

## Heterothermy and the water economy of free-living Arabian oryx (*Oryx leucoryx*)

Stéphane Ostrowski<sup>1,\*</sup>, Joseph B. Williams<sup>2</sup> and Khairi Ismael<sup>1</sup>

<sup>1</sup>National Wildlife Research Center, PO Box 1086, Taif, Saudi Arabia and <sup>2</sup>Department of Evolution, Ecology and Organismal Biology, Ohio State University, 1735 Neil Avenue, Columbus, OH 43210, USA

\*Author for correspondence (e-mail: ostrowski@nwrc-sa.org)

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### Summary

To test the idea that large, free-living, desert ungulates use heterothermy to reduce water loss, we measured core body temperature ( $T_b$ ) of six free-ranging, adult Arabian oryx (*Oryx leucoryx*) during 2 years in the arid desert of west-central Saudi Arabia. We report the first case of heterothermy in a free-living ruminant in a desert environment:  $T_b$  varied by  $4.1 \pm 1.7^\circ\text{C day}^{-1}$  during summer (June to September) and by  $1.5 \pm 0.6^\circ\text{C day}^{-1}$  during winter (November to March). Over both seasons, mean  $T_b$  was  $38.4 \pm 1.3^\circ\text{C}$ . During the day in both summer and winter,  $T_b$  increased continually, suggesting that oryx store heat instead of dissipating it by evaporation, whereas at night  $T_b$  decreased. The minimum  $T_b$  was lower in summer ( $36.5 \pm 1.16^\circ\text{C}$ ) than in winter ( $37.5 \pm 0.51^\circ\text{C}$ ) despite the fact that the temperature gradient between  $T_b$  and air temperature ( $T_a$ ) was larger and solar radiation was lower in winter. Throughout the year, daily variation in  $T_b$  appeared to reflect thermal load ( $T_{a,\text{max}} - T_{a,\text{min}}$ ) rather than an endogenous rhythm. Behavioural thermoregulation was used by oryx to cope with thermal

stress during summer: animals lay down in shade in the morning shortly before  $T_a$  exceeded  $T_b$  and remained there until evening when  $T_b - T_a$  became positive. The use of heterothermy by oryx resulted in storage of  $672.4 \text{ kJ day}^{-1} \text{ animal}^{-1}$  in summer and  $258.6 \text{ kJ day}^{-1} \text{ animal}^{-1}$  in winter, if heat storage is based on calculations involving mean  $T_b$ . To dissipate this heat by evaporation would require  $0.28 \text{ litres H}_2\text{O day}^{-1} \text{ animal}^{-1}$  and  $0.11 \text{ litres H}_2\text{O day}^{-1} \text{ animal}^{-1}$  in summer and winter, respectively. Without heat storage in summer, we estimated that oryx would have to increase their water intake by 19%, a requirement that would be difficult to meet in their desert environment. If heat storage was calculated based on the daily change in  $T_b$  rather than on heat storage above mean  $T_b$  then we estimated that oryx saved  $0.538 \text{ litres H}_2\text{O day}^{-1} \text{ animal}^{-1}$  during summer.

Key words: Arabian oryx, desert, heterothermy, *Oryx leucoryx*, thermoregulation, water saving.

### Introduction

Many species of endotherms control their core body temperature ( $T_b$ ) within narrow limits ( $\pm 2^\circ\text{C}$ ) even when subjected to a wide range of environmental temperatures, a process called homeothermy (International Union of Physiological Sciences Thermal Commission, 1987). However, some species indigenous to desert environments reputedly allow their  $T_b$  to increase during the hot portion of the day, losing stored heat by non-evaporative means during the night (Schmidt-Nielsen, 1957; Taylor, 1969, 1970; Langman and Maloiy, 1989). Heterothermy, fluctuations in  $T_b$  exceeding  $\pm 2^\circ\text{C}$ , is thought to be used by desert animals to minimize water losses in an environment where water balance can be difficult (Willmer et al., 2000; Randall et al., 2002). Although heterothermy and its use by free-living desert animals are described in textbooks of animal physiology and reviews on thermoregulation (Bartholomew, 1964; Willmer et al., 2000; Jessen, 2001; Randall et al., 2002), data documenting

heterothermy in free-living animals is scant to non-existent (Walsberg, 2000). Indeed Walsberg (2000) pointed out that a well-known example of heterothermy, that of variation in  $T_b$  in the antelope ground squirrel (*Ammospermophilus leucurus*; Bartholomew, 1964), a diurnal rodent living in the Sonoran desert, was based on data for  $T_b$  observed in squirrels held in the laboratory not data on free-living individuals.

Diurnal variation in  $T_b$  has been reported in a number of large ruminants, including the dromedary camel (*Camelus dromedarius*), Grant's gazelle (*Gazella granti*), Thomson's gazelle (*Gazella thomsonii*), fringe-eared oryx (*Oryx beisa callotis*) and Cape eland (*Taurotragus oryx*) (Schmidt-Nielsen et al., 1957; Taylor and Lyman, 1967; Taylor, 1969, 1970), but these studies were also done on captive animals, so our knowledge about use of heterothermy and its physiological significance among free-living ungulates remains limited (Parker and Robbins, 1985). In these studies, fluctuations in  $T_b$  were often

as much as 4–7°C when captive ungulates were deprived of drinking water but only 1–2°C when hydrated, suggesting that hydration state influences the use of heterothermy.

Because measurements of  $T_b$  have been made in captivity, where opportunities for behavioural thermoregulation by individuals may be limited, the extent to which, and under what circumstances, heterothermy is used by ungulates in their natural environment remains unclear, despite statements to the contrary (Willmer et al., 2000; Randall et al., 2002). Investigations on free-ranging mule deer (*Odocoileus hemionus*; Sargeant et al., 1994) and black wildebeest (*Connochaetes gnou*; Jessen et al., 1994), both inhabitants of semi-arid areas, and on springbok (*Antidorcas marsupialis*; Mitchell et al., 1997) and Cape eland (Fuller et al., 1999), both occurring in arid habitats, did not find that these species routinely employed heterothermy, despite daily variation in air temperature ( $T_a$ ) of >15°C in some cases. Because  $T_b$  of Cape eland was relatively invariant when they were allowed to seek shade, Fuller et al. (1999) argued that the heterothermy observed by Taylor and Lyman (1967) was “probably an experimental artefact occurring in animals denied access to behavioural thermoregulation”.

The Arabian oryx (*Oryx leucoryx*), a desert antelope (body mass, 80–100 kg) that once ranged throughout most of the Arabian peninsula, was extirpated from the wild by 1972 (Henderson, 1974). In 1990, Arabian oryx were reintroduced into Mahazat as-Sayd, a large protected area 160 km north-east of Taif, Saudi Arabia. Captive-reared animals survived and reproduced without supplemental food and water; the population has increased significantly over the past decade and now numbers more than 450 individuals (Ostrowski et al., 1998; Treydte et al., 2001). Arabian oryx can live without access to drinking water in arid and hyperarid deserts (Williams et al., 2001), including the Rub al-Khali, one of the driest regions in the world (Meigs, 1953). Survival of oryx in such harsh areas is noteworthy when one considers its large size, its inability to shelter in burrows and that herbivory is typically associated with high rates of water turnover (Nagy and Peterson, 1988). Arabian oryx have one of the lowest mass-specific water-influx rates among ungulates living in hot environments: 76.9% below allometric prediction in summer (Nagy and Peterson, 1988; Williams et al., 2001; Ostrowski et al., 2002).

In the present study, we tested the hypothesis that heterothermy is a mechanism employed by free-ranging Arabian oryx in their natural environment. We found that their mean daily  $T_b$  varied by 4.1±1.7°C during summer, the first documentation of heterothermy in a free-living ungulate, but only by 1.5±0.6°C during winter. We used data on heterothermy of Arabian oryx during summer and winter to estimate their daily heat storage and concomitant water savings.

## Materials and methods

### Study area

Designated as a protected area in 1988, our study area, Mahazat as-Sayd, consisted of 2244 km<sup>2</sup> tract of flat, open

steppe desert in west-central Saudi Arabia (28°15' N, 41°40' E). Other than temporary pools after infrequent rain, Mahazat as-Sayd provides no surface water for oryx.

Characterized by hot summers and mild winters, the arid climate of this region has an annual mean rainfall of 96±41 mm ( $N=11$  years). The mean daily maximum ( $T_{a,max}$ ) and minimum ( $T_{a,min}$ ) air temperatures are 42.4°C and 26.6°C, respectively, in June, the hottest month, and 23.8°C and 11.5°C, respectively, in January (National Wildlife Research Center, unpublished report). During 1998, 1999, 2000 and 2001, annual rainfall was 79 mm, 34 mm, 45 mm and 136 mm, respectively. Weather data were measured continuously at an automatic meteorological recording station situated within the protected area. Solar radiation was measured using a pyranometer (Li-Cor, Lincoln, NB, USA).

The sparse vegetation of Mahazat as-Sayd is dominated by perennial grasses, including *Panicum turgidum*, *Lasiurus scindicus*, *Stipagrostis* spp. and *Ochthochloa compressa* (Mandaville, 1990). Small acacia (*Acacia* spp.) and maeru trees (*Maerua crassifolia*), sporadically distributed along dry wadis (water courses), provide shade for the oryx.

### Handling of oryx

We darted six wild-born Arabian oryx [*Oryx leucoryx* (Pallas, 1777); three males and three females] with a mixture of 4.9 mg ml<sup>-1</sup> etorphine (M99; C-Vet, Leyland, UK; mean dose, 4.2±0.4 mg) and 50 mg ml<sup>-1</sup> xylazine (Rompun; Bayer, Leverkusen, Germany; dose, 25 mg), a combination of drugs that induced anaesthesia within 10 min (Machado et al., 1983). All animals were sexually mature and >3 years old, judging from wear on their teeth (Ancrenaz and Delhomme, 1997). After oryx were anaesthetized, we weighed them (±0.5 kg) using a Salter scale attached to a tripod and moved them to a truck. Mean body mass was 92.9±4.26 kg (range, 88.9–99.1 kg). Using aseptic procedures, we sutured temperature-sensitive radio-transmitters (model IMP/400 equipped with a S4 thermistor; Telonics, Mesa, AZ, USA), embedded in synthetic resin and coated with paraffin and beeswax (3.3 cm×9.7 cm; 85–90 g), into a fold of the omentum. We injected each individual with 1 g of long-acting amoxicillin intramuscularly, attached a second radio-transmitter around its neck, and reversed the anaesthetic with 9 mg diprenorphine (M50-50; C-Vet; 12 mg ml<sup>-1</sup>) and 10 mg atipamezole (Antisedan; Orion, Espoo, Finland; 5 mg ml<sup>-1</sup>). Experimental animals were ambulatory within 2 min following drug reversal and were released, on average, 42.2±5.8 min after they were darted. Radio-transmitters affixed to collars were long-range and motion-sensitive (MOD-400/S11 sensor; Telonics), with a faster pulse rate when animals were active. Our experimental protocol was approved by the National Commission for Wildlife Conservation and Development, Riyadh, Saudi Arabia.

### Temperature-sensitive radio-transmitters

We calibrated (±0.1°C) temperature-sensitive radio-transmitters in a temperature-controlled water bath against a

mercury thermometer with a certificate traceable to the US National Institute of Standards and Technology. We determined the interpulse interval of these radio-transmitters using a digital data processor (TDP-2; Telonics) connected to a portable multichannel receiver (TR-2; Telonics) over a temperature range of 32–46°C. After log transformation of temperatures and interpulse intervals, we derived least-squares linear regression equations relating interpulse interval to  $T_b$ ; all regressions had an  $r^2$  of  $>0.995$ . We surgically removed two radio-transmitters 22 months after implantation to check for deviations in calibration. Between 32°C and 46°C, the change from our initial calibrations of these two transmitters was  $-0.1^\circ\text{C}$  and  $-0.2^\circ\text{C}$ . We concluded that temperature-sensitive radio-transmitters provided an accurate measurement of oryx  $T_b$ .

#### Data collection

Beginning 30 days after implanting radio-transmitters, we used a hand-held antenna (range, 600–800 m) to record  $T_b$  every 30 min for a total of 828 h during the day and 81 h at night, with measurement periods equally distributed among six oryx. We monitored  $T_b$  of oryx from 17 May 1998 to 29 September 2001. Daytime was considered to be between 06.00 h and 19.00 h, and night-time between 19.30 h and 05.30 h. We also measured  $T_a$  ( $\pm 0.1^\circ\text{C}$ ) in the shade at the same intervals with an electronic thermometer (Type T; Omega Engineering, Stamford, CT, USA) and a 38-gauge copper–constantan thermocouple, 30 cm above ground. When oryx were in deep shade,  $T_a$  crudely approximates to operative temperature (Bakken, 1976, 1992). To document oryx shading behaviour, we monitored their movements by radiotracking them at long distance from our vehicle using the radio signal from their neck collar. When visible through binoculars, oryx were described every 15 min as resting in shade, standing outside of shade or active (walking, feeding or interacting). During the night, we classified behaviour as active or inactive based on differences in pulse interval of radio-collar signals. At night, some oryx were sensitive to our presence, even at long distance. Observations of behaviour were terminated and  $T_b$  data were eliminated if we suspected that oryx were more active because of our presence. Hence, total night-time observations were fewer than those in daytime.

#### Calculation of water savings

To calculate water savings as a result of hyperthermia, we assumed that oryx had a uniform body and surface temperature, a reasonable approximation at the high  $T_a$ s experienced by animals during summer in this study. Skin temperature was probably lower than  $T_b$  in winter but, because the heat of vaporization of water is only 0.7% higher at 30°C than at 38°C (Kleiber, 1975), errors are probably small because of this assumption. We used the following equation:  $W = \Delta T_b C_p M_b / H_v$ , where  $W$  is water saved (in litres) per time interval,  $\Delta T_b$  is the difference between  $T_b$  observed and mean  $T_b$  (in °C),  $C_p$  is the specific heat of tissue ( $3.48 \text{ kJ kg}^{-1} \text{ deg}^{-1}$ ; Taylor, 1970; International Union of Physiological Sciences

Thermal Commission, 1987),  $M_b$  is mean body mass (in kg), and  $H_v$  is the heat of vaporization of water ( $2404 \text{ kJ litre}^{-1}$  at 38°C; Kleiber, 1975; Schmidt-Nielsen, 1998).

Because of the complexity of heat exchange of an animal with its environment (Porter and Gates, 1969), we recognize the limitations of our simplifying assumptions involved in estimating water savings. However, given that we computed water savings only when  $T_b > T_{b,\text{mean}}$ , and given that  $T_a$  exceeded  $T_{b,\text{mean}}$  in summer only for an average of 4 h per day, our estimates of water savings are conservative.

#### Data analysis

To test for differences between mean daily  $T_b$  and daily variation in  $T_b$  ( $T_{b,\text{max}} - T_{b,\text{min}}$ ), we used a repeated-measures two-way analysis of variance [ANOVA; with season (winter/summer) and time of day (night/day) as fixed factors and individuals as a random factor (model type III)]. We investigated the relationship between total heat storage, expressed as  $C_p(T_{b,\text{max}} - T_{b,\text{min}})M_b$ , and  $T_a$  with linear regression. We tested for differences in  $T_a$  between seasons by comparing half-hour means with a Wilcoxon matched pairs signed-rank test.

For each season, the proportion of time spent in shade per 24 h-day was calculated for each animal. The effect of climate on behaviour was examined by correlating activity with  $T_a$ ,  $T_{a,\text{max}}$  and  $T_{a,\text{min}}$ . All proportions were arcsine transformed prior to analyses (Zar, 1996). To determine if animals were resting in shade when their  $T_b$  was decreasing, and if they were active in sun when their  $T_b$  was increasing, we used a binomial test ( $H_0$ ;  $P=0.5$ ). Means  $\pm 1$  s.d. are reported. We assumed statistical significance at  $P < 0.05$  (Zar, 1996).

## Results

### Climate

During summer (15 June to 15 September), maximum air temperature ( $T_{a,\text{max}}$ ; mean =  $43.5 \pm 1.7^\circ\text{C}$ ) occurred between 15.00 h and 15.30 h, and minimum air temperature ( $T_{a,\text{min}}$ ; mean =  $29.4 \pm 2.1^\circ\text{C}$ ) occurred at dawn between 05.00 h and 05.30 h (Fig. 1A), whereas during winter (15 November to 15 March),  $T_{a,\text{max}}$  (mean =  $27.0 \pm 3.5^\circ\text{C}$ ) occurred between 15.00 h and 15.30 h and  $T_{a,\text{min}}$  (mean =  $13.3 \pm 2.7^\circ\text{C}$ ) occurred at dawn between 06.30 h and 07.00 h (Fig. 1B). Mean diurnal  $T_a$  was higher in summer than in winter ( $P < 0.001$ ). Solar radiation peaked around noon at approximately  $1050 \text{ W m}^{-2}$  in summer and  $850 \text{ W m}^{-2}$  in winter.

### Body temperature

With data from summer and winter combined, mean body temperature ( $T_b$ ) was  $38.4 \pm 1.3^\circ\text{C}$ ; it did not vary significantly between seasons or between day and night ( $F_{1,59} = 1.1$ ,  $P = 0.30$ ). However, the daily variation in  $T_b$ , ( $T_{b,\text{max}} - T_{b,\text{min}}$ ), was significantly higher in summer ( $4.13 \pm 1.7^\circ\text{C}$ ;  $F_{1,56} = 148.9$ ,  $P < 0.0001$ ) than in winter ( $1.5 \pm 0.6^\circ\text{C}$ ).

During summer,  $T_{b,\text{max}}$  and  $T_{b,\text{min}}$  averaged  $40.5 \pm 0.66^\circ\text{C}$  and  $36.5 \pm 1.16^\circ\text{C}$ , respectively, during day and  $39.8 \pm 0.20^\circ\text{C}$  and

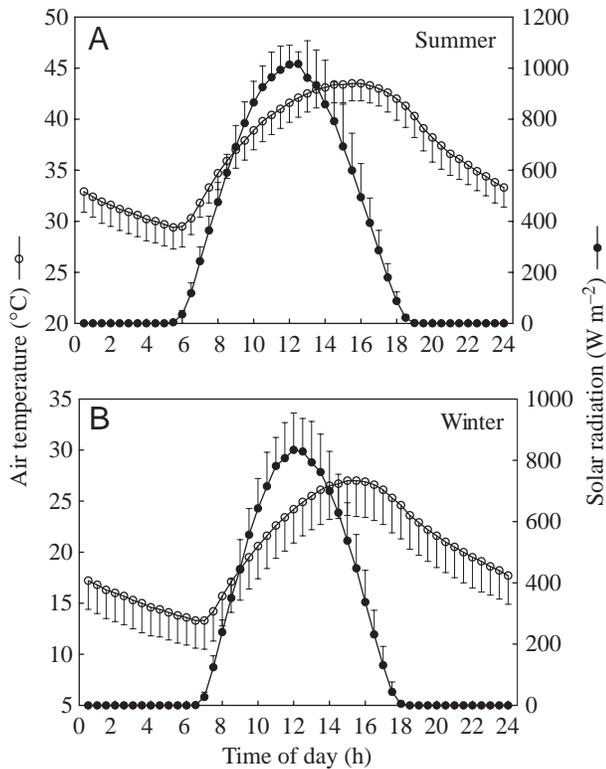


Fig. 1. Air temperature (open circles) and solar radiation (filled circles) versus time of day in Mahazat as-Sayd for summer and winter between May 1998 and September 2001. Values are means  $\pm$  S.D.

$38.1 \pm 0.36^\circ\text{C}$  during night.  $T_{b,\text{min}}$  occurred around 08.30 h, which is 3 h later than  $T_{a,\text{min}}$ .  $T_{b,\text{max}}$  occurred near 18.30 h, shortly before sunset, and decreased during the night (Fig. 2). Mean  $T_b$  was  $38.3 \pm 0.44^\circ\text{C}$  during day and  $38.8 \pm 0.16^\circ\text{C}$  during night. The largest change in  $T_b$  during one day was  $7.5^\circ\text{C}$ , from  $34.5^\circ\text{C}$  to  $42.0^\circ\text{C}$  (in July), in a male that weighed 99.1 kg, the heaviest oryx in our cohort.

During winter, the mean  $T_{b,\text{max}}$  and  $T_{b,\text{min}}$  were  $39.2 \pm 0.29^\circ\text{C}$  and  $37.5 \pm 0.51^\circ\text{C}$ , respectively, during day, and  $39.2 \pm 0.22^\circ\text{C}$  and  $37.9 \pm 0.18^\circ\text{C}$  during night.  $T_{b,\text{min}}$  occurred around 07.00 h, 30–60 min after sunrise.  $T_b$  increased until 18.00 h and monotonically decreased during the night (Fig. 2). Mean  $T_b$  was  $38.3 \pm 0.59^\circ\text{C}$  during the day and  $38.5 \pm 0.22^\circ\text{C}$  during the night. The largest change in  $T_b$  during one day was  $2.5^\circ\text{C}$ , from  $36.6^\circ\text{C}$  to  $39.1^\circ\text{C}$  in February, in a female that weighed 89.7 kg.

During the summer, mean  $T_{b,\text{max}}$  was significantly higher ( $t=290.4$ , d.f.=57,  $P<0.001$ ), and mean  $T_{b,\text{min}}$  significantly lower ( $t=159$ , d.f.=57,  $P<0.001$ ) than during winter. There was no statistically significant correlation ( $P>0.5$ ) between mean  $T_a$  and  $T_b$  in summer or winter. However, there was a significant correlation between the total heat stored and the amplitude of variation in  $T_a$  during the day in summer (Fig. 3A;  $F_{1,24}=4.9$ ,  $P=0.03$ ,  $r^2=0.17$ ) and in winter ( $F_{1,20}=22.2$ ,  $P<0.001$ ,  $r^2=0.53$ ). There was also a correlation between the total heat stored and

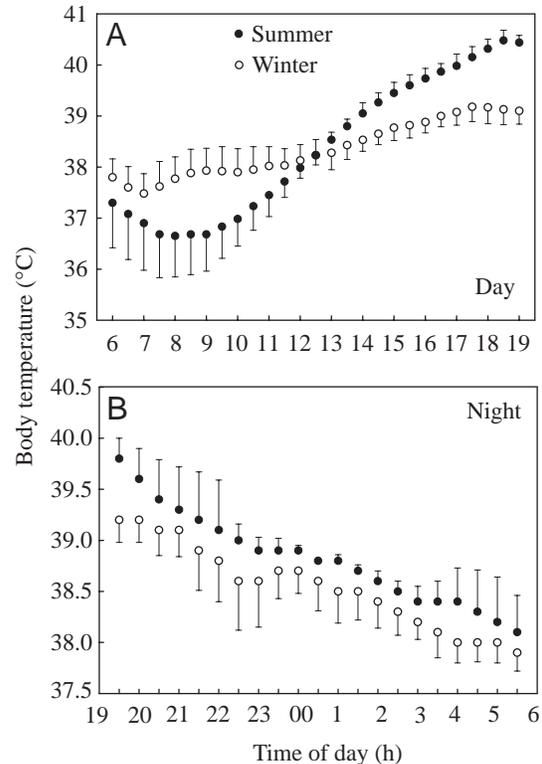


Fig. 2. Mean body temperature of six free-ranging Arabian oryx as a function of time of day. Means  $\pm$  S.D. for 59 days and 12 nights between May 1998 and September 2001.

$T_{a,\text{max}}$  and  $T_{a,\text{min}}$  during the summer (Fig. 3B,C;  $F_{1,24}=14.4$ ,  $P<0.001$ ,  $r^2=0.37$  and  $F_{1,24}=242.8$ ,  $P<0.001$ ,  $r^2=0.91$ , respectively) and between total heat stored and  $T_{a,\text{max}}$  during the winter (Fig. 3B;  $F_{1,20}=9.0$ ,  $P=0.007$ ,  $r^2=0.32$ ). There was no correlation between total amount of heat stored and  $T_{a,\text{min}}$  in winter (Fig. 3C;  $F_{1,20}=0.1$ ,  $P=0.78$ ,  $r^2=0.04$ ).

#### Behavioural thermoregulation

To search for correlations between behaviour and changes in  $T_b$ , we recorded oryx activity between 06.00 h and 08.30 h, when  $T_b$  was typically decreasing, and between 08.30 h and 18.30 h, when  $T_b$  was increasing. During summer, between 06.00 h and 08.00 h, animals were more frequently active outside shade than resting under shade (Fig. 4A;  $P<0.001$ ,  $N=20$ ). During periods when  $T_b$  was increasing, animals were resting under shade more frequently than active outside shade (Fig. 4A;  $P<0.001$ ,  $N=20$ ). In winter, there was no relationship between behaviour and  $T_b$  (Fig. 4B).

#### Shading pattern

During summer, when diurnal  $T_a$  was  $>35^\circ\text{C}$ , oryx sought shade as early as 06.30 h, typically under the dense foliage of maeru trees. They stayed in the shade, on average, for 9 h 21 min and began foraging at around 18.30 h. Time spent in the shade by oryx was positively correlated with mean  $T_a$

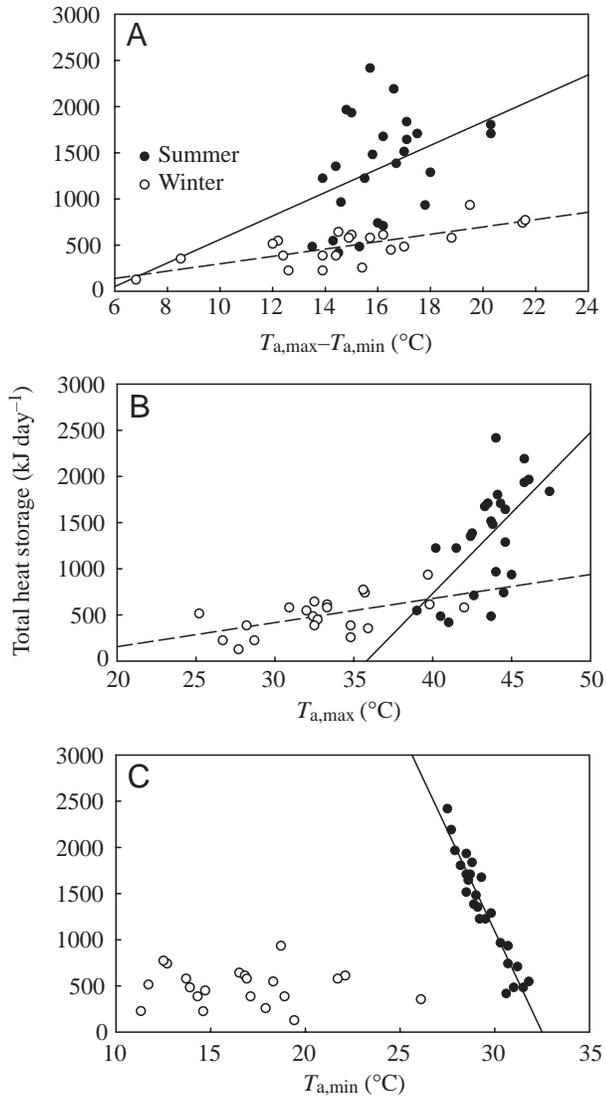


Fig. 3. Heat storage of six free-ranging Arabian oryx *versus* (A) daily variation in air temperature ( $T_{a,max}-T_{a,min}$ ), (B) maximum air temperature ( $T_{a,max}$ ) and (C) minimum air temperature ( $T_{a,min}$ ) during the summer and winter in Mahazat as-Sayd.

( $r_s=0.70$ ,  $P<0.01$ ,  $N=20$ ),  $T_{a,max}$  ( $r_s=0.67$ ,  $P<0.01$ ,  $N=20$ ) and  $T_{a,min}$  ( $r_s=0.65$ ,  $P<0.01$ ,  $N=20$ ). Shading time was also positively correlated with  $T_{b,max}$  ( $r_s=0.77$ ,  $P<0.01$ ,  $N=20$ ). During winter, time spent in the shade was not correlated with any of the variables we measured.

#### Water savings by heat storage

The gradient between the temperature of the animal's surface and  $T_a$  drives heat flux (Gates, 1962), but often the approximation  $T_b-T_a$  is used (McNab, 1980; McClure and Porter, 1983; Parker and Robbins, 1985). During summer,  $T_b-T_a$  was positive in late afternoon, night and early morning. During the morning, as  $T_a$  approached  $T_b$ , the outward flow of heat was reduced. Then, between 09.00 h and 17.30 h,  $T_b-T_a$

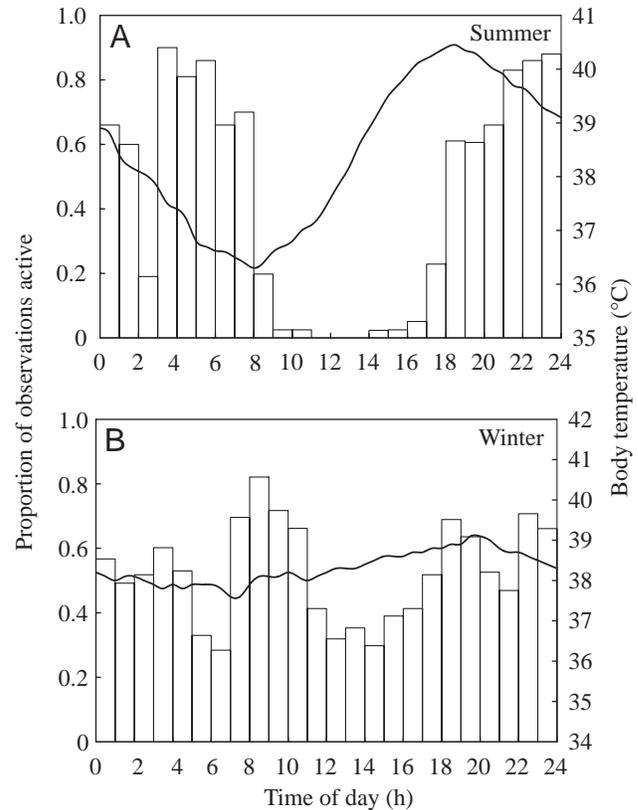


Fig. 4. Proportion of time spent active (bars) and mean body temperature (line) for Arabian oryx during summer ( $N=14$  oryx) and winter ( $N=17$  oryx) in Mahazat as-Sayd. Where there was more than one sample from an individual, a single mean was calculated.

was negative, indicating heat flow to the animals from their environment (Fig. 5). During winter,  $T_b$  of animals was always higher than  $T_a$ . Heat storage was  $112.1 \text{ kJ h}^{-1}$  in summer *versus*  $36.9 \text{ kJ h}^{-1}$  in winter, and the rate of heat gain was also higher in summer ( $t_{\text{slope}}=10.3$ ,  $d.f.=21$ ,  $P<0.001$ ;  $b_{\text{summer}}=44.9$ ,  $r^2=0.98$ ;  $b_{\text{winter}}=16.3$ ,  $r^2=0.84$ ).

Assuming mean  $T_b=38.4^\circ\text{C}$ ,  $T_{b,max}=40.48^\circ\text{C}$  and body mass= $92.9 \text{ kg}$ , heat storage was  $672.4 \text{ kJ day}^{-1}$  in summer and  $258.6 \text{ kJ day}^{-1}$  in winter. To dissipate this amount of heat by evaporation would require  $0.28 \text{ litres H}_2\text{O day}^{-1}$  in summer and  $0.11 \text{ litres H}_2\text{O day}^{-1}$  in winter.

#### Discussion

Although several authors have suggested that hyperthermia reduces evaporative water loss in large ungulate species (Schmidt-Nielsen et al., 1957; Taylor, 1969, 1970; Taylor and Lyman, 1967), these observations were made on animals in pens or environmental chambers. We provide the first documentation of a large desert herbivore, the Arabian oryx, using heterothermy under free-living conditions.

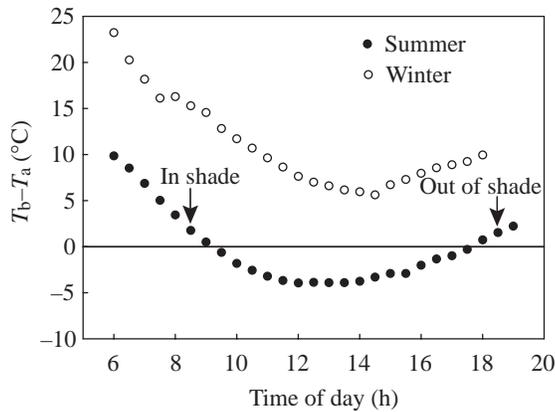


Fig. 5. Gradient between body temperature and air temperature ( $T_b - T_a$ ) as a function of time of day in six Arabian oryx during summer and winter in Mahazat as-Sayd.

In a vanguard study, Schmidt-Nielsen et al. (1957) showed that the camel ( $N=2$ ; mean body mass=260 kg), under penned conditions and deprived of drinking water, varied its rectal  $T_b$  from 3.5°C to 6.2°C and as much as 2.8°C above mean  $T_b$  during summer. If we calculate heat storage for the camel as we have done for oryx, then camels stored approximately 2500 kJ day<sup>-1</sup> and potentially saved approximately 1 litre H<sub>2</sub>O day<sup>-1</sup>. With a daily variation in core  $T_b$  of 1.5–7.5°C, and a potential water saving of 0.28 litres H<sub>2</sub>O day<sup>-1</sup> during summer, the Arabian oryx, which is about a third the size of a camel and therefore has a larger surface-to-volume ratio, appears to employ heterothermy in the wild as effectively as does the legendary domestic camel.

Although studies on free-ranging Cape eland and springbok failed to find heterothermy (Mitchell et al., 1997; Fuller et al., 1999), these studies were conducted when climatic conditions were moderate ( $T_a < 35^\circ\text{C}$ ) and over short periods (<2 months; Fuller et al., 1999). Had we measured  $T_b$  of Arabian oryx only during winter, we would have found variation of  $<1.5 \pm 0.6^\circ\text{C day}^{-1}$ . During summer, arid-zone antelopes are often exposed to  $T_a$ s of  $>40^\circ\text{C}$ , a temperature above the mean  $T_b$  for bovid ungulates, and do not have access to drinking water. Under such conditions, these species may also use heterothermy to limit evaporative water losses.

The extent to which hydration state influences heterothermy remains uncertain. In captivity, at  $T_a > 35^\circ\text{C}$ , the variation in rectal  $T_b$  increased for camels, Grant's gazelles, Thomson's gazelles and fringe-eared oryx when they were water-deprived compared with when they were hydrated (Schmidt-Nielsen et al., 1957; Taylor, 1970). However, Cape eland, African buffalo (*Syncerus caffer*) and wildebeest did not significantly elevate rectal  $T_b$  when water-deprived (Taylor and Lyman, 1967; Taylor, 1970). Because free-living Arabian oryx have a remarkably low rate of water influx during summer, on average 1310 ml H<sub>2</sub>O day<sup>-1</sup> (Williams et al., 2001), it could be that

they are somewhat dehydrated at this time. In support of this idea, they have higher haematocrit, plasma protein concentration and plasma osmolality during summer than during winter (S. Ostrowski, unpublished data). Hydration state during summer may influence use of heterothermy by oryx.

During summer, oryx stored 112.1 kJ h<sup>-1</sup> of heat during the day and dissipated this heat by non-evaporative means at night. They defended their  $T_b$  by evaporative cooling, primarily panting, only when  $T_b$  approached 41.5–42°C (S. Ostrowski, unpublished data). Between 06.00 h and 08.30 h,  $T_b$  continued to decline despite the fact that  $T_a$  and solar radiation were increasing and oryx were active during this period, a pattern that was also observed for the camel (Schmidt-Nielsen et al., 1957), red kangaroo (*Megaleia rufa*; Brown and Dawson, 1977) and Cape eland (Fuller et al., 1999). Allowing  $T_b$  to decrease to a lower level would presumably permit oryx to store additional heat during the hot part of the day, as is also suggested by the correlation between  $T_{a,\text{min}}$  and total heat storage (Fig. 3C). In winter, oryx also increased their  $T_b$  during the day, storing 36.9 kJ h<sup>-1</sup>. However,  $T_{b,\text{min}}$  was higher in winter than in summer despite the fact that the gradient between  $T_b$  and  $T_a$  was larger, suggesting that they limit the decrease in  $T_b$  during winter.

During winter,  $T_b$  of oryx always exceeded  $T_a$ , indicating that heat stored in their body was endogenous (Fig. 5). Williams et al. (2001) reported that oryx during spring, with a mean body mass of 89.0 kg, had a mean field metabolic rate of 920 kJ h<sup>-1</sup>. The fact that oryx stored 258.6 kJ during the 12.5 h that  $T_b$  was higher than  $T_{b,\text{mean}}$  suggests that, during winter days, a modest 2.2% of heat production was stored, assuming that oryx were in energy balance. Our results indicate that, during winter, oryx adjust their thermoregulatory behaviour and attendant water savings to a decrease in  $T_a$ .

Our estimates of water savings as a result of heat storage indicate that this is an important mechanism in the water economy of Arabian oryx. Our calculations show that they saved 0.28 litres H<sub>2</sub>O day<sup>-1</sup> and 0.11 litres H<sub>2</sub>O day<sup>-1</sup> in summer and winter, respectively, when we used mean  $T_b$  in our calculations. The mass-corrected water-influx rate of oryx in summer is 22.7 ml H<sub>2</sub>O day<sup>-1</sup> kg<sup>-0.922</sup>, where 0.922 is the slope of the allometric relationship between water influx (ml day<sup>-1</sup>) and body mass (kg) among large ungulates in hot environments (Ostrowski et al., 2002). If oryx maintained a constant  $T_b$  of 38.4°C, their water-influx rate would have to increase 19% (to 27 ml H<sub>2</sub>O day<sup>-1</sup> kg<sup>-0.922</sup>) to offset water losses.

Our use of mean  $T_b$  in our calculation of water savings assures that our estimate is a conservative one. Given that oryx allowed their  $T_b$  to decline to a mean of 36.5°C during summer, one could argue that heat storage was 1293.2 kJ day<sup>-1</sup> ( $4.0^\circ\text{C} \times 3.48 \text{ kJ kg}^{-1} \text{ deg}^{-1} \times 92.9 \text{ kg}$ ) and that water savings were 0.538 litres day<sup>-1</sup>.

Although Arabian oryx avoid solar radiation during the day

in summer, they still depend on heterothermy at this time. Our calculations of water savings as a result of heterothermy, coupled with their low daily water-influx rate (Ostrowski et al., 2002), suggest that oryx can not obtain sufficient preformed water during summer to maintain homeothermic  $T_b$  without disrupting their hydration state. Contrary to what was suggested for the Cape eland (Fuller et al., 1999), behavioural thermoregulation in the oryx does not result in homeothermy.

An endangered species, the Arabian oryx has been the focus of re-introduction projects throughout the Middle East (Stanley Price, 1989; Ostrowski et al., 1998). Formerly, this species was distributed over much of the Arabian peninsula, but now the only viable free-living herds occur in the desert of central Saudi Arabia and the western Rub al-Khali or Empty Quarter. Current models of climate change attributable to global warming predict that the Arabian peninsula may experience as much as a 5°C increase in mean  $T_a$  over this century; night-time mean  $T_{a,min}$  may increase proportionately more than daytime  $T_{a,max}$  values (Mitchell and Hulme, 2000). Our data highlight the importance of minimum night-time  $T_a$  to daytime heat storage of oryx and their attendant water conservation. If night-time  $T_a$  increases as models predict, this will undoubtedly impact the ability of oryx to live in some areas, a major concern for conservationists.

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