

**Drought-induced starvation of aardvarks in the Kalahari:  
an indirect effect of climate change**

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## **Abstract**

Aardvarks (*Orycteropus afer*) are elusive burrowing mammals, predominantly nocturnal and distributed widely throughout Africa except for arid deserts. Their survival may be threatened by climate change via direct and indirect effects of increasing heat and aridity. To measure their current physiological plasticity, we implanted biologgers into six adult aardvarks resident in the semi-arid Kalahari. Following a particularly dry and hot summer, five of the study aardvarks and eleven other aardvarks at the study site died. Body temperature records revealed homeothermy (35.4-37.2°C) initially, but heterothermy increased progressively through the summer, with declining troughs in the nycthemeral rhythm of body temperature reaching as low as 25°C before death, likely due to starvation. Activity patterns shifted from the normal nocturnal to a diurnal mode. Our results do not bode well for the future of aardvarks facing climate change. Extirpation of aardvarks, which play a key role as ecosystem engineers, may disrupt stability of African ecosystems.

## **Keywords**

climate change, body temperature, physiological flexibility

## **Introduction**

Aardvarks (*Orycteropus afer*) are nocturnal fossorial mammals, distributed throughout sub-Saharan Africa but absent from arid deserts [1]. As ecosystem engineers, their prodigious excavation of burrows provides shelters to multiple commensal species [2]; a decline of aardvark populations may thus have dire consequences for African ecosystems. The semi-arid zones, which aardvarks inhabit, are likely to become hotter and drier with climate change, with increased frequency and duration of droughts [3]. Hotter and drier habitats will have direct effects on aardvarks through greater heat gain from the environment and increased water requirements. There also may be indirect effects, through changes in resource quality and availability, altered habitats, and other ecosystem changes. Alterations in trophic interactions may be more pervasive than direct effects of climate change [4,5].

Aardvarks are committed myrmecophages [6], and the primary factor determining their habitat suitability is the abundance and distribution of ants and termites [7]. Hotter and drier conditions are likely to alter distributions and availability of these prey species [8]. Aardvarks may have to adjust their activity and feeding patterns in response to changes in activity of prey, potentially at the cost of other homeostatic systems, such as thermoregulation. As large, long-lived mammals, aardvarks will have to rely on physiological plasticity to buffer the effects of climate change [9,10].

To investigate their current physiological plasticity, we implanted temperature and activity biologgers into six adult aardvarks in the Kalahari. During the course of our study, 16 aardvarks, including five of our implanted aardvarks, were found dead on site during a severe summer drought.

## **Methods**

### *Aardvark body temperature and activity data collection*

The study took place at Tswalu Kalahari Reserve (27°14'57"S, 22°22'52"E) in South Africa. In July 2012, we implanted temperature- and motion-sensitive biologgers and tracking transmitters (supplementary material S1) into six free-living adult aardvarks (37-45kg) under anaesthesia [11]. Following surgery, aardvarks were released at their capture sites. We tracked the aardvarks occasionally, but mostly they functioned free of human presence. Only one of the six aardvarks survived the summer of 2013. We recovered the temperature and activity loggers from the carcasses, and explanted them from the survivor.

### *Climatic variables*

We assessed ambient temperature at the study site using a 150mm diameter black globe thermometer (Hobo U30-NRC, Onset Computer Corporation, USA). We assessed local climatic variables over the previous 35 years using the Global Land Data Assimilation System (supplementary material S2).

### *Data analyses*

We analysed two periods with similar ambient temperatures, namely early (November 2012) and late (March 2013) summer (Table 1). We compared climatic data between these two periods with Mann-Whitney rank sum tests. Changes in aardvarks' body temperature and activity patterns were investigated by fitting linear mixed models by entering 'period' as an explanatory variable with two modalities (November and March) and individual identity as a random factor.

Some of the biologgers were lost after an aardvark's death, so analyses were restricted to four individuals. Analyses were performed using the 'nlme' R software package (<http://cran.at.r-project.org>).

## **Results**

During the 2012-2013 summer, monthly precipitation was in the lower quartile range of data recorded over 35 years (supplementary material S2). Substantial summer rainfall (>100 mm) occurred late, i.e., only at the end of March. Concomitantly, mean air temperatures were the hottest since records began in 1980, with air temperature in January 2013 almost 3°C higher than the 35-year mean. Mean wind speed was 32% higher than that averaged over 35 years. This combination of climatic conditions resulted in a severe drought; the soil moisture content was 23% lower than average (supplementary material S2). Daily black globe temperature, which integrates air temperature, wind speed and solar radiation, typically exceeded 40°C and reached 55°C (Fig. 1a).

At the beginning of summer, the aardvark were homeothermic with daily body temperature varying between 35-37°C (Table 1, n=4), however, the mean, minimum and maximum 24h body temperature decreased progressively throughout summer in aardvarks that died later (see example in Fig 1c, d). Because minimum 24h body temperature decreased to a greater extent than did maximum 24h body temperature, heterothermy (as indexed by the 24h amplitude of the body temperature rhythm) increased progressively over the summer in these aardvarks (reaching an amplitude of 8.6°C). Visual observations of the implanted but also non-implanted aardvarks indicated a decline in the aardvarks' body condition as the summer progressed. Poor body condition was evidenced by prominent ribs, spine and pelvic bones

(Fig. 1b). The single study armadillo that survived (Fig. 1e and f) also exhibited heterothermy during summer ( $3.9^{\circ}\text{C}$ ), an effect that resolved partially at the end of summer.

The body temperature rhythm changed from a bimodal pattern in November (start of summer), when body temperature elevation coincided with activity, to a more-cosinor rhythm in March (end of summer), with body temperature peaking just after sunset when armadillos were inactive in their burrows (see example in Fig. 2). Despite similar ambient conditions in these two months (Fig. 2a, Table 1), armadillos regulated their body temperature at a lower level and showed increased heterothermy in March compared to in November ( $n=4$ , Table 1, see example in Fig 2b). Armadillos shifted activity from an almost exclusively nocturnal pattern in November to mainly diurnal activity in March (Table 1,  $n=4$ ), with the length of the circadian activity periods being 30% shorter in March than in November. This effect was more pronounced in the armadillo that did not survive the summer (see example in Fig. 2c).

## **Discussion**

We have shown that armadillos did not exhibit sufficient physiological plasticity to survive a summer drought in a semi-arid desert. Despite shifting from a nocturnal to diurnal activity pattern, the armadillos experienced a progressive decline in body temperature over the dry summer, most until death. We propose that the decrease in body temperatures reflects a negative energy balance, as indicated by the loss of body condition, and as demonstrated for other food-deprived mammals [12].

The severe drought was likely to have reduced armadillo prey availability. Soil moisture directly affects activity, development and survival of subterranean insects such as ants and

termites [13, 14], on which aardvarks depend [7]. Furthermore, the low soil moisture severely affected grassland phenology and overall vegetation productivity, as evidenced by MODIS derived time-series Enhanced Vegetation Indices [15], which would further compromise aardvark prey availability [16].

It has been argued that aardvark activity patterns are dictated by ambient temperatures, with aardvarks emerging from their burrows earlier in winter months [17,18] to avoid cold temperatures at night, and avoiding activity during summer days to prevent overheating [1]. However, we have shown that activity patterns differed in March and November despite similar ambient temperatures (Fig. 2c). Moreover, body temperature of the aardvarks was lower in March, when they were diurnally active (Fig. 2b) and when they could benefit from warmer ambient temperatures during foraging. Phenotypic plasticity in activity pattern, particularly temporal niche shifting toward a diurnal phenotype, appears to allow endotherms to reduce thermoregulatory costs when energetically challenged [19]. Despite the aardvarks' low body temperatures, which would have reduced energy demand, and adjusted activity times, most died at the end of summer. Body temperatures dropped critically to as low as 25°C (Fig. 1d), from which the aardvarks did not recover. Sudden mortality of aardvarks in response to drought has been reported previously [20]. Rather than being a direct consequence of exposure to heat or aridity, we suggest that secondary effects of drought on prey availability compromised the aardvarks' welfare. With climate change predicted to increase the frequency and duration of droughts, aardvarks may be extirpated from much of their current range as a result of disrupted trophic interactions. The burrows excavated by aardvarks provide thermal refugia for at least 27 vertebrate species [2]; with climate change, these refugia will become increasingly important for those species to buffer climatic extremes [21]. The extirpation of aardvarks that function as physical ecosystem engineers therefore

may disrupt ecosystem stability [22] and result in an undesirable ecological cascade, as seen with digging mammals in Australia [23]. We may face a similar scenario in African ecosystems.

### **Ethics**

All procedures were approved by the Northern Cape Department of Environment and Nature Conservation and the Animal Ethics Screening Committee of the University of the Witwatersrand (2011/10/04).

### **Competing interests**

We have no competing interests.

### **Data accessibility**

Data used can be found in Dryad (doi:10.5061/dryad.tr360):

<http://dx.doi.org/10.5061/dryad.tr360> [24].

### **Authors' contributions**

All authors contributed to study design, data collection and interpretation, and manuscript writing. BR and RH conducted data analyses. All authors agree to be held accountable for the content therein and approved the final version of the manuscript.

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## **Figure and table captions**

### **Figure 1**

Hourly recordings of black globe temperature (a) and 30-min recordings of body temperature from a representative aardvark that died (c) and one that survived (e) the summer drought. Right panels represent body temperatures (zoomed in from rectangles in c and e) during the month of March, during which 16 aardvarks were found dead. The upper right photograph (b) illustrates poor body condition of an aardvark.

### **Figure 2**

Nychthemeral rhythm of black globe temperature (a), body temperature (b) and activity (c), double plotted for clarity, of a single representative aardvark at the beginning (November, grey lines) and at the end (March, black lines) of a particularly hot and dry summer. Black/grey bars represent night for the respective periods.

### **Table 1**

Body temperature and activity patterns from four aardvarks (three that died and one that survived summer 2013), together with prevailing ambient conditions at Tswalu Kalahari Reserve during early (November) and late (March) summer.

**Table 1**

<b>Time of year</b>	<b>Early summer (November 2012)</b>	<b>Late summer (March 2013)</b>		
<i>Black globe temperature (°C)</i>			<i>z</i> -values	<i>p</i> -values
24h mean	28.3 ± 3.5	29.5 ± 2.3	-1.212	0.22
24h minimum	15.5 ± 3.2	13.8 ± 4.0	-0.894	0.37
24h maximum	44.8 ± 6.7	46.8 ± 3.4	-1.493	0.13
24h amplitude	29.3 ± 7.4	33.0 ± 4.6	-1.567	0.12
<i>Light/dark cycle (h:min)</i>			<i>z</i> -values	<i>p</i> -values
Sunrise (local time)	05:34 (05:30-05:42)	06:34 (06:27-06:42)	-6.48	<b>&lt;0.001</b>
Sunset (local time)	19:06 (18:55-19:18)	18:52 (18:38-19:07)	-4.88	<b>&lt;0.001</b>
Day light duration	13:32 (13:12-13:48)	12:17 (11:55-12:39)	-6.47	<b>&lt;0.001</b>
<i>Body temperature (°C)</i>			<i>F</i> -values	<i>p</i> -values
24h mean	36.1 ± 0.5	34.2 ± 0.5	56.94	<b>&lt;0.001</b>
24h minimum	35.4 ± 0.7	32.2 ± 0.7	94.98	<b>&lt;0.001</b>
24h maximum	37.2 ± 0.5	35.8 ± 0.3	47.39	<b>&lt;0.001</b>
24h amplitude	1.7 ± 0.3	3.8 ± 0.3	149.94	<b>&lt;0.001</b>
<i>24h activity</i>			<i>F</i> -values	<i>p</i> -values
Total time active per (h:min)	7:34 ± 38	5:21 ± 42	43.18	<b>&lt;0.001</b>
Proportion of diurnal activity (%)	13.6 ± 6.4	67.4 ± 6.7	263.34	<b>&lt;0.001</b>

Figure 1

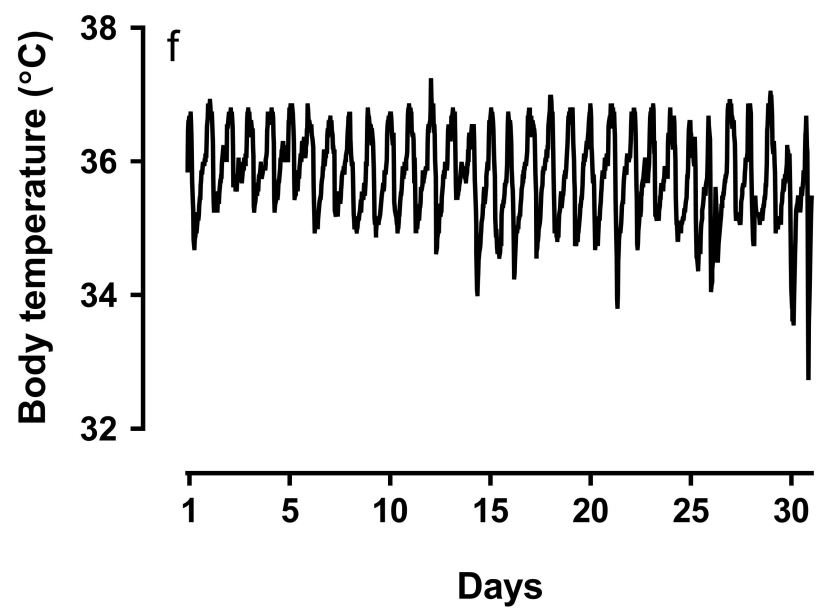
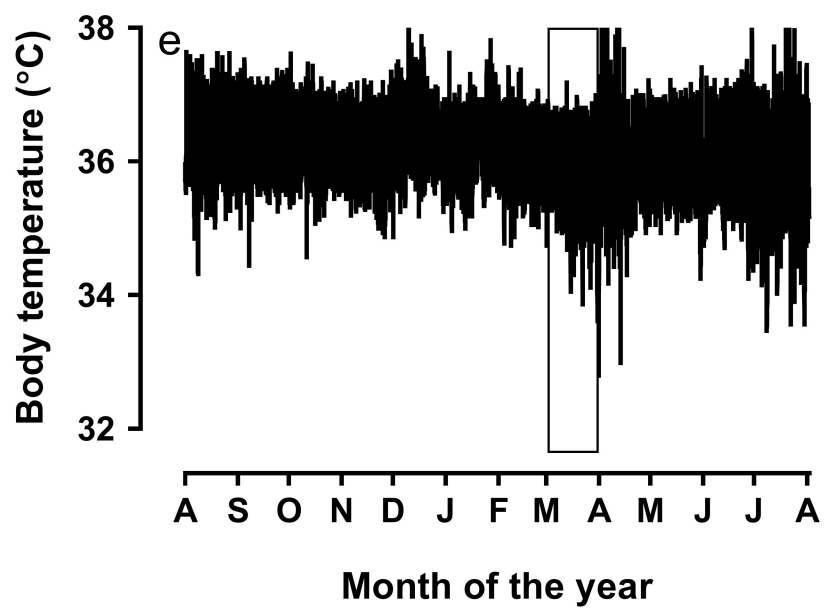
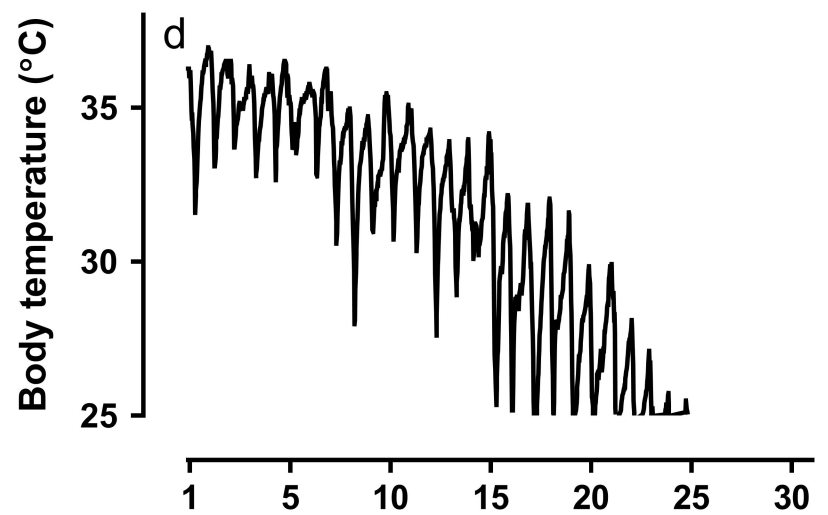
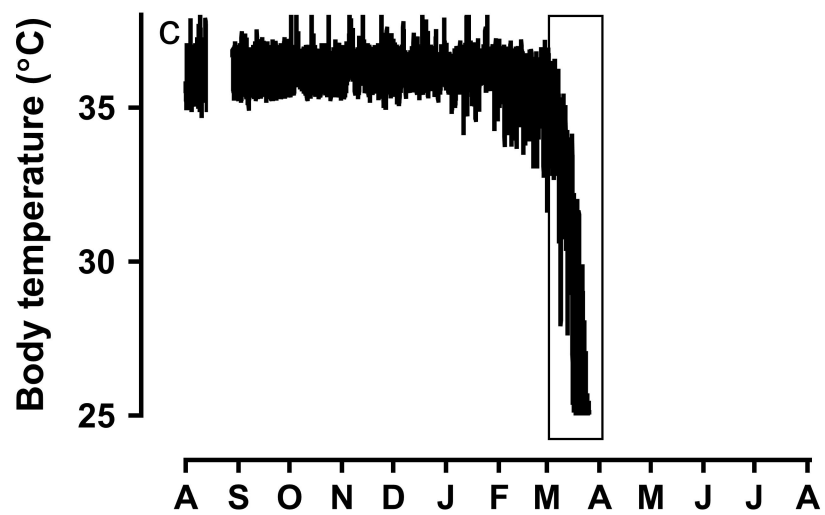
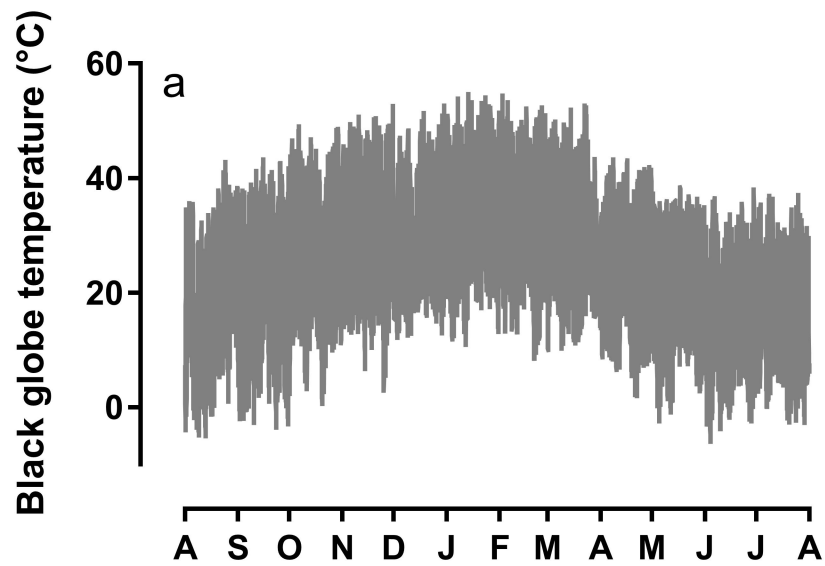


Figure 2

