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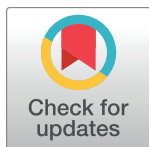
RESEARCH ARTICLE

Living on the edge: Daily, seasonal and annual body temperature patterns of Arabian oryx in Saudi Arabia

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Abstract

Heterothermy, the ability to allow body temperature (T_b) to fluctuate, has been proposed as an adaptive mechanism that enables large ungulates to cope with the high environmental temperatures and lack of free water experienced in arid environments. By storing heat during the daytime and dissipating it during the night, arid-adapted ungulates may reduce evaporative water loss and conserve water. Adaptive heterothermy in large ungulates should be particularly pronounced in hot environments with severely limited access to free water. In the current study we investigated the effects of environmental temperature (ambient, T_a and soil, T_s) and water stress on the T_b of wild, free-ranging Arabian oryx (*Oryx leucoryx*) in two different sites in Saudi Arabia, Mahazat as-Sayd (MS) and Uruq Bani Ma'arid (UBM). Using implanted data loggers we took continuous T_b readings every 10 minutes for an entire calendar year and determined the T_b amplitude as well as the heterothermy index (HI). Both differed significantly between sites but contrary to our expectations they were greater in MS despite its lower environmental temperatures and higher rainfall. This may be partially attributable to a higher activity in an unfamiliar environment for translocated animals in UBM. As expected T_b amplitude and HI were greatest during summer. Only minor sex differences were apparent that may be attributable to sex-specific investment into reproduction (e.g. male-male competition) during rut. Our results suggest that the degree of heterothermy is not only driven by extrinsic factors (e.g. environmental temperatures and water availability), but may also be affected by intrinsic factors (e.g. sex and/or behaviour).

Introduction

Deserts sustain life, despite being hot and dry with low and unpredictable precipitation, intense solar radiation, low primary production and soil fertility, extreme span of ambient temperatures as well as an overall lack of free standing water [1–3]. Water availability is likely to be the most important factor affecting life in deserts and primary productivity often closely parallels rainfall in desert ecosystems [4]. Similarly, since free standing water is usually scant in deserts, secondary productivity is usually indirectly linked to water availability as the rate of food consumption by desert herbivores tends to be linked to the water content of the plants consumed [5–8]. As a result animals living in desert environments make use of behavioural and physiological adaptations to reduce water loss and conserve energy [9,10]. Among mammals behavioural responses in the form of seasonal migrations, such as the large scale migrations of wildebeest (*Connochaetus taurinus*) in East Africa and springbok (*Antidorcas marsupialis*) in southern Africa but also the more localized movements of gemsbok (*Oryx gazelle*) in the Namib, are well documented [9]. Migration is, however, usually restricted to larger mammals in which locomotion is not too costly and the use of retreats can provide short-term relief [9]. Consequently, many desert-dwelling mammals exhibit nocturnal activity and use burrows during the day [9,11]. Their body size prevents large mammals from the use of the latter strategy. Instead shade seeking behaviour is commonly observed while in the absence of shade ungulates have also been observed to orientate themselves in a way that the least body surface is exposed to the sun [9,12,13]. Although their larger body size is associated with a reduction in evaporative water loss (EWL), the more limited benefits of the behavioural strategies employed, probably means that they have to rely on physiological mechanisms to a greater extent for water and energy conservation than small mammals [9].

Endotherms generally regulate and maintain their core body temperatures (T_b) within a narrow range, and when inhabiting deserts, large mammals such as ungulates have developed unique adaptations for thermoregulation [14–17]. Selective brain cooling and adaptive heterothermy are among the main strategies employed by large ungulates [9,13–15,18]. Adaptive heterothermy is a strategy whereby an endotherm relaxes its strict T_b limits and allows the T_b to increase during the day. Subsequently, these animals may lose stored heat by non-evaporative means during the night allowing them to reduce EWL [19].

Both energy constraints as well as water shortage may induce heterothermy in large mammals [18]. Although both of these factors (i.e. energy and water) may induce heterothermy the physiological mechanism and the resulting T_b patterns may differ substantially. Energetic bottlenecks as a result of food shortage and/or higher energetic demands due to cooler climatic conditions can be expected to lead to lower minimum and mean T_b (i.e. hypothermia) as a result of a reduction in metabolic rate (MR) in response to low food availability. Consequently, this type of heterothermy is more likely to occur in winter. Even if ambient conditions and energy supply are comparable between the sexes higher reproductive investment of one sex may result in sex-specific heterothermy as has been shown for male camels where males exhibited lower minimum T_b than females during rut when males reduce their foraging time in favour of energetically costly vigilance, territoriality and fighting [20]. In contrast, if ambient temperature exceeds T_b and low water availability is low the competing demands of body fluid and thermal homeostasis make a reduction in EWL by increasing maximum T_b (hyperthermy) a more sustainable strategy for large mammals [10,18].

Heterothermy has been studied in a number of large ungulates in captivity, but studies on free-living ungulates, where the movement of animals have not been restricted, have only been conducted on two species of desert ungulates, the Arabian oryx (*Oryx leucoryx*) and the Arabian sand gazelle (*Gazella subgutturosa marica*) [15,21–23]. The former is the only species of

oryx occurring outside of Africa [24]. Once widespread throughout the Arabian Peninsula, the Arabian oryx was extirpated from the wild in 1972 [15,25]. Saudi Arabia currently hosts the two largest free-ranging Arabian oryx populations one in Mahazat as-Sayd, ca. 200 km north-east of Taif, and one in Uruq Bany Ma'arid, in the western Rub-al Khali, one of the driest regions of the world both of which lack permanent water bodies [26–29]. The Arabian oryx is a highly mobile species that can survive months without access to free standing water [15,24]. As a predominantly grazing species they obtain most of their water from several grass species but may supplement their diet by browsing and digging for underground tubers, particularly in summer, due to the deterioration of nutritional value and water content of their main food species [7,8,30–33]. Considered an exploratory species Arabian oryx exhibit highly flexible home ranges with large distance migration being observed after rainfall (mostly during spring in Saudi Arabia) while it will contract again during hot and dry periods (e.g. summer) when shade seeking appears to govern movement patterns [8,15,31,33]. In addition, ranging patterns and feeding strategies may differ between the sexes with older, dominant males becoming territorial at greater population sizes and may change over time since the release in a new habitat [8,30,31,34]. As additional behavioural adaptation to the desert climate Arabian oryx exhibit a switch from diurnal to nocturnal activity in response to high ambient temperatures and water shortage and spend substantial amounts of the daytime in the shade of Acacia trees or grass tussocks where they may dig shallow depressions to facilitate heat exchange [8,31,35–37]. Rainfall has also been shown to affect reproduction in Arabian oryx and although birth may occur throughout the year, both in captivity and in the wild, conception is more likely to occur after rainfall [8,29,31,37,38].

Like most artiodactyls, Arabian oryx have been found to employ selective brain cooling in response to water limitations [39]. However, compared with other arid-adapted ungulates including the closely related gemsbok, Arabian oryx exhibited a lower threshold and increased frequency of selective brain cooling while the magnitude was similar [39,40]. The authors found furthermore some evidence that the use of this water conservation mechanism may be modified by behaviour and one dominant male in their study did employ brain cooling to a lesser degree and at higher thresholds [39].

Both in captivity and in free-ranging populations Arabian oryx respond with T_b reduction to food restriction while maintaining a high digestive efficiency [6,7,41]. In addition, Arabian oryx show a remarkably low EWL when food and water restricted and have one of the lowest water influx rates reported for desert ungulates including camels [7,41]. However, these may be increased in lactating females due to their higher water requirements [7].

The T_b in the Arabian oryx has previously been studied in one of the free-ranging Saudi Arabian populations Both studies found that Arabian oryx employ adaptive heterothermy with maximum T_b amplitudes in summer of 4.1 and 7.7°C, respectively, presumably as a strategy to reduce water loss and energy costs [15,21]. Although both the highest and the lowest T_b were recorded during summer (hot-dry season) the seasonal patterns of heterothermy were largely attributed to water restrictions [21]. Both of these studies had relatively low sample sizes and/or were only conducted during restricted periods in Mahazat as-Sayd and comparative data from other localities experiencing a different climate as well as data allowing investigating possible sex-specific patterns are currently lacking. Consequently, in the current study we examined T_b of free-ranging male and female Arabian oryx at two different localities in Saudi Arabia that differ greatly in the mean annual rainfall receive. We hypothesized that (1) we would observe that Arabian oryx employ adaptive heterothermy. Furthermore, we predicted that (2) the frequency and amplitude of heterothermy would be larger in the more arid site and (3) during summer when high temperatures coincide with low precipitation. Lastly,

we anticipated to observe sex differences in heterothermy patterns coinciding with reproductive activity (i.e. rut and the calving season)

Material and methods

Study areas

Mahazat as-Sayd. Mahazat as-Sayd (MS) is a fenced protected area located in west-central Saudi Arabia (22°15' N, 41°40'E), comprised of 2553 km² of open steppe desert. The substrate composition at MS is loose sand, gravel and alluvial clays [42]. The mean minimum and maximum temperatures recorded between 1991 and 2009 were 9°C and 42°C respectively [27]. Characteristic of an arid climate, MS experiences hot summers and mild winters with very low rainfall [15]. Data for the past 18 years show great inter-annual variation in rainfall, with an average of ±7 mm rainfall per month from 1991 to 2009 [27]. Vegetation is sparse, predominated consisting of perennial grasses with sporadically distributed small *Acacia* trees providing shade for animals [43].

MS was the first release site for the reintroduction of Arabian oryx in Saudi Arabia [26,28]. Between 1990 and 1994 a total of 76 captive-bred were released in MS. These included individuals from the breeding programme at the National Wildlife Research Center (NWRC) in Taif (derived from the donation of 57 animals from the farm of late King Khaled in Thumamah) and supplemented by captive bred animals from the World Heard (comprising of descendants of founders from Aden Protectorate, Kuwait, Saudi Arabia as well as wild-caught individuals from London Zoo), Jordan, Bahrain and Qatar [26,28,29]. The population size now exceeds 300 individuals and based on management recommendations for this population, animals above an estimated carrying capacity of 70% are regularly removed and either incorporated in the NWRC breeding programme or relocated to other suitable habitats such as Uruq Bani Ma'arid. Since the first reintroduction in 1995 from the NWRC breeding herd into Uruq Bani Ma'arid it has grown to one of more than 200 individuals [26,28].

Uruq Bani Ma'arid. Uruq Bani Ma'arid (UBM) is Saudi Arabia's largest unfenced protected area and covers a surface area of approximately 12787 km² [42]. It is located at the western edge of the Empty Quarter, 200 km north of Najran in southern Saudi Arabia, (19.10° N, 45.3° E) [42]. UBM is characterized by a hyper-arid climate, very low to sporadic rainfall (less than 25 mm per annum), with rainfall absent for a few years, extremely high ambient temperatures and very low floristic diversity, providing little to no shade for animals [44,45]. Annual ambient temperature and average monthly rainfall from 1985 to 2009 were 28.4°C and 3.2 mm respectively [27]. Accordingly, UBM is one of the driest and harshest regions in the world [26,42,46].

We obtained measurements of ambient (T_a) and soil temperature (T_s) routinely recorded by the reserve staff in MS and UBM every 15 min throughout the year at weather stations located within the respective reserves (MS: Rumrumiyah, UBM: Sharurah). Daily rainfall measurements made at the same weather stations were also obtained.

Anaesthesia and logger implantation

Twenty animals (8 males, 12 females) were captured in MS and after implantation, half of the animals were released back into MS (4 males, 6 females) and the other half was released at UBM (4 males, 6 females). All animals were remote injected using a Dan-Inject dart gun (Daninject, Børkop, Denmark) with etorphine hydrochloride (CaptivonTM 98, Wildlife Pharmaceuticals Ltd., White River, South Africa; 19µg/kg; a semi-synthetic opioid that has an analgesic effect and is an opioid receptor antagonist), Ketamine (Ketaminol[®] Vet., MDS Animal Health, Intervet International B.V., Boxmeer, The Netherlands; 0.3mg/kg; a dissociative

anaesthetic agent which is an NMDA receptor antagonist), Midazolam (Midazolam, Wildlife Pharmaceuticals Ltd., White River, South Africa; 0.13mg/kg; a benzodiazepine class anaesthetic agent that acts by enhancing the effect of GABA on GABAA receptors), and Medetomidine (Zalopine 10 mg/ml, Orion Pharma, Espoo, Finland; 5µg/kg; a sedative analgesic that is an alpha-2 adrenergic agonist). All animals received oxytetracycline (Terramycin LA, Pfizer, Brazil, 20mg/kg IM; a broad spectrum antibiotic) and ketoprofen (Ketovet, Vetmedim Animal Health, Cantho City, Vietnam, 2mg/kg IM; a propionic acid class of nonsteroidal anti-inflammatory which acts to inhibit the production of prostaglandin). After the operations, anaesthesia was reversed using naltrexone hydrochloride (Naltrexone, APL, Kungens Kurva, Sweden; 40mg IM; an opiate antagonist) and atipamezole hydrochloride (Antisedan, Orion Pharma; 2mg IM; a synthetic 2 adrenergic receptor antagonist). Using aseptic techniques, a data logger that measured temperature was inserted intra-abdominally (AIC001: Abdominal implant, Africa Wildlife Tracking, South Africa). The T_b device was calibrated against an accurate thermometer in an insulated water bath, providing an accuracy of better than 0.06°C. A small incision (less than 80 mm in length) was made through the skin at the implantation site and the muscle layers of the abdominal wall were separated using blunt dissection. The implant, pre-coated in inert wax and sterilized within a container with formalin pellets for 48 hr prior to implantation, was inserted untethered into the abdomen, the incisions closed, and liberally sprayed with Necrospray. A satellite collar with a GPS unit was attached to the neck of each animal (iridium satellite collar, Africa Wildlife Tracking, South Africa, Model: SBU202). Following reversal of anaesthesia, the animals were monitored in holding pens with access to food and water for 10 days, before being released into the two protected areas for the year-long recording period. The animals were not recaptured following the recording period, the collars and implants being left *in situ*.

Body temperature measurement

The T_b of Arabian oryx were monitored in both habitats and the precise location of each oryx were traced using iridium satellite collars with connections to a body temperature logger (<http://www.atstrack.com>). In standard operation the tracking device will upload the location of the collar and temperature of the implant to the database immediately after position acquisition. Thus, data were made available immediately eliminating the wait for bulk uploads. Uploads for the T_b occurred every 10 min throughout the day and night. The on-board temperature sensor made measurements of T_b to an accuracy of 0.5 of a °C for 6 equal intervals each and every hour.

Statistical analysis

The daily variance in T_b was calculated for each animal in MS and UBM using two different methods. First, we calculated the daily temperature amplitude by subtracting the minimum from the maximum T_b for each animal every 24 hours [15,22]. As a second index of daily variance in T_b we quantified the variation in T_b using the Heterothermy Index (HI) of Boyles *et al.* [47]:

$$HI = \sqrt{\frac{\sum (T_{b-mod} - T_{b-i})^2}{n - 1}}$$

where T_{b-mod} is the modal T_b , T_{b-i} is the T_b measurement at time i and n is the number of times T_b is sampled. The HI quantifies deviation away from the theoretically optimal temperature for performance as approximated by T_{b-mod} . T_{b-mod} was calculated as the modal T_b for

individuals that displayed unimodal distributions of T_b and the mode of the highest peak for individuals that displayed bimodal distributions of T_b [48,49] HI values were calculated for each animal over each 24 h period [47].

We compared the body mass between male and female Arabian oryx released in MS and UBM, respectively, using a general linear model (GLM). We included sex and site (MS or UBM) as well as the interaction between sex and site as independent variables in the model.

We explored the fluctuations of mean hourly T_a and T_s using linear mixed models (LMMs). We included site (MS, UBM), hour and season (winter: December-February, spring: March-May, summer: June-August and autumn: September-November, [21]) as well as all 2- and 3-way interactions between these variables in our model.

To evaluate the possible contributions of study site, season and an animal's sex on mean daily T_b amplitude and HI, respectively, we employed linear mixed models (LMMs). All 2- and 3-way interactions between these variables were included in the model. Oryx ID was included as random effect in our models to account for the repeated measurement of the same individual. These analyses were carried out using the 'lme' function from the 'nlme' package in R using restricted maximum likelihood. Non-significant terms were dropped sequentially from the model based on the Δ AIC [50] and only the results of the final model are reported.

To determine the relationship between T_b and extrinsic factors, we tested for a correlation between hourly average T_b and T_a and T_s for both sites over the entire study period as well as for each season in each site. All statistical tests were completed using the software package R (version 2.15.3). All data are presented as mean \pm SD and $p < 0.05$ was considered significant.

Ethical clearance for the current study was obtained from the University of the Witwatersrand Animal Ethics Committee (clearance certificate number 2014/53/D) and all animals were treated according to the guidelines of this committee, which parallel those of the National Institute of Health of South Africa (NIH) for the care and use of animals in scientific studies. Permission to work in MS and UBM was granted by the President of the Saudi Wildlife Authority (SWA).

Results

Climate

During the study period the average annual T_a in MS was $26.85 \pm 8.15^\circ\text{C}$ and the T_s was $30.44 \pm 9.54^\circ\text{C}$. The T_a fluctuated during the four seasons and was lowest in winter ($14.93 \pm 5.44^\circ\text{C}$) and highest in summer ($33.05 \pm 4.91^\circ\text{C}$, Table 1). The T_s was consistently higher than the air temperature (Table 1).

In UBM, the average yearly T_s was $33.81 \pm 8.06^\circ\text{C}$ and the T_a was $30.32 \pm 8.60^\circ\text{C}$. The T_a varied during the four seasons and was lowest in winter ($18.25 \pm 5.22^\circ\text{C}$) and highest in summer ($33.9 \pm 4.21^\circ\text{C}$, Table 1). Just as in MS, the T_s was always higher than the air temperature in UBM (Table 1).

The mean hourly T_a did not differ significantly between the two study sites ($df = 1$, 15874; $F = 0.18$; $p = 0.67$). At the same time, T_a differed significantly between the seasons ($df = 3$, 334; $F = 340.04$; $p < 0.0001$) and during the day ($df = 1$, 15874; $F = 1101.57$; $p < 0.0001$, Fig 1). The interaction between site and season was significant ($df = 3$, 15874; $F = 53.34$; $p < 0.0001$, Fig 1). Similarly, the interaction between site and hour was significant ($df = 1$, 15874; $F = 8.392$; $p = 0.0038$, Fig 1). In contrast, the interaction between season and hour was not significant ($df = 3$, 15874; $F = 1.61$; $p = 0.19$). The 3-way interaction between site, season and hour was significant ($df = 3$, 15874; $F = 3.43$; $p = 0.0164$, Fig 1).

The mean hourly T_s did not differ significantly between the study sites ($df = 1$, 15874; $F = 1.90$; $p = 0.17$). In contrast, it differed significantly between the seasons ($df = 3$, 334;

Table 1. The mean T_b , T_a , T_s , and rainfall in MS and UBM during winter (Dec—Feb), spring (Mar—May), summer (Jun—Aug), autumn (Sep—Nov) and for the whole year (March 2014 to February 2015).

	Annual	Winter	Spring	Summer	Autumn
	mean \pm SD	mean \pm SD	mean \pm SD	mean \pm SD	mean \pm SD
T_b MS (n = 8)	38.23 \pm 0.80°C	38.20 \pm 0.50°C	38.29 \pm 0.81°C	38.35 \pm 1.00°C	38.01 \pm 0.81°C
T_a	26.85 \pm 8.15°C	14.93 \pm 5.44°C	23.52 \pm 8.88°C	33.05 \pm 4.91°C	26.07 \pm 6.41°C
T_s	30.44 \pm 9.54°C	16.77 \pm 5.91°C	26.74 \pm 10.34°C	37.64 \pm 6.81°C	29.49 \pm 7.59°C
Rainfall	28.81 mm	0.34 mm	112.1 mm	0 mm	3.22 mm
T_b UBM (n = 6)	38.26 \pm 0.77°C	38.00 \pm 0.47°C	38.43 \pm 0.47°C	38.43 \pm 0.84°C	38.14 \pm 0.65°C
T_a	30.32 \pm 8.60°C	18.25 \pm 5.22°C	27.72 \pm 5.17°C	33.9 \pm 4.21°C	26.39 \pm 5.80°C
T_s	33.81 \pm 8.06°C	20.9 \pm 4.78°C	31.31 \pm 6.35°C	37.39 \pm 5.81°C	30.32 \pm 6.33°C
Rainfall	0.87 mm	0 mm	3.14 mm	0 mm	0 mm

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$F = 470.96$; $p < 0.0001$) and hours ($df = 1, 15874$; $F = 2375.30$; $p < 0.0001$). In addition, the interaction between site and season was significant ($df = 3, 15874$; $F = 15.92$; $p < 0.0001$). The T_s did not differ significantly with hours between seasons ($df = 1, 15874$; $F = 3.52$; $p = 0.061$). Conversely, the interaction between season and hour was significant ($df = 1, 15874$; $F = 6.56$; $p = 0.0002$). Similarly, the 3-way interaction between site, season and hour was significant ($df = 3, 15874$; $F = 3.65$; $p = 0.0120$).

Rainfall was low in MS throughout the year, but summer was the only season during which no precipitation was recorded. In contrast, the only rainfall recorded for UBM occurred in spring which also coincided with the greatest mean precipitation in MS (Table 1).

Body mass of Arabian oryx

The mean body mass of oryx released in the MS was 70.5 ± 13.7 kg, $n = 10$ range 48–88 kg (males 77.6 ± 12 kg, $n = 4$; range 54–88 kg and females 63 ± 11.4 kg, $n = 6$, range 48–78 kg) while it was 67.0 ± 13.1 kg, $n = 10$ range 48–90 kg (males 69.8 ± 2.4 kg, $n = 4$; range 68–74 kg

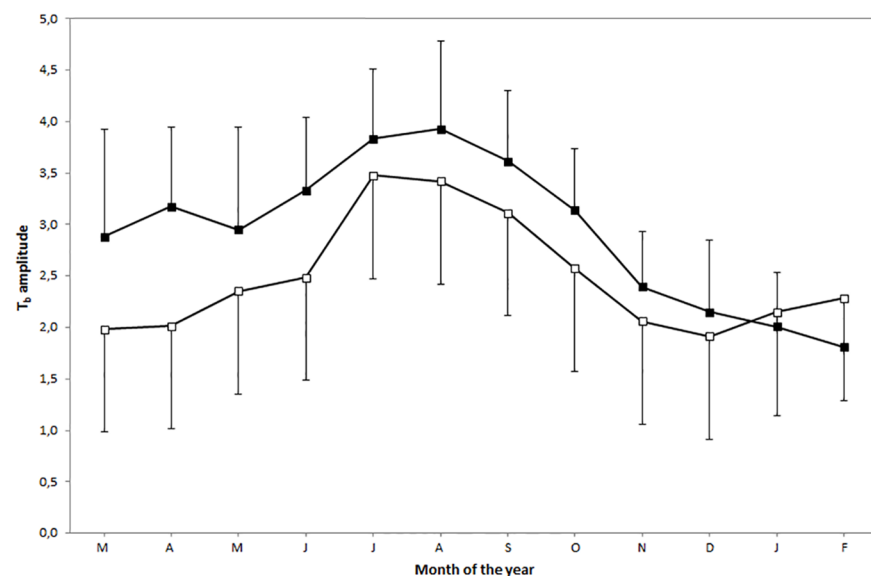


Fig 1. The mean monthly T_b amplitude (\pm SD) for oryx in MS (filled squares) and UBM (open squares) from March 2014 to February 2015.

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and females 64.2 ± 20 kg, $n = 6$, range 48–90 kg) for animals released in UBM. The body mass of our study animals did neither differ significantly between sites ($F = 1.44$, $df = 1$, $p = 0.248$) nor between the sexes ($F = 4.11$, $df = 1$, $p = 0.060$). Similarly, the interaction between site and sex was not significant ($F = 1.24$, $df = 1$, $p = 0.281$). Due to the remote nature of the current study no additional body mass measurements could be taken during the course of the study.

Mean T_b

Several study animals were lost due to poaching and in other instances the transmitters failed. Of the released animals T_b data could be retrieved from 8 (3 males, 5 females) and six (2 males, 4 females). For these oryx we recovered T_b data for a mean of 318.07 ± 20.87 days (range: 99–365). The mean yearly T_b for 8 individuals in MS was $38.24 \pm 0.93^\circ\text{C}$. It varied between seasons and ranged from $38.20 \pm 0.50^\circ\text{C}$ in winter to $38.35 \pm 1.00^\circ\text{C}$ in summer (Table 1). In UBM the mean yearly T_b for 6 animals was $38.26 \pm 0.77^\circ\text{C}$. The mean T_b ranged from $38.00 \pm 0.47^\circ\text{C}$ in winter to $38.43 \pm 0.84^\circ\text{C}$ in summer (Table 1). We found a significant effect of season on average T_b in UBM (ANOVA: $df = 3$, $F = 8.47$, $p < 0.01$).

There were no seasonal differences between MS and UBM, except during winter (Mann-Whitney U test: $W = 3179.5$, $p = 0.02$). The average T_b was lower in UBM ($38.00 \pm 0.47^\circ\text{C}$) when compared with MS ($38.20 \pm 0.50^\circ\text{C}$).

Daily T_b variation

The LMM indicated that the mean T_b amplitude was significantly greater in MS ($2.97 \pm 0.98^\circ\text{C}$) compared with UBM ($2.53 \pm 0.83^\circ\text{C}$; $df = 1,11$; $F = 8.44$; $p = 0.0143$). It also differed significantly between seasons ($df = 3,4468$; $F = 736.65$; $p < 0.0001$, Fig 1). Oryx had the lowest mean daily T_b amplitude during winter ($2.05 \pm 0.62^\circ\text{C}$) and the highest during summer ($3.41 \pm 0.82^\circ\text{C}$, Fig 2). Mean T_b amplitude did not differ significantly between the sexes ($df = 1,11$; $F = 4.57$; $p = 0.0559$). The interaction between site and season was significant ($df = 3,4468$; $F = 61.95$; $p < 0.0001$). The mean T_b amplitude was lower in UBM than in MS in spring but not the other seasons. In addition, the interaction between season and sex was significant ($df = 3,4468$; $F = 6.48$; $p = 0.0002$) with males, but not females exhibiting a significantly larger amplitude in summer compared with winter.

Heterothermy index

The HI was significantly greater in MS (1.56 ± 0.53) compared with UBM (0.91 ± 0.44 ; $df = 1,11$; $F = 13.17$; $p = 0.0040$). In addition, the HI varied significantly between seasons and was greatest in summer ($df = 3,4430$; $F = 427.47$; $p < 0.0001$, Table 1). However, HI did not differ significantly between the sexes ($df = 3,4430$; $F = 3.71$; $p = 0.080$). The interaction between site and season was significant ($df = 3,4430$; $F = 38.56$; $p < 0.0001$) and in spring but not the other seasons HI was greater in MS than UBM (Fig 3). Similarly, the interaction between season and sex was significant ($df = 3,4430$; $F = 4.66$; $p = 0.0030$) with male but not female HI being significantly greater in summer compared with winter.

Correlation between T_a , T_s and T_b

Throughout the year in both MS (Spearman: $S = 24076.07$, $\rho = 0.99$, $p < 0.01$) and UBM (Spearman: $S = 173116$, $\rho = 0.96$, $p < 0.01$) there was a positive correlation between T_a and T_s (Fig 4). In addition, T_a and T_b (Spearman: $S = 2141865$, $\rho = 0.46$, $p < 0.01$) as well as T_s and T_b (Spearman: $S = 2058695$, $\rho = 0.49$, $p < 0.01$) were significantly correlated in MS (Fig 4c and 4e).

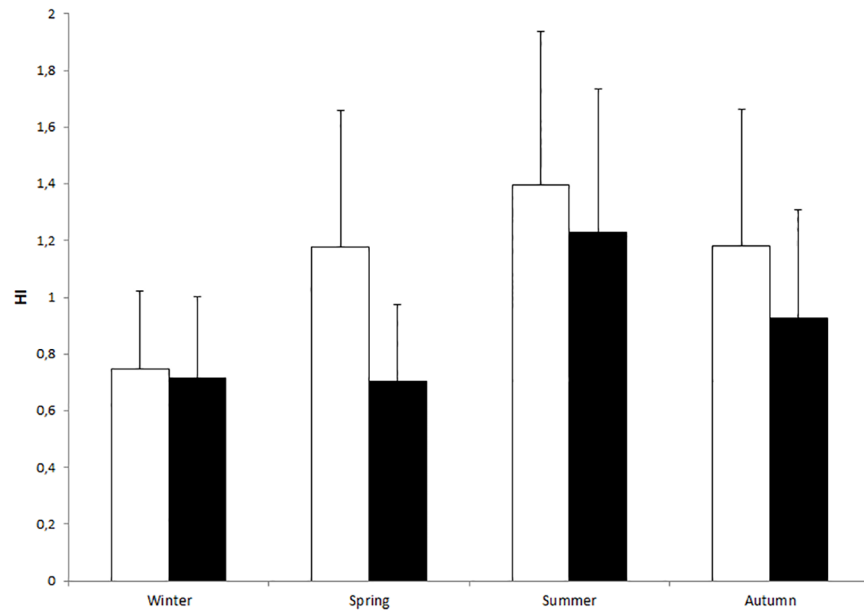


Fig 2. Traces of T_b of an oryx for five consecutive days during February (grey line, representing winter) and five consecutive days during August (black line, representing summer) from (a) MS and (b) UBM.

<https://doi.org/10.1371/journal.pone.0180269.g002>

In MS, when we compared hourly average T_b to T_a and T_s for every season, we detected a significant correlation for winter (T_a : Spearman: $S = 30030.64$, $\rho = 0.52$, $p < 0.01$; T_s : Spearman: $S = 31306.02$, $\rho = 0.50$, $p < 0.01$), spring (T_a : Spearman: $S = 28224.58$, $\rho = 0.55$, $p < 0.01$; T_s : Spearman: $S = 27674.56$, $\rho = 0.56$, $p < 0.01$) and autumn (T_a : Pearson: $t = 5.41$,

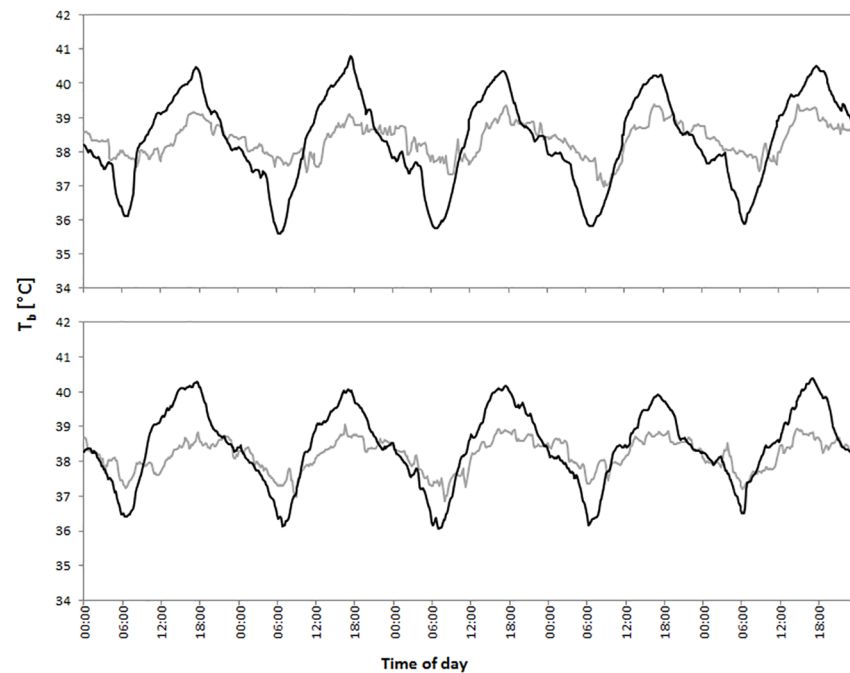


Fig 3. Seasonal variation in HI (\pm SD) in MS (open bars) and UBM (closed bars).

<https://doi.org/10.1371/journal.pone.0180269.g003>

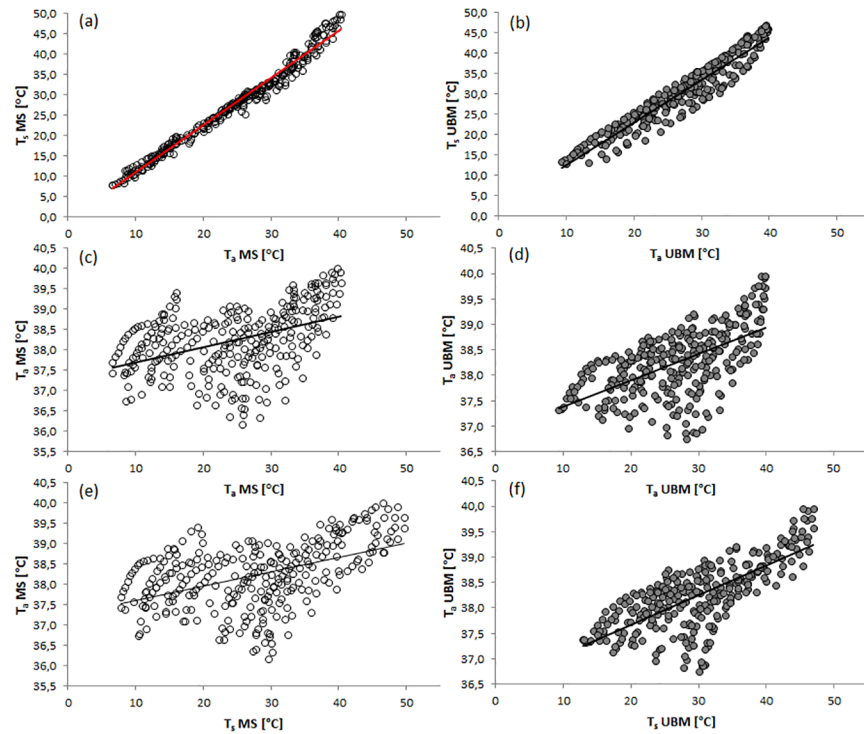


Fig 4. Correlation between (a) T_a and T_s as well as T_a and T_b and T_s and T_b in MS (a, c, e) and UBM (b, d, f).

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df = 70, rho = 0.54, $p < 0.01$; T_s : Pearson: $t = 6.67$, df = 70, rho = 0.62, $p < 0.01$) and summer (T_a : Spearman: $S = 10230.73$, rho = 0.84, $p < 0.01$; T_s : Spearman: $S = 8221.86$, rho = 0.87, $p < 0.01$) (Fig 5). We found a significant correlation between T_a and T_s for all four seasons (Fig 5). Similarly, T_b increased significantly with increasing T_a in UBM (Spearman: $S = 1612055$,

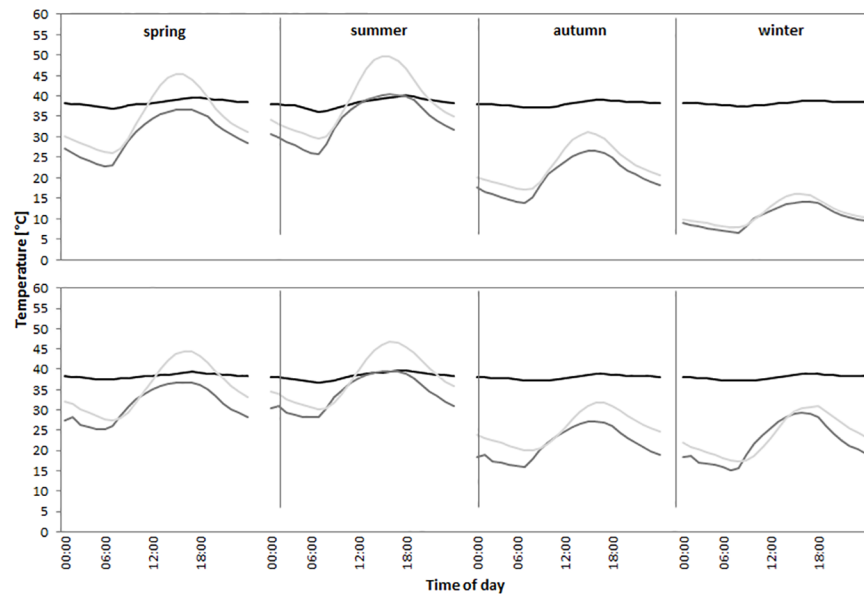


Fig 5. Correlation between the seasonal variation of mean hourly T_b (black line), T_a (dark grey line) and T_s (light grey line). Displayed are temperature traces for MS (top panel) and UBM (bottom panel).

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$\rho = 0.60$, $p < 0.01$, Fig 4b) for the whole year. Likewise, T_b was significantly correlated with T_s (Spearman: $S = 1106835$, $\rho = 0.72$, $p < 0.01$, Fig 4d and 4e).

In UBM, when we looking at hourly average T_b , T_a and T_s for every season, we detected significant correlations for all seasons: winter (T_a : Spearman: $S = 23792.68$, $\rho = 0.62$, $p < 0.01$; T_s : Spearman: $S = 8144.92$, $\rho = 0.87$, $p < 0.01$), spring (T_a : Spearman: $S = 25066.93$, $\rho = 0.60$, $p < 0.01$; T_s : Spearman: $S = 14057.42$, $\rho = 0.77$, $p < 0.01$) and autumn (T_a : Spearman: $S = 25552.23$, $\rho = 0.59$, $p < 0.01$; T_s : Spearman: $S = 12291.59$, $\rho = 0.80$, $p < 0.01$) and summer (T_a : Spearman: $S = 9433.18$, $\rho = 0.85$, $p < 0.01$; T_s : Spearman: $S = 3246.75$, $\rho = 0.95$, $p < 0.01$, Fig 5). We found a significant positive correlation between T_a and T_s for all four seasons (Fig 5).

Discussion

Our study provides the first continuous body temperature measurements for an entire calendar of free-living Arabian oryx in UBM within the 'Empty Quarter' in Saudi Arabia. Our data show that, as has previously been reported for MS [21], oryx in UBM display the characteristics typically associated with adaptive heterothermy—an increase in the daily amplitude of T_b rhythm where maximum T_b increased and minimum T_b decreased, particularly during the dry and hot months (i.e. summer). As predicted the two methods we used to quantify body temperature fluctuations, T_b amplitude and HI, both confirmed that oryx in UBM employ adaptive heterothermy. The use of HI, suggested to provide an objective reference for heterothermy measurements, has been criticized because of its reliance on the upper mode of the bimodal temperature distribution typical for small mammals that may not necessarily reflect the optimal temperature and does not account for variation in MR [18,47,51,52]. However, although the inclusion of simultaneous MR and T_b measurements has been suggested to provide a more accurate indication of the use of heterothermy this is logistically challenging in studies like ours [53]. The similar results obtained for T_b amplitude and HI furthermore suggest that the disadvantages of the latter are negligible in our study.

Our study provides the first comparison of T_b patterns between Arabian oryx from two different areas in Saudi Arabia, MS (a rocky desert) and UBM (a sandy desert). However, contrary to our expectations both T_b amplitude and HI were significantly greater in the less water restricted habitat (i.e. MS). At the same time, the annual average T_b for six oryx in UBM was $38.26 \pm 0.77^\circ\text{C}$ and comparable to the T_b in MS and what has previously been reported from the latter site ($38.24 \pm 0.93^\circ\text{C}$) for which water has been suggested as important cue for adaptive heterothermy during periods of water restriction [15,18,21]. This suggests that, contrary to what has been hypothesized [21], water shortage is unlikely to be the key driver of heterothermy in our study animals. Similarly, based on their observations in Arabian sand gazelles Ostrowski and Williams [22] stated that heterothermy is not a response to water stress in desert-adapted ungulates. The significance of water restriction as driver for heterothermy in ungulates has furthermore been questioned by Grigg et al. [20] who observed greater heterothermy in rutting camel males during winter when water was freely available. Also, our data confirm that water is substantially more restricted in UBM than in MS throughout the year with rainfall only recorded during spring in UBM while it was absent only during summer in MS. At the same time, while T_a and T_s in summer are similar in both sites they are substantially lower during winter and spring in MS compared with UBM. Alternatively, animals in UBM may have exerted a stronger control over their T_b by employing behavioural mechanisms, such as seeking out shade or shifting their activity period to the cooler periods of the day, to a greater extent than oryx in MS [15,23,35,36]. Indeed, a heavy reliance on acacia trees for shade on the escarpment in UBM that supersedes foraging requirements has been reported for Arabian oryx in UBM [8]. At the same time studies in UBM as well as of other oryx

populations suggest that Arabian oryx released in a new environment range over much larger distances than those already familiar with their environment [8,30,31,33]. In addition, territorial aggression expressed by dominant males [34] may have forced the newly introduced individuals to exhibit greater activity. In contrast, the individuals re-released in MS were already familiar with the habitat in MS may have quickly resumed their previous home ranges and hence not have experienced changes in their activity patterns. Thus, the additional body heat generated by a greater general activity may at least partially account for the observed difference in heterothermy patterns.

As predicted both the amplitude of T_b and the HI varied significantly between seasons and was highest during summer and lowest during winter for both sites. This is likely to be linked to the combined stress of food limitation and water shortage during the hot, dry summer while in winter the cooler temperatures meant that food shortage alone was probably responsible for the observed pattern [6,7,41]. However, although slightly lower than previously reported [15,21] both T_b amplitude and HI were significantly greater in MS compared with UBM. This result was unexpected given the harsher environmental conditions faced by oryx in UBM and further refutes the hypothesis that adaptive heterothermy is linked to water limitations or high ambient temperatures [21,22]. This is further supported by the fact that (almost) no rainfall was recorded during both winter and summer while T_a and T_s and were substantially higher during the latter season in both sites.

In accordance with our predictions we only found a significant interaction between season and sex with males, but not females exhibiting larger amplitudes of T_b and HI in summer, when environmental temperatures peaked, compared with winter with precipitation being low during both of these seasons. Since the sexes did not differ in their body mass we can largely exclude body mass as a contributing factor to this pattern [9,18,23]. Rather, the different reproductive investment between the sexes may have contributed to the observed sex-effects on oryx T_b amplitude and HI in our study. Although Arabian oryx in Saudi Arabia may have offspring at any time of the year reproduction is closely tied with rainfall and birth peaks occur in spring [8,29,37]. The species exhibits a postpartum oestrus and the gestation length is roughly 9 months suggesting that rutting mostly occurs in summer [38]. Hence, similar to what has been reported for camels, the additional nutritional stress caused by a reduction in foraging activity in favour of energetic investment in territorial behaviour and fighting among males may account for the observed larger change in our heterothermy measures in males from summer to winter [8,20,34].

Our data suggest that as previously reported for populations in MS Arabian oryx in UBM employ adaptive heterothermy, a process which reduces evaporation by storing body heat during the day, as a strategy to cope with their harsh habitat. However, despite the lower temperatures and greater water availability indices of heterothermy were greater in the cooler, more humid site suggesting that behavioural factors may override the expression of heterothermy in the study species. At the same time the greater variance in T_b during the hottest time of the year supports the role of both energy and water limitations on the expression of heterothermy in ungulates. In addition, seasonal variation in sex-specific patterns of heterothermy further suggest that sex differences in reproductive investment may modify the expression of heterothermy in our study animals. Thus, results suggest that the degree of heterothermy was not only driven by extrinsic factors such as environmental temperatures and rainfall but may also be affected by intrinsic factors such as sex and behaviour.

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