



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 (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-h body temperature amplitude did not differ between the study sites, regardless of season. Conversely, wildebeest in Mapungubwe showed a higher variability in the 24-h amplitude of body temperature and also a lower 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 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.

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1. 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 behavioral 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 and Henry, 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 behavioral adjustments to cope with the changing climatic conditions. Furthermore, it has been argued that a population at or

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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 behavior 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.

2. Materials and methods

2.1. 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 to 780 m a.s.l., whereas the range in Asante Sana varies between 1000 and 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-h 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-h 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 day) (Kerley and Boshoff, 1997). The summer can be hot with maximum ambient temperatures reaching 38 °C. About 70% of the total 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 *Merxmuellera 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*, *Eriocephalus 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*.

2.2. 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, 2010). These animals were radio tracked regularly (2–3 times per month) for monitoring purposes. We recorded body temperature (T_b) at 15-min 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 1 m 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.

2.3. 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.

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).

3. Results

3.1. 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 1). 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.

3.2. 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. 1a). 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 ($F_{2,6}=0.39$, $P=0.69$) (Fig. 1b). Therefore, impala and eland were able to maintain homeothermy throughout the year despite being exposed to different climates and habitats.

The daily T_b amplitude of wildebeest differed significantly between the study sites ($F_{1,6}=14.18$, $P=0.009$) and across the

Table 1

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)									
24-h Mean	21.47 \pm 0.4	13.38 \pm 0.4	*	29.0 \pm 0.4	19.45 \pm 0.4	*	31.16 \pm 0.4	25.34 \pm 0.4	*
24-h Maximum	40.96 \pm 0.6	28.8 \pm 0.6	*	46.8 \pm 0.6	36.49 \pm 0.6	*	51.01 \pm 0.6	43.22 \pm 0.6	*
24-h Minimum	8.63 \pm 0.4	2.15 \pm 1.3	*	17.18 \pm 0.4	5.76 \pm 0.4	*	20.75 \pm 0.5	11.48 \pm 0.5	*
24-h Amplitude	32.32 \pm 0.7	26.65 \pm 0.7	*	29.62 \pm 0.7	30.73 \pm 0.7	ns	30.26 \pm 0.7	31.74 \pm 0.7	ns
Ambient temperature (°C)									
24-h Mean	19.76 \pm 0.4	12.02 \pm 0.4	*	26.99 \pm 0.4	16.66 \pm 0.4	*	28.35 \pm 0.4	21.63 \pm 0.4	*
24-h Maximum	32.69 \pm 0.5	20.77 \pm 0.5	*	37.98 \pm 0.5	26.18 \pm 0.5	*	38.04 \pm 0.5	30.89 \pm 0.5	*
24-h Minimum	9.89 \pm 0.4	3.49 \pm 0.4	*	18.21 \pm 0.42	7.06 \pm 0.4	*	21.52 \pm 0.4	12.77 \pm 0.5	*
24-h Amplitude	22.8 \pm 0.6	17.28 \pm 0.6	*	19.77 \pm 0.6	19.13 \pm 0.6	ns	16.54 \pm 0.6	18.12 \pm 0.6	ns
Total rainfall (mm)	0	86		46	23		222	81	
Daylight hour	12.04 \pm 0.05	10.44 \pm 0.05		12.75 \pm 0.05	12.86 \pm 0.05	ns	13.93 \pm 0.05	13.93 \pm 0.05	ns

ns: non-significant; $P > 0.05$.

* $P < 0.0001$.

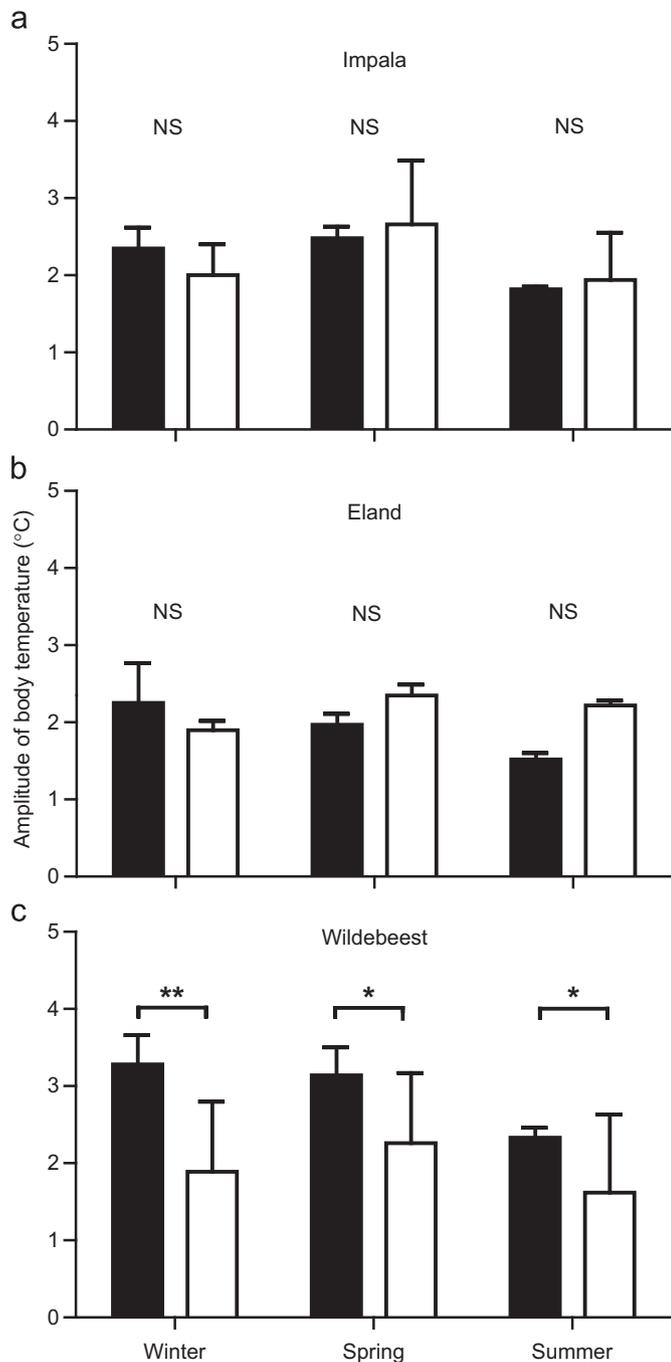


Fig. 1. Mean (\pm SEM) 24-h amplitude of body temperature ($^{\circ}$ C) in impala (a), eland (b) and wildebeest (c) inhabiting the less seasonal site (Mapungubwe, black bars) and the more seasonal site (Asante Sana, white bars) across three seasons. NS: not significant, **: $P < 0.001$, *: $P < 0.05$.

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. 1c). 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. 2a and b).

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 ($F_{1,6} = 0.83$,

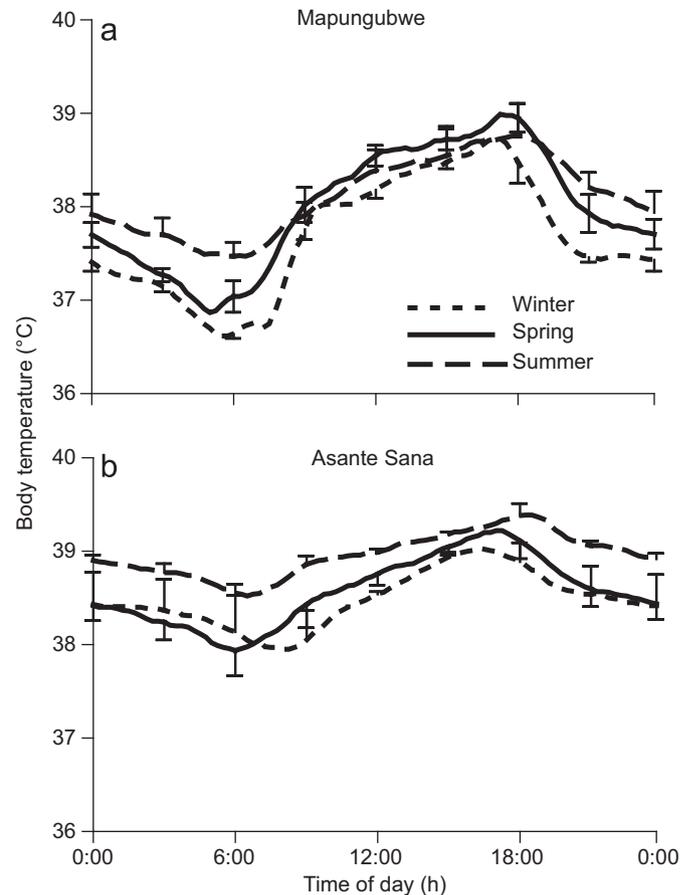


Fig. 2. 24-h Rhythm of body temperature (mean \pm SD) ($^{\circ}$ C) of wildebeest in the less seasonal site (Mapungubwe, a) and the more seasonal site (Asante Sana, b) during winter, spring and summer.

$P = 0.40$) or across seasons ($F_{1,10,6.62} = 0.16$, $P = 0.056$) (Fig. 3a). 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. 3b). 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. 3b). Therefore, the larger T_b amplitude among the wildebeest in Mapungubwe is the result of the lower Min T_b during winter and spring. Furthermore, the frequency of occurrence of daily Min T_b was more skewed to the left in winter (Fig. 4a) and spring (Fig. 4b) than it was in summer (Fig. 4c) in Mapungubwe. In contrast, in Asante Sana, the Min T_b was skewed to the right in all seasons providing further evidence that the Min T_b was lower in Mapungubwe than in Asante Sana and these low Min T_b occurred frequently in winter and spring (Fig. 4a and b).

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 ($B_{T_a} = 0.05$, $P < 0.0001$; $B_{\text{rainfall}} = -0.01$, $P < 0.0001$). The mean daily Min T_b of wildebeest at Mapungubwe was positively influenced by the mean daily Min T_a and bi-weekly cumulative rainfall ($B_{\text{min } T_a} = 0.061$, $r^2 = 0.69$, $P < 0.0001$; $B_{\text{rainfall}} = 0.005$, $P < 0.0001$). 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 ($B_{\text{rainfall}} = -0.0003$; $P = 0.86$) did not have any effect. In Asante Sana, moreover, only the mean daily Min T_a accounted for the variability in the mean daily Min T_b ($B_{\text{min } T_a} = 0.054$, $r^2 = 0.45$, $P < 0.0001$; $B_{\text{rainfall}} = 0.001$, $P = 0.63$).

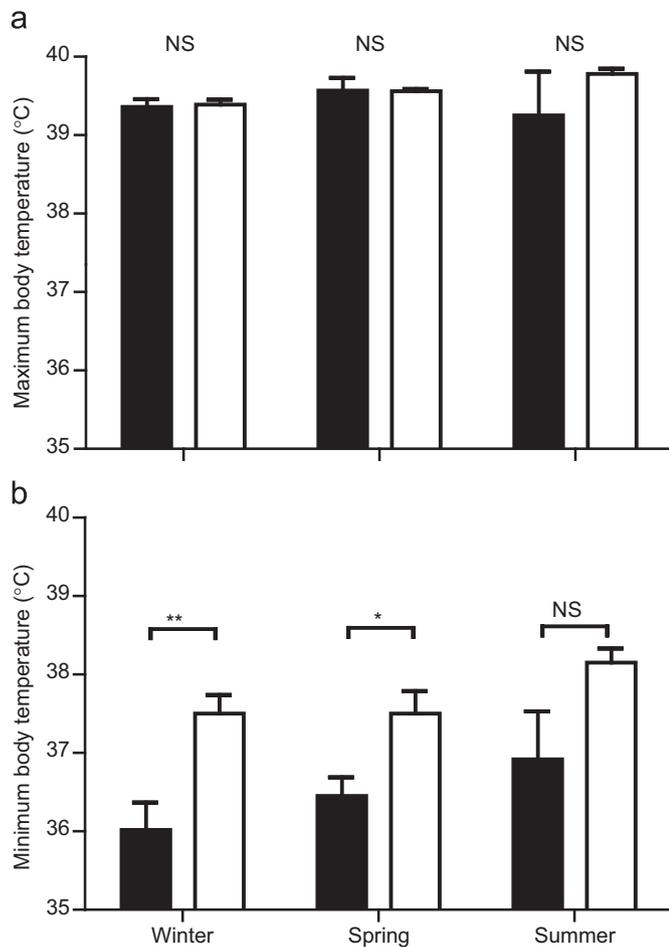


Fig. 3. Mean (\pm SEM) 24-h maximum (a) and minimum (b) body temperature of wildebeest inhabiting the less seasonal site (Mapungubwe, black bars) and the more seasonal site (Asante Sana white bars) across three seasons. NS: not significant, **: $P < 0.001$, *: $P < 0.05$.

4. 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 $\text{Min } T_b$, 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, 2006; Hetem et al., 2009, 2010; Glanville and Seebacher, 2010a, b; 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; Yoda et al., 2000; 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 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 modeling 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; Redfren 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 favor water points in the form of dams and drinking troughs (Smit et al., 2007), we suggest that

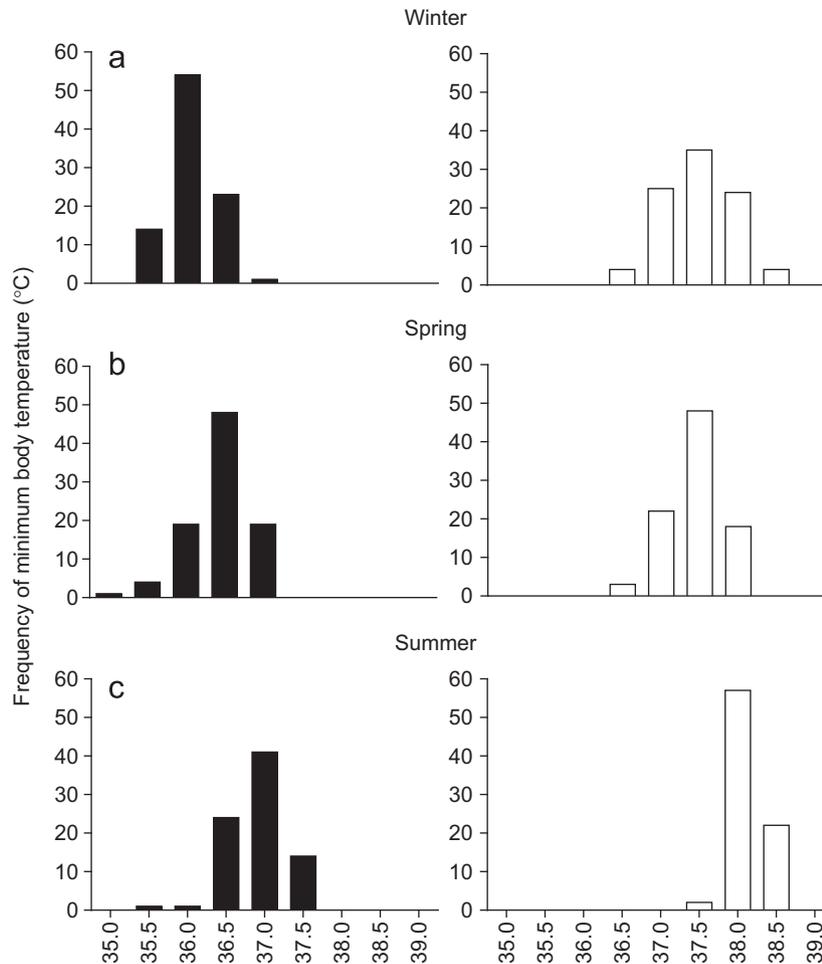


Fig. 4. Frequency distribution of minimum body temperature ($^{\circ}\text{C}$) of wildebeest in winter (a), spring (b) and summer (c) in the less seasonal site (Mapungubwe, black bars) and the more seasonal site (Asante Sana, white bars).

surface water and hence the hydration state, should not be limiting for these antelopes during the dry season. Lowering $\text{Min } T_b$ 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 $\text{Min } T_b$, 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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