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Larger antelopes are sensitive to heat stress throughout all seasons but smaller antelopes only during summer in an African semi-arid environment

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Abstract Heat stress can limit the 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 whether the activity pattern during the day of three antelope species of different body size—eland, blue wildebeest and impala—is negatively correlated with the pattern of black globe temperature (BGT) during the day of the ten hottest days and each season in a South African semi-arid ecosystem. Furthermore, we tested whether the larger bodied eland and wildebeest are less active than the 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 activity of the larger bodied eland and wildebeest was negatively influenced by BGT, but not for the smallest of the three species, the 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.

Keywords 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 and Dill 1990; Lima and 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 and 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 and 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 or at least there would be an increase in the energy cost of existence.

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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 and Kearney 2009) and the thickness of the boundary layer in the air next to the animals (Porter et al. 2000). Indeed, smaller ungulates have a greater surface area to volume ratio and thinner boundary layer than large bodied ungulates, and therefore higher thermal conductance and lower thermal inertia (Porter and Gates 1969; Calder 1984; Schmidt-Nielsen 1984; Peter 1986; Haim and 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 and thicker boundary layer of large ungulates reduce the rate of heat dissipation to the environment, which is disadvantageous in hot weather but may be beneficial in a cold climate (Bradley and Deavers 1980; Phillips and Heath 1995; Porter et al. 2000; McNab 2002).

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 and 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 rises 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; Natori and Porter 2007). 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 et al. 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 *Aepyceros 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 h' time zone and the climate is semi-arid with mean rainfall ranging from 350 to 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 and 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 and 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 and 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 *Taurotragus oryx*, kudu *Tragelaphus strepsiceros*, blue wildebeest *Connochaetes taurinus*, zebra *Equus burchelli*, red hartebeest *Alcelaphus buselaphus*, gemsbok *Oryx gazella*, water buck *Kobus ellipsiprymnus*, impala *Aepyceros melampus*, bushbuck *Tragelaphus scriptus*, and warthog *Phacochoerus aethiopicus*.

Data collection

We captured, collared and implanted a waxed miniature activity data logger ($50 \times 30 \times 20$ mm; African Wildlife Tracking, South Africa) into the retroperitoneal area in the right side lateral aspect of the abdomen of five eland, five wildebeest and five impala (late April 2008) (Shrestha et al. 2012). The surgical procedure was similar to that used previously (Fuller et al. 1999; Hetem et al. 2009; Hetem et al. 2010). The miniature activity data logger was equipped with a radio-transmitter with omni-directional 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 min for eland and wildebeest (N/day=288) but of 10 min 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). Standard black globe temperature (accuracy ±0.2 °C, onset, USA) and ambient temperature (accuracy ±0.2 °C, onset, USA) were recorded from June 2008 to April 2009 with an interval of 5 min (N/day=288). A standard black globe temperature is a hollow copper globe of 150 mm in diameter painted with matt black to measure the mean radiant temperature (Vernon 1932). 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 2 h (i.e. the mean for 0:00 h includes activity data from 00:00 to 01:55, and so on) for each day. Then, we calculated the mean monthly activity and its variance for each 2 h as a percentage of the maximum reading each logger recorded to correct for the sensitivity of individual activity data loggers (Hetem et al. 2008). As this maximum activity score refers to running animals, we can say that, for example, 30 % activity is similar for each animal relative to the maximum activity.

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 (06:00–18:00 h; local times) and nocturnal (20:00–4:00 h) activity between the three seasons separately for each species using a GLM. Then, the activity pattern during the day (06:00–18:00 h) of each species was regressed with the pattern of the corresponding BGT during the day (06:00–18:00 h) for each season to test hypothesis 1, followed by a Bonferroni multiple comparison to test the differences between the slopes of the regression lines. This approach allowed us to analyse the adjustment of the activity pattern of the animals during the day when temperature changes, as the daily fluctuation in temperature and light cycles are dominant ecological factors which determine the range of adaptations among animals (Hut et al. 2012). Moreover, we can also compare these relationships between different diurnal activities and temperatures between seasons to test hypothesis 1. 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 ten hottest days based on black globe temperature to test hypothesis 2 under the hottest conditions.

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 minima at dawn, dusk and night while BGT was always highest at midday (between 12:00 and 14:00 h) (Fig. 1). Summer exhibited the highest mean BGT (31 °C±11.5), followed by spring (29 °C±11.2) and winter (21 °C± 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 2 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.
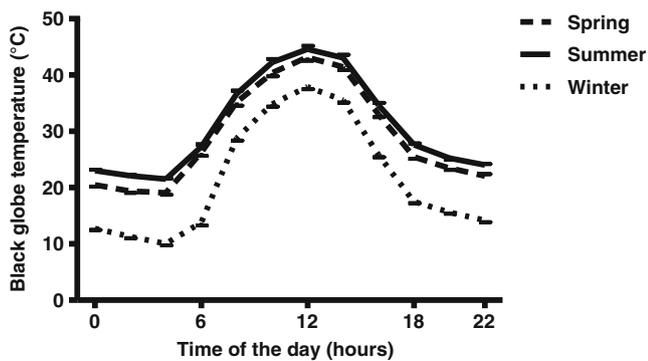
Fig. 1 The mean two-hourly black globe temperature (mean, 95 % upper and lower bound) over the day during spring, summer and winter in Mapungubwe National Park (2008–2009)

Daily and seasonal activity rhythm

All species exhibited a typical bimodal activity pattern with peaks 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 18:00 h (i.e.18:00–19:55) whereas in winter it was at 16:00 h (16:00–17:55). In line with this, the activity at dusk in spring peaked between 16:00 and 18:00 h (Fig. 2).

Mean 24-hour activity of eland was significantly different between the seasons ($F_{2, 189}$=3.59, P=0.029) (Fig. 3a). Mean 24-hour activity in summer was significantly higher than that in winter (P=0.032), whereas summer 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. 3b), whereas nocturnal activity (20:00–4:00) of eland did not differ between the seasons ($F_{2, 77}$=0.952; P=0.391) (Fig. 3c). 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. 3a). 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. 3b). 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. 3c). 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).
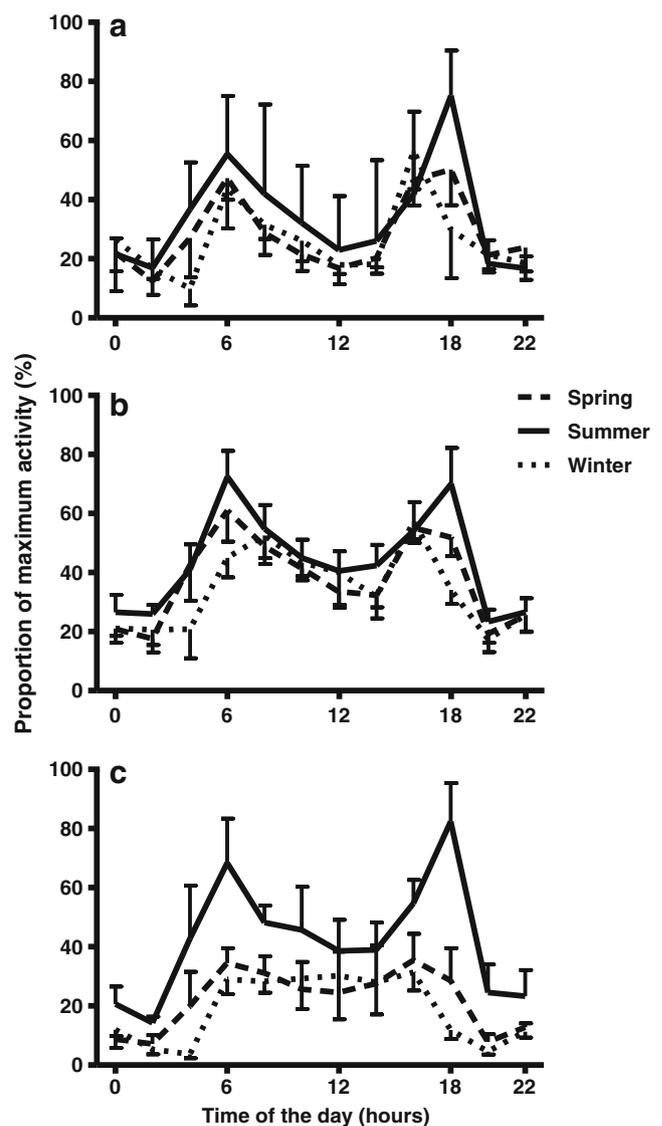

Fig. 2 Daily activity pattern (mean, 95 % upper and lower bound) during spring, summer and winter as proportion of the maximum activity of eland (N=2) (a), wildebeest (N=4) (b) and impala (N=2) (c)

Also for impala, mean 24-hour activity differed between the seasons ($F_{2, 213}$=37.87; P<0.001) (Fig. 3a). 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. 3b). 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. 3c). 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).
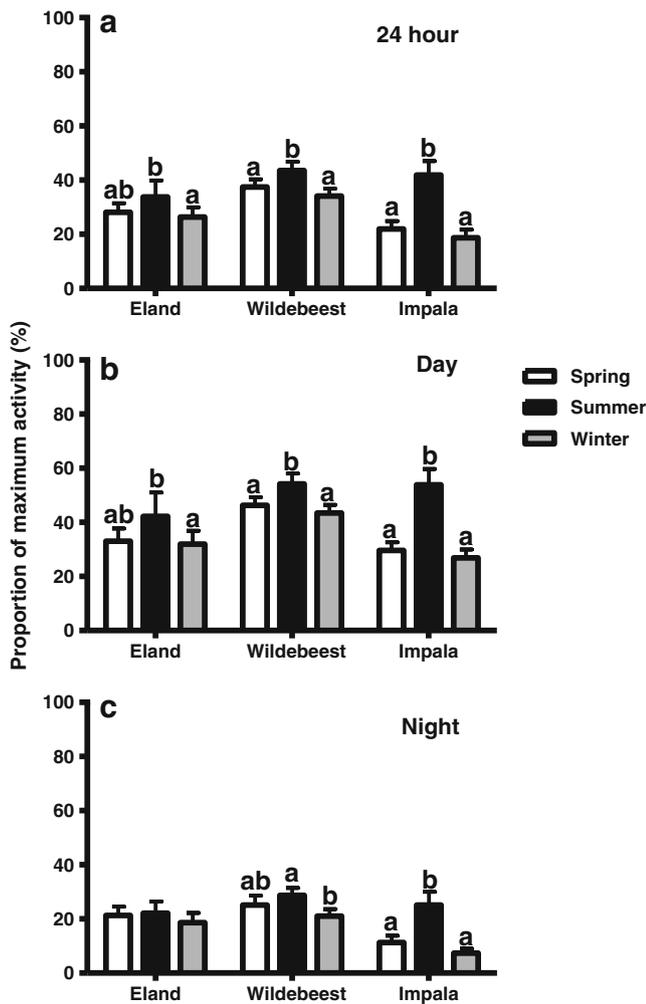
Fig. 3 Seasonal mean activity levels as proportion of the maximum activity (mean, 95 % upper and lower bound) for eland ($N=2$), wildebeest ($N=4$) and impala ($N=2$) during the 24-hour period (**a**), the day light period (**b**) and the night (**c**). *Letters* indicate significantly different activity levels between season within each species after post-hoc test ($P<0.05$)

Heat stress and diurnal activity

Each line of Fig. 4 shows the response of a species to temperature differences over the day—a decreasing line means that the animals become less active during the day when temperatures during the day increase. Comparing the different lines gives information about the different activity levels of the animals between the different seasons and, moreover, the response of the activity level during the day to temperature. The diurnal activity of eland was negatively related with BGT for spring ($\beta_1=-1.92$, $P<0.001$, $R^2=0.80$), summer ($\beta_1=-2.34$, $P=0.001$, $R^2=0.60$) and winter ($\beta_1=-0.928$, $P=0.028$, $R^2=0.34$) (Fig. 4a). The slope of the regression lines describing the effect of BGT on activity (β) were significantly different between the seasons ($F_{2,\ 36}=3.312$, $P=0.047$), i.e. 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 more pronounced in summer than in winter.

The diurnal activity of wildebeest was only negatively related with BGT during spring ($\beta_1=-1.359$, $P<0.0001$, $R^2=0.60$) and summer ($\beta_1=-1.359$, $P<0.0001$, $R^2=0.60$), but not in winter ($\beta_1=-0.267$, $P=0.65$, $R^2=0.008$) (Fig. 4b). The βs 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.
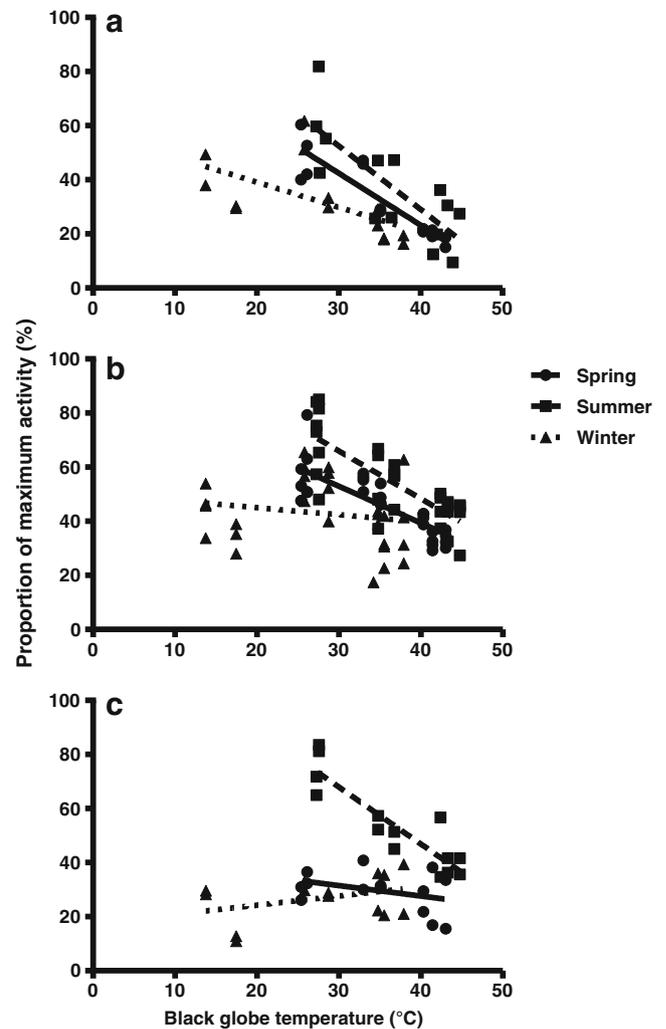

Fig. 4 Relationship between black globe temperature (°C) and diurnal activity as a proportion of the maximum activity (%) in spring, summer and winter for eland ($N=2$) (**a**), wildebeest ($N=4$) (**b**) and impala (**c**) (7 data points per day per individual averaged for 2-hour time intervals over each season)

For impala, the diurnal activity was only negatively related with BGT in summer ($\beta_1 = -2.106$, $P<0.0001$, $R^2 = 0.79$). However, the activity patterns in spring ($\beta_1 = -0.387$, $P=0.228$, $R^2 = 0.11$) and winter ($\beta_1 = 0.340$, $P=0.205$, $R^2 = 0.13$) were not significantly related to BGT (Fig. 4c). In line with this, the βs 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.

Comparing the βs 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 ($P=0.247$). 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 correlated with diurnal activity during winter. During spring, only the larger bodied antelopes were negatively influenced by BGT.

For the ten hottest days, the diurnal activity of eland ($\beta_1 = -1.501$, $P<0.0001$, $R^2 = 0.83$) and wildebeest ($\beta_1 = -0.502$, $P=0.004$, $R^2 = 0.27$) was negatively correlated with BGT, while the diurnal activity of impala was not significantly related with BGT ($\beta_1 = -0.577$, $P=0.164$, $R^2 = 0.15$). This confirms that the activity pattern of the larger bodied antelopes is correlated with BGT, but not that of the smallest antelope, the impala.

Discussion

We investigated how the activity pattern of three antelope 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 correlated with 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 and Fairall 1986; Owen-Smith 1998; du Toit and 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 (Porter and 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 and 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 heat stress is at its highest, all three species exhibited a similar response to heat with a higher BGT (i.e., steeper negative slope of BGT regressed on activity), indicating that the higher heat 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 and 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 and 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). The high activity level of wildebeest in spring and summer might be explained by their higher water and food requirements (Prins and Van Langevelde 2008; Bunnell and Gillingham 1985). A similar pattern was observed for other African ungulates which are found in resource-limited systems in Africa (Beekman and 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 greater effort expended to acquire more available forage and to avoid heat stress (Fig. 2). 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. However, note that ungulates may also employ the alternative strategy of feeding longer to store energy for when the quality and quantity of forage is reduced during the dry season.

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 (the latter might be caused by the low activity at low BGT; Fig. 4; hypothesis 2), which is confirmed by the results from the ten 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; Peter 1986; Owen-Smith 1988) and also the thickness of boundary layer in the air next to the animals (Porter et al. 2000). We thus argue that during spring these large species are less active during periods of high temperature, probably to avoid the risk of hyperthermia. Further, pelage characteristics such as thickness and colour also influence the ability to gain or lose heat (Lewis 1977; Hofmeyr 1981; Hetem et al. 2009; Maloney et al. 2009). Our large species had a thinner mean pelage depth (eland: 1.0 mm, wildebeest: 2.7 mm, impala: 3.9 mm) (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 in spring such elevated heat stress and water scarcity caused the large antelopes to reduce their activity with increasing temperature (Fig. 4), 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 and 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. An alternative explanation for the observed activity patterns might be related to reproduction. However, all studied antelope species give birth in the wet season and the species have a gestation period of 6 (impala), 8 (wildebeest) and 9 (eland) months (Ahrestani et al. 2012). This excludes possible explanations of lactation or mating during spring (late dry season).

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 and Leuthold 1978; Klein and Fairall 1986; Owen-Smith 1998; du Toit and 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 and Van Soest 1985; Illius and 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 micro-climate 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, although daily activity of all three antelope species was higher in summer (Fig. 3b). 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. We hypothesize that this increased activity in summer reflects foraging activities due to increased food availability. 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 et al. 2007; Lyon 2009). Therefore, abilities to cope with future climate change by these species will primarily depend on their ability to track resources during the resource scarce season and shifting their activity pattern to the cooler part of the day.

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