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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.

Keywords: Activity level; Body size; Thermoregulation; iButton

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 [2,3]. 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 [7,8]. 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 [14,15].

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

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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 [28,29] 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)