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

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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±1.7°C day^{-1} during summer (June to September) and by 1.5±0.6°C day^{-1} during winter (November to March). Over both seasons, mean T_b was 38.4±1.3°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±1.16°C) than in winter (37.5±0.51°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 ($T_{a,max}$–$T_{a,min}$) 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 kJ day^{-1} animal^{-1} in summer and 258.6 kJ day^{-1} 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 litres H_2O day^{-1} animal^{-1} and 0.11 litres H_2O day^{-1} 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 litres H_2O day^{-1} 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 (±2°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 ±2°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^2 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^{-1} etorphine (M99; C-Vet, Leyland, UK; mean dose, 4.2±0.4 mg) and 50 mg ml^{-1} 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 amoxycillin intramuscularly, attached a second radio-transmitter around its neck, and reversed the anaesthetic with 9 mg diprenorphine (M50-50; C-Vet; 12 mg ml^{-1}) and 10 mg atipamezole (Antisedan; Orion, Espoo, Finland; 5 mg ml^{-1}). 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°C and –0.2°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 (±0.1°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_as 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, ΔT_b is the difference between T_b observed and mean T_b (in °C), C_p is the specific heat of tissue (3.48 kJ kg^{-1}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 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 $T_b > T_{b,mean}$, and given that T_a exceeded $T_{b,mean}$ 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 ($T_{b,max}$–$T_{b,min}$), 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 $C_p(T_{b,max}-T_{b,min})M_b$, 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, $T_{a,max}$ and $T_{a,min}$. 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_o; P=0.5). Means ± 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 ($T_{a,max}$; mean=43.5±1.7°C) occurred between 15.00 h and 15.30 h, and minimum air temperature ($T_{a,min}$; mean=29.4±2.1°C) occurred at dawn between 05.00 h and 05.30 h (Fig. 1A), whereas during winter (15 November to 15 March), $T_{a,max}$ (mean=27.0±3.5°C) occurred between 15.00 h and 15.30 h and $T_{a,min}$ (mean=13.3±2.7°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 W m^{-2} in summer and 850 W m^{-2} in winter.

Body temperature

With data from summer and winter combined, mean body temperature (T_b) was 38.4±1.3°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, ($T_{b,max}$–$T_{b,min}$), was significantly higher in summer (4.13±1.7°C; $F_{1,56}$=148.9, $P<0.0001$) than in winter (1.5±0.6°C).

During summer, $T_{b,max}$ and $T_{b,min}$ averaged 40.5±0.66°C and 36.5±1.16°C, respectively, during day and 39.8±0.20°C and

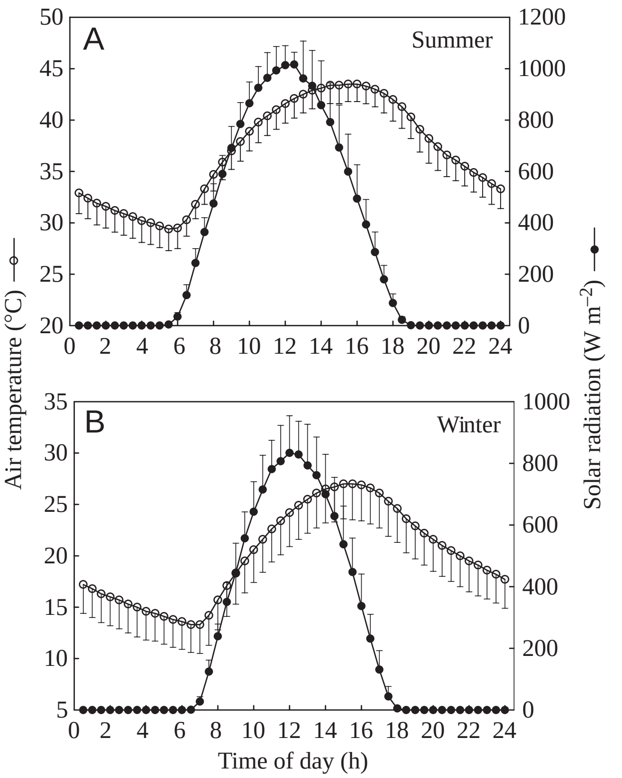

Fig. 1. Air temperature (open circles) and solar radiation (filled circles) *versus* time of day in Mahazat as-Sayd for summer and winter between May 1998 and September 2001. Values are means ± S.D.

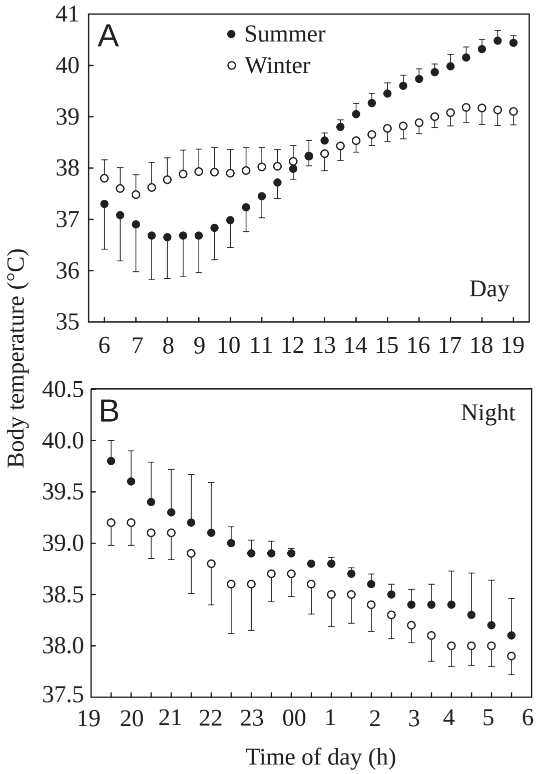

Fig. 2. Mean body temperature of six free-ranging Arabian oryx as a function of time of day. Means ± S.D. for 59 days and 12 nights between May 1998 and September 2001.

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

During winter, the mean $T_{\mathrm{b,max}}$ and $T_{\mathrm{b,min}}$ were 39.2±0.29°C and 37.5±0.51°C, respectively, during day, and 39.2±0.22°C and 37.9±0.18°C during night. $T_{\mathrm{b,min}}$ 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±0.59°C during the day and 38.5±0.22°C during the night. The largest change in T_{b} during one day was 2.5°C, from 36.6°C to 39.1°C in February, in a female that weighed 89.7 kg.

During the summer, mean $T_{\mathrm{b,max}}$ was significantly higher (t=290.4, d.f.=57, P<0.001), and mean $T_{\mathrm{b,min}}$ 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 $T_{\mathrm{a,max}}$ and $T_{\mathrm{a,min}}$ 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 $T_{\mathrm{a,max}}$ 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 $T_{\mathrm{a,min}}$ 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°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}

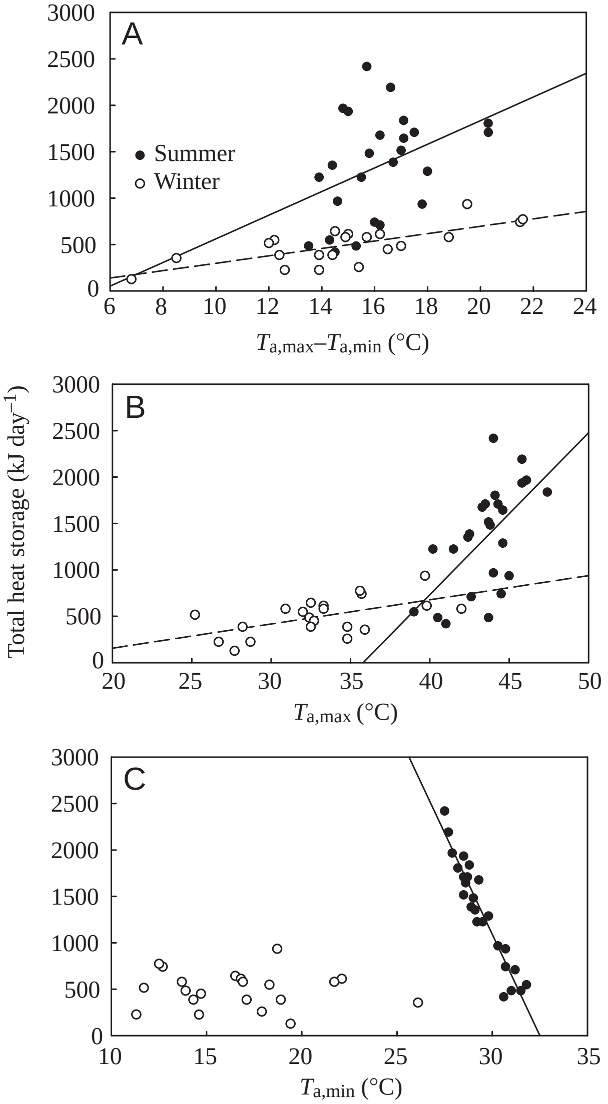

Fig. 3. Heat storage of six free-ranging Arabian oryx *versus* (A) daily variation in air temperature ($T_{a,max}$–$T_{a,min}$), (B) maximum air temperature ($T_{a,max}$) and (C) minimum air temperature ($T_{a,min}$) during the summer and winter in Mahazat as-Sayd.

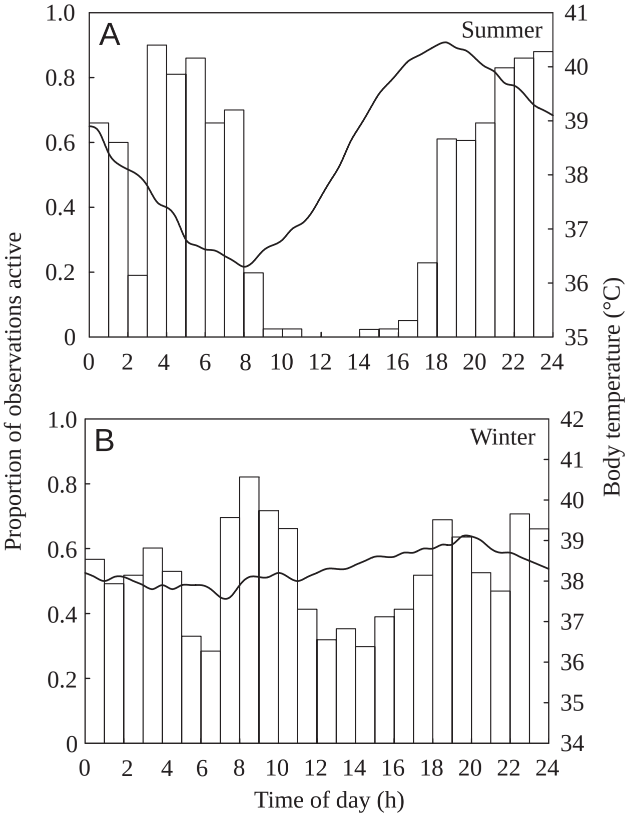

Fig. 4. Proportion of time spent active (bars) and mean body temperature (line) for Arabian oryx during summer (N=14 oryx) and winter (N=17 oryx) in Mahazat as-Sayd. Where there was more than one sample from an individual, a single mean was calculated.

(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 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 kJ h^{-1} in summer *versus* 36.9 kJ h^{-1} in winter, and the rate of heat gain was also higher in summer (t_{slope}=10.3, d.f.=21, P<0.001; b_{summer}=44.9, r^2=0.98; b_{winter}=16.3, r^2=0.84).

Assuming mean T_b=38.4°C, $T_{b,max}$=40.48°C and body mass=92.9 kg, heat storage was 672.4 kJ day^{-1} in summer and 258.6 kJ day^{-1} in winter. To dissipate this amount of heat by evaporation would require 0.28 litres H_2O day^{-1} in summer and 0.11 litres H_2O 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.

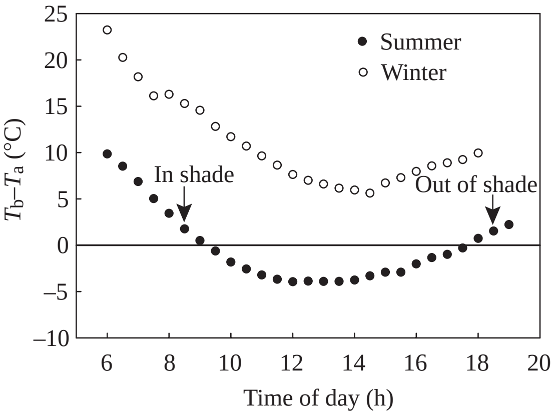

Fig. 5. Gradient between body temperature and air temperature (T_b–T_a) as a function of time of day in six Arabian oryx during summer and winter in Mahazat as-Sayd.

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^{-1} and potentially saved approximately 1 litre H_2O day^{-1}. With a daily variation in core T_b of 1.5–7.5°C, and a potential water saving of 0.28 litres H_2O day^{-1} 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°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±0.6°C day^{-1}. During summer, arid-zone antelopes are often exposed to T_as of >40°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°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_2O day^{-1} (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^{-1} 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 $T_{a,min}$ and total heat storage (Fig. 3C). In winter, oryx also increased their T_b during the day, storing 36.9 kJ h^{-1}. However, $T_{b,min}$ 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^{-1}. The fact that oryx stored 258.6 kJ during the 12.5 h that T_b was higher than $T_{b,mean}$ 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_2O day^{-1} and 0.11 litres H_2O day^{-1} 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_2O day^{-1} kg$^{-0.922}$, where 0.922 is the slope of the allometric relationship between water influx (ml day^{-1}) 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_2O day^{-1} kg$^{-0.922}$) 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^{-1} (4.0°C×3.48 kJ kg^{-1} deg.$^{-1}$×92.9 kg) and that water savings were 0.538 litres day^{-1}.

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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