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Body temperature daily rhythm adaptations in African savanna elephants (*Loxodonta africana)*

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Abstract

The savanna elephant is the largest extant mammal and often inhabits hot and arid environments. Due to their large size, it might be expected that elephants have particular physiological adaptations, such as adjustments to the rhythms of their core body temperature (T_b) to deal with environmental challenges. This study describes for the first time the T_b daily rhythms in savanna elephants. Our results showed that elephants had lower mean T_b values (36.2 ± 0.49 °C) than smaller ungulates inhabiting similar environments but did not have larger or smaller amplitudes of T_b variation (0.40 ± 0.12 °C), as would be predicted by their exposure to large fluctuations in ambient temperature or their large size. No difference was found between the daily T_b rhythms measured under different conditions of water stress. Peak T_b's occurred late in the evening (22:10) which is generally later than in other large mammals ranging in similar environmental conditions.

Article Outline

1. Introduction

Haldane [1] noted that biological diversity was largely a matter of size, which varies by over 21 orders of magnitude. Increasing physiological and morphological complexity observed from small micro-organisms such as bacteria to large macroscopic organisms such as elephants, therefore, is an inevitable consequence of an increase in size. Various ecological and physiological characteristics can be predicted by body mass and are described by allometric scaling equations [2] and [3]. In mammals, metabolic heat production scales with body mass and large mammals have smaller surface area: volume ratio [4]. As a result, larger mammals have smaller areas available for heat transfer compared with smaller mammals [5]. In hot and arid environments therefore, large mammals face physiological challenges to prevent hyperthermia.

Body temperature (T_b) is considered to be a consequence of the “balance between heat production and heat dissipation” [6] and is a well documented biological rhythm in homeothermic species. Biological rhythms generally represent adaptations of organisms to variations in cyclical environmental conditions [7] and [8]. Although some studies suggest that ambient temperature and activity patterns may influence T_b daily rhythms in large mammals inhabiting arid environments (e.g. eland *Tragelaphus oryx*, [9]; savanna elephants, [10]; camel *Camelus dromedarius*, [11]; Arabian oryx *Oryx leucoryx*, [12]; springbok *Antidorcas marsupialis*, [13]), others have suggested that with exception of the camel they are in fact largely endogenous [14] and [15].

Hot, arid environments may impose restrictions on food and water availability, as well as exposing animals to large fluctuations in ambient temperature. Therefore, large homeothermic animals that inhabit these habitats are expected to have adaptations that deal with these environmental stresses. These can include a lower average (mesor) T_b and adjustments to the T_b daily rhythm, which may enable an animal to reduce energy consumption and water loss [16]. The savanna elephant (*Loxodonta africana*) is the largest extant terrestrial mammal and occurs in a wide range of habitats from savannas to deserts [18]. In these habitats, water sources are often sparse and peak ambient temperatures may reach up to 50 °C at certain times of the year [18] with hot dry season daily fluctuations in some regions ranging from approximately 8 °C at night to well over 40 °C during the day (A.A Kinahan unpublished data). Elephants do not possess sweat glands but cool themselves using transepidermal water loss [19]. They also often make use of free standing water in which to wallow and bathe [19] and their large ears act as thermal windows [20]. In addition, recent work has shown that during the hot dry season in Zambia, free-ranging elephants select shaded habitats in the heat of the day and select landscapes that facilitate heat loss during the cool evenings [21]. However, due to the difficulty in obtaining physiological parameters from such animals, little information is available on the body temperature of savanna elephants (with the exception of 10, 22, 23) and no studies that we are aware of have attempted to examine their T_b daily rhythms. The aims of the current study therefore were to (i) measure and describe T_b daily rhythms in savanna elephants, (ii) determine whether these rhythms were consistent with expectations of animals living in a hot environment with large daily fluctuations in ambient temperature, independent of body size, and (iii) determine whether T_b daily rhythms varied with water stress.

2. Materials and methods

2.1. Animals and housing

Four individual adult African elephants (ranging 20–30 years) (1 male [M] and 3 females [F1 F2 and F3]) from the National Zoological Gardens in Pretoria, South Africa were used for this study. Elephants were housed in an outdoor enclosure during the day and at night throughout this study (9143 m^2) but were moved to a smaller enclosure each morning (300 m^2) whilst the larger enclosure was being cleaned (approximately 08:00–09:00). During this time the male was housed in a non-climate controlled indoor enclosure (314 m^2). We were not able to measure body mass directly but we estimated the male to weight between 5.5 and 7.0 metric tonnes and the females to weigh between 2.0–3.0 metric tonnes [24], with shoulder heights averaging 3.3 m for adult males and 2.7 m for adult females [25]. Data were obtained between October and November 2005, during the hot season and before the onset of heavy summer rains. A daily ration of 40 kg pumpkin, 20 kg gem squash, 15 kg butternut, 20 kg carrots, 30 kg beetroot, 20 loaves of bread, 20 kg potatoes and *ad libitum* dry teff was offered. Ambient temperature was recorded every 30 min for the duration of the experiment by placing three iButtons® (Thermochron, Dallas Semiconductors, Maxim Integrated Products, Inc., Sunnyvale, CA) (model DS1921G; ± 0.5 °C) at different locations around the enclosure. The iButtons were placed below plastic discs so they were shaded from direct sunlight and secured in three different random locations around the enclosure at a height of approximately 2 m, to obtain the mean ambient temperature of the enclosure.

2.2. Daily rhythms of body temperature (T_b)

Body temperatures of elephants were obtained by hand-feeding them iButtons that were set to record every 30 min. This technique has previously been used to measure T_b in African and Asian circus elephants during transportation [26]. Gastrointestinal temperatures recorded by ingested temperature sensors have been shown to be reliable indicators of core body temperature in hindgut fermenters [27]. Initially, we used model DS1921G iButtons but since this did not give us sufficient resolution to measure T_b we used model DS1922 L (± 0.0625 °C). iButtons were sewn into pockets of rip-stop nylon [26] which included a 30 cm strand of trailing material. They were inserted into the centre of an apple before being fed to elephants. This provided some protection and also allowed iButtons to be readily identified in dung that had been passed. iButtons were retrieved by examining the dung in the enclosure each morning. Data were downloaded using iButton-TMEX software version 3.21 (2004 Dallas Semiconductor MAXIM Corporation). Using the data traces, we were able to determine how long iButtons remained in the stomach of the elephants (in which temperatures were slightly variable, because of the ingestion of food and water which was at a lower temperature) and how long they remained in the lower intestine (in which recorded temperatures provided reliable measurements of core body temperature).

2.3. Experimental design

Elephants were fed iButtons under two different conditions in which we varied water stress. Individuals were enticed to the edge of their enclosure (by feeding them part of their daily ration) and trained to stand under hosepipes for 10-minute periods. We were careful to wet the entire animal (head, neck, ears, back and stomach). This was done twice per day at approximately 11:00 and 15:00. During weeks 1–2, individuals M and F1 were sprayed (F2 and F3 were not sprayed). During weeks 3–4, F2 and F3 were sprayed (M and F1 were not sprayed). We fed the elephants iButtons at approximately 8:00 and 15:00 on alternate days in an attempt to obtain at least 5 days worth of measurements for each animal under each treatment. Throughout the study the elephants were allowed continuous access to their normal water supply, which included a pool (300 m^2 and up to 2 m deep) and a drinking trough.

2.4. Data analysis

We used cosinor analysis to determine the T_b daily rhythms of measured individuals [28] and [29] using the program *Chrono2* (J.W.H. Ferguson, University of Pretoria). The period was assumed to be 24 h. We calculated the mean (mesor) values, the amplitude and the phase angle (Acrophase) of the T_b daily rhythms for each individual. The significances of the fitted curves were tested against the null hypothesis that the amplitude was zero [29]. The percentage of the variability in the data that could be accounted for by the fitted curve (percentage rhythm) was also calculated. We determined the curves that described groups of individuals within treatments (unsprayed and sprayed) and whether they were significantly different from one another. We also determined whether T_b daily rhythms differed between treatments (i.e. unsprayed versus sprayed) [30].

3. Results

3.1. Ambient conditions

A one-way repeated measures ANOVA showed that no inter-variation occurred between the ambient temperatures around the enclosure recorded by each of the iButtons. Mean ambient temperature throughout the study period was 21.5 ± 0.19 °C (maximum = 37.7 °C, minimum = 11.2 °C).

3.2. Data retrieval

iButtons were recovered between 2 and 7 days after they had been fed to elephants. The mean gut transit period was 65.2 ± 36.5 h. The mean period that the iButtons remained in the animals stomach was 4.4 ± 2.2 h (range 2 to 9 h). The overall success in retrieving data from iButtons was low. Of the 40 that were fed to elephants, 2 were never retrieved and 32 appeared to be intact when retrieved however could not be read. We were only able to obtain data from the male and two of the females (F1 and F2). We therefore present data from six iButtons. It should be noted, that changing the feeding regime from placing the apples in the elephant's trunk to directly placing them in their mouths improved chances of successfully retrieving data from the iButtons.

3.3. Daily rhythms of body temperature (T_b)

Across all individuals, the average mesor was 36.2 ± 0.49 °C, the amplitude was 0.40 ± 0.12 °C (range of oscillation 0.8 °C) and the acrophase was at 22:03. All individuals (M, F1 and F2) had amplitudes that differed significantly from zero and had high percentage rhythmicities, both during times when they were not sprayed and when they were sprayed (Table 1). In addition, there were differences in the mesor values between individual animals with the male typically having lower mesor values than the females.

Table 1.

Body temperature daily rhythm values for each individual under each condition

	Male no spray	**Male spray**	**F1 no spray**	**F1 spray**	**F2 no spray**	**F2 spray**
Mesor (°C)	35.8	35.7	35.5	36.0	36.2	37.0
Amplitude (°C)	0.50	1.00	1.04	0.48	0.84	0.62
Acrophase (time)	23.25	22.05	20.55	20.40	23.15	0:10
Percentage rhythm	73.9	63.8	69.0	58.1	60.0	69.1
Zero-amplitude test	$F_{2,45}$ = 63.61	$F_{2,93}$ = 82.11	$F_{2,237}$ = 263.19	$F_{2,45}$ = 31.18	$F_{2,141}$ = 105.94	$F_{2,45}$ = 50.33
P-value	$P < 0.001$	$P < 0.001$	$P < 0.001$	$P < 0.001$	$P < 0.001$	$P < 0.001$

Mesor values (the mean value based on the parameters of the cosine function), amplitudes (the differences between the peak or trough values and the mean value), acrophases (the time at which the peak of T_b occurs), percentage rhythms (the proportion of the variance accounted for by the fitted 24-hour cosine model), and the corresponding *P*-value from the zero-amplitude (no rhythm) tests are shown.

There were significant differences in the T_b daily rhythms of the 3 individuals when they were not sprayed ($F_{2,423} = 429.4$, $P < 0.001$ for the mesor and $F_{4,423} = 41.7$, $P < 0.001$ for the phase/amplitude). The overall T_b daily rhythm of all three non-sprayed individuals had a mesor value of 36.2 °C, amplitude of 0.8 °C and an acrophase at 22:10 (Table 1). There were also significant differences in the T_b daily rhythms of the individuals when they were sprayed ($F_{2,183} = 902$, $P < 0.001$ for the mesor and $F_{4,183} = 13.0$, $P < 0.001$ for the phase/amplitude). The overall T_b daily rhythm of the three individuals that were sprayed had a mesor value of 36.2 °C, an amplitude of 0.4 °C and an acrophase at 21:56 (Table 1). Because there was a large amount of variation in the T_b daily rhythms within treatments (sprayed and not sprayed), there was no significant difference in the T_b daily rhythms between treatments ($t_4 = 0.125$, $P = 0.45$ for the mesors and Hotelling's $T_2 = 0.290$, $P = 0.93$ for the phase/amplitudes).

Fig. 1 and Fig. 2 show an example of T_b daily rhythms for two females, one sprayed and one non-sprayed and the corresponding ambient temperatures. The graphs show that the T_b of elephants were generally higher during lower ambient temperatures (night) compared to warmer ambient temperatures (daytime) and that T_b gradually increases during the day into late evening after sundown and decreases throughout the night and early morning.

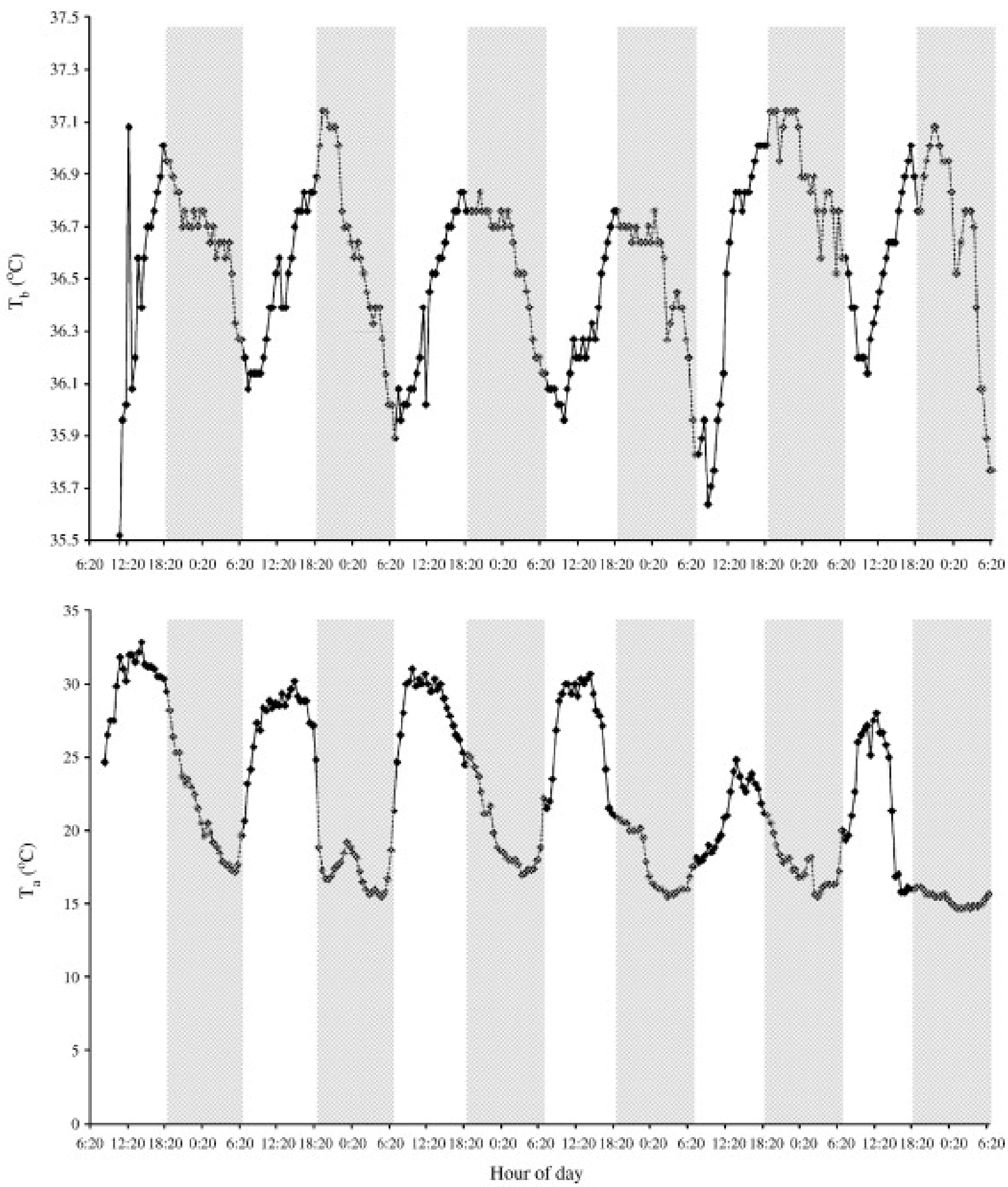

Fig. 1. Graph showing an example of Female: F2 (not sprayed) (above) T_b daily rhythm and the corresponding ambient temperatures (below). The elephant ingested the iButton at 8:20, it remained in the stomach for 6 h where we assume it moved into the intestinal tract at approximately 14:20 the same day. The iButton remained in the intestinal tract of this individual for a period of 138 h before it was assumedly (since a marked drop in temperatures were observed) excreted in the faeces at approximately 07:20 6 days after initial ingestion (not shown in this graph). Shaded areas represent night time data.

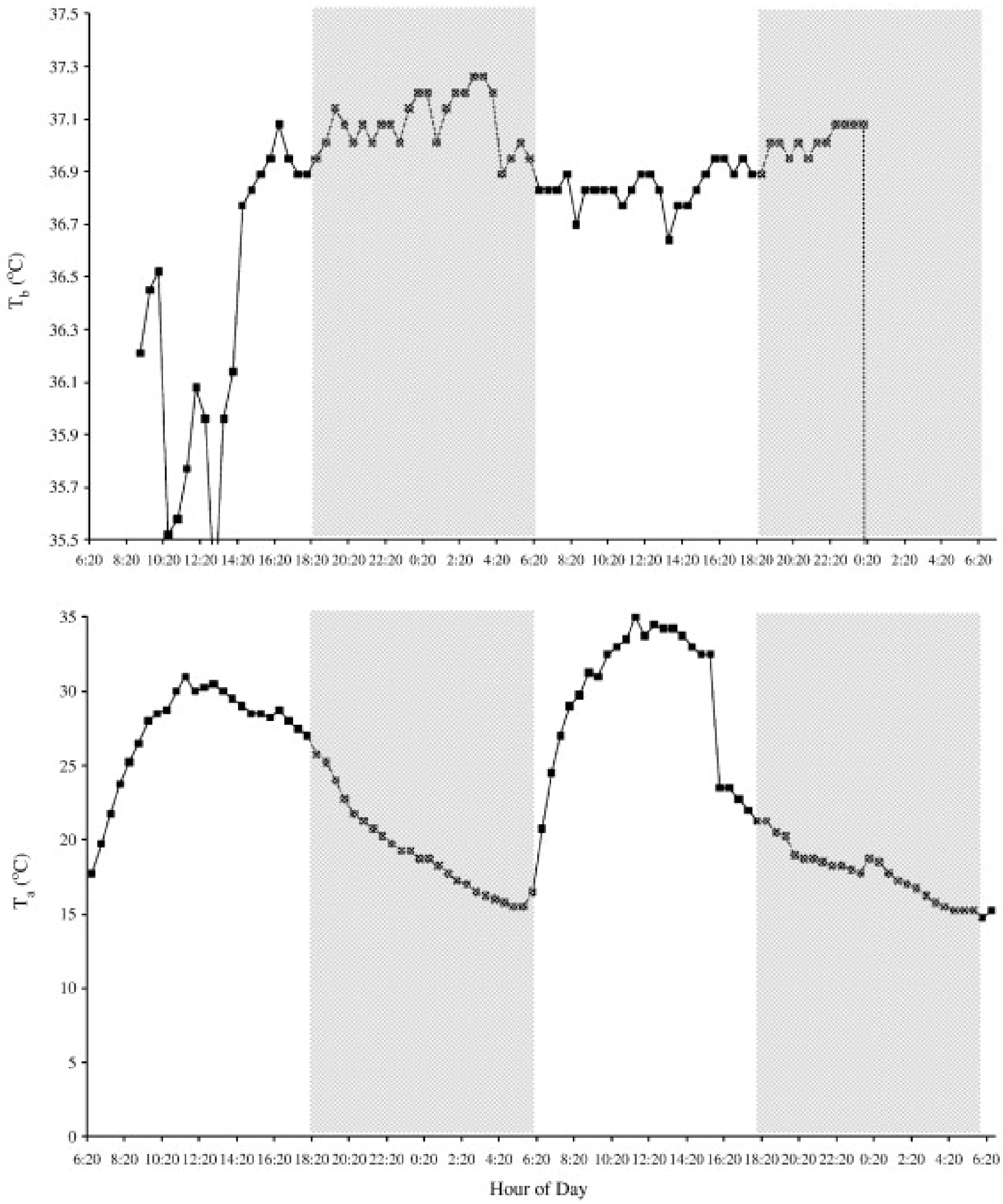

Fig. 2. Graph showing an example of Female: F1 (sprayed) (above) T_b daily rhythm and the corresponding ambient temperatures (below). The elephant ingested the iButton at 8:20, it remained in the stomach for 7 h where we assume it moved into the intestinal tract at approximately 15:20 the same day. The iButton remained in the intestinal tract of this individual for a period of 33 h before it was excreted in the faeces at approximately 00:20 the following day. Shaded areas represent night time data.

4. Discussion

Savanna elephants are the largest extant terrestrial mammal and often inhabit areas in which daytime ambient temperatures exceed that of their core body temperature, but in which night-time temperatures can be relatively cool [18]. Although behavioural thermoregulation is well documented for savanna elephants (e.g. [19] and [20]), due to the difficulty of obtaining physiological parameters, little is known about the T_b of elephants and nothing known of their T_b daily rhythms.

In the current study we measured the T_b daily rhythms in savanna elephants for the first time. In addition, we attempted to provide the individuals with different levels of water stress i.e. sprayed with water (representing a lower level of water stress) and when they were not sprayed (representing a higher level). However, because there was a large variation in the T_b daily rhythms between different individuals, we found that there were no significant differences in the T_b daily rhythms between the two treatments (sprayed and not sprayed). In addition, due to welfare considerations, individuals had continuous access to free water. Thus, our attempts to manipulate water stress may have been insufficient to alter the T_b daily rhythms. Moreover, since daily fluctuations in ambient temperature occurring throughout this study (11 to 38 °C) were we assume, generally within the thermal 'comfort' range for elephants, it is unlikely that they were heat stressed. We suggest, therefore, that our results are indicative of normal (i.e. non-heat or water stressed conditions) temperature circadian rhythms in savanna elephants.

The mesor values of the elephants (36.2 ± 0.5 °C) were low compared with other large herbivores such as the Arabian oryx (*Oryx leucoryx*) (38.4 ± 1.3 °C)[12], springbok, (*A.*

marsupialis) (39.43 ± 0.15 °C) [13] and the eland (*T. oryx*) (38.03 ± 0.15 °C) [31]. However, they fell within the range of temperatures measured in earlier studies on the body temperatures of other African elephants [10], [22] and [23] (which used rectal probes and urine and faecal temperature measurements). Likewise, in a study on circus elephants during transportation [26], using a method and within environmental temperature ranges (10–38 °C) similar to this study, the authors also found that T_b in elephants ranged between 35–37.5 °C. The lower T_b observed in elephants compared to other smaller species may be one way in which elephants adapt their daily rhythms to the thermal constraints their large sizes impose on them. The fact that the largest individual (the male) consistently had a lower average mesor compared to the smaller females seems to support this notion. It should be noted however, that in large domestic livestock there is much interspecies variation that cannot be accounted for by size (e.g. 39.3 °C in sheep, 39.04 °C in cattle and 38.0 °C in horses) [7], [32] and [33] and so, whether the observed lower mesor occurring in elephants is a function of body size should be interpreted with caution. Alternatively, it may be that the lower mesor values in elephants may be in response to their intra-abdominal testes [23] since spermatogenesis usually occurs at 37 °C and can be disrupted if the temperature is raised by a few degrees [34]. Indeed, in an earlier study, a correlation was found between the location of testes and body temperature T_b in mammals, with species that had intra-abdominal testes generally having the lower body temperatures T_b's [34].

Elephants typically showed a high rhythmicity in their T_b daily rhythms and all showed measured amplitudes significantly different from zero. Aschoff [6] suggested that due to thermal inertia larger species should generally have lower amplitudes than smaller species. The amplitudes of variation found in the current study (0.4 °C; half excursion; 0.8 °C full excursion) were lower than those measured in other ungulates inhabiting hot arid environments [12] and [15]. However, no evidence for a relationship between body mass and amplitude of variation was found in large ungulates weighing between 41 kg–900 kg [16]. Our elephants had amplitudes of variation similar to that measured in the black wildebeest (*Connochaetes gnou*) [35], which is much smaller, further suggesting that extremely large body size in elephants does not necessarily predispose them to having small amplitudes of T_b variation. Whether amplitudes of T_b variation may increase when much larger daily fluctuations in temperatures occur remains to be determined. Elephants in this study showed peak T_b occurring later in the evening (typically around 22:00), which is later than that measured in other large ungulates in which peak values occur at or near the end of the thermal heat load (approximately 17:00–19:00) [14], [15], [16] and [17]. However, in horses and sheep T_b rhythms did not appear to be related to activity rhythms [32] and acrophases occurred at the beginning of night despite them being diurnal animals [7]. In addition, studies on arid-inhabiting ungulates have generally found no relationship between acrophases and thermal loads (with the exception, 12). T_b daily rhythms in large ungulates therefore are thought to be largely endogenous [13], [15] and [35]. While this may be also true of elephants, the fact that their acrophases occur later than other large ungulates studied to date, and indeed whether their T_b rhythms are endogenous, warrants further investigation.

One possible concern regarding the significance of our data may be the use of captive individuals [36]. However, the animals in the current study were neither restrained nor were they prevented from normal behavioural modes of thermoregulation thus we are confident that observed T_b daily rhythms in this study are not an artefact of a captive environment. Furthermore, this study was carried out in the same geographical area (sub Saharan Africa) in which they would naturally inhabit.

In summary, this study describes for the first time T_b daily rhythms of African savanna elephants. Our results show that elephants, which can be over seven times larger than the largest ungulate studied to date, typically had lower T_b and amplitudes and later acrophases than other large ungulates inhabiting similar environments. This study utilised a novel non-invasive technique to examine T_b daily rhythms in a species where such measurements can be difficult to attain. We suggest that this method provides accurate measures of T_b and could be used for a wide range of species that are free ranging or semi-free ranging. Such a method therefore, has the potential to play an important role in greatly improving our understanding of the physiology of animals in relation to their ecology, which otherwise would be extremely difficult to ascertain.

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