ungulates may select optimal microhabitats defined here as “thermal refuge”, that minimize absorption of heat at high temperatures or habitats that maximize the absorption of heat at low temperatures to maintain homeothermy. Such behavioural thermoregulation of microhabitat selection is considered to be the first line of defence by animals (Bartholomew 1964; Willmer et al. 2005) when they become exposed to inhospitable environments. This is because behavioural thermoregulation requires low energetic demands, which can be sustained longer than the energetically expensive autonomic responses (Cabanac 1996; Maloney et al. 2005). Therefore, movements of animals to select suitable thermal habitats (thermal refuge) to avoid hyperthermia or hypothermia is important for survival and fitness (Wang et al. 2010; Zeng et al. 2010; de Knecht et al. 2011).

A number of studies demonstrated that ungulates use particular habitats, e.g., forested or open habitat (Irwin & Peek 1983) or higher or lower altitudes (Parrini et al. 2003; Aublet et al. 2009; Rice 2008; Bačkor 2010) disproportionately to their availability at certain times of a day and in certain seasons. For example, Alpine ibex (*Capra ibex*) in Gran Paradiso National Park, Italy, moved to higher altitudes to cope with heat stress in summer (Aublet et al. 2009), whereas mountain goats (*Oreamnos americanus*) in the Cascade mountain range in Washington moved to lower altitudes during the winter (Rice 2008). This selective use of certain habitats and altitudes under certain circumstances was suggested to be a response to avoid hyperthermia or hypothermia provided by vegetation cover and topography (Merrill 1991; Bowyer & Kie 2009). However, most of these studies used coarse climatic and altitude data, which might not represent the actual environmental conditions experienced by animals.

Biophysical models demonstrate that microhabitats can significantly differ in their thermal properties and consequently metabolic energy cost (Bakken 1976) and therefore, selection of a microhabitat has a direct influence on an animal's thermal balance which needs to be quantified at fine temporal scales to understand the animal's adaptive capacity properly. This is because the diverse microhabitats provide a range of microclimates which can increase foraging time and the time needed for reproductive activities even during extreme climatic conditions (Sih et al. 2010; Sears et al. 2011) and therefore increase survival and fitness. This is particularly relevant with the predicted increase in temperature and extreme events (heat waves and warm spell) due to climate change (IPCC 2011; Rahmstorf & Coumou 2011) which makes dissipation of metabolic heat to become difficult for endotherms (Sherwood & Huber 2010). Therefore, the risk of death through exposure to lethal temperatures will be near certain in some habitats compared to the risk of death through predation or from forgone forage, which may be high but will rarely be certain (Dexter 1998). Despite a growing interest in the behavioural adaptation of animals in relation to climate change (Boyles et al. 2011), few studies have been carried out on microhabitat selection by tropical ungulates,

although the selection of thermally suitable microhabitats is particularly important for these animals, not only because their behavioural and physiological processes are temperature dependent (Fuller et al. 2005; Kinahan et al. 2007), but also because these tropical animals are already near their maximum thermal tolerance (Tewksbury et al. 2008).

It has been demonstrated that habitats at the edge of an animal's distributional range can be sub-optimal in terms of food and climatic condition. Therefore, animals living at or near the range margins are more likely to experience stressful and lethal weather events (Hoffman & Parsons 1997). In response to a changing climate, animals are predicted to expand their range to track their climatic envelope (Feder 2010). Hence, many of the animals may have to live at their present-day range limits and beyond in the future. Therefore, understanding how animals living at the range of their distribution respond to changing climatic condition is critical for predicting the effect of climate change on the distribution and abundance of animals, and is thus at the core of modern animal ecology.

We studied daily and seasonal movements of the largest African antelope, the eland (*Taurotragus oryx* ~ 420 kg), to test if it selects optimal microhabitats (both in relation to altitude and microclimate) at the southern edge of its distribution in South Africa (in this case Asante Sana Game Reserve). Asante Sana is situated at higher altitudes south of the tropic of Capricorn where the climate is very seasonal with long and cold winters with freezing ambient temperatures but also with a hot summer when diurnal temperatures can routinely increase to more than 40° C (Mucina & Rutherford 2006; Lindsay et al. 2009). African antelopes evolved in less seasonal environments under hot and dry conditions, and their physiological responses to cold temperatures are limited due to their high critical minimum temperature, narrow zone of thermo-neutrality and low insulation value due to a thin pelage (Scholander 1955; Taylor & Lyman 1967; Hofmeyr 1981). Habitats with cold winters are suboptimal for them and therefore will present an energetic challenge for the maintenance of

homeothermy. With this limited ability to physiological respond to cold temperatures, African antelopes should employ behavioural thermoregulation through microhabitat selection to maintain homeothermy when exposed to long cold winter conditions.

Eland antelope with their low critical temperature (Taylor & Lyman 1967) and a thinner pelage (Hofmeyr 1981) have a limited physiological ability to cope with cold stress. Probably, eland are even better adapted to heat dissipation than to heat conservation (Hofmeyr 1981) thus making it likely that they have evolved or developed behavioural mechanisms to cope with cold. Therefore, we hypothesize that the eland should select lower altitudes with a relative warmer microclimate during cold periods in winter to prevent hypothermia. Within a day, eland should select lower altitudes with a warmer microclimate during the cooler part of the day (morning, and late afternoon and night) as during this time in winter the temperature is often below their thermal neutral zone.

In Asante Sana, not only the winter can be harsh but the summer can be hot with the maximum diurnal temperature of 40°C which is beyond their thermal neutral zone. During such extremely high temperatures, dissipation of heat will become a problem particularly for large animals like the eland due to their high surface area to volume ratio (Peters 1986). Therefore, eland should select higher altitudes with a cooler microclimate during warm periods in summer to prevent hyperthermia whereas within a day, they should select relatively higher altitudes with a cooler microclimate during the hottest part of the day (midday and afternoon) as temperatures can peak around 40°C during this time of the day in the summer.

Material and Methods

Study area

Asante Sana Game Reserve (32°15' - 32°21' S; 24°52' - 25°04' E), is situated south of the tropic of Capricorn in South Africa. The altitudinal range varies from 1000 to 2400 m a.s.l.

The climate is seasonal in terms of temperature. The winter can be long and cold with an average 24-hour temperature of 13°C with many days of freezing temperatures and even a few days of snowfall. The mean number of frost days in the region is about 25 (range: 8-40 days) (Kerley & Boshoff 1997). The summer can be hot with maximum ambient temperatures reaching 40°C. Most of the rainfall (about 70%) occurs during the summer months. However, precipitation can also occur during winter and is associated with sporadic cold fronts (Kerley & Boshoff 1997). The long-term mean annual rainfall (1948-1996) recorded at 1000 m is 318 mm (range: 171-706 mm; SD = 112 mm) while at a higher altitude (1300 m), the rainfall is 550 mm (range: 177-853 mm; SD = 152 mm) (Boshoff & Kerley 1997). In Asante Sana, there are three perennial streams which ensure availability of water throughout the dry periods (Boshoff & Kerley 1997).

Data collection

We captured five eland (all female) and fitted GPS collars during late May 2008. The GPS collars recorded location (latitude, longitude in WGS 1984) at 2-hour intervals with an accuracy of ~10m (African Wildlife Tracking, Pretoria, South Africa). Each GPS collar was attached with a miniature black globe thermometer (MBGT), which recorded the real time microclimate as experienced by the animals at 5 minute intervals. This technique of quantifying microclimate selection was previously validated for other African ungulates living in semi-wild condition in South Africa (Hetem et al. 2007). A MBGT is a matt-black hollow copper sphere of 30mm diameter, equipped with a small temperature-sensitive thermistor (accuracy of ~0.1°C) inserted in the centre of the MBGT. The thermistor was attached to the data card (an electronic chip) of the GPS/UHF collar unit, which records the miniature black globe temperature (MBGT). The MBGT was attached to the collar with a brass screw with a 5 mm spacer between the MBGT and the collar (African Wildlife Tracking, Pretoria, South Africa). A weight on the ventral side of the collar ensured that the MBGT remained at the dorsal side of the neck and could not be shaded by the animal's body.

Daily and seasonal microhabitat selection

We regularly monitored collared animals using radio-telemetry (2-3 times per month). All experimental procedures were approved by the Animal Ethics Screening Committee of the University of the Witwatersrand (protocol no. 2007/60/4) and South African National Parks.

Out of five individuals, four eland yielded data for 11 months, and one individual yielded 8 months of data.

We collected weather data from a portable weather station (Hobo Weather Station, Onset Computer Corporation, Pocasset, MA, USA) installed approximately at 1m above the ground on a mown lawn in Asante Sana (altitude: ca. 1000 m; 32° 18'S; 24° 58'E). Standard (150 mm) black globe temperature (BGT, °C), mini black (30 mm) globe temperature (MBGT, °C) and ambient temperature (dry-bulb, °C) were recorded from June 2008 to February 2009.

Data analysis

Using Arc GIS 9.3.2.1 (ESRI, USA) with the Hawth analysis extension, we assigned altitude to each GPS fix for each eland by extracting it from the Advanced Space-borne Thermal Emission and Reflection Radiometer (ASTER) Digital Elevation Model (DEM). ASTER DEM satellite image has estimated accuracies of 20 m at 95% confidence for vertical data and a 30m at 95% confidence for horizontal data (METI/ERSDAC & NASA/LPDAAAC 2009).

With these data to test the hypothesis of within-day and seasonal altitude selection, we used marginality (M) defined as the difference between the average environmental conditions (altitude in this case) selected by the species (species mean: m_s) and the average environmental condition (altitude) of the study area (global mean: m_g), divided by 1.96 standard deviations (σ_g) of the global distribution (Hirzel et al. 2002):

$$M = \frac{m_s - m_g}{1.96 * \sigma_g}$$

Marginality (M) measures whether the average environmental condition selected by the species is different from that of the average environmental condition of the study area. Generally, the absolute value of the marginality ranges from 0 to 1 (can be positive or negative), where a larger value indicates the selection of a more extreme environmental condition by the species relative to what is available in the study area. Negative values of M indicate selection of environmental conditions (altitude in our case) that are lower than the average environmental condition of the study area, whereas positive M values indicate the selection of environmental conditions higher than the average environmental condition of the study area.

To calculate the within day (2 hourly) altitude species means (m_s), we first calculated the 2 hourly mean altitude for each eland for each season and then pooled the data from all individuals to calculate the 2 hourly mean altitude (within day) for the winter (June-August) and the summer (December to February) period. For the seasonal altitude species means (m_s), we calculated the overall average altitude for each individual eland for each season and then pooled the data from all individuals. Further, we also calculated the species mean (altitude) for the first month of winter (June) and for the first month of summer (December) to investigate how eland adapt to location during the first month of the coldest and the hottest seasons. For the global means (m_g), we calculated the average altitude of the entire study area and corresponding standard deviation (σ_g) as a reference base.

To test the daily and seasonal microclimate selection, we used the same Marginality index as described above. For this, we calculated the overall average seasonal (seasonal m_s) and daily 2-hourly (within day seasonal m_s) MBGT for each season from the collar as described above. We also calculated the average (m_g) and the standard deviation (σ_g) of the corresponding MBGT (seasonal and daily 2-hourly for each season) from the weather station as reference base.

Daily and seasonal microhabitat selection

To test the selection of microclimate during extreme climatic conditions, we identified the 5 coldest days and the 5 hottest days on the basis of mean daily BGT. Then, we calculated the average MBGT (m_g , weather station) and its standard deviation (σ_g) for each of these 5 coldest days and 5 hottest days separately. To calculate species mean (m_s), we calculated the average MBGT (from the collars) for each of the 5 coldest days and 5 hottest days separately. For comparison of the daily 2-hourly temperatures (within day) during these extreme periods, we calculated m_g and σ_g for each 2-hourly MBGT from the weather station and m_s for each 2-hourly MBGT from the collar by pooling data from all the 5 coldest days and all the 5 hottest days separately.

Table 1. Environmental conditions (mean \pm SD) during winter and summer in Asante Sana Game Reserve.

	Winter	Summer
Black globe temperature (BGT°C)		
24- h mean	13.4 \pm 4.1	25.1 \pm 2.9
24-h maximum	28.8 \pm 4.2	43.1 \pm 4.3
24-h minimum	2.2 \pm 5.0	11.7 \pm 3.3
Ambient temperature (°C)		
24- h mean	12 \pm 4.5	21.5 \pm 2.7
24-h maximum	20.8 \pm 4.2	30.7 \pm 3.9
24-h minimum	3.5 \pm 5.1	12.9 \pm 3.1
Mini-black globe temperature (MBGT°C)		
24- h mean	12.8 \pm 4.8	23.2 \pm 2.7
24-h maximum	25.0 \pm 4.5	36.9 \pm 3.8
24-h minimum	1.9 \pm 5.3	12.2 \pm 3.1

Results

Daily and seasonal environmental condition

The standard black globe temperature (BGT) and miniature black globe temperature (MBGT) was always highest at midday (between 10:00 to 14:00 h) with minima at dawn, dusk and night (Fig. 6). Winter was colder with the lowest mean BGT and the lowest mean MBGT and with the lowest daily mean minimum temperature whereas the summer was milder with the highest mean BGT and MBGT followed by the highest daily mean maximum temperature (Table 1). The average altitude of the study area was 1521 \pm 372 m (mean \pm SD). During

winter the average altitude selected by eland was 1322 ± 227 m (mean \pm SD, N=5), whereas for summer it was 1444 ± 212 m (mean \pm SD, N=5).

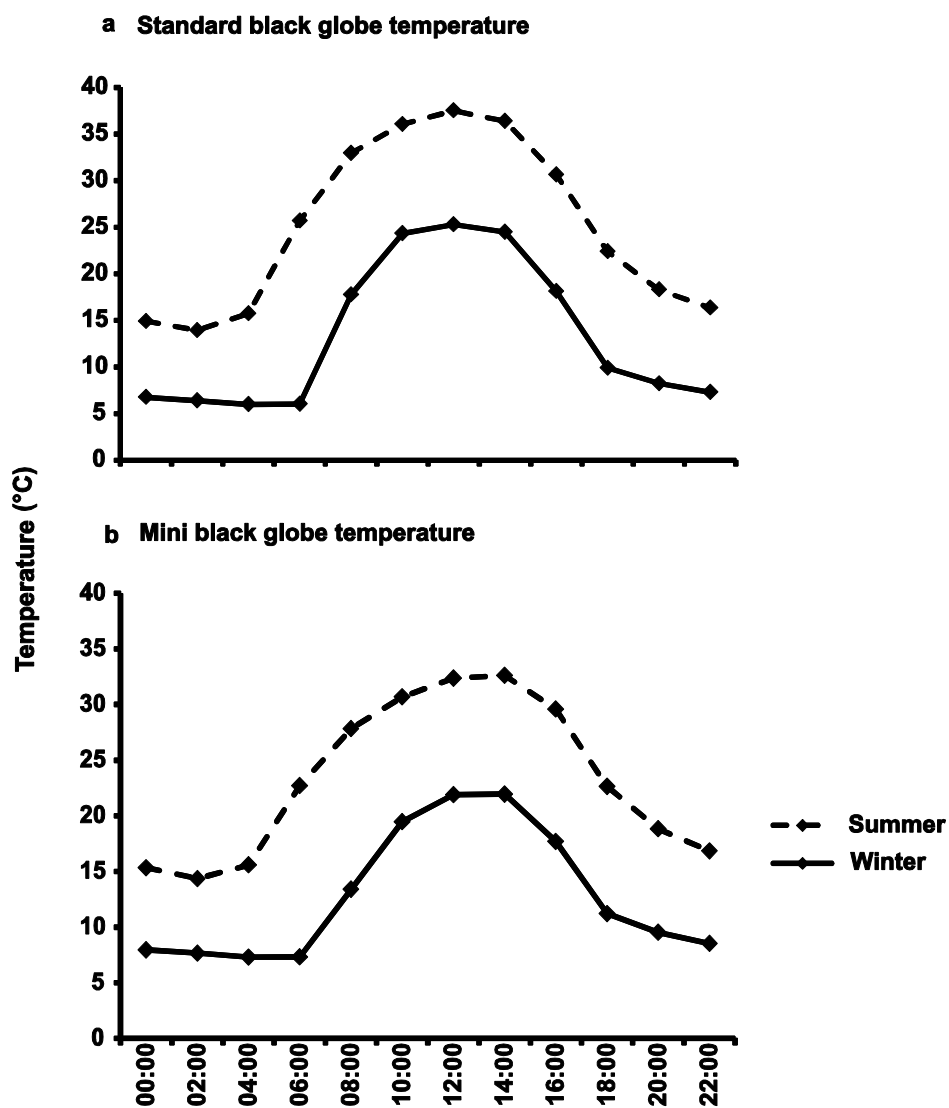


Figure 6. Daily rhythm of standard black globe temperature (BGT) (a) and mini-globe temperature (MBGT) (b) in winter and summer.

Daily and seasonal altitude selection

During winter, eland selected a lower altitude than the average altitude of the study area ($M=-0.3$). In contrast, during summer eland selected a lower altitudes compared to the average altitude of the study area ($M=-0.1$). However, it should be noted that the summer altitudes selected by eland were higher than the altitudes selected during the winter. During June, the eland selected a lower altitude than the average altitude of the study area ($M=-0.4$), whereas during December eland were at an altitude similar to that of the study area ($M=0.0$). Within a day, only during winter eland slightly selected lower altitudes in the evening ($M=-0.3$), whereas they selected relatively higher altitudes during the mid-day ($M=-0.2$), which was not the case in summer (Fig.7).

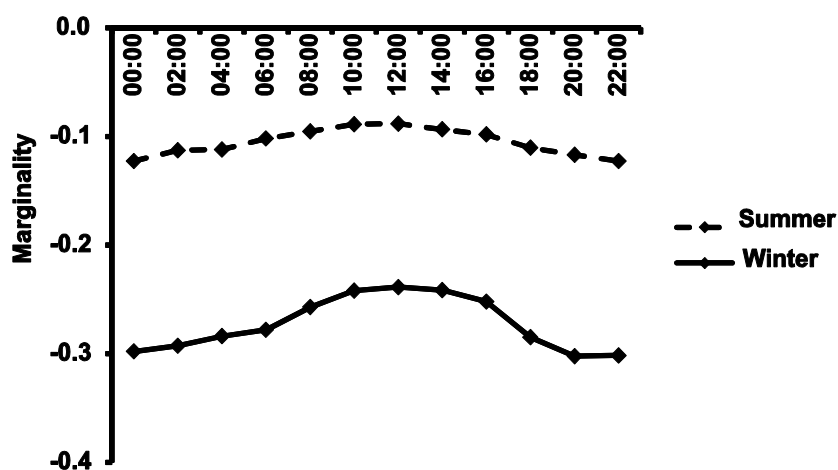


Figure 7. Seasonal marginality for altitude selected by eland within a day relative to the average altitude in the study area. Negative values of the marginality indicate that eland selected lower altitudes than the average of the study area.

Daily and seasonal microclimate selection

During winter, eland selected a relative warmer than average microclimate of the study area ($M=0.1$). In contrast, during summer, eland selected microclimates similar to that of the study area ($M=0.0$). The selection of sites based on microclimatic conditions was more evident only in the five coldest days and five hottest days. The eland actively selected warmer microclimates than the average of the study area during the five coldest days (Table 2), while during the five hottest days, eland selected cooler than average microclimates at least for the three hottest days (Table 2).

Table 2. Marginality value for microclimates selected by eland during the five coldest days and the five hottest days measured by the black globe in the weather station. A positive value of marginality indicates that eland selected microclimates warmer than the average of the study area, while negative values indicate that eland selected microclimates cooler than the average of the study area. Marginality value of zero indicates that eland selected on average similar microclimates relative to the average of the study area.

Five coldest days (°C)	Marginality	Five hottest days(°C)	Marginality
2.9	+ 0.3	30.1	-0.1
3.3	+ 0.3	29.0	-0.1
4.3	+ 0.3	27.8	-0.1
4.5	+ 0.2	27.7	0.0
4.6	+ 0.2	27.6	0.0

During early morning and evening, eland selected warm microclimates both in winter and summer (Figs. 8a & 8b). However, the eland selected warmer habitats in the late afternoon (14:00-18:00) during the winter (Fig. 8a), whereas during the summer eland selected cooler habitats in the early morning (6:00-8:00) (Fig. 8b). Surprisingly, in the midday eland did not appear to select microclimates different from the average microclimate of the study area during winter ($M = 0.09$) or summer ($M = 0.07$); however, note that the value of M was <0.1 (Fig. 8a & 8b).

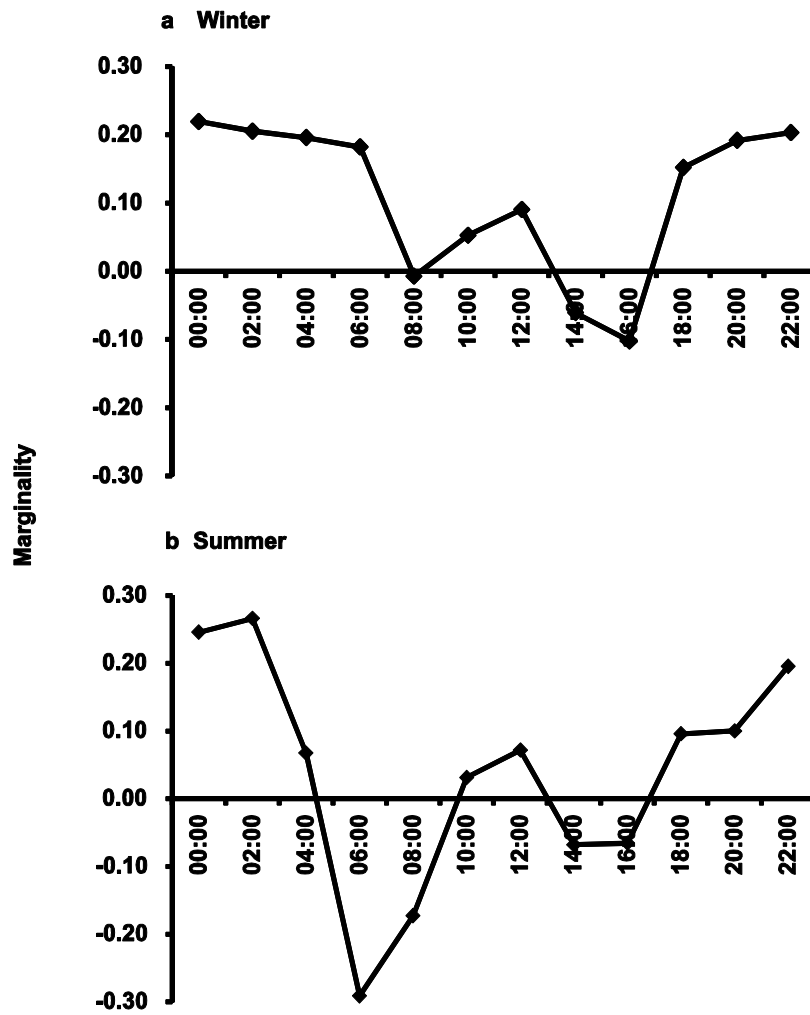


Figure 8. Seasonal marginality for microclimates selected by eland within a day relative to the average microclimate in the study area during (a) winter and (b) summer. A positive value of the marginality indicates that eland selected microclimates warmer than the average of the study area, while negative values indicate that eland selected microclimates cooler than the average of the study area.

On the five coldest days, eland selected warmer microclimates all the time, except during late afternoon when they selected microclimates similar to the study area (Fig.9a). In contrast, during the five hottest days, eland preferred to be in cooler habitats in the morning (06:00–

08:00) and late in the afternoon (16:00), whereas they preferred relatively warmer habitats during the evening. During midday they selected microclimates similar to the study area (Fig. 9b).

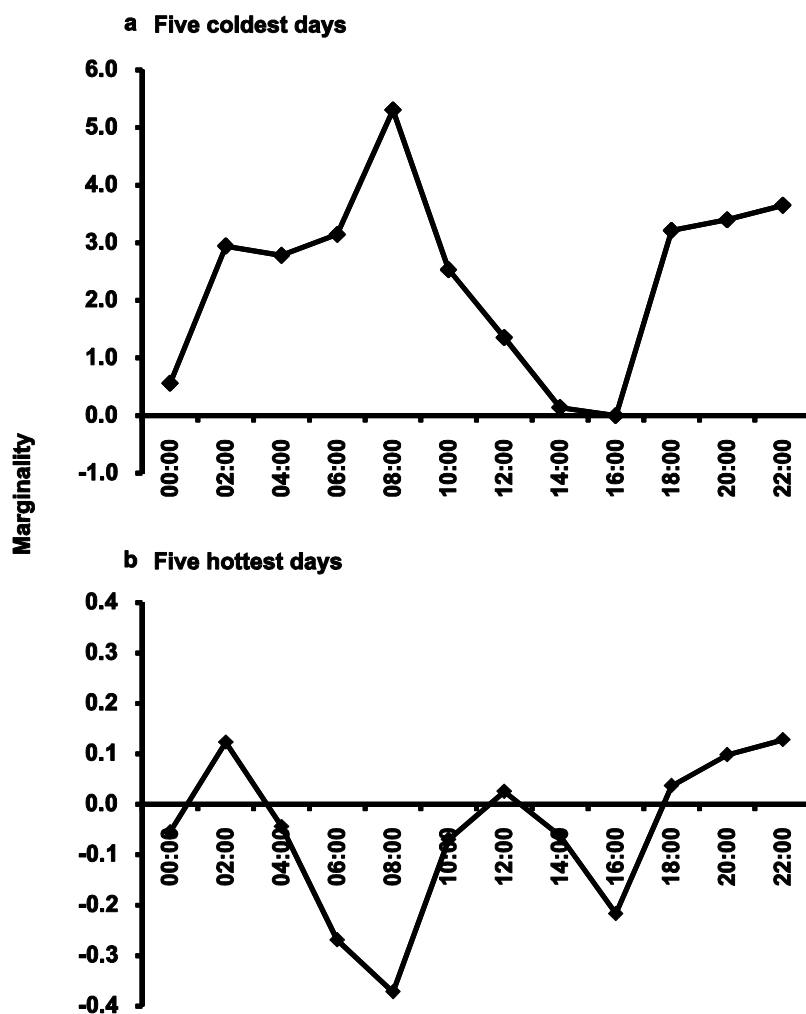


Figure 9. Marginality for microclimates selected by eland within a day relative to the average microclimate in the study area during (a) the five coldest days and (b) the five hottest days. A positive value of marginality indicates that eland selected microclimates warmer than the average of the study area, while negative values indicate that eland selected microclimates cooler than the average of the study area. When marginality is zero, then eland selected on average similar microclimates relative to the average of the study area.

Discussion

We investigated the daily and seasonal selection of sites that differed in altitude and microclimate by eland at the southern edge of their distributional range. The results of our study show that eland adjust their daily and seasonal movements to select particular altitudes and microclimates. In agreement with our two hypotheses, eland selected lower altitudes during winter, particularly in the cool night-time period, whereas higher altitudes were selected during midday. The explanation might be given by the daily and seasonal change in temperature in the study area with respect to altitude. Winter in Asante Sana is harsh with a daily average temperature of 12°C and a daily average minimum temperature of 3°C, which is below the thermal neutral zone for most of the African mammals including eland as it increased its metabolic rate by 19% when exposed to 14 °C compared to 22 °C (Taylor & Lyman 1967). The cold stress during winter might get further worsened by many days of freezing temperatures and even a few days of snowfall. We argue that these tropical antelopes with their higher low critical temperature (Taylor & Lyman 1967) and a thinner pelage (Hofmeyr 1981) than temperate and arctic ungulates have a limited physiological ability to tolerate the cold stress, thus making it likely that they have developed behavioural mechanisms such as microhabitat selection to cope with cold stress. As lower altitudes are generally warmer than higher altitudes (Barry 2008), particularly in South Africa, South of the Capricorn, where microclimate depends on altitude (Werger 1986; Mucina & Rutherford 2006), lower altitudes are likely to be warmer than higher altitudes during the day. Therefore, we suggest that selection of lower altitudes by eland help to gain more heat to maintain homeothermy during winter when temperature is below their thermal neutral zone without employing an energetically expensive physiological response. Further, the special feature of lower altitudes in Asante Sana may provide a warmer climate: Asante Sana is a small valley (bowl) with the valley bottoms situated at lower altitudes with flat and undulated terrain with drainage lines. We suggest that these valley bottoms at lower altitude receive more solar

radiation for longer periods of time throughout the day, i.e., more heating, than the sites at higher altitudes because the sun is always high in the sky, which is particularly true in the tropics (Price 1981).

The valley bottom, however, can be colder than the higher altitude, particularly during the night in winter because the cold air, which is denser than warm air, accumulates in the valley bottoms at night (Barry 2008): night frost is typically observed in the valley bottoms. During behavioural observations, we observed that eland spent most of their time in the open valley bottom area grazing or resting during the day, whereas just before sunset they moved towards the drainage lines and nearby slopes of the foot-hill with small trees and shrubs, which might be warmer during the night. Indeed, such drainage lines with trees and shrubs and foot hill slopes were suggested to be in use as night-time refuges by African ungulates to prevent them from cold stress (Acocks 1976; Skead 1980). Therefore, we suggest that eland selected the open valley bottoms during the day when there was sun to absorb solar radiation while they moved to warmer areas such as drainage lines and foot hill slopes during the night when the open valley was cold. This idea is supported by the result of the seasonal and daily selection of sites based on microclimatic conditions. During the winter season, eland selected warmer microclimates than the average microclimate of the study area. The selection of a warmer microclimate was more evident during the five coldest days when it was freezing in Asante Sana. Further, within the day, microclimatic selection during winter and during the five coldest days also support the idea that eland were actively seeking warmer microclimates particularly during the coolest part of the day.

Consistent with this observation are findings that many Temperate, Arctic and Himalayan ungulates, even with their low lower critical temperature and thicker pelage than tropical ungulates, showed similar behavioural responses of moving to lower altitudes (Nelson 1995; Brinkman et al. 2005; Rice 2008) and selecting warmer microclimates during the winter

(Signer et al. 2011; Zeng et al. 2010; Liu et al. 2011), apparently to avoid cold stress. To our knowledge, such a behavioural response of selection of lower altitudes with warmer temperatures in response to cold stress is recorded here for the first time among African antelopes in their natural habitat.

However, such altitudinal migration during the cold winter could also be attributed to the acquisition of forage resources (Wiersema 1984; Zeng et al. 2008; Zeng et al. 2010; Monteith et al. 2011); in that case the selection of thermally acceptable areas is a side-effect of a food acquisition strategy. Since we did not measure the availability of food resources during the study, we cannot rule out this possible role of food. However, selection of lower altitudes corresponds with the warmer microclimatic selection not only during winter and the coldest days, but also within the day, which supports that eland antelopes have a strategy for behaviourally preventing heat loss. We suggest that by selecting such thermal refuges of lower altitude and warmer microclimate during winter and the cooler part of the day when temperature was below the thermal neutral zone, eland might be able to reduce the thermal gradient between body temperature and ambient temperature ($T_b - T_a$). Hence, eland were able to maintain homeothermy, which is supported by the results of our body temperature study which showed that there were no differences in amplitude of body temperature between the seasons (Shrestha et al. 2012). Though for this study we did not quantify the energetic advantage of this behavioural response, a biophysical model study carried out in the same area during winter showed that indeed the model of eland maintained homeothermy with little or no increment in endogenous energy during the midday with the presence of solar radiation, i.e., in a warmer habitat. However, the eland model needs to spend as much as 150 to 180 J.s⁻¹ to maintain homeothermy in the absence of solar radiation during night (Hetem et al. 2011). Therefore, we propose that selection of a lower altitude and a warmer microclimate might have such energetic advantages for these eland as well.

In contrast to our hypothesis, eland selected relatively lower altitudes during the summer and similar altitudes compared to the average altitude of the study area in December. They also did not show the daily rhythm of altitude selection as expected. This discrepancy indicate that either the selected altitudes, although they were higher than the altitudes during winter, were sufficient to avoid summer heat stress for eland or that, the magnitude of the heat stress was not high enough that force eland to actively seek higher altitudes. In line with this idea, eland selected a cooler habitat, at least in the morning during summer (Fig. 8b), when they were more active, perhaps while foraging. Further, the selection of cooler habitats was more evident during the three hottest days when the average temperature of the study area was between 28 °C and 30°C, which is close to the upper end of the thermo-neutral zone of the eland (Taylor & Lyman 1967). During these hot days, eland were selecting not only cooler microclimates, but they also were selecting cooler habitats during the morning (6:00-8:00) and late after-noon (14:00-16:00) (Fig. 9b), when they were more active perhaps while foraging. This active behaviour, such as foraging, can increase heat production fivefold when compared to standing idle, as has been found in cattle (Malechek & Benton 1976). However, during midday they did not select cooler habitats as expected. We do not have a clear explanation for this discrepancy, except that during midday eland were not active. Being less active at the time of maximum ambient temperature and solar radiation perhaps decreases the thermal heat load generated from muscular activity. Support for this comes from behavioural studies in Kenya (Lewis 1977), Namibia (Fuller et al. 1999) and South Africa (Shrestha *et al.* in preparation), which showed that eland were inactive during midday when heat stress was high. Hence, we suggest that eland selected a cooler microclimate only when temperatures were near to the upper end of its thermo-neutral zone to avoid high temperature.

We have demonstrated that eland at its southern distributional range use a range of behavioural adaptations to cope with hot and cold temperatures. This tropical antelope with a limited capacity to physiologically respond to cold stress selected lower altitudes and warmer

microclimates on a daily and seasonal scale to cope with daily and seasonal variation in ambient temperatures. In contrast, during summer eland selected cooler microclimates only when temperatures were near to the upper end of its thermo-neutral zone, suggesting that the selected altitudes were either sufficient to avoid heat stress or that the magnitude of the heat stress was not high enough to make them to actively seek sites at higher altitude with cooler temperatures. Selection of these microhabitats of altitude and microclimate can help individuals to find thermal refuge in extreme events which predicted to increase due to climate change. Understanding such behavioural responses of animals to local climatic and topographical variation at fine temporal scales contributes to accurately predict effects of climate change on the distribution of animals, something which is largely ignored by statistical and mechanistic models applied to date. Current models might overestimate the effects of climate change (Sears et al. 2011; Dobrowski 2011) because these models do not take into account behavioural adaptations, such as the ability of animals to actively select the best or least detrimental microclimate. Because large mammals can actively locate themselves within the larger landscape, their tolerance to climate change may be larger than generally assumed and this ability may therefore mask the effect of climate change.

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Chapter 4

Buffering resource variability: Adaptive
home range size of three antelope
species over time and space in South
Africa

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Abstract

Adjusting home range size over time and space can be a primary behavioural mechanism of an individual to maximize access to limited resources. We investigated home range size variation of eland, wildebeest and impala over time (seasons) and between two climatically contrasting areas in South Africa (Mapungubwe National Park and Asante Sana Game Reserve) using GPS collars. First, we tested the hypothesis that the home range size of antelopes are larger in resource-poor seasons such as winter (cold, dry season) and spring (hot, dry season) than in the resource-rich summer (hot, wet season) within a study area (the habitat productivity hypothesis). Secondly, we hypothesized that the home range size of antelopes from populations at the edge of their distribution (Asante Sana with long, cold winters) will be larger than the home range size of conspecifics within their core distribution range (Mapungubwe with short, mild winters) (the core vs. edge hypothesis). In agreement with the habitat productivity hypothesis, the home range size of wildebeest in Mapungubwe was 3 to 4 times larger during the dry season (winter: **38** ha, and spring: **65** ha) than the one in the wet season (**14** ha), but their home range size did not differ across any season in Asante Sana. Contrary to the core vs. edge hypothesis, the wildebeest in Mapungubwe showed a 4 to 7 times larger home range size in the dry season than the wildebeest in Asante Sana (edge, winter: **9** ha and spring: **9** ha). For impala, the home range size was larger during the dry season than during the wet season in Asante Sana but not in Mapungubwe. Impala in Asante Sana showed a 4 to 14 times larger range size during the dry season (winter: **28** ha, and spring: **13** ha) than the impala in Mapungubwe (winter: **2** ha and spring: **3** ha). The home range size of eland was not different across any season in Asante Sana and Mapungubwe, while their home range size in Mapungubwe (**150** ha) was larger than that in Asante Sana (**71** ha). Our results suggest that the home range size of antelope species is a response to resource quality and availability specific to the local habitat. Although the ability to adjust the size of the home range can buffer the impact of climate change to some extent, the survival of these

Adaptive home range size over time and space

antelope species will primarily depend on sporadic dry season rainfall and their ability to track the heterogeneously distributed resources.

Key words: home range, adaptive behaviour, climate change, Mopane veld, subtropical thicket

Introduction

A home range is an area utilized by an animal to obtain resources for its survival and reproduction (Burt 1943; Jewell 1966). Therefore, the home range size is expected to be large enough to satisfy the requirements for metabolic energy (McNab 1963; Lindstedt et al. 1986; Reiss 1988), reproduction and the raising of offspring (Jewell 1966) with, over time, important consequences for population dynamics (Mosnier et al. 2003; Wang & Grimm 2007; Gaillard et al. 2010). Interspecific variation in home range size has a strong link with body size as there is a clear allometric relationship between body size and home range (McNab 1963; Du Toit 1990; Kelt & Van Vuren 1999; Ottaviani et al. 2006). In contrast, intraspecific variation in home range size is thought to be mainly affected by availability of resources (Lacher & Mares 1996; Tufto et al. 1996; McLoughlin & Ferguson 2000; Dussault et al. 2005; Relyea et al. 2000; Shannon et al. 2010; Van Beest et al. 2011). Most of these studies of home range sizes focussed either on interspecific comparisons based on meta-data or on single species in one specific area for a specific time period. Comparisons of home range size across various spatial and temporal scales are lacking (Saïd et al. 2009; Romeo et al. 2010).

Understanding the dynamics of behavioural traits such as home range size across spatial and temporal scales will enhance knowledge on behavioural flexibility with respect to the prevailing environment. For instance, animals inhabiting resource-poor areas may have larger home range size to satisfy their energetic needs than their conspecifics from resource-rich areas (Koprowski et al. 2008). Further, quality and quantity of the food differs over time in many ecosystems and hence, home range size is expected to be larger during periods when resources are low in quality and quantity than in periods with resources of higher quality and quantity: this is named ‘the habitat productivity hypothesis of home range size’ (Harestad & Bunnell 1979; Relyea et al. 2000; Shannon et al. 2006; Dussault et al. 2005). Understanding such adjustment in home range size could be particularly relevant for African antelopes,

which inhabit arid and semi-arid ecosystems in unpredictable environments where food availability depends on erratic rainfall (Rutherford 1980; Chamaille-Jammes & Fritz 2009). In the present context of climate change, antelopes from southern Africa are likely to experience an increased variability in climatic condition together with an increased frequency of drought periods (Lyon 2009). This situation could further worsen with the predicted reduction of rainfall and an increased frequency of droughts in the coming years in the region (IPCC 2007).

It has been argued that habitats at or near the edge of an animal's distribution are marginal and suboptimal in terms of food and climatic conditions (Parsons 1991; Spicer & Gaston 1999; Gaston et al. 2009; Busch et al. 2011). Therefore, a population of a species at or near the edge of its distributional range is likely to have a relatively larger home range than their conspecific at or near the core of the distribution due to suboptimal food and climatic conditions (Koprowski et al. 2008; Coleman & Downs 2010; Romeo et al. 2010). To persist with changing climatic conditions, an animal has to track its climatic envelope or it must be able to expand its tolerance limits by means of behavioural or physiological adjustment (Huey & Tewksbury 2009; Berg et al. 2010). Whatever the options available for the animals, behavioural adjustments such as adjusting home range size might be one of the immediate responses to cope with the changing climatic conditions because such a phenotypic response could provide increased environmental tolerance (Via et al. 1995). Therefore, knowledge of home range size dynamics in core and edge habitats of an animal's distribution is important to understand the adaptive capacity of a species to cope with a changing climate.

We investigated variation of home range size of three African antelopes *Taurotragus oryx* (\approx 420 kg), blue wildebeest *Connochaetes taurinus* (\approx 180 kg) and impala *Aepycerus melampus* (\approx 50 kg) across different seasons with variation in resource availability and in a core area (that is, in Mapungubwe National Park) versus an area at the edge of the geographical

distribution (in this case, Asante Sana Game Reserve) in South Africa. We first compared the seasonal home range sizes of each species within each area between three different seasons. Food is the most important factor determining an individual's home range size (McLoughlin & Ferguson 2000), but resources in these semi-arid to arid areas can drastically vary over time and space (Chamaille-Jammes & Fritz 2009). Therefore, we hypothesize that the seasonal home range size of a species will vary across the seasons. We therefore predict that the home range size of animals of the same species will be larger in the resource-poor season, i.e. winter (the cold and dry season) and in spring (the hot and dry season), than in the resource-rich summer (hot and wet season) in line with the habitat productivity hypothesis.

Mapungubwe National Park is situated in the northern part of South Africa where the climate is less seasonal with hot summers and mild winters (O'Connor & Kiker 2004; Mucina & Rutherford 2006), whereas Asante Sana is situated at higher altitudes in the Karoo where the climate is more seasonal with long and cold winters with freezing ambient temperatures and even with occasional snow (Mucina & Rutherford 2006; Lindsay et al. 2009). Since many African artiodactyls including South African antelopes evolved in less seasonal environments under hot and dry conditions (Haltenorth & Diller 1994; Flagstad et al. 2001; Mitchell & Lust 2008), and their physiological responses to cold temperatures are limited due to their high critical minimum temperature, narrow zone of thermo-neutrality and high conductance (low insulation value) (Scholander 1955; Taylor & Lyman 1967; Hofmeyr 1981), we hypothesize that the habitats with long and cold winters at the edge of the geographical range (Asante Sana) are suboptimal for these tropical antelopes. Therefore, to investigate the differences in home range sizes in core and edge habitat, we compared the seasonal home range size of each species between Mapungubwe National Park (taken as 'core habitat') and Asante Sana Game Reserve (taken as 'edge habitat'). We hypothesize that the seasonal home range size of antelopes from Mapungubwe will be smaller than the range size of conspecifics from Asante Sana (which we named 'core vs. edge hypothesis').

Methods and Materials

Study area

The study was carried out in Mapungubwe National Park (29°12' - 29°23'E; 22°15' - 22°30'S, hot, less seasonal) and in Asante Sana Game Reserve (24°52' - 25°04'E; 32°15' - 32°21'S, the more seasonal area with cold winters), situated in the northern and southern part of South Africa respectively. The altitudinal range in Mapungubwe varies from 300m - 780m asl, whereas in Asante Sana it varies between 1000m - 2400m asl.

The climate of both areas is semi-arid to arid. In Mapungubwe, the winter is mild with an average daily air temperature of 20°C while summer temperatures can reach 45°C. Most of the rainfall occurs strictly during the summer months with an annual mean of 300-400mm (O'Connor & Kiker 2004; Mucina & Rutherford 2006). The vegetation type of Mapungubwe can be classified as Mopani Veld (Acocks 1988). More than 80% of the area is covered by *Colophospermum mopane* woodland (O'Connor & Kiker 2004). Riverine and flood plain vegetation includes *Acacia xanthophloea*, *Hyphaine petersiana*, *Salvadora australis*, whereas *Acacia stuhlmanni* communities were found in old abandoned land.

In Asante Sana, winter can be harsh with an average daily temperature of 13°C coupled with many days of freezing temperature and even a few days of snowfall. The summer can be hot with air temperatures of more than 35°C. The number of frost days in the region is about 25 (range: 8-40 days). About 70% of the total rainfall occurs during the summer months but it also gets rain during the winter season associated with the cold fronts and run off provided by the infrequent snowfalls (Kerley & Boshoff 1997). The long-term annual mean rainfall (1948-1996) recorded at 1000m was 318mm (range: 171-706mm; SD = 112mm), while at higher altitude (1300m), it was relatively higher: 500-550mm (range: 177-853mm; SD = 152mm). There are three streams supplemented by a number of springs, which keep water throughout drought periods (Boshoff & Kerley 1997).

The vegetation type of Asante Sana is associated with Camdeboo escarpment thicket and Karoo escarpment grassland (Mucina & Rutherford 2006). The montane grassland occurs on the higher altitude with *Merxmuellera disticha* and *Themeda triandra* grasses as the dominant species. The mesic valley thicket, dry open valley thicket, riverine woodland and Karoo shrubland are the other main vegetation types with *Olea europea*, *Rhamnus prinoides*, *Acacia karroo*, *Rhus lucida*, *Eriocephalus ericoides* and *Pentzia incana* as dominant species (Furstenburg 2000).

Data collection and analysis

We captured and fitted GPS collars to five eland, five wildebeest and five impala in Mapungubwe National Park (late April 2008) and the same number in Asante Sana Game Reserve (except only 3 impala) during late May 2008. The GPS collars recorded location (latitude, longitude in WGS 1984) at 2-hour intervals with an accuracy of ~10m (African Wildlife Tracking, Pretoria, South Africa). Out of five individuals of each species sampled in each area, only two impala, three eland and five wildebeest yielded data for about 10 months in Mapungubwe, whereas in Asante Sana, only three impala, four eland and four wildebeest yielded data for about 11 months. All experimental procedures were approved by the Animal Ethics Screening Committee of the University of the Witwatersrand (protocol no. 2007/60/4) and South African National Parks.

We collected weather data from a portable weather station (Hobo Weather Station, Onset Computer Corporation, Pocasset, MA, USA) installed approximately at 1m above the ground on a mown lawn in the middle of Mapungubwe National Park (29° 24'E, 22° 12'S) and in Asante Sana (24° 58'E 32° 18'S). Standard (150 mm) black globe temperature (°C) and ambient (dry-bulb) temperature (°C) were recorded from June 2008 to February 2009. We obtained daily rainfall data during the study period from each study site.

Adaptive home range size over time and space

Using Arc View 3.3 (ESRI, USA) with the animal movement extension software, we estimated monthly home range size of each animal using a fixed kernel (90%) with the reference method for calculation of the smoothing factor h (Kernohan et al. 2001; Rivrud et al. 2010). Monthly home range sizes (ha) were \log_{10} transformed to meet the assumption of normality and homogeneity of variance. Then, we performed a General Linear Model (GLM) with season as fixed factor, separately for each species per area to test the effect of season on home range size variation (for testing ‘habitat productivity hypothesis’). Further, a Sidak multiple comparison was performed to identify differences between the seasons. To test the effect of study area on the seasonal home range of each species (for the ‘core vs. edge hypotheses’), we carried out a GLM for each species separately with season and area as fixed factors including their interaction, followed by Sidak multiple comparison. All the statistical tests were two-tailed with 0.05 significance level.

We only used data from June 2008 to February 2009 and defined three seasons: winter (June–August), spring (September–November) and summer (December–February) based on prevailing climatic conditions (Table 3).

Table 3. Environmental conditions (mean \pm SEM) during winter, spring and summer in the less seasonal site (Mapungubwe) and the more seasonal site (Asante Sana).

	Winter		Spring		Summer	
	Mapungubwe	Asante Sana	Mapungubwe	Asante Sana	Mapungubwe	Asante Sana
Globe temperature (°C)						
Daily mean	21.5 \pm 2.8	13.4 \pm 4.1	29 \pm 4.5	19.5 \pm 5	31.2 \pm 3.2	25.3 \pm 3
Daily maximum	41.0 \pm 5	28.8 \pm 4.2	46.8 \pm 7.4	36.5 \pm 6.4	51.0 \pm 5.6	43.1 \pm 4.3
Daily minimum	8.6 \pm 3.6	2.2 \pm 5	17.2 \pm 4	5.8 \pm 5.2	20.8 \pm 1.9	11.7 \pm 3.3
Air temperature (°C)						
Daily mean	19.8 \pm 2.6	12 \pm 4.5	27.0 \pm 4	16.7 \pm 5	28.3 \pm 2.7	21.7 \pm 3
Daily maximum	32.7 \pm 3.4	20.8 \pm 4.2	38.0 \pm 6	26.2 \pm 5.6	38.0 \pm 4.3	30.7 \pm 3.9
Daily minimum	9.9 \pm 3.6	3.5 \pm 5.1	18.2 \pm 3.7	7.0 \pm 5	21.5 \pm 1.9	12.9 \pm 3.1
Total rainfall (mm)		86	46	23	222	81

The total rainfall during the study period was 268 mm in Mapungubwe and 190 mm in Asante Sana (Table 3). Mapungubwe received about 83% of its rainfall during summer while it had no rain in winter and only two days of rain in spring. In Asante Sana, although the total

amount of rain was less than in Mapungubwe, it was more evenly distributed and was also supplemented by melting snow on the mountains particularly in winter. Winter was dry and cold, whereas summer was wet and hot, and spring was hot and dry in both study areas (Table 3).

Results

Intra-specific comparison of home range size between seasons

The home range size of eland was not different between the three seasons in Asante Sana ($F_{2,40}=0.31$, $P=0.74$, $R^2=0.02$, Fig.10a) and in Mapungubwe ($F_{2,22}=1.4$, $P=0.27$, $R^2=0.11$, Fig.10b).

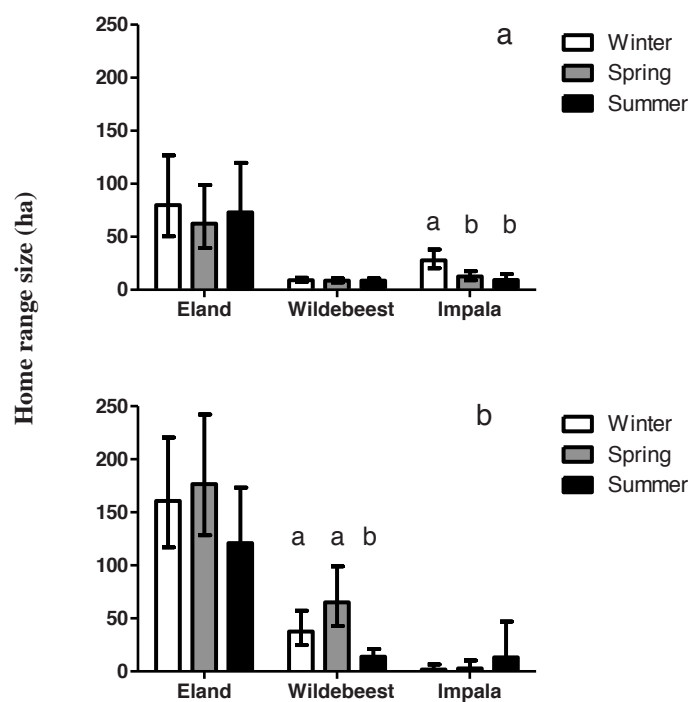


Figure 10. Seasonal home range sizes of eland, wildebeest and impala in (a) Asante Sana and (b) Mapungubwe National Park. Shown are the back-transformed estimated means from a log10 scale. The 95%-CI error bars are asymmetrical because of this back transformation. Letters indicate significant differences.

Adaptive home range size over time and space

Wildebeest in Asante Sana did not differ in their home range size between the three seasons ($F_{2,41}=0.04$, $P=0.96$, $R^2=0.002$, Fig.10a), while home range sizes of wildebeest in Mapungubwe differed significantly between the seasons ($F_{2,42}=14.24$, $P<0.0001$, $R^2=0.40$, Fig.10b). The summer home range sizes of wildebeest were significantly smaller than the one in spring ($P<0.0001$, Fig.10b) and winter ($P<0.0001$, Fig.10b), whereas spring and winter did not differ ($P=0.19$, Fig.10b). Impala had significantly different home range sizes in the three seasons in Asante Sana ($F_{2,19}=11.26$, $P=0.001$, $R^2=0.49$, Fig.10a) but not in Mapungubwe ($F_{2,15}=3$, $P=0.08$, $R^2=0.29$, Fig.10b). Winter home ranges of impala in Asante Sana were significantly larger than in spring ($P=0.005$, Fig.10a) and summer ($P=0.001$, Fig.10a), whereas spring and summer were not different ($P=0.486$, Fig.10a).

Table 4. Comparative average seasonal home range sizes (in ha) of eland, wildebeest and impala in winter, spring and summer in Asante Sana and Mapungubwe. Shown are the back-transformed estimated means from a \log_{10} scale. The 95%-CI are asymmetrical because of this back transformation. NS indicated no significant differences, *** indicates significant differences.

Species/Season	Asante Sana	Lower	Upper	Mapungubwe	Lower	Upper	
Eland							
Winter	80.0	54.0	118.3	160.7	96.9	266.4	NS
Spring	62.5	42.2	92.4	176.5	106.4	292.6	NS
Summer	73.0	47.9	111.1	121.0	68.2	214.7	NS
Wildebeest							
Winter	9.1	6.5	12.7	37.6	27.0	52.4	***
Spring	8.6	6.0	12.0	65.2	46.8	90.8	***
Summer	8.6	6.1	12.1	13.9	9.9	19.4	NS
Impala							
Winter	27.7	13.7	56.1	1.8	.8	4.4	***
Spring	12.6	6.0	26.7	2.9	1.2	6.8	***
Summer	9.3	3.2	26.8	13.2	5.6	31.3	NS

Intra-specific comparison of home range size between study areas

The home range size of eland was significantly different between the two study areas ($F_{1,62}=14.54$, $P<0.0001$, $R^2=0.22$). Eland in Mapungubwe had a larger home range size (151 ha, 95% CI 111 to 205) than those in Asante Sana (71 ha, 95% CI 57 to 90; $P<0.0001$). Season ($F_{2,62}=0.312$, $P=0.733$) and the interaction between season and study area

($F_{2,62}=0.664$, $P=0.519$) was not different (Table 4). The home range size of wildebeest was significantly different between the two study areas ($F_{1,83}=82.78$, $P<0.0001$, $R^2=0.61$, Table 4) and seasons ($F_{2,83}=11.12$, $P<0.0001$) including the interaction between study area and season ($F_{2,83}=10.75$, $P<0.0001$). Interestingly, the spring ($P<0.0001$) and winter ($P<0.0001$) home range of wildebeest in Mapungubwe was significantly larger than the ones in Asante Sana. Their summer home range did not differ between the two study areas ($P=0.091$). Impala exhibited significantly different home range sizes in the two study areas ($F_{1,34}=15.97$, $P<0.0001$, $R^2=0.52$), season was not different ($F_{2,34}=1$, $P=0.376$), whereas there was a significant interaction between season and study area ($F_{2,34}=6.39$, $P=0.004$). The home range size of impala in Asante Sana was significantly larger in spring ($P=0.006$) and winter ($P<0.0001$) than in Mapungubwe. However, impala did not differ in their summer home range between the study areas ($P=0.66$).

Discussion

We investigated home range size variation of three antelopes over time (three seasons) and space (core vs. edge habitat) in a semi-arid system in South Africa. We show that the wildebeest in Mapungubwe exhibited (3-7 times) larger home range sizes during the resource-poor season (dry season) compared to the resource-rich season (wet season), which agrees with the habitat productivity hypothesis. However, the wildebeest in Asante Sana did not exhibit significantly different home range sizes over the three seasons. The comparison of intra-specific home range sizes between the two areas revealed that wildebeest in Mapungubwe (core habitat) had larger home range sizes in winter and spring than in Asante Sana (edge habitat) thus rejecting the core vs. edge hypothesis. A plausible explanation for such discrepancy might be given by the poor quality and availability of forage in Mapungubwe during the dry season. Indeed, in Mapungubwe, there was no rainfall at all during the winter season and very little rain late in the spring, while rainfall is the main driver of the quality and quantity of grass in these semi-arid systems (Rutherford 1980; O'Connor &

Kiker 2004; Chamaille-Jammes & Fritz 2009; Buitenwerf et al. 2011). For example, in Mapungubwe National Park, the biomass of grass was reported to reduce by 40% in the dry scenario (510 kg/ha) compared to the wet scenario (829 kg/ha) (O'Connor & Kiker 2004). Not only the availability but also the nutritional quality of grass can decline drastically during the dry season in this semi-arid ecosystem. For example, in Etosha National Park in southern Africa (with a similar amount of rainfall as in Mapungubwe), crude protein in grass was declined from 17.7% during the rainy season to a mere 4.1% in the dry season (Berry 1982), which is less than the assumed minimum maintenance requirement (5-6%) for a large ruminant (Sinclair 1974; Robbins 1993; Van Soest 1994). Therefore, we suggest that forage quality and quantity for wildebeest in Mapungubwe declined much during the dry season (winter and spring) due to lack of rainfall. Hence, wildebeest had to increase their home range to acquire discretely distributed grass resources leading to large range sizes during the dry season.

In contrast, wildebeest in Asante Sana inhabited short grass habitats at higher altitude (1300-1400m), where rainfall events occurred even during the winter and spring in the form of rainfall and snowfall, perhaps maintaining sufficient quality and quantity of grasses over the seasons. Further, we also suspect that the higher altitude (1300-1400 m), where wildebeest in Asante Sana mainly lived, received more rain, a common feature in this system (Kerley & Boshoff 1997; Mucina & Rutherford 2006). For the wildebeest in Asante Sana, food quality and quantity is not expected to be a limiting factor because of the rainfall even during the dry season (winter and spring). Therefore, we did see smaller home range size in Asante Sana than in Mapungubwe which support the habitat productivity hypothesis (Harestad & Bunnell 1979; Relyea et al. 2000; McLoughlin & Ferguson 2000).

For impala, their home range size in Asante Sana was almost two times larger during the resource-poor seasons (winter and spring) compared to the resource-rich season (summer).

In contrast, the range size of impala in Mapungubwe did not differ at any season.

The comparison of home range size between the two areas showed that impala in Asante Sana had larger home range sizes during the resource-poor winter (14 times) and spring (4 times) than the impala in Mapungubwe. However, their home range size during the resource-rich summer was not different. This can be explained by the idea that the habitat in Asante Sana for impala was comparatively less productive and also, the food resources perhaps more discretely distributed in the landscape at least during the dry season than in the habitat in Mapungubwe. Impala in Asante Sana strictly inhabited the lower Karoo shrub land and dry open valley thickets dominated by *Acacia karroo*, *Rhus species* and annual grasses such as *Stipagrostis obtusa*, *Eragrostis curvula* and *Aristida diffusa*, which are deciduous during the dry season (except *Rhus species*) (Boshoff & Kerley 1997; Kerley & Boshoff 1997). Therefore, the larger home range size of impala in Asante Sana during the dry season was presumably a response to the search and acquisition of other evergreen food resources such as *Rhus spp*, *Grewia spp* and *Rhigosum obovatum*, when their principle food resources such as *Acacia karroo* and annual grasses were not available. In line with this argument, giraffe in the Eastern Cape, which diet primarily depends on *Acacia karroo*, switched to evergreen species such as *Rhus species* going from the wet to the dry season (Parker & Bernard 2005). Further, impala shifted their diet from predominantly grass in the wet season to browse during the dry season (Sponheimer et al. 2003; Kos et al. 2011). Interestingly, during the summer season (wet season), when there were enough food resources (*Acacia karroo* and grasses), the impala in Asante Sana did not extend their home range size and home range size was similar between the study areas.

However, for impala in Mapungubwe we argue that the availability of food is expected not to be limiting because they inhabited the riparian habitats along the Limpopo river where availability of food is less variable between the seasons due to higher soil moisture availability in the riparian habitat (Pettit & Naiman 2007). As a result, we suggest that impala did not exhibit seasonal variation in home range size.

The home range size of eland in Mapungubwe (151 ha) was larger (2 times) compared to the eland in Asante Sana (71 ha) but there was neither a seasonal effect nor an interaction effect between area and season on home range size despite the result that the mean home range size of eland in Mapungubwe was larger (>2 times) in winter and spring (Table 4). Such discrepancy might be explained by the larger variation among individual home range sizes (Fig 10). We suggest that the observed large home range size of eland in Mapungubwe might reflect the need to track the patchily distributed forage such as Mopane (*Colophospermum mopane*) twigs and green leaves during the dry season when other browse species are not available due to their deciduousness. Indeed, this semi-arid veld of Mapungubwe is dominated by Mopane vegetation (> 80%) (O'Connor & Kiker 2004), while most of the other dominant trees and shrubs species (*Acacia spp*, *Combretum spp*) are deciduous during the dry season. Mopane, a deciduous tree with a long leaf carriage duration and a very short leafless period is an important food resource for eland during the dry season (Dekker & Smit 1996). Further, we observed that the leaf senescence and leaf flush of Mopane in Mapungubwe occurs patchily over time and space, which may result in a mosaic of patches with or without food for eland during the dry season. Hence, we argue that eland in Mapungubwe had to range over large areas to acquire patchily distributed Mopane twigs and green leaves to satisfy their high energetic demands, particularly during the dry season. In support of this argument, eland in Northern Tuli Reserve in Botswana with similar vegetation and climate (reserve adjacent to Mapungubwe) heavily browsed on nutritious and palatable twigs of

Mopane during the winter (Styles & Skinner 2000) and young green leaves at the end of the spring season when other browse was unavailable (Styles & Skinner 1997).

In contrast, eland in Asante Sana did not differ in their home range size over the seasons while their range size was smaller compared to the eland in Mapungubwe. A plausible explanation might be that the availability of forage resources, particularly browse, within their habitat remains fairly constant throughout the year. Indeed, in Asante Sana, the dominant vegetation type is subtropical thicket vegetation, which consists of evergreen and nutritious trees and shrubs (such as *Grewia spp*, *Olea spp*, *Rhus spp*, *Euclea spp*, *Rhigozum obovatum*) throughout the year (Seydack & Bigalke 1992; Stuart-Hill & Aucamp 1993). Since the diet of eland is predominantly browse (Hofmann & Stewart 1972; Watson & Owen-Smith 2000), the quality and quantity of browse might decline less drastically between the wet and the dry season in Asante Sana, which is dominated by the evergreen species, than in the deciduous Mopane veld in Mapungubwe. Hence, we observed a smaller home range size in eland in Asante Sana than in Mapungubwe.

We studied the adaptive response in home range size of three South African antelopes at a spatio-temporal gradient and demonstrated that these antelopes adjusted their home range size temporally and spatially in accordance with their habitat characteristics and forage requirement. In agreement with the habitat productivity hypothesis, impala in Asante Sana and wildebeest in Mapungubwe exhibited a larger home range size during the dry than during the wet season. In contrast, eland in both areas, impala in Mapungubwe and wildebeest in Asante Sana did not show different home range sizes between the seasons. Further, intra-specific comparison between the two study areas (core vs. edge habitat) revealed that only impala in Asante Sana (edge habitat) showed a larger home range size during the dry season, as expected. In contrast, eland and wildebeest in Mapungubwe (core habitat) showed larger home range sizes than their conspecifics in Asante Sana (edge habitat). The observed

variation in range size is most likely a response of the species to forage quality and availability specific for the local habitat. We interpret this behaviour as a remarkable adaptive response to changing environment. Although the ability to adjust the size of the home range can buffer the impact of global climate change to some extent, human barriers to movement and an increased level of habitat destruction, coupled with an expected increase in frequency of drought in Southern Africa (IPCC 2007; Lyon 2009), indicates that the survival of these antelopes will primarily depend on dry season rainfall and hence on their ability to track the heterogeneously distributed resources.

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Chapter 5

Body temperature variation of South African antelopes in two climatically contrasting environments

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Abstract

To understand the adaptive capacity of a species in response to rapid habitat destruction and climate change, we investigated variation in body temperature (T_b) of three species of antelope, namely eland, blue wildebeest and impala, using abdominally-implanted temperature data loggers. The study was conducted at two climatically contrasting environments in South Africa, one with a less seasonal and mild winter (Mapungubwe National Park) and the other with a more seasonal, long and cold winter (Asante Sana Game Reserve). Since the habitat with long and cold winters would be suboptimal for these African antelopes, which evolved in less seasonal and hot environments, antelopes in Asante Sana were expected to exhibit a larger amplitude in T_b and a lower minimum body temperature ($\text{Min}T_b$) during winter to reduce T_b and the ambient temperature (T_b-T_a) gradient to save energy. In both eland and impala, 24-hour body temperature amplitude did not differ between the study sites, regardless of season. Conversely, wildebeest in Mapungubwe showed a higher variability in the 24-hour amplitude of body temperature and also a lower $\text{Min}T_b$ during winter and spring than the wildebeest in Asante Sana. This variation in T_b among Mapungubwe wildebeest was influenced by both the amplitude of ambient temperature (positive) and cumulative rainfall (negative), which was not the case for wildebeest in Asante Sana. We propose that the low $\text{Min}T_b$ of wildebeest in Mapungubwe was the result of nutritional stress during winter and spring; an evident response even during a year of average rainfall. Therefore, these wildebeest apparently live in a physiologically stressful environment. With the predicted increase in the frequency and intensity of drought periods in southern Africa, wildebeest, and other grazers, will likely experience greater nutritional stress in the future.

Key words: body temperature, macro-physiology, physiological plasticity, homeothermy, heterothermy, nutritional stress

Introduction

Animals exhibit physiological plasticity to cope with daily and seasonal variations in ambient temperature within their environment (Garland and Adolph, 1991; Angilletta et al., 2010). As ambient conditions vary considerably across temporal and spatial scales, populations are expected to exhibit distinct physiological responses across these scales (Dunbar and Brigham, 2010). Understanding intra- and inter-variability of physiological traits along these temporal and spatial scales in relation to ambient temperature, a domain of macro-physiology (Chown et al. 2004; Chown and Gaston, 2008) is essential to understand the adaptive capacity of a species, defined here as the evolutionary changes and plastic physiological and / or behavioural responses of a species to adapt to changing conditions (Williams et al. 2008). Understanding adaptive capacity may help to explain species distribution and may lead to a causal understanding of biodiversity patterns and community ecology. In the present context of rapid habitat destruction and climate change, understanding the physiological plasticity, therefore the adaptive capacity of a species in relation to a changing environment is essential to comprehend the ecological impact of environmental changes on animal populations (Chown et al., 2004; Gaston et al., 2009; Canale et al., 2010; Chown et al., 2010).

The field of macro-physiology predicts that populations of a species inhabiting different environments and microhabitats should exhibit different physiological strategies (Chown et al., 2004; Chown and Gaston, 2008; Gaston et al., 2009). Yet, to date, very little research has focused on the macro-physiology of long-lived endotherms, such as antelopes (Fuller et al., 2010; Boyles et al., 2011). Most traditional physiological studies on long-lived endotherms were conducted under controlled conditions where animals did not have the opportunity to use their suite of behavioural adjustments to cope with the changing climatic conditions. Furthermore, it has been argued that a population at or near the edge of its distribution range might be physiologically stressed because these habitats would be suboptimal in terms of food and climatic conditions (Parsons, 1991; Spicer and Gaston, 1999; Gaston et al., 2009;

Busch et al., 2011). With a rapidly changing climate, animals are predicted to expand their range to track their climatic envelope (Feder 2010). Due to these changes, many animals that occupied habitats within their range have then to live at their range limits and beyond, which might be sub-optimal in terms of food and climate. An understanding of the dynamics of behaviour and physiological plasticity of populations living at their range margins at present is important to predict how well a species will be able to cope with climate change.

We carried out the first macro-physiological study of three species of free-ranging antelope. We simultaneously measured body temperature (T_b) variability both temporally, over three seasons, and spatially, as the antelopes were distributed in two climatically contrasting environments in the northern and southern part of South Africa. At the northern field site, north of the tropic of Capricorn, the climate is less seasonal with hot summers and mild winters (O'Connor and Kiker, 2004; Mucina and Rutherford, 2006) whereas at the southern field site, the climate is more seasonal with long and cold winters during which ambient temperatures frequently drop below zero and with occasional snow in the mountains (Mucina and Rutherford, 2006; Lindsay et al., 2009). We selected three widely distributed antelopes of different body sizes, namely eland *Taurotragus oryx* (~ 420 kg), blue wildebeest *Connochaetes taurinus* (~ 180 kg) and impala *Aepycerus melampus* (~ 50 kg), as our study species. Since African antelopes evolved in less seasonal environments under hot and dry conditions (Haltenorth and Diller, 1994; Flagstad et al., 2001; Mitchell and Lust, 2008), these species might be adapted to dissipate heat rather than to conserve heat (Hofmeyr, 1981), hence their physiological responses to cold might be limited as a result of their high critical minimum temperature, narrow zone of thermo-neutrality and high conductance (low insulation value) (Scholander, 1955; Taylor and Lyman, 1967; Hofmeyr, 1981; Owen-Smith, 2000). Therefore, we hypothesize that habitats with cold winters, which are at the southern edge of their distribution range, are suboptimal for these antelopes and will present an energetic challenge for the maintenance of homeothermy. We predict that, in response to this

climatic challenge, antelopes in the southern field site will have a larger amplitude of T_b rhythm and a lower minimum T_b in winter compared to the antelopes in the less seasonal site with mild winters.

Materials and Methods

Study site

The study was carried out in Mapungubwe National Park (22°15' - 22°30' S; 29°12' - 29°23' E, the hot, less seasonal site) and in Asante Sana Game Reserve (32°15' - 32°21' S; 24°52' - 25°04' E, the more seasonal site with long and cold winters), situated in the northern and southern part of South Africa, respectively. The altitudinal range in Mapungubwe varies from 300 - 780 m a.s.l., whereas the range in Asante Sana varies between 1000 – 2400 m a.s.l.

The climate of both sites is semi-arid to arid. In Mapungubwe, the winter is mild with an average 24-hour ambient temperature of 20°C while summer ambient temperatures can reach a maximum of 45°C. Most rainfall occurs during the summer months with an annual mean of 300-400 mm (O'Connor and Kiker, 2004; Mucina and Rutherford, 2006). Though Mapungubwe is bordered by the Limpopo river, many of the rivers and streams are ephemeral and dry up during the winter and spring season (O'Connor and Kiker, 2004), however, Schroda dam consists of water throughout the year. The vegetation type of Mapungubwe can be classified as Mopani Veld (Acocks, 1988). More than 80% of the site is covered by *Colophospermum mopane* woodland (O'Connor and Kiker, 2004). Riverine and flood plain vegetation include *Acacia xanthophloea*, *Hyphaine petersiana*, *Salvadora australis* whereas *Acacia stuhlmanni* communities were found in old abandoned land.

In Asante Sana, winters can be harsh with an average 24-hour temperature of 13°C with many days of freezing temperature and even a few days of snowfall. The number of frost days in the region is about 25 (range: 8-40 days) (Kerley and Boshoff, 1997). The summer can be hot with maximum ambient temperatures reaching 38°C. About 70% of the total

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rainfall occurs during the summer months, but precipitation also occurs during the winter season and is associated with sporadic cold fronts (Kerley and Boshoff, 1997). The long-term mean annual rainfall (1948-1996) recorded at 1000 m was 318 mm (range: 171-706 mm; SD = 112 mm) while at a higher altitude (1300 m), the rainfall was 550 mm (range: 177-853 mm; SD = 152 mm) (Boshoff and Kerley, 1997). There are three perennial streams onsite supplemented by a number of permanent springs, which contain water throughout the drought periods (Boshoff and Kerley, 1997). The vegetation type of Asante Sana is associated with Camdeboo escarpment thicket and Karoo escarpment grassland (Mucina and Rutherford, 2006). The montane grassland occurs at the higher altitude with *Merxmüllera disticha* and *Themeda triandra* grasses as the dominant species. Mesic valley thicket, dry open valley thicket, riverine woodland and Karoo shrubland are the other main vegetation types with *Olea europea*, *Rhamnus prinoides*, *Acacia karroo*, *Rhus lucida*, *Erioccephalus ericoides* and *Pentzia incana* as the dominant species (Furstenburg, 2000).

Common ungulates found in the study sites are giraffe *Giraffa camelopardalis*, eland, kudu *Tragelaphus strepsiceros*, blue wildebeest, zebra *Equus burchelli*, gemsbok *Oryx gazella*, water buck *Kobus ellipsiprymnus*, impala and warthog *Phacochoerus aethiopicus*.

Data collection

We captured, collared (GPS/radio-telemetry, Africa Wildlife Tracking, South Africa) and implanted miniature thermometric data loggers (StowAway XTI, Onset Computer, Pocasset, MA, USA), covered in an inert wax, into the retroperitoneal in the right side lateral aspect of the abdomen of five eland, five wildebeest and five impala in Mapungubwe National Park (late-April 2008) and five eland, five wildebeest and three impala in Asante Sana Game Reserve (mid-May 2008). Surgical procedure was similar to that used previously (Fuller et al., 1999; Hetem et al., 2009; Hetem et al., 2010). These animals were radio tracked regularly (2-3 times per month) for monitoring purposes. We recorded body temperature (T_b) at 15-

minute intervals from May 2008 to February 2009. Before implantation, we calibrated each data logger in an insulated water bath with a high accuracy thermometer (Quat 100, Heraeus, Hanau, Germany). The data logger had a resolution of 0.04 °C with a measurement range from + 34 to + 46 °C. All experimental procedures were approved by the Animal Ethics Screening Committee of the University of the Witwatersrand (protocol no. 2007/60/4) and South African National Parks.

We collected weather data from a portable weather station (Hobo Weather Station, Onset Computer Corporation, Pocasset, MA, USA) installed approximately at 1m above the ground on a mown lawn in the middle of Mapungubwe National Park (29° 24'E, 22° 12'S) and in Asante Sana (24° 58'E 32° 18'S). Standard (150 mm) black globe temperature (°C) and ambient (dry-bulb) temperature (°C) were recorded from June 2008 to February 2009. We obtained daily rainfall data during the study period from each study site.

Data analysis

Out of 15 individuals sampled in Mapungubwe, only two impala, four wildebeest and three eland yielded complete data sets for nine months, whereas in Asante Sana, out of 13 individuals sampled, only two impala, four wildebeest and two eland yielded complete datasets for nine months. Therefore, we only used these data for all our analyses. For various reasons, the other data loggers yielded no or incomplete data. Two impala in Mapungubwe were killed by predators and we could not retrieve two (eland) data loggers in Mapungubwe and one (impala) in Asante Sana due to early battery failure. Moreover, two data loggers in Mapungubwe (one wildebeest and one impala) and four in Asante Sana (three eland and one wildebeest) stopped recording data early due to technical failure. We used data from June 2008 to February 2009 to give the animals at least two weeks to recover from surgery. We defined three seasons: winter (June-August), spring (September-November) and summer (December-February) based on prevailing climatic conditions.

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We calculated daily averages of the mean, maximum, minimum and amplitude of black globe and ambient temperature and compared the seasonal periods between the two study sites using a General Linear Model (GLM). To test the hypotheses about the T_b amplitude, we first calculated the amplitude (Maximum T_b – Minimum T_b of each day) of the daily rhythm of body temperature for successive 24-h periods, for each individual of each species. We averaged the amplitude of the body temperature for each individual of each species for each seasonal period. Then, we used two way repeated-measure ANOVA to test the hypothesis about the amplitude of body temperature variation between the two study sites and within the different seasons for each species separately, because the sample sizes for each species were not equal. ANOVAs were followed by a Bonferroni multiple comparison test.

We calculated the average daily maximum and minimum T_b for each seasonal period for each individual for each species, and performed two-way repeated-measure ANOVA followed by a Bonferroni multiple comparison test. While performing repeated-measure ANOVA, the degrees of freedom were corrected using the Greenhouse-Geisser correction for sphericity, if the sphericity assumption was violated (Field, 2009).

We also performed regression analysis to investigate the environmental influence on the measured body temperature variables. To do this, we regressed the daily amplitude of body temperature, averaged for all the individuals of a species in each study site, against the daily amplitude of ambient temperature (T_a) and bi-weekly cumulative rainfall. We also regressed the mean daily minimum T_b against the mean daily minimum T_a and bi-weekly cumulative rainfall. We used bi-weekly cumulative rainfall as a proxy for food and surface water availability because in a semi-arid system like our study sites, food availability mostly depends on rainfall (Deshmukh, 1984; Prins, 1988; Prins and Loth, 1988; Edwards, 1991; O'Connor and Kiker, 2004; Chamaille-Jammes and Fritz, 2009).

Results

Climate

The daily mean, maximum and minimum ambient temperature (T_a) and black globe temperature (BGT) were significantly higher in Mapungubwe in all three seasons than they were in Asante Sana (Table 5). The daily amplitude of T_a and BGT between the study sites differed only during the winter but not during spring and summer. The total rainfall during the study period was 268 mm in Mapungubwe and 190 mm in Asante Sana. Mapungubwe received about 83% of its rainfall during summer while it had no rain in winter and only two days of rain in spring. In Asante Sana, although the total amount of rain was less than in Mapungubwe, it was more evenly distributed and was also supplemented by melting snow on the mountains particularly in winter. In summer and spring, Mapungubwe was hotter and drier than Asante Sana whereas in winter, Asante Sana was much colder than Mapungubwe.

Table 5. Environmental conditions (mean \pm SEM) during winter, spring and summer in the less seasonal site (Mapungubwe) and the more seasonal site (Asante Sana).

	Winter			Spring			Summer		
	Mapungubwe	Asante Sana		Mapungubwe	Asante Sana		Mapungubwe	Asante Sana	
Globe temperature ($^{\circ}\text{C}$)									
24-h mean	21.4 \pm 0.4	13.4 \pm 0.4 *		29.0 \pm 0.4	19.5 \pm 0.4 *		31.2 \pm 0.4	25.3 \pm 0.4 *	
24-h maximum	41.0 \pm 0.6	28.8 \pm 0.6 *		46.8 \pm 0.6	36.5 \pm 0.6 *		51.0 \pm 0.6	43.2 \pm 0.6 *	
24-h minimum	8.6 \pm 0.4	2.2 \pm 1.3 *		17.2 \pm 0.4	5.8 \pm 0.4 *		20.8 \pm 0.5	11.5 \pm 0.5 *	
24-h amplitude	32.3 \pm 0.7	26.7 \pm 0.7 *		29.6 \pm 0.7	30.7 \pm 0.7 ns		30.3 \pm 0.7	31.7 \pm 0.7 ns	
Ambient temperature ($^{\circ}\text{C}$)									
24-h mean	19.8 \pm 0.4	12.0 \pm 0.4 *		27.0 \pm 0.4	16.7 \pm 0.4 *		28.4 \pm 0.4	21.6 \pm 0.4 *	
24-h maximum	32.7 \pm 0.5	20.8 \pm 0.5 *		38.0 \pm 0.5	26.2 \pm 0.5 *		38.0 \pm 0.5	30.9 \pm 0.5 *	
24-h minimum	9.9 \pm 0.4	3.5 \pm 0.4 *		18.2 \pm 0.4	7.0 \pm 0.4 *		21.5 \pm 0.4	12.8 \pm 0.5 *	
24-h amplitude	22.8 \pm 0.6	17.3 \pm 0.6 *		19.8 \pm 0.6	19.1 \pm 0.6 ns		16.5 \pm 0.6	18.1 \pm 0.6 ns	
Total rainfall (mm)	0	86		46	23		222	81	
Daylight hour	12.0 \pm 0.1	10.5 \pm 0.1		12.8 \pm 0.1	12.9 \pm 0.1 ns		13.9 \pm 0.1	13.9 \pm 0.1 ns	

* : $P < 0.0001$; ns : non-significant $P > 0.05$

Variation in body temperature

The daily T_b amplitude of impala did not significantly differ between the study sites ($F_{1,2}=0.001$, $P=0.98$) and seasons ($F_{2,4}=6.74$, $P=0.052$) (Fig.11a). The daily T_b amplitude of eland did also not differ between the study sites ($F_{1,6}=3.27$, $P=0.11$) and seasons ($F_{2,6}=0.39$,

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P=0.69) (Fig.11b). Therefore, impala and eland were able to maintain homeothermy throughout the year despite being exposed to different climates and habitats.

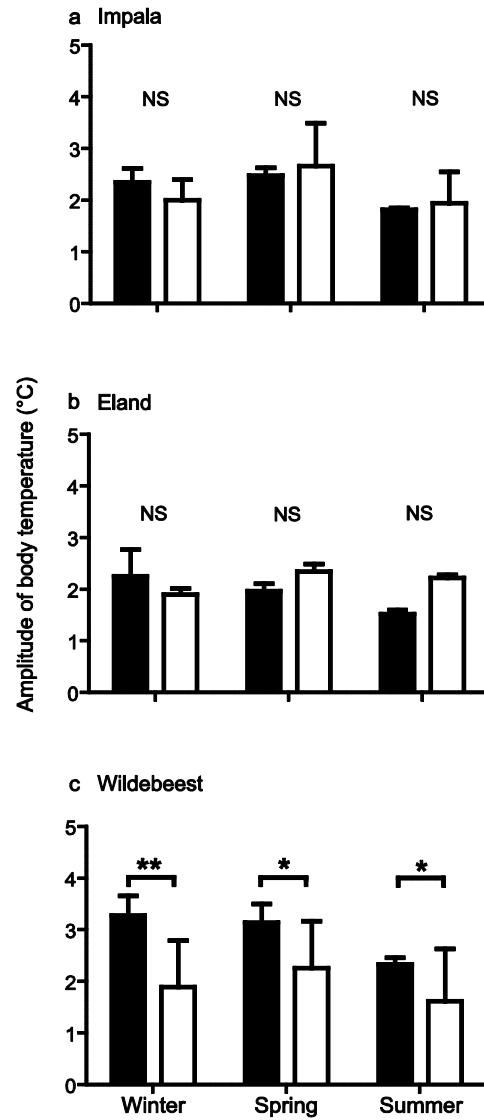


Figure 11. Mean (\pm SEM) 24-hour amplitude of body temperature ($^{\circ}$ C) in impala (a), eland (b) and wildebeest (c) inhabiting the less seasonal site (Mapungubwe, black bars) and the more seasonal site (Asante Sana, white bars) across three seasons. NS: not significant,

** $;$ $P < 0.001$, * $;$ $P < 0.05$.

The daily T_b amplitude of wildebeest differed significantly between the study sites ($F_{1,6}=14.18$, $P=0.009$) and across the seasons ($F_{2,12}=18.63$, $P<0.001$) including the interaction between the study site and season ($F_{2,12}=10.34$, $P=0.002$). The daily T_b amplitude was significantly larger in Mapungubwe than it was in Asante Sana in all three seasons, with winter having the largest amplitude (Fig. 11c). The increased T_b amplitude of wildebeest in Mapungubwe was caused by their reduced T_b in the morning, especially in winter and spring as compared to the wildebeest in Asante Sana (Fig. 12a & 12b).

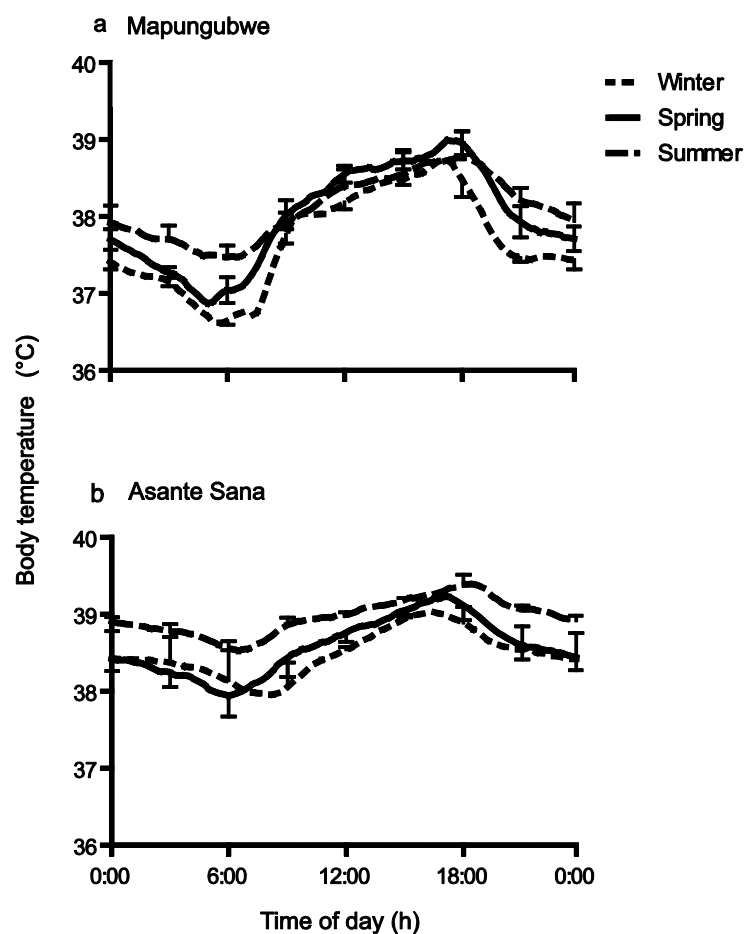


Figure 12. 24-hour rhythm of body temperature (mean \pm SD) (°C) of wildebeest in the less seasonal site (Mapungubwe, a) and the more seasonal site (Asante Sana, b) during winter, spring and summer.

Variation of body temperature in two contrasting environments

We further investigated if the daily maximum T_b (Max T_b) or the minimum T_b (Min T_b) or both were responsible for the larger amplitude of T_b among the wildebeest. The daily Max T_b did not significantly differ between the two study sites ($F_{1,6}=0.83$, $P=0.40$) or across seasons ($F_{1,10,6,62}=0.16$, $P=0.056$) (Fig. 13a).

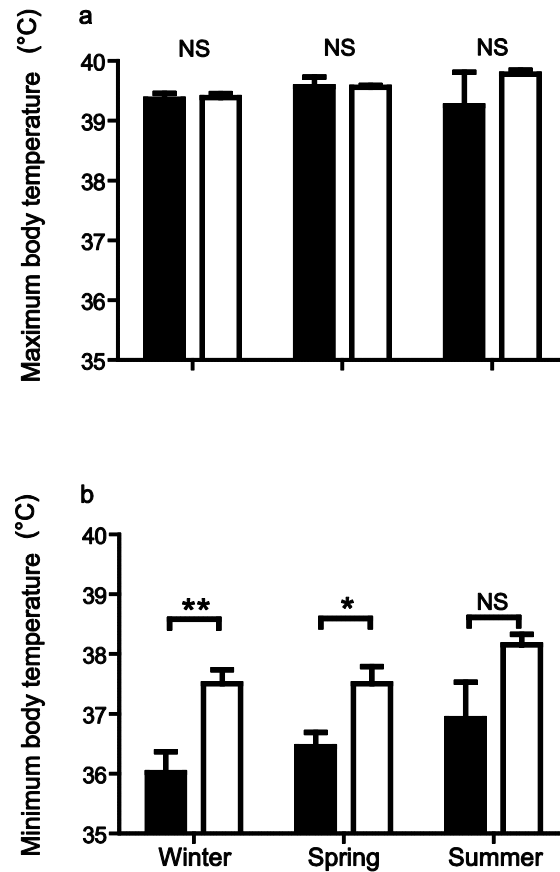


Figure 13. Mean (\pm SEM) 24-hour maximum (a) and minimum (b) body temperature of wildebeest inhabiting the less seasonal site (Mapungubwe, black bars) and the more seasonal site (Asante Sana white bars) across three seasons. NS: not significant, **: $P < 0.001$, *: $P < 0.05$.

However, the Min T_b did significantly differ between the study sites ($F_{1,6}=18.37$, $P=0.005$) and across seasons ($F_{1,074,6,44}=6.23$, $P=0.043$) (Fig. 13b). The Min T_b of wildebeest in Mapungubwe was significantly lower than that of the wildebeest in Asante Sana in winter

($P=0.002$) and spring ($P=0.009$), but it was not significantly different in summer ($P=0.10$) (Fig. 13b). Therefore, the larger T_b amplitude among the wildebeest in Mapungubwe is the result of the lower $\text{Min}T_b$ during winter and spring.

Furthermore, the frequency of occurrence of daily $\text{Min}T_b$ was more skewed to the left in winter (Fig. 14a) and spring (Fig. 14b) than it was in summer (Fig. 14c) in Mapungubwe.

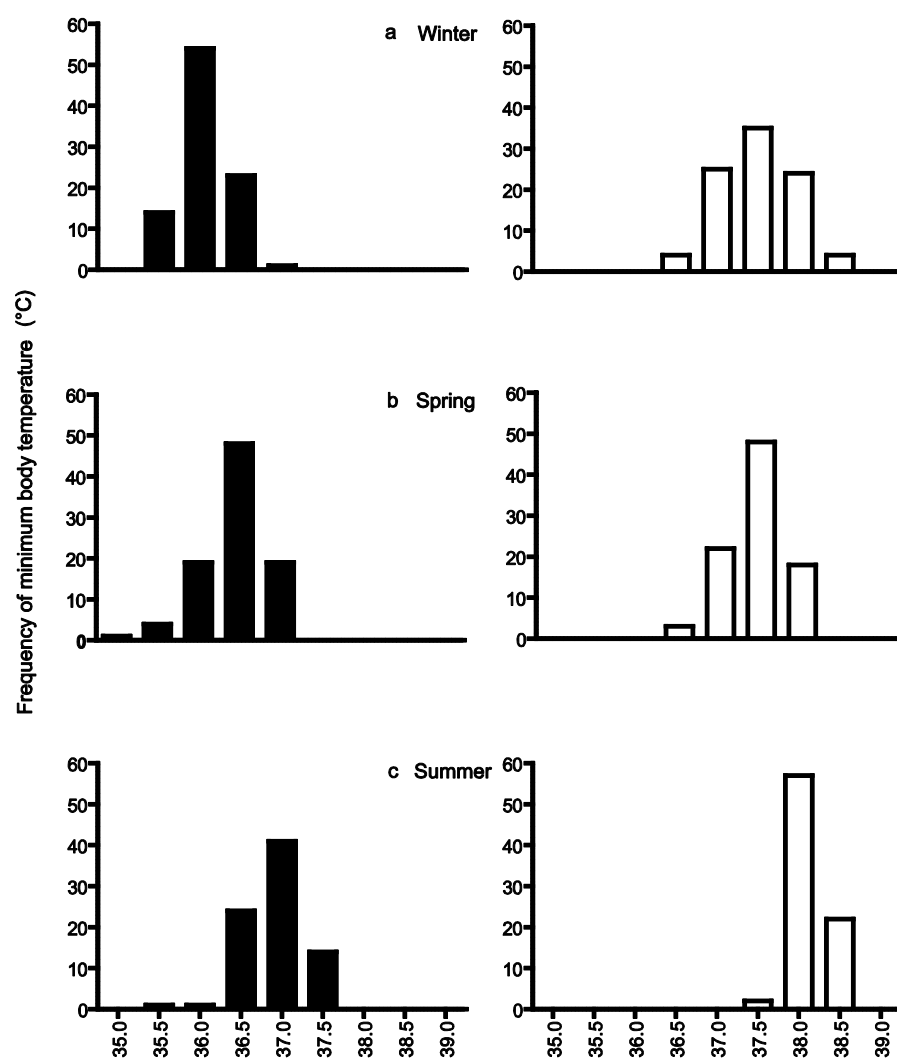


Figure 14. Frequency distribution of minimum body temperature (°C) of wildebeest in winter (a), spring (b) and summer (c) in the less seasonal site (Mapungubwe, black bars) and the more seasonal site (Asante Sana, white bars).

Variation of body temperature in two contrasting environments

In contrast, in Asante Sana, the $MinT_b$ was skewed to the right in all seasons providing further evidence that the $MinT_b$ was lower in Mapungubwe than in Asante Sana and these low $MinT_b$ occurred frequently in winter and spring (Fig. 14a and 14b).

The mean daily amplitude of T_a and bi-weekly cumulative rainfall together explained 48% of the variation in mean daily T_b amplitude of wildebeest from Mapungubwe ($B_{T_a}=0.05$, $P<0.0001$; $B_{rainfall}=-0.01$, $P<0.0001$). The mean daily $MinT_b$ of wildebeest at Mapungubwe was positively influenced by the mean daily $MinT_a$ and bi-weekly cumulative rainfall ($B_{minT_a}=0.061$, $r^2=0.69$, $P<0.0001$; $B_{rainfall}=0.005$, $P<0.0001$). In the wildebeest from Asante Sana, daily amplitude of T_a accounted for only 18% of the variation in the daily mean T_b amplitude ($B_{T_a}=0.03$, $P<0.0001$), but cumulative rainfall ($B_{rainfall}=-0.0003$; $P=0.86$) did not have any effect. In Asante Sana, moreover, only the mean daily $MinT_a$ accounted for the variability in the mean daily $MinT_b$ ($B_{minT_a}=0.054$, $r^2=0.45$, $P<0.0001$; $B_{rainfall}=0.001$, $P=0.63$).

Discussion

Our study is the first that simultaneously compares variation in body temperature of three large mammalian species over three seasons in two climatically contrasting environments. The amplitude of body temperature for impala and eland did not differ between the study sites, regardless of season, therefore the hypothesis for impala and eland was rejected. In contrast, the wildebeest in the less seasonal site (Mapungubwe) showed a larger amplitude of T_b , as a result of a lower $MinT_b$, than wildebeest in the more seasonal site (Asante Sana). This large fluctuation of body temperature suggests that the wildebeest in the less seasonal site were temporarily abandoning homeothermy. A diverse group of endothermic mammals also show this pattern in body temperature when they are exposed to climatic or nutritional stress, or both (Ostrowski et al., 2003; Ostrowski et al., 2006; Hetem et al., 2009; Glanville and Seebacher, 2010a; Glanville and Seebacher, 2010b; Hetem et al., 2010; Maloney et al., 2011; Signer et al., 2011).

A low $\text{Min}T_b$ in endothermic mammals is often attributed to a response to cope with low ambient temperatures to reduce the T_b-T_a differential, which lowers the demand for metabolic heat production and subsequently saves energy (Pereira et al., 2002; Brown and Downs, 2006). Contrary to such a hypothesis, the wildebeest in the less seasonal site showed a reduced $\text{Min}T_b$ in winter and spring despite being exposed to relatively higher ambient temperatures than the wildebeest in the more seasonal site. Therefore, the ambient temperature alone (both the amplitude and low temperature) could not be responsible for the observed physiological differences between the two populations of wildebeest. Another factor responsible for such low body temperature in our wildebeest in the less seasonal site could be poor nutrition. Many field and laboratory studies have demonstrated a similar response in $\text{Min}T_b$ of endothermic mammals when they were exposed to a nutritionally stressful environment (Buffenstein, 1985; Lane et al., 1996; Pereira et al., 2002; Ostrowski et al., 2006; Canale et al., 2011). Interestingly, the amplitude of T_a (positive effect) and cumulative rainfall (negative effect), a proxy for food availability, explained 48% of the variation in T_b amplitude in wildebeest which inhabited the less seasonal site, whereas only the amplitude of ambient temperature (positive effect) weakly explained the observed variation in T_b amplitude of wildebeest in the more seasonal site. These findings are supported by the analysis of the $\text{Min}T_b$ of wildebeest in the less seasonal site, which was positively influenced by the mean daily minimum T_a and bi-weekly cumulative rainfall.

In the less seasonal site, there was no rainfall in winter and little rain in late spring. In these semi-arid systems, rainfall is the main driver for the quality and quantity of grass. Low rainfall reduces grass quality and quantity during the dry season from mid-winter to late spring just before summer rainfall (Grunow et al., 1980; Rutherford, 1980; Owen-Smith, 1990; O'Connor et al., 2001; O'Connor and Kiker, 2004; Chamaille-Jammes and Fritz, 2009). In Etosha National Park in Southern Africa (with a similar amount of rainfall as in Mapungubwe), crude protein in grass was reduced from 17.7% during the rainy season to a

Variation of body temperature in two contrasting environments

mere 4.1% in the dry season (Berry, 1982), which is less than the assumed minimum maintenance requirement (5-6%) for a large ruminant (Sinclair, 1974; Robbins, 1993). Not only the quality of the grass, but also its availability can decline drastically during the dry season. For example, a modelling study in the less seasonal site (Mapungubwe) estimated that the biomass of grass was 40% lower in the dry scenario (510 kg.ha⁻¹) than in the wet scenario (829 kg.ha⁻¹) (O'Connor and Kiker, 2004). In Mapungubwe, rainfall generally peaks around October (O'Connor and Kiker, 2004) but during our study period the rainfall started late, only at the end of December, which would have delayed the growth of grass. Therefore, we argue that the quality and quantity of the grass declined in this semi-arid system during dry season (winter and spring) due to lack of a timely rainfall.

In contrast, in the more seasonal site (Asante Sana), rainfall occurred even in winter and spring in the form of rainfall and snowfall, maintaining quality and availability of the grasses. Further, we also suspect that the higher altitude (1300-1400 m) inhabited by our wildebeest received more rain compared to the lower altitudes where impala and eland were found (around 1000 m) (Kerley and Boshoff, 1997; Mucina and Rutherford, 2006). Because of the rainfall during the dry season, food quality and quantity is not expected to be a limiting factor for the wildebeest in Asante Sana. Therefore, we suggest that the higher variability of T_b amplitude and reduced minimum T_b among the wildebeest in Mapungubwe is a response to nutritional stress rather than a response to cold climate.

However, note that the heterothermy among dromedary camels (*Camelus dromedarius*; Schmidt-Nielsen et al. 1957), hartebeest (*Alcelaphus buselaphus* ; Harthoorn et al. 1970) and zebu steers (*Bos primigenius indicus*; Taylor 1970) was reported while they were deprived of water. Indeed, surface water availability during the dry season in this semi-arid system can be a limiting resource (Western 1975; Redfern et al. 2003). However, in the less seasonal site (Mapungubwe), there was permanent surface water available, even during the dry season in

the form of dams (Schroda dam), artificial water holes, natural springs and water pools from the Limpopo river. Since wildebeest are known to favour water points in the form of dams and drinking troughs (Smit et al. 2007), we suggest that surface water and hence the hydration state, should not be limiting for these antelopes during the dry season. Lowering $MinT_b$ during the dry season by wildebeest in the less seasonal site might be associated with a lowering of metabolic activity, which helps these grazers to operate at low maintenance cost at the time of poor resource conditions.

We did not see a similar variation of T_b in the sympatric eland and impala in the less seasonal site (Mapungubwe). A plausible explanation could be their different foraging niche and ability to cope with food stress compared to the wildebeest. As typical mixed feeders, the diet of eland and impala in the dry season (winter and spring) is predominantly browse (impala: Dunham, 1980; Monro, 1980; Sponheimer et al., 2003; eland: Hofmann and Stewart, 1972; Watson and Owen-Smith, 2000). Unlike grass, the quality and quantity of browse is less dependent on rainfall and therefore the forage availability and nutrient content declines less drastically between the wet and dry season (Rutherford, 1984; Owen-Smith, 1994). Hence, forage quality and quantity are not expected to be a major constraint for eland and impala in Mapungubwe in the dry season.

In conclusion, eland and impala are able to maintain their T_b within narrow limits both in the core and at the edge of their distributional range. Contrary to our expectation, the wildebeest in the less seasonal site showed a high variability in T_b resulting from a lower $MinT_b$, which we attribute to nutritional stress during the dry season. With a predicted increase in the frequency of drought periods in southern Africa because of climate change (IPCC, 2007; Lyon, 2009), wildebeest, and other grazers, will likely experience greater nutritional stress in the future.

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Chapter 6

Synthesis

Anil Kumar Shrestha

Synthesis: Phenotypic plasticity of behaviour and physiology of African antelopes

Climate change, habitat loss and fragmentation, and their synergetic effects are key threats to biodiversity conservation (Opdam & Wascher 2004; Joubert & Bijlsma 2010; Mantyka-Pringle et al. 2011). To persist in a rapidly changing environment, an animal must either track its climatic envelope using behavioural mechanisms (e.g., adjustment in activity pattern and home range, habitat tracking) or show physiological plasticity (e.g., adjustment of metabolic rate, body temperature) (Huey & Tewksbury 2009; Feder 2010; Berg et al. 2010). Such phenotypic plasticity may be the first response of an individual organism and the only option available, especially for long-lived species, to cope with the changing environment (Fuller et al. 2010). Furthermore, the adaptive capacity of a species might vary depending on species traits such as body size (small vs. large), feeding type (grazer vs. browser) or niche width (specialist vs. generalist).

As environmental conditions vary considerably across temporal and spatial scales, individual animals are expected to exhibit distinct behavioural and physiological responses across these scales (Dunbar & Brigham 2010). Therefore, understanding intra- and inter-variability of behavioural and physiological traits along these temporal and spatial scales in relation to their natural habitats is essential to understand the adaptive capacity of a species (Chown et al. 2004; Chown & Gaston 2008). Yet, to date, very little research has focused on these traits in long-lived endotherms such as antelopes (Fuller et al. 2010; Boyles et al. 2011). The central theme of this thesis was therefore to understand the behavioural and physiological plasticity of three species of African antelopes of different body sizes and feeding types across different temporal and spatial scales, in their natural habitat. The first three chapters focussed on the behavioural plasticity of these antelopes, while the fourth chapter focussed on the physiological plasticity of their body temperature.

Adaptive daily and seasonal activity patterns: Trading off climate and resource variability

A timely organization of daily and seasonal activity patterns by ungulates is important for the optimization of their energy balance, and therefore, for their survival and fitness, especially in a dynamic environment with varying levels of stress and resource availability (Dunbar et al. 2009). Since the daily activity pattern is species-specific and adaptive within its ecological niche (Sharma 2003), we would expect an animal to exhibit plasticity in its activity pattern when it is exposed to stressful conditions. For antelopes in a semi-arid ecosystem in South Africa where temperature frequently increases above 40°C, heat stress could limit the activity time budget due to hyperthermia. Body size influences this thermal sensitivity because large-bodied ungulates have a lower surface area to volume ratio than smaller ungulates, and therefore a reduced capacity to dissipate heat (Phillips & Heath 1995). In the second chapter, I have shown that the diurnal activity of all three species of antelopes of different body size that I studied, namely, eland *Taurotragus oryx* (≈ 420 kg), blue wildebeest *Connochaetes taurinus* (≈ 180 kg) and impala *Aepycerus melampus* (≈ 50 kg) were negatively influenced by heat stress as measured by black globe temperature devices during summer when heat stress was at its highest. Against expectations, all three species were more active during summer than in spring and winter, but they shifted the timing of their active behaviour more to the early morning (eland) or late in the evening, or both (wildebeest and impala), which suggests that they were avoiding heat stress in order to maximize food intake in a season when forage is abundant. During spring, the larger antelopes such as eland and wildebeest were negatively influenced by heat stress, but the smaller impala was apparently unaffected. Furthermore, during the 10 hottest days over the entire study period, the diurnal activity of the larger antelopes was negatively influenced by heat stress but not that of the smaller impala. Based on these findings, I conclude that these large African antelopes apparently suffer from heat stress during spring and the hottest days due to their limited capacity to dissipate heat.

With an expected increase in temperature of 2.5 °C to 5.5 °C by the end of this century in Southern Africa (IPCC 2007), the body temperature to ambient temperature differential ($T_b - T_a$) will become smaller, in particular during mid-day in summer and spring when there is high heat stress. This will make dissipating body heat even more difficult for these antelopes. Therefore, as a proximate response to avoid high heat stress, we might expect that they would shift their active behaviour such as foraging to a cooler part of the day when the ($T_b - T_a$) gradient is higher (i.e., early morning or late evening, or even night). At least in summer, these species demonstrated such shifts in their activity patterns to the cooler part of the day to avoid heat stress while acquiring sufficient resources. The consequences of such adaptive behaviour in relation to their interaction with predators are, however, largely unknown. Perhaps an increase in nocturnal activity to avoid heat stress may make them more vulnerable to predation due to a more synchronized activity pattern with predators. Research should therefore focus on what I call “community behavioural ecology” defined here as understanding the activity patterns of prey and predator simultaneously in a community, which will enhance our knowledge of the effect of climatic stress such as heat stress on the activity patterns of both prey and predator. If predator pressure is very high, these antelopes are forced to avoid predation, by becoming active even during the unfavourable time of the day, or by foraging in the shade if it is available, or they have to employ an energetically expensive physiological mechanism such as adaptive heterothermy.

As an ultimate response to excess heat stress due to climate change, endotherms suffering from increased temperature might be subjected to an increase in surface area to volume ratio by natural selection favouring smaller individuals (Sheridan & Bickford 2011). This would enhance dissipation of heat at the time of heat stress (Smith et al. 1998). Indeed, during the early Eocene, when the highest mean temperatures of the entire cenozoic era prevailed, the sizes of the major mammalian taxa such as carnivora, artiodactyles, and perrisodactyles were

smaller by a factor of about 10 (Alroy et al. 2000; Smith et al. 2004) and the current era, the wood rats (*Neotoma sp*) (Smith et al. 1998), Soay sheep (*Ovis aries*) (Ozgul et al. 2009), red deer (*Cervus elaphus*) (Post et al. 1997) and many other species have become smaller since the end of the Pleistocene. Being smaller at a time of excess heat stress may also help animals to select cooler microhabitats effectively. Therefore, declining body size of animals could be a universal response to global warming (Gardner et al. 2011).

Microhabitat: Buffering effect of thermal stress

To cope with inhospitable environmental conditions caused by high or low temperatures, animals may select optimal habitats that minimize absorption of heat at high temperatures or habitats that maximize the absorption of heat at low temperatures. Understanding such microhabitat selection patterns of animals in relation to thermal constraints is highly pertinent in the present context of climate change because these habitats can provide thermal refuges which can help to buffer the adverse effects of climate change. Hence in the third chapter, I investigated selection of microhabitat of the largest African antelope, the eland, at the southern limits of its distributional range, since the implications of microhabitat selection are supposed to be greater for these animals living at or near their range limits (Hoffman & Parsons 1997). I found that eland actively selected microhabitat at low altitudes with warm microclimates when it was cold in the winter and the ambient conditions were below its thermal neutral zone. In contrast, eland did not show selection of higher altitudes or cooler climate when it was warm in the summer. Selection of cooler microhabitats was only evident when heat stress was close to the upper end of the thermal neutral zone. The eland thus showed a behavioural adaptation in the daily and seasonal selection of altitude and microclimate to buffer the adverse effect of both cold and very hot conditions. Therefore, I argue that adaptive animal behaviour to track local variation in climate due to a diverse topography must be incorporated into species distribution models with respect to climate

change studies. I demonstrated that complex topography can offer thermal refuges, which may enable species to persist during extreme climate events (Rull 2009). Species distribution models which usually use a coarse climatic resolution of kilometres or even more, may therefore overestimate the effect of climate change on species persistence.

Indeed, during glacial (cold period) and interglacial (warm period) periods of the Quaternary, several species are reported to have used climate refugia (microrefugia) that occurred at local scales to cope with the changing climate (Dobrowski 2011). These microrefugia were smaller areas than the macrorefugia (for details see Ashcroft 2010) and were thought to provide suitable microclimate at times of unfavourable regional climate which helped species to persist beyond their range boundaries (Rull 2009; Dobrowski 2011). For example, some temperate species such as small mammals (Deffontaine et al. 2005), amphibians (Teacher et al. 2009), fresh water fish (Hänfling et al. 2002) and some plant species (Tyler 2002; Trewick et al. 2002) at higher latitudes in the Northern hemisphere were reported to use microrefugia to escape the cold climate during the glacial period. It is thought that these microrefugia were located in deeply incised valleys which provided warm microclimates during the cold glacial period (Stewart & Lister 2001). Two glacial microrefugia were also reported for North American mountain sheep (*Ovis spp*) between the Laurentide and Cordilleran glaciers in North America (Loehr et al. 2006).

Some cold-adapted temperate species at lower latitudes are thought to have used southern microrefugia to escape from the warm climate during the interglacial period, for example rock ptarmigan *Lagopus mutus*, Arctic hare *Lepus timidus* and dwarf birch *Betula nana* (Angus 1983), and ibex *Capra ibex* and chamois *Rupicapra rupicapra* (Stewart et al. 2003). These microrefugia were situated in mountainous areas such as in the Scottish highlands, the Alps and the Pyrenees which are believed to have provided a cooler microclimate than the regional warm climate during the interglacial period (Stewart et al. 2010).

Mosaics of microrefugia are also reported to have occurred in Africa during the Last Glacial Maximum. It is hypothesized that these microrefugia provided shelter to small isolated populations of antelope species such as Grant's gazelle *Nanger granti* (Lorenzen et al. 2007) and eland *Taurotragus oryx* (Lorenzen et al. 2010) in East Africa and the southern African gemsbok *Oryx gazella* in South Africa (Osmers et al. 2011) at times of unfavourably cold regional climate conditions. These isolated populations later helped to recolonize large areas during post-glacial periods via local dispersal (Loehr et al. 2006; Lorenzen et al. 2010).

Microrefugia provided safe havens for many plant and animal species all over the world during extreme climatic events, not only in the glacial and interglacial periods but also at present as I have shown in this chapter. In the present context of climate change, with increasing temperatures and frequency of drought in Africa (IPCC 2007), microrefugia with a cooler microclimate and mesic environment (including a range of altitudes, different aspects, slopes and valley depression) are likely to play an important role in buffering the effects of climate change. Therefore, designing protected areas and modelling species distribution must take into account local variations in climate due to diverse topography to ensure future availability of microrefugia.

Adaptive home range size: Buffering the variability of resources

In semi-arid ecosystems such as the study areas used in this thesis, the quality and quantity of forage primarily depends on rainfall, which is erratic and low and is predicted to decrease in the future due to climate change (LeHou  rou 1996; IPCC 2007). Therefore, the availability of forage and water resources to animals in these systems is highly variable. As a response to these highly variable resources, we would expect animals to adjust their home range sizes over time and space as their primary behavioural adaptive mechanism to maximize access to limited resources. The home range size is therefore expected to be larger during periods when resources are low in quality and quantity than in periods with resources of higher quality and

quantity: the habitat productivity hypothesis of home range size (Harestad & Bunnell 1979; Relyea et al. 2000). Animals in resource-poor areas, for example at their distributional range margin, may also need larger home ranges than their conspecifics from resource-rich core areas, to satisfy their energetic needs (Koprowski et al. 2008).

To understand the adaptive behavioural responses of African antelopes, in the fourth chapter I investigated the variations in home range sizes of eland, impala (both mixed feeders) and wildebeest (a grazer) over time (seasons) and between two climatically contrasting areas in South Africa, taking Mapungubwe National Park as the core area and Asante Sana Game Reserve as the edge area. The home range size of wildebeest in Mapungubwe was larger during the dry season when resource availability was lower compared to the resource-rich wet season, while their home range size did not differ across seasons in Asante Sana. The wildebeest in Mapungubwe showed a four to seven times larger home range size in the dry season than those in Asante Sana.

For impala, the home range size was larger during the dry season only in Asante Sana but not in Mapungubwe. Impala in Asante Sana showed a three to 14 times larger range size during the dry season than those in Mapungubwe. Surprisingly, the home range size of eland did not differ across any season between Asante Sana and Mapungubwe, while their average year-round home range size in Mapungubwe was larger than that in Asante Sana.

So, in these semi-arid habitats with variable forage resources, impala in Asante Sana, wildebeest in Mapungubwe and eland in both areas were foraging in a wide range of habitats whereas impala in Mapungubwe and wildebeest in Asante Sana typically occupied habitats that provided sufficient quantity of high-quality food year-round. These results suggest that the home range size of antelope species is most likely a response to resource quality and availability specific to the local habitat, which corresponds with the “habitat productivity

hypothesis". Although the ability to adjust the size of the home range can buffer the impact of climate change to some extent, the survival of these antelope species is expected to depend primarily on dry season rainfall and their ability to track the heterogeneously distributed resources.

Tracking heterogeneously distributed resources (habitat tracking) has already been widely accepted as a prime behavioural response of mammals in times of pre-historic climate extremes (Raia et al. 2012). For example, during the Late Pleistocene epoch when the northern hemisphere was undergoing repeated global cooling, mammals moved longer distances from the North to the South to track their habitats (Hewitt 2000). Recently, it has been reported that Neogene large mammals which moved longer distances and were able to track their habitat, enhanced their survival in the face of climatic changes (Raia et al. 2012). However, the extant mammals may not have had the same opportunity as their pre-historic counterparts to track their climatic niche and resources in the face of climatic changes due to the added pressure of anthropogenic habitat destruction and fragmentation. This is especially true in Southern Africa, where protected areas are well fenced and therefore these animals are forced to live inside parks even during extreme climatic conditions and consequently cannot track the heterogeneously distributed resources as they used to do in the past. For example, in Kruger National Park, one of the three subpopulations of wildebeest was reduced by 87% between 1965 and 1978, possibly due to fencing at the western boundary of the park, which prevented these wildebeest from tracking forage and water resources during periods of drought (Whyte & Joubert 1988). In the 1980s, there was also a massive die-off of wildebeest (~80,000) and hartebeest (~10,000) in the Southern Kalahari due to the building of a fence that prevented these animals gaining access to water and forage at a time of extreme drought (Spinage 1992). Although these antelopes in South Africa have shown behavioural plasticity in tracking heterogeneously distributed resources during the dry season, the recently fenced

protected areas make it less likely that they will be able to track scarce resources during extreme climatic conditions. Therefore, to buffer the effect of increased drought conditions in future, the connectivity of the current network of isolated protected areas must be improved. This will enhance possibilities for these antelopes to track heterogeneously distributed resources during extreme climatic stress.

Plasticity of body temperature: Coping with climatic or nutritional stress

In the first three chapters, I demonstrated how South African antelopes adjusted their behaviour such as activity patterns, daily and seasonal selection of microhabitat, and home range size dynamics when they were exposed to a stressful environment of climate and resources. In chapter 5, I investigated the variations in body temperature (T_b) of eland, blue wildebeest and impala to understand the physiological plasticity of these antelopes. The study was conducted in two climatically contrasting environments in South Africa, one with a less seasonal pattern and a mild winter (Mapungubwe National Park) and the other with a more seasonal pattern and a long and cold winter (Asante Sana Game Reserve). I showed that for eland and impala (both mixed feeders) the 24-hour body temperature amplitude did not differ between the study sites, regardless of season, suggesting they were able to maintain homeothermy although they were exposed to two contrasting environments. Conversely, the grazer (wildebeest) at a less seasonal site showed a higher variability in the 24-hour amplitude of body temperature ($\sim 4^\circ\text{C}$) and also a lower daily minimum body temperature $\text{Min}T_b$ ($\sim 2^\circ\text{C}$) compare to the normothermic level during winter and spring than the wildebeest at a seasonal site. I suggest that such differences in homeothermic and heterothermic response of the studied species can be explained by their different foraging niches and by the effect of rainfall on the quality and quantity of food resources, i.e. grass and browse. As a typical grazer, the main food resource of wildebeest is grass, and the quality and quantity of grass mainly depends on the rainfall in this semi-arid system (Rutherford 1980;

Prins 1988). No rainfall in winter and late rainfall only at the end of December in Mapungubwe could have delayed the growth of grass. Therefore, the quality and quantity of the grass in the dry season (winter and spring) declined in this semi-arid system during our study period. During very dry years, in the semi-arid system, the green fraction of grass can be reduced to zero, thereby drastically declining in nutrient content (Prins 1988) (Fig. 15a), and the grass biomass can also severely decline (Mosienyane 1979; Grunow et al. 1980; Prins 1988) (Fig. 15b).

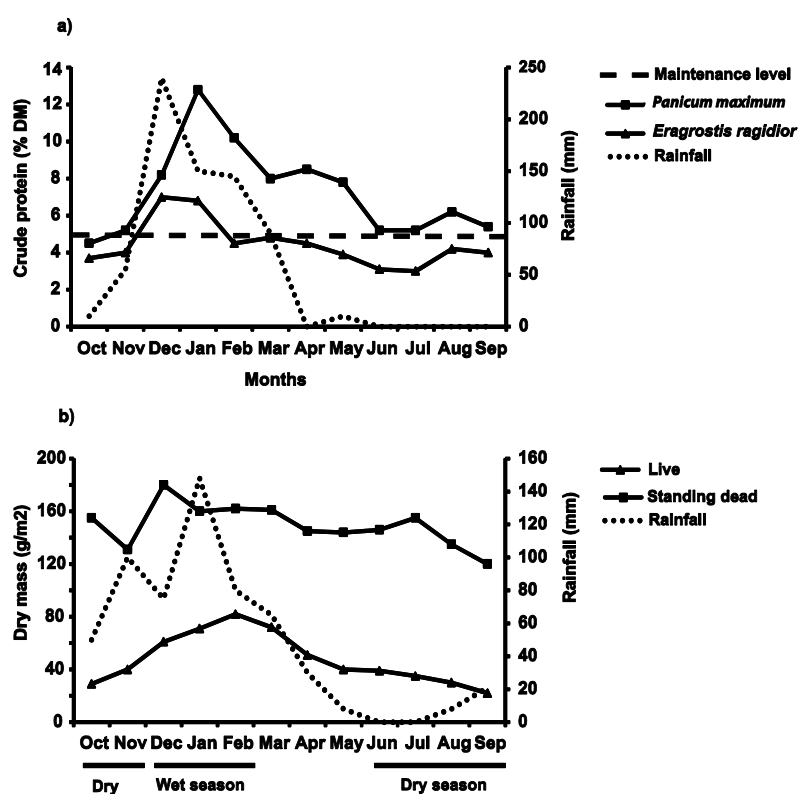


Figure 15. Seasonal changes in crude protein content in the individual grass species *Panicum maximum* and *Eragrostis rigidior* in Botswana (a: modified from Mosienyane 1979) and biomass in Nylsvley nature reserve, South Africa (b: modified from Grunow et al. 1980).

Even during years of normal rainfall, the wildebeest in Mapungubwe exhibited a higher amplitude of body temperature due to low $\text{Min}T_b$ during the dry season. This variation in T_b

among Mapungubwe wildebeest was influenced by both the amplitude of ambient temperature (positive) and cumulative rainfall (negative), which was not the case for wildebeest in Asante Sana. Wildebeest in Mapungubwe not only showed lower MinT_b but they also extended their home range sizes four to seven times larger than the wildebeest in Asante Sana. I propose that this physiological (the low MinT_b) and behavioural adjustment (extended home range size) of wildebeest in Mapungubwe was caused by scarcity of grass during the dry season, and therefore the result of nutritional stress. Such a physiological response of lowering MinT_b might be associated with a lowering of metabolic activity, which would help these grazers to operate at low maintenance cost at the time of poor resource conditions. Indeed, a reduced MinT_b among western grey kangaroos *Macropus fuliginosus* has similarly been proposed as a response to poor nutritional conditions in Australia (Maloney et al. 2011). It has also been shown that lowering the body temperature by as little as 0.6°C in dromedary camels *Camelus dromedarius* during the rutting season helps the males to conserve energy and is advantageous in sustaining their mating rituals (Grigg et al. 2009). I suggest that the heterothermy due to low MinT_b of wildebeest and extended home range size in Mapungubwe was the result of nutritional stress during the dry season; an evident response even during a year of average rainfall (Shrestha et al. 2012). Therefore, these wildebeest apparently live in a physiologically stressful environment. An indication that the wildebeest, and other grazers, have been under physiological stress are the occasional mass mortality events that occur during below average dry and wet rainfall seasons in Southern Africa (Ogutu & Owen-Smith 2003; Dunham et al. 2004; Mills et al. 1995; Walker et al. 1987; Child 1972; Williamson & Williamson 1984; Williamson & Mbano 1988; Spinage 1992; Knight 1995) and Eastern Africa (Hillman & Hillman 1977; Simon et al. 1999; Ottichilo et al. 2000; Ottichilo et al. 2001; Estes et al. 2006; Western 2009).

Low rainfall negatively influences both the population dynamics of adult grazers and the number of new born to them (topi *Damaliscus korrigum*, waterbuck and warthog), which was also best explained by monthly rainfall averaged over the preceding 5-6 months (Ogutu et al. 2008). In contrast, for giraffe *Giraffa camelopardalis* (browser), impala (mixed feeder) and kongoni *Alcelaphus buselaphus* (drought tolerant grazer), this relationship was best explained by seasonal rainfall averaged over 2-5 years, suggesting a likely negative influence of drought on production of new born calves among the grazers (Ogutu et al. 2008). Droughts not only delayed the onset of calving by ~ 1.5 months and reduced the synchrony of calving among topi and warthog in Masai Mara Nature Reserve in Kenya, but their natality rate was also reduced to far below that of average years (Ogutu et al. 2010). With a predicted increase in the frequency of droughts in Southern Africa (IPCC 2007) and Eastern Africa (Williams & Funk 2011), the population dynamics of these grazers is expected to be increasingly influenced by adult mortality as well as by changing calving and natality rates. This situation of drought may get worse when these animals are forced to confine themselves to areas such as those close to water holes, or when they are not able to track their dry season habitat because of fencing. As a result, the grass resource will be rapidly depleted, leading to starvation among the grazers, making them more vulnerable to predation (Walker et al. 1987; Spinage 1992; Ogutu et al. 2008). Reduction of quality and quantity of grass will further worsen due to climate change because the combined effect of increased temperature and low rainfall have been shown to cause reduced dietary crude protein and digestible matter in grasses (Craine et al. 2010). As a consequence, grazers which are nitrogen limited are likely to experience nutritional stress in future.

The diets of eland and impala, which are typical mixed feeders, are predominantly browse in the dry season (winter and spring) (impala: (Sponheimer et al. 2003; Kos et al. 2011); eland: (Watson & Owen-Smith 2000)). Unlike grass, the quality and quantity of browse is less

dependent on current rainfall and therefore the forage availability and nutrient content declines less drastically between the wet and dry seasons than that of grass (Fig. 16a & 16b) (Rutherford 1984; Owen-Smith 1994).

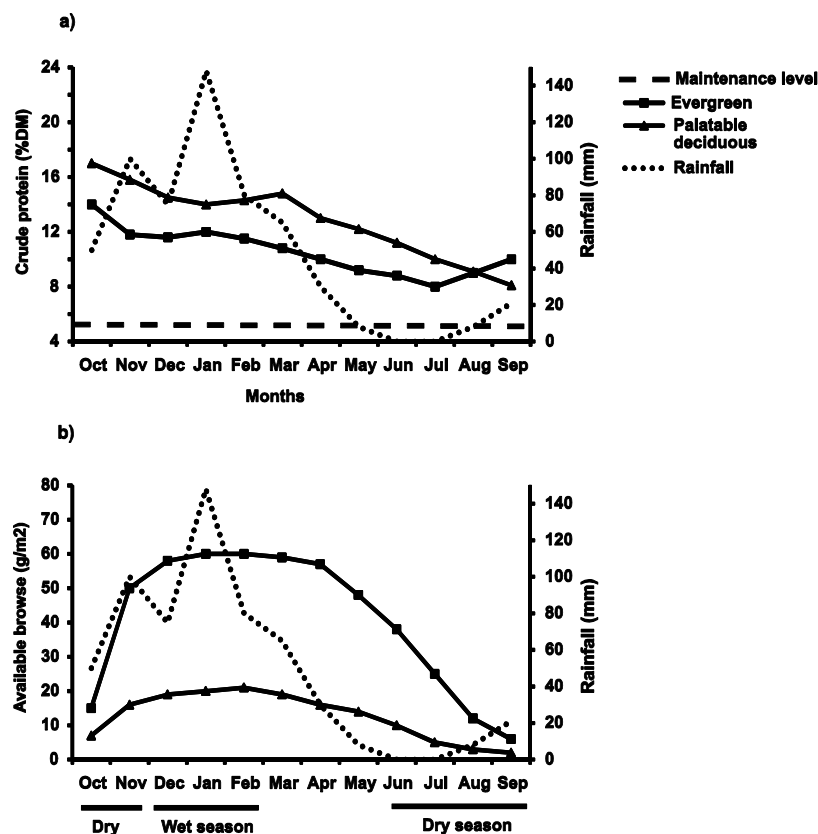


Figure 16. Seasonal changes in crude protein of browse (a) and biomass (b) in Nylsvley nature reserve, South Africa (modified from Owen-Smith 1994).

Therefore, mixed feeders such as eland and impala, which can switch their diet from grass to browse or vice versa from the wet to the dry seasons, have a greater opportunity to buffer drought-modulated food scarcity. Hence, I suggest that the mixed feeders, eland and impala, were able to maintain homeothermy throughout the year although impala in Asante Sana also had to extend their home ranges to offset a shortage of their principal food item i.e. *Acacia karroo* leaves.

Climate change is also expected to affect vegetation structure due to increased CO₂ levels. With increasing CO₂ levels, shrubs and trees will grow faster than grass, and therefore woody plants are likely to increase in the African savanna (Bond & Midgley 2000; Kgope et al. 2010; Buitenwerf et al. 2012) and the nutritional value of browse is likely to increase more than that of grass (Gordon & Prins 2008). With these changes in the vegetation community structure of the savanna in future, browsers and mixed feeders seem likely to benefit more than the ruminant grazers which are nitrogen limited (Gordon & Prins 2008). Apart from the effects on food quality and quantity, browsers and mixed feeders have relatively faster life histories (earlier age at first breeding, higher fecundity rate and a shorter life span) compared to grazers (Gaillard et al. 2008) which might make grazers, which are already physiologically and behaviourally stressed, even less able to adapt to changes in climate.

Following this reasoning, I suggest that grazers such as wildebeest which are drought-sensitive and nitrogen-limited will be less able to adapt to the expected climate change compared to mixed feeders and browsers.

Conclusion and outlook

This research is the first simultaneous investigation of the behavioural and physiological responses of African antelopes to changes in climatic and resource parameters in their natural habitats. This was only possible thanks to the state of the art technology of GPS collars with mini-black globe temperature measuring devices, and telemetric activity and body temperature data loggers. This novel technology enabled me to record behavioural and physiological traits of African antelopes not only for long time periods in their natural habitats, but also without disturbing them, so that they freely employed their behavioural and physiological adaptation mechanisms, thus overcoming the constraints of previous behavioural and physiological studies. Using this technology, I showed that homeothermic mammals cannot cope well with heat, and that large ones will suffer more than small ones.

This became clear in areas and at times that were very warm, but at these times, mammals can overcome stress by shifting their activity patterns to cooler parts of the day or by selecting optimal microhabitats that minimize absorption of heat at high temperatures or that maximize the absorption of heat at low temperatures. Animals can survive better in diverse topography which provides shelter from extreme climatic events (hot, cold and drought) than the habitats without diverse topography. With this knowledge, I predict that animals in less diverse topography will become more susceptible to extinction due to climate change. If the climate warms up further -as has happened since the Pleistocene- then natural selection will continue favouring small individuals (Sheridan & Bickford 2011; Gardner et al. 2011) not only because their higher surface area to volume ratio favours dissipation of excess heat more efficiently than that of large ones, but also because small individuals may have more opportunities to select cooler microhabitats more effectively. The mechanism by which large animals suffer more from heat stress and are less efficient at selecting favourable microhabitat compared to small animals improves understanding of the mega-fauna extinctions in the Pleistocene, at least in the case of musk ox *Ovibos moschatus* (Campos et al. 2010).

The fact that the amount of rainfall directly determines the quality and quantity of grass in the semi-arid and arid areas of Africa, while the production of browse is less dependent on rainfall, means that grazers and mixed feeders/browsers have different physiological and behavioural mechanisms to adapt to seasonal fluctuations in forage resources. The observation that the wildebeest, a grazer, reduced its body temperature and extended its home range during the dry season but that the mixed feeders/browsers did not, emphasizes that grazers will become more nutritionally stressed than mixed feeders and browsers at times of low rainfall. With the predicted increase in low rainfall events in many parts of the world and changes in vegetation structure in savanna due to climate change, browsers and mixed feeders will be likely to benefit more in future than the ruminant grazers.

Understanding behavioural and physiological traits among a range of species using bio-logging technology in their natural habitats along temporal and spatial scales proved to be a powerful method for investigating the adaptive capacity of animal species in the face of a changing environment. These valuable insights should greatly benefit biodiversity conservation in the light of a changing climate.

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Summary

Climate change, habitat loss and fragmentation individually or synergistically force species to live in a sub-optimal condition in terms of climate and resource posing threat to fitness and survival of the species. Hence, a very pressing issue for biodiversity conservation at present is to understand if species are able to keep pace with these rapidly changing environment conditions. To persist with these changes, phenotypic plasticity of behaviour and physiology may be the most likely response for long-lived endothermic species because of their longer generation times. Therefore, the central aim of this thesis is to investigate intra- and inter-variability of behavioural and physiological adaptation of range of African antelopes along spatio-temporal scales in their natural habitats.

With the aim to understand the behavioural plasticity of African antelopes to the climatic stress, in Chapter 2, I investigated effect of heat stress on diurnal activity pattern of three species of antelopes of different body size and feeding types namely, eland *Taurotragus oryx* (≈ 420 kg; mixed feeders), blue wildebeest *Connochaetes taurinus* (≈ 180 kg; grazer) and impala *Aepycerus melampus* (≈ 50 kg; mixed feeder) across season and extreme climatic condition as indicated by the 10 hottest days. During summer when the heat stress was its highest, the heat stress negatively influenced diurnal activity of all the three species. However, they shifted the timing of their activity more to the early morning (eland) or late in the evening, or both (wildebeest and impala) to avoid heat stress and maximize intake of food in a season when forage is abundant. During the spring and the 10 hottest days over the entire study period, only the diurnal activity of the larger antelopes (eland and wildebeest) was negatively influenced by the heat stress whereas the smaller impala was unaffected. Therefore, these large African antelopes apparently suffer from heat stress during spring and the extreme hottest days due to their limited capacity to dissipate heat.

In chapter 3, to understand possible behavioural adaptation of the largest African antelope eland against the thermal stress, I investigated the daily and seasonal selection of microhabitats based on altitude and microclimate at the southern limits of its distributional range. Eland actively selected lower altitudes with warm microclimates during the winter and the five coldest days when the ambient conditions were below its thermal neutral zone. In contrast, eland did not select higher altitudes or cooler climate when it was warm in the summer. However, selection of cooler microhabitats was only evident in the three extremely hottest days when the heat stress was close to the upper end of its thermal neutral zone. Hence, the eland was able to use diverse topography as a thermal refuge to buffer the adverse effect of both cold and very hot condition.

In the fourth chapter, to study behavioural response of African antelopes to variation in food resources which is predicted to exacerbate due to climate change and habitat loss and fragmentation, I investigated adaptation of home range sizes of eland, impala (both mixed feeders) and wildebeest (a grazer) over time (seasons) and between two climatically contrasting areas in South Africa, taking Mapungubwe National Park as the core area and Asante Sana Game Reserve as the edge area. This comparative study not only showed the home range size of wildebeest in Mapungubwe was larger during the resource-poor dry season compared to the resource-rich wet season but their home range size in the core area was also a four to seven times larger in the dry season than those in the edge area. In contrast, the home range size of impala was 3-14 times larger in the edge area than those in the core area. Surprisingly, the home range size of eland neither differs across any season within study areas nor between Asante Sana and Mapungubwe, while their average year-round home range size in core area was larger than that in edge area. These results suggest that the home range size of these African antelope is most likely a response to resource quality and availability specific to the local habitat.

With an attempt to investigate physiological plasticity of African antelopes over a spatio-temporal context, in Chapter 5, I compared intraspecific variation of body temperature, as measured by amplitude, of the eland, blue wildebeest and impala in the two climatically contrasting areas: one with a less seasonal pattern and a mild winter (Mapungubwe National Park) and the other with a more seasonal pattern and a long and cold winter (Asante Sana Game Reserve). The 24-hour amplitude of body temperature of both mixed feeder (eland and impala) did not differ between the study sites, regardless of season. In contrast, the grazer (wildebeest) at a less seasonal site exhibited not only a higher variability in the 24-hour amplitude of body temperature (T_b)(~4°C) but also a lower daily minimum body temperature by ~2 °C compare to the normothermic level during the dry season than the wildebeest at a seasonal site. Further, the variation in T_b amplitude were influenced both by temperature (positive effect) and rainfall (negative effect), a proxy for food availability only among the wildebeest from less seasonal site. This suggest that these physiological response of higher variability of T_b amplitude and reduced minimum T_b among the wildebeest in Mapungubwe is a response to nutritional stress rather than a response to cold climate.

These behavioural (home range) and physiological (body temperature) response of African antelopes to stressful conditions are specific for species and habitats. The smallest impala, which is a mixed feeder, maintained homeothermy even though they were exposed to stressful habitats by selecting the most productive habitat, i.e., riparian habitat in Mapungubwe. In Asante Sana, impala maintained homeothermic status by extending their dry season home range size when their principle food *Acacia Karoo* was not available. The largest antelope (eland) maintained homeostasis by ranging over large areas to track heterogeneously distributed resources, which is only possible due to their large size and ability to cope with lower quality food. Eland in Mapungubwe had larger home range sizes compared to Asante Sana which was most probably due to the poor quality of the habitat in Mapungubwe. Interestingly, the wildebeest in Mapungubwe did not maintain homeothermy

particularly in dry season. Not only their amplitude of T_b was much larger ($\sim 4^\circ\text{C}$) and Minimum T_b lowered by 2°C compared to normothermic level, they also extended their home range size four to seven folds compared to the wildebeest in Asante Sana. This failure to maintain homeothermy and extension of home range size was due to nutritional stress and therefore these antelopes are living in a physiologically stressful environment. With the predicted increase in the frequency and intensity of drought periods in southern Africa due to climate change, wildebeest, and other grazers, will likely experience greater nutritional stress in the future.

To conclude, this thesis shows importance of studying behavioural and physiological traits among a range of species along temporal and spatial scales in their natural habitats to understand the adaptive capacity, therefore sensitivity of animal species. Apparently, homeothermic mammals cannot cope well with heat stress, which negatively influence the larger ones more than the smaller ones. However, mammals can overcome these stresses by shifting time of their activity to cooler parts of the day or by selecting optimal microhabitats that minimize absorption of heat at high temperatures or that maximize the absorption of heat at low temperatures. The behavioural (larger home range size) and physiological (reduced body temperature) response of wildebeest, a grazer to dry season but not that of the mixed feeder emphasizes that grazers will become more nutritionally stressed than mixed feeders at times of low rainfall. With the predicted increase in low rainfall events in many parts of the world and changes in vegetation structure in savannas due to climate change, browsers and mixed feeders will be likely to benefit more in future than the ruminant grazers.

Samenvatting

De afzonderlijke en gezamenlijke effecten van klimaatsverandering, habitatverlies en fragmentatie dwingen soorten te leven in suboptimale klimatologische en energetische omstandigheden, wat negatieve gevolgen kan hebben voor *fitness* en overleving. Voor het behoud van biodiversiteit is het daarom van groot belang inzicht te krijgen in de vraag of soorten zich kunnen aanpassen aan hun snel veranderende leefomgeving. In het geval van warmbloedige, langlevende soorten, die een lange generatietijd hebben, is fenotypische plasticiteit in gedrag en fysiologie de meest waarschijnlijke aanpassing om in dergelijke veranderende omgevingen te kunnen overleven. Het hoofddoel van dit proefschrift is daarom het onderzoeken van de intra- en interindividuele variabiliteit in ethologische en fysiologische aanpassingen van verschillende Afrikaanse antilopen in hun natuurlijke habitat, hierbij rekening houdend met de invloed van ruimtelijke en temporele schalen.

Met als doel inzicht te verkrijgen in de plasticiteit van het gedrag van Afrikaanse antilopen met betrekking tot klimatologische stress, heb ik in hoofdstuk 2 het effect van hittestress op het dagelijkse activiteitenpatroon van antilopen onderzocht. Dit heb ik gedaan voor drie soorten met verschillende lichaamsgewichten, namelijk elandantilope *Taurotragus oryx* (≈ 420 kg), blauwe gnoe *Connochaetes taurinus* (≈ 180 kg) en impala *Aepycerus melampus* (≈ 50 kg). Ik hield hierbij rekening met het seizoen en extreme klimatologische omstandigheden, gedefinieerd als de 10 warmste dagen. Gedurende de zomer, wanneer hittestress het sterkst was, vertoonden alle drie de soorten de minste activiteit. Om oververhitting te vermijden en toch gebruik te maken van de overvloedige voedselbronnen in de zomer, verschoven antilopen perioden van activiteit naar de ochtend (elandantilope), avond, of beide (gnoe en impala). Voor de grotere antilopen (elandantilope en gnoe), maar niet de impala, was dit patroon ook zichtbaar gedurende de lente en de 10 warmste dagen van de studieperiode. De grotere Afrikaanse antilopen lijden derhalve blijkbaar meer onder hittestress, omdat zij vanwege een kleinere oppervlak-/inhoudverhouding minder makkelijk warmte verliezen.

Om te begrijpen hoe de grootste Afrikaanse antilope zich in zijn gedrag aanpast aan thermische stress, onderzocht ik in hoofdstuk 3 de dagelijkse en seizoensmatige selectie van microhabitats door de elandantilope in het meest zuidelijk deel van zijn verspreidingsgebied. Hierbij beschreef ik microhabitats middels de variabelen 'hoogte- boven- zee' en 'microklimaat'. Elandantilopen selecteerden laaggelegen gebieden met warm microklimaat in de winter en tijdens de vijf koudste dagen, wanneer de temperatuur lager was dan de thermische neutrale zone. Echter, omgekeerd selecteerden elandantilopen niet hogere of koudere gebieden tijdens de zomer. Dit gebeurde alleen tijdens de drie warmste zomerdagen, wanneer hittestress bijna hoger was dan de bovengrens van de thermisch neutrale zone van de elandantilope. Elandantilopen waren dus in staat om variaties in topografie te gebruiken als thermische buffer voor zowel koude als warme omstandigheden.

Het doel van het vierde hoofdstuk was te bestuderen hoe Afrikaanse antilopen hun gedrag aanpassen aan schommelingen in voedselbeschikbaarheid, welke naar verwachting zullen toenemen als gevolg van klimaatsverandering habitatverlies en fragmentatie. Ik onderzocht daartoe hoe de grootte van *home ranges* van elandantilopen, impala (beide '*mixed feeders*') en blauwe gnoe (een grazer) verschillen over tijd en tussen twee klimatologisch tegengestelde gebieden in Zuid-Afrika. Deze gebieden waren Mapungubwe National Park, een kerngebied, en Asante Sana Game Reserve, een randgebied. Deze vergelijkende studie toonde aan dat de *home range* van de gnoe in Mapungubwe groter was gedurende het droge seizoen dan tijdens het natte seizoen. Daarnaast was de *home range* van gnoes drie tot zeven maal groter in het kerngebied dan in het randgebied. Echter, voor impala's was de *home range* juist drie tot veertien maal groter in randgebieden. Het is opmerkelijk, dat er geen verschil was in de grootte van de *home ranges* van de elandantilope, niet tussen seizoen en ook niet tussen Asante Sana en Mapungubwe. Deze resultaten suggereren dat de grootte van *home ranges* van Afrikaanse antilopen gestuurd wordt door lokale verschillen in de kwaliteit en beschikbaarheid van voedsel. Om de fysiologische plasticiteit van Afrikaanse antilopen te

bestuderen in een ruimtelijke en temporele context, heb ik in hoofdstuk 5 gekeken naar de intraspecifieke variatie in lichaamstemperatuur (gekwantificeerd als de dagelijkse amplitudo in lichaamstemperatuur T_b) van elandantilopen, blauwe gnoe en impala in twee klimatologisch tegengestelde gebieden. Deze gebieden waren Mapungubwe National Park, gekenmerkt door weinig seizoensverschillen en zachte winters, en Asante Sana Game Reserve, waar de temperatuursverschillen tussen de seizoenen groter zijn en winters koud en lang zijn. Er was geen verschil in de amplitudo van T_b van beide ‘*mixed feeders*’ (elandantilope en impala) tussen de twee studiegebieden. De grazer (gnoe) daarentegen vertoonde in het gebied met duidelijke seizoenswerking wel een grotere variabiliteit in de T_b amplitudo ($\sim 4^\circ\text{C}$), alsmede een lagere minimum T_b ($\sim 2^\circ\text{C}$), in vergelijking met het gebied met weinig seizoensverschillen. Tevens vond ik dat voor de gnoe in het gebied met weinig seizoensverschillen de variatie in T_b beïnvloed werd door temperatuur (positief effect) en regenval, een indicator voor voedselbeschikbaar (negatief effect). Dit suggereert dat de variabiliteit in T_b -amplitudo en de lagere T_b -minimum van gnoes in Mapungubwe meer een respons is op voedselschaarste dan een aanpassing aan het koude klimaat.

Deze gedragsmatige (*home range*) en fysiologische (lichaamstemperatuur) reacties van Afrikaanse antilopen op stress zijn soort- en habitatspecifiek. De kleine impala, die een ‘*mixed feeder*’ is, behield homeothermie in Mapungubwe, ondanks blootstelling aan stressvolle situaties, door middel van het selecteren van het meest productieve habitat, namelijk oeverstroken. In Asante Sana waarborgden impala’s een constante lichaamstemperatuur door het vergroten van de *home range* wanneer hun belangrijkste voedselcomponent, *Acacia karoo*, niet beschikbaar was. De grootste antilope (elandantilope) behield homeostatisch evenwicht door grote gebieden te doorkruisen om zodanig heterogeen verspreide voedselbronnen op te kunnen sporen. Dit is alleen mogelijk door de grote lichaamsmassa van elandantilopen en hun vermogen te overleven op voedselbronnen van lage kwaliteit. Elandantilopen in Mapungubwe hadden een grotere *home range* dan

elandantilopen in Asante Sana, wat hoogstwaarschijnlijk verklaard kan worden door de lage kwaliteit van het habitat in Mapungubwe. Interessant genoeg waren gnoes in Mapungubwe niet in staat een homeothermische situatie te behouden, met name in het droge seizoen. Niet alleen was de T_b -amplitudo veel groter ($\sim 4^\circ\text{C}$) en de minimum T_b verlaagd met 2°C ten opzichte van de normothermische situatie, ook vergrootten zij hun *home range* drie tot vier maal in vergelijking tot gnoes in Asante Sana. Deze afwijking van homeothermie en uitbreiding van de *home range* werden veroorzaakt door voedseltekort en als zodanig leven blauwe gnoes in Mapungubwe in een fysiologisch stressvolle omgeving. Door de als het gevolg van klimaatsverandering voorspelde toename in de frequentie en intensiteit van droogteperiodes in zuidelijk Afrika zullen gnoes en andere grazers in de toekomst waarschijnlijk meer stress door voedselgebrek ervaren..

Concluderend onderstreept dit proefschrift de relevantie van het bestuderen van ethologische en fysiologische kenmerken van meerdere soorten in hun natuurlijke habitat en in relatie tot verschillende ruimtelijke en temporele schalen. Dit helpt ons om een beter begrip te krijgen van het aanpassingsvermogen en daarmee ook de gevoeligheid van diersoorten. Zoals gebleken kunnen warmbloedige zoogdieren, vooral de grotere, moeilijk omgaan met hittestress. Echter, zoogdieren kunnen deze stress vermijden door hun activiteit te verleggen naar koudere gedeelten van de dag of door een microhabitat te selecteren waarin absorptie van warmte geminimaliseerd of juist gemaximaliseerd wordt bij respectievelijk hoge en lage temperaturen. De ethologische (grotere *home range*) en fysiologische (lagere lichaamstemperatuur) aanpassingen, die alleen waargenomen werden bij de gnoe (een grazer) in het droge seizoen, geven aan dat in tijden van weinig neerslag grazers meer te lijden hebben onder stress door voedselgebrek dan '*mixed feeders*'. Met de voorspelde toename in droogteperiodes in grote delen van de wereld en veranderingen in vegetatiestructuur in savannes, beide het gevolg van klimaatverandering, zijn '*browsers*' en '*mixed feeders*' in de toekomst meer in het voordeel dan grazende herkauwers..

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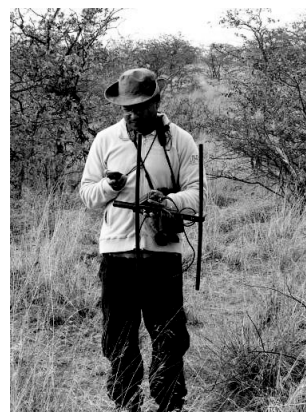
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Biography

Anil Kumar Shrestha was born on 6 June 1973 in Hetauda, Nepal. After completing primary and secondary school, he went to Tribhuvan University, Nepal, where he received the Technician Certificate in Forestry at the Institute of Forestry (IOF), Hetauda Campus, in 1991. He then worked as a Forest Ranger in the same institute until 1995. He went back to Tribhuvan University to study for a Bachelor's degree in



Forestry at the Institute of Forestry, Pokhara Campus, which he completed in 1999. While studying for his BSc degree, he did research on the conservation biology of some lowland grassland birds species with small grants from UNDP Nepal and the Partridge, Quail and Francolin Specialist Group of IUCN.

In 2000 he rejoined the Institute of Forestry, Hetauda Campus, Tribhuvan University, but now as a Deputy Instructor, where he was involved in teaching and research on the following subjects: Wildlife Ecology, Protected Area Management, Eco-tourism and Range Management. During his tenure at IOF, he also collaborated as Researcher and Agro-forestry officer with NGOs on biodiversity conservation and sustainable land development of the Himalayas and lowland regions of Nepal.

In 2003, he received a NORAD Fellowship from the Government of Norway to study for a MSc Natural Resource Management and Sustainable Agriculture at the University of Life Sciences (UMB) in Ås, Norway. Reflecting his interest in wildlife ecology, his MSc research focused on “Dry season diets of sympatric ungulates in flood plain grassland of Royal Bardia National Park, Nepal”, under the supervision of Prof. Per Wegge and Dr. Stein R. Moe. After completing his MSc degree in 2005, he worked as a research assistant in the Department of

Ecology and Natural Resource Management at UMB on the ecology and conservation of South Asian and Arctic ungulates.

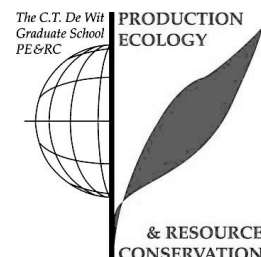
In 2006, he moved to Wageningen University, the Netherlands, to study for a PhD degree at the Resource Ecology Group under supervision of Prof. Herbert Prins, Prof. Steven de Bie and Dr. Sip van Wieren, and in collaboration with Prof. Andrea Fuller, University of Witwatersrand, South African National Park (SANPARKs) and Asante Sana Game Reserve in South Africa. His PhD research investigated the behavioural and physiological adaptation of African antelopes along climatic gradient in their natural habitat.

Publications

1. **A.K. Shrestha**, S.E. van Wieren, F. van Langevelde, A. Fuller, R.S. Hetem, L.C.R. Meyer, S. de Bie and H.H.T. Prins. (2012). Body temperature variation of South African antelopes in two climatically contrasting environments. *Journal of Thermal Biology* 37: 171-178.
2. **A.K. Shrestha**, S.E. van Wieren, F. van Langevelde, A. Fuller, R.S. Hetem, L.C.R. Meyer, S. de Bie and H.H.T. Prins. Larger antelopes suffer more from heat stress than smaller antelopes in tropical semi-arid South Africa (**Submitted and paper under review**).
3. N.M.B. Pradhan, P. Wegge, S. Moe and **A. K. Shrestha** (2008). Resource partitioning between Asian wild elephant (*Elephas maximus*) and Greater one-horned rhinoceros (*Rhinoceros unicornis*) in Lowland Nepal. *Journal of Wildlife Biology* 14:147-154.
4. P. Wegge, **A. K. Shrestha** and S. Moe (2006). Dry season diets of sympatric ungulates in lowland Nepal: competition and facilitation in alluvial tall grassland, *Journal of Ecological Research* 21: 698-706.

PE&RC PhD Education Certificate

With the educational activities listed below the PhD candidate has complied with the educational requirements set by the C.T. de Wit Graduate School for Production Ecology and Resource Conservation (PE&RC) which comprises of a minimum total of 32 ECTS (= 22 weeks of activities)



Review of literature (6 ECTS)

- Behavioural and physiological adaptation of ungulates in nature (2006/2007)

Writing of project proposal (4.5 ECTS)

- Behavioural and physiological plasticity of South African antelopes in two contrasting environments

Post-graduate courses (10.8 ECTS)

- Consumer resource interaction; PE&RC, SENSE, FE (2006)
- Survival analysis; PE&RC (2007)
- Advanced statistics; PE&RC (2010)
- A practical post graduate GIS; PE&RC (2010)
- GLM for ecologist; Groningen University (2010)
- Animal movement analysis; IBED, UvA (2010)
- Geo-ecological data analysis; IBED, UvA (2010)
- Mixed linear Model; PR&RC/SENSE (2010)

Laboratory training and working visits (3 ECTS)

- Handling and calibration of micro-metrological instrument; University of Witwatersrand, South Africa (2008)
- Development/test/calibration of GPS collar and telemetric activity and body temperature data logger; Africa Wildlife tracking, South Africa (2008)

Competence strengthening / skills courses (1.2 ECTS)

- Techniques for writing and presenting scientific papers; PE&RC, WAS, WIMEK, VLAG ,EPS, WSS (2011)

PE&RC Annual meetings, seminars and the PE&RC weekend (1.5 ECTS)

- PE&RC Weekend (2007)
- PE&RC Day (2009/2010)

Discussion groups / local seminars / other scientific meetings (2.7 ECTS)

- Ecological theory and application (2011)
- Oral presentation at climate related research within centre of ecosystem mini-ecosystem; Wageningen University (2011)
- Mini symposium: how to write a world class paper (2010/2011)
- Wildlife surveillance using GPS: from moment tracking to behaviour recognition; Eindhoven, the Netherlands (2011)

Training and Education Statement Form

International symposia, workshops and conferences (11.9 ECTS)

- Oral presentation at world congress international association of landscape ecology, 25 years of landscape ecology: scientific principles & practice; Wageningen, the Netherlands (2007)
- Poster presentation at 5th annual Kruger national Park science network meeting; Sukukuza, South Africa (2007)
- Oral presentation at 8th annual savannah science network meeting; Sukukuza, South Africa (2010)
- Oral presentation at annual main meeting of society for experimental biology; Prague, Czech Republic (2010)
- Oral presentation at annual main meeting of society for experimental biology; Glasgow, Scotland (2011)

Supervision of MSc 4 students; 60 days

- Antelopes have sixth sense (Tamara Bore de Oliveira & Eveline Hoppers)
- Activity patterns and body temperature amplitude of African lion in semi-arid environment (Rob de Boer)
- The effect of ambient temperature on home range of African lion at different temporal scales (Carline van Vliet)

