

Heterothermy of free-living Arabian sand gazelles (*Gazella subgutturosa marica*) in a desert environment

Stéphane Ostrowski^{1,*} and Joseph B. Williams²

¹National Wildlife Research Center, PO Box 1086, Taif, Saudi Arabia and ²Department of Evolution, Ecology and Organismal Biology, Ohio State University, 300 Aronoff Lab, 318 W 12th Avenue, Columbus, OH 43210, USA

*Author for correspondence at present address: UMR 5123, Université Claude Bernard Lyon 1, 43 bd du 11 Novembre 1918, 69622 Villeurbanne, France (e-mail: stephane.ostrowski@laposte.net)

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Summary

To test whether free-living desert ungulates employ heterothermy to reduce water loss, we measured core body temperature (T_b) of six free-living Arabian sand gazelles (*Gazella subgutturosa marica*), a small desert antelope (12–20 kg) that lives in the deserts of Saudi Arabia, where air temperature (T_a) often exceeds 40°C. We found that the mean daily T_b varied by $2.6 \pm 0.8^\circ\text{C}$ during summer (June–July) and $1.7 \pm 0.3^\circ\text{C}$ during winter (January–February); over both seasons, mean T_b was $39.5 \pm 0.2^\circ\text{C}$. During the day, in summer, T_b increased by more than 2°C when $T_a > T_b$ and declined at night when $T_a < T_b$, suggesting that gazelles stored heat during day and dissipated it by non evaporative means during night. The minimum T_b was lower in summer ($38.2 \pm 0.5^\circ\text{C}$) than in winter ($38.6 \pm 0.3^\circ\text{C}$) despite the fact that the gradient between T_b and T_a was larger and solar radiation was lower in winter. Correlation between daily variation of T_b and mean, maximal T_a s were significant in summer, but not in winter. To dissipate the amount of heat stored by gazelles would require an evaporative water loss of $33.5 \text{ ml H}_2\text{O day}^{-1}$ in summer and $23.2 \text{ ml H}_2\text{O day}^{-1}$ in winter.

We tested whether the amplitude of daily variation in T_b

was influenced by the level of water provided to six captive sand gazelles maintained under controlled conditions in summer. The daily amplitude of T_b was increased by 1.4°C when gazelles were denied drinking water but supplied with pre-formed water in food, and by 1.1°C when they were denied both water and food. Gazelles denied only drinking water increased the amplitude of variation in T_b , whereas when denied both food and water, they seemed to undergo a dehydration-hyperthermia, with increased mean and maximal T_b values but no decrease of minimal T_b .

Free-ranging and captive gazelles surviving on pre-formed water in natural food used heterothermy during summer with no elevation of plasma osmolality, indicating that they were not in a state of dehydration. Our data on variation in T_b of gazelles provide an example of a small desert ungulate employing heterothermy to reduce evaporative water loss that would otherwise be required to maintain normothermic T_b .

Key words: Arabian sand gazelle, dehydration, desert, *Gazella subgutturosa marica*, heterothermy, thermoregulation, water saving.

Introduction

When exposed to high thermal loads, many endotherms maintain their body temperature (T_b) within narrow limits (less than $\pm 2^\circ\text{C}$), either behaviourally, such as seeking shade, or by panting or sweating, these requiring evaporative water loss (Jessen, 2001). Species indigenous to desert environments, without access to drinking water, can ill afford profligate use of evaporative water for cooling, and therefore must minimize reliance on this mechanism for maintenance of T_b (Wilson, 1989; Degen, 1997; Schmidt-Nielsen, 1997). One mechanism, thought to be important in reducing evaporative water loss among large desert ungulates, is heterothermy, the storage of body heat during the day, under positive thermal load, and

dissipation of this heat at night by non-evaporative means, thereby reducing evaporative water loss in maintenance of normothermic T_b (International Union of Physiological Sciences Thermal Commission, 1987; Willmer et al., 2000).

The concept of heterothermy was originally espoused by Schmidt-Nielsen et al. (Schmidt-Nielsen et al., 1957), who measured 24 h rhythms of T_b in captive camels (*Camelus dromedarius*) during summer; T_b of camels increased during the day, decreased at night, and variation in T_b was amplified when animals were water-deprived. Extending these observations to captive Cape eland (*Tragelaphus oryx*), Taylor and colleagues demonstrated that, in environmental chambers set to 40°C during the day, but 22°C at night, eland increased

their rectal T_b by 4°C during the day, saving approximately 0.5 l of evaporative water (Taylor and Lyman, 1967; Taylor, 1969).

In an insightful series of articles, Mitchell and colleagues have criticized early studies of heterothermy because test animals were captive and did not have opportunities for behavioural thermoregulation (Mitchell et al., 2002; Fuller et al., 2004). From measurements of T_b using miniature data loggers on free-ranging black wildebeest (*Connochaetes gnou*) (Jessen et al., 1994), springbok (*Antidorcas marsupialis*) (Mitchell et al., 1997; Fuller et al., 2005), eland (Fuller et al., 1999), zebra (*Equus burchelli*) (Fuller et al., 2000), impala (*Aepyceros melampus*) (Mitchell et al., 2002) and gemsbok (*Oryx gazella*) (Maloney et al., 2002), this coterie of authors found that 24 h rhythms of T_b were not related to environmental heat load as indexed by daily variation of air temperature (T_a) and or 'globe temperature', the latter the internal temperature of a copper sphere painted black (Mitchell et al., 2002). They concluded that heterothermy was an artifact of captive conditions and that free-ranging ungulates in nature did not employ this mechanism of water savings.

In 2003 we reported the first case of heterothermy in free-living Arabian oryx (*Oryx leucoryx*; $N=6$), a species that is often exposed to T_a in excess of mean T_b during summer, lives in areas receiving less than 100 mm rain, and has no access to drinking water (Ostrowski et al., 2003). In this species, during summer, T_b increased from $36.5 \pm 1.2^\circ\text{C}$ around 08:30 h in the morning to $40.5 \pm 0.7^\circ\text{C}$ shortly before sunset, and decreased during night. In the early morning hours, T_b continued to decline despite the fact that T_a was increasing, a mechanism that presumably permitted the oryx to store additional heat during the hot part of the day. The use of heterothermy allowed oryx to potentially save 280 ml H_2O day⁻¹.

Heterothermy is variation in T_b , by more than 2°C, in response to environmental heat load that permits a savings of evaporative water loss. We agree with Fuller and colleagues that T_b should be measured on free-living animals, and thus behavioural thermoregulation should be component of our thinking about whether ungulates use heterothermy or not. Under the heterothermy model, during the day, when operative temperature (T_e) exceeds T_b of animals, heat is transferred from the environment to the animal. Instead of dissipating this heat load by evaporative water loss, thus maintaining normothermic T_b , animals increase T_b above normothermic levels storing heat in their body to reduce evaporative water losses. At night, when T_e is lower than T_b , stored heat is dissipated by non-evaporative means. The amplitude of daily T_b variation ought to be positively correlated with amplitude of heat load. Although neither T_a nor 'globe temperature' reflect actual thermal load of an ungulate, at least in full sun (S.O., unpublished data), both parameters have been used to approximate heat load in arid-zone antelopes (Ostrowski et al., 2003; Fuller et al., 2005). Because T_a is a weak index of thermal load, and because T_a may exceed T_b for only a short period of time during the day, it follows that T_a will not fully explain variation in T_b . Finally, the heterothermy model

predicts that water deprivation ought to increase the amplitude of T_b .

Arabian sand gazelles (*Gazella subgutturosa marica*; 12–20 kg) occur naturally in the northern deserts of Saudi Arabia, and in the Rub' al-Khali, one of the driest regions in the world (Meigs, 1953; Mallon and Kingswood, 2001). In 1990, they were reintroduced into Mahazat as-Sayd, a protected area 160 km north-east of Taif, Saudi Arabia (Haque and Smith, 1996). The population now numbers more than 2000 individuals (Mohammed et al., 2003). Gazelles have no access to drinking water apart from ephemeral pools that occur in the desert landscape after infrequent rains. An ungulate with small body mass such as a gazelle, a relatively large surface area-to-volume ratio and a lower thermal inertia would be less likely to employ heterothermy than a larger ungulate (Fuller et al., 1999; Mitchell et al., 2002; Fuller et al., 2005). But if gazelles were found to employ heterothermy, it would suggest that desert ungulates of most any size could employ this mechanism (Mitchell et al., 2002; Fuller et al., 2005).

In this study, we tested the hypothesis that heterothermy is a mechanism employed by free-ranging sand gazelles in their natural environment to reduce evaporative water losses. We measured T_b of gazelles over the course of seven months, spanning both winter and summer and found that they used heterothermy during summer, but not winter. In a lab experiment, we found that water deprivation influenced the magnitude of variation in T_b .

Materials and methods

Study area

Designated as a protected area in 1988, our study site, Mahazat as-Sayd, an area of 2244 km², consisted of a tract of flat, open steppe desert in west-central Saudi Arabia (28°15'N, 41°40'E). Mahazat as-Sayd provides no artificial sources of water for gazelles.

Characterized by hot summers and mild winters, this region has an annual average rainfall of 93 ± 56 mm ($N=14$ years) with a coefficient of variability >60%. The mean daily maximum ($T_{a,\text{max}}$) and minimum ($T_{a,\text{min}}$) air temperatures were 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 data). Between January 1st and July 31, 2004, the period of this study, 91 mm of rain fell in the reserve. Weather data were measured continuously at an automatic meteorological recording station situated within the protected area. Solar radiation was measured using a pyranometer (Licor, Lincoln, NB, USA). In addition, we measured T_a ($\pm 0.1^\circ\text{C}$) in the shade of a maeru tree (*Maerua crassifolia*) at 20 min intervals with a Campbell Scientific data logger (model 21X) and a 38-gauge copper-constantan thermocouple, 30 cm above ground, during the entire study. When gazelles were in deep shade, most often under maeru trees, T_a crudely approximated T_e (Bakken, 1976; Bakken, 1992; S.O., unpublished data).

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, sporadically distributed along dry wadis (dry water courses), provide shade for gazelles.

Procedures

Implantation of data loggers

In October 2003, we captured six adult Arabian sand gazelles (*Gazella subgutturosa marica* Gldenstaedt 1780), three males and three females, using a pop-up coral system. Animals were sedated with diazepam 5 mg ml⁻¹ (Valium; Roche, Neuilly-sur-Seine, France; dose 5 mg) and 100 mg ml⁻¹ perphenazine enanthate (Trilifan; Shering-Plough, Levallois, France; dose 20 mg) and relocated to a nearby (5 km) research facility where we anaesthetized them with a mixture of 100 mg ml⁻¹ ketamine (Imalgne; Merial, Lyon, France; mean dose 110.5±15.6 mg) and 100 mg ml⁻¹ xylazine (Rompun; Bayer, Leverkusen, Germany; dose 132.8±9.8 mg), a combination of drugs that induced anaesthesia within 10 min (Mubarak, 1997). Using aseptic procedures, we implanted miniature data loggers (StowAway XTI, Onset Computer Corporation, Pocasset, MA, USA) embedded in synthetic resin and coated with biologically inert wax (Paraffin/Elvax; Mini-Mitter Corporation, Sunriver, OR, USA) into the abdominal cavity of each animal. Average duration of surgery was 14 min. We treated surgical wounds with povidone iodine antiseptic (Vetidine, Vetoquinol, Lure, France), injected each individual with 15 mg kg⁻¹ of long-acting amoxicillin (Clamoxyl L.A., Pfizer, Orsay, France) intramuscularly, and reversed the anaesthesia with 10 mg atipamezole (Antisedan; Orion, Espoo, Finland; 5 mg ml⁻¹). Experimental animals were ambulatory within 25 min following drug reversal and were released into 10 m² individual pens, on average 67.2±12.1 min after they were captured. Two days after implantation of data loggers, gazelles were equipped with radio-transmitters affixed to neck-collars (model MOD305/S; Telonics, Mesa, AZ, USA) and released into a 200 ha enclosure located inside the reserve, for post-surgery monitoring. At the end of October 2003 we released all six gazelles back into the reserve. 9–10 months later, between August and early September 2004, we re-darted the gazelles with a mixture of 4.9 mg ml⁻¹ etorphine (M99; C-Vet, Leyland, UK; mean dose 0.45±0.08 mg) and 50 mg ml⁻¹ xylazine (Rompun; Bayer, Leverkusen, Germany; dose 15 mg). We surgically removed data loggers, and released the gazelles at their final capture site.

Food and or water deprivation experiment

To explore the effect of water deprivation on the amplitude of variation in T_b of gazelles, we designed an experiment wherein we controlled their intake of water, both drinking water and pre-formed water in natural food. We selected three male and three female Arabian sand gazelles from the captive herd of the King Khaled Wildlife Research Center (KKWRC), Thumamah, Saudi Arabia (25°20'N, 45°35'E), transported

them to Mahazat as-Sayd, and implanted them with miniature data loggers following the same procedures as on free-living gazelles. Animals were kept in outdoor 1200 m² enclosures that contained natural vegetation for shade, but natural food was collected and provided to them daily along with water (S.O., unpublished data). Food provided to gazelles consisted of green twigs/stems, leaves, and fruits of *Acacia tortillis*, *Panicum turgidum*, *Lasiurus scindicus*, *Stipagrostis* spp., *Tribulus macropterus* and *Monsonia nivea*, species commonly eaten by sand gazelles (Roberts, 1977). We sampled natural foods, dried them at 65°C, and found that they contained on average 470–560 ml H₂O kg⁻¹ wet mass, depending on species. In our water deprivation experiment, in mid August 2004, we provided gazelles a daily ration of 350 ml drinking water and 1 kg natural food for 3 days (Treatment 1), a regime previously determined to be sufficient for them to maintain body mass, then we removed drinking water but provided 1 kg natural food for 3 days (Treatment 2), then after a 5 day period of food and water again, we deprived them of both food and drinking water for 3 additional days (Treatment 3). We weighed gazelles using an electronic hanging scale (±0.05 kg) at the beginning and end of each treatment. Two weeks after final measurements, we anaesthetized the gazelles, and removed data loggers. Our experimental protocols were approved by the National Commission for Wildlife Conservation and Development, Riyadh, Saudi Arabia.

Data loggers for measurements of T_b

We used miniature data loggers custom-modified to have a storage capacity of 32 kb, a measurement range from +34 to +46°C, and a resolution of 0.04°C (Kammerman et al., 2001; Fuller et al., 2005). After wax-coating the data-loggers, we calibrated (±0.1°C) them over a temperature range of 34–46°C in a temperature-controlled water bath against a precision mercury thermometer with a certificate traceable to the US National Institute of Standards and Technology. We set the scan interval on loggers at 20 min, allowing more than 1 year of recordings. After retrieval of data loggers at the end of the experiment, we re-calibrated them again to check for drift. The change from our initial calibration in loggers used on free-ranging gazelles was –0.2°C, –0.1°C, –0.1°C, –0.1°C, 0.0°C, +0.1°C, respectively. We assumed that the temperature drift was linear over the course of the sampling period and made small corrections in T_b for loggers that displayed drift. There was no drift in loggers over the short period of our deprivation experiments.

Osmolality of plasma

Since hydration state is predicted to influence T_b in the heterothermy model, we measured plasma osmolality of both free-ranging gazelles, at initial and final handling, and in our deprivation trials, at the end of each treatment. We collected blood from the jugular vein, within 2 min of capture of gazelles, into glass tubes containing lithium–heparin, and then centrifuged it for 15 min at 700 g. We measured plasma osmolality (±1 mOsm) of each sample, in triplicate, with a

freezing-point depression osmometer (Type 13, Roebling, Berlin, Germany).

Calculation of potential water savings by heat storage

To calculate the potential water savings of gazelles as a result of using heterothermy, we assumed that their surface temperature equalled their T_b , a reasonable approximation at 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 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 ml) 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, 1970a; 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 (2.404 kJ ml⁻¹ at 38°C) (Kleiber, 1975; Schmidt-Nielsen, 1997).

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 1.3 h per day, our estimates of water savings are conservative.

Data collection

A priori, we purposed to discard T_b measurements on our loggers for the first 2 months following implantation to avoid possible bias related to post-surgical recovery. We compiled T_b measurements on six gazelles between 1 January 2004 and 26 July 2004. For the purpose of this paper we used only T_b measurements of the two coldest (January and February) and two hottest (June and July) months that were termed 'winter' and 'summer', respectively. Daytime was considered to be between 06:30 h and 18:15 h in winter and between 05:25 h and 19:30 h during summer. On 15 March 2004 one implanted free-ranging gazelle died, impaled during what appeared to be a fight with another male. We recovered the undamaged data logger on 18 March. Hence T_b was recorded for this animal only during winter.

Data analysis

We verified normality and homoscedasticity of variables with Kolmogorov-Smirnov goodness of fit and Levene's tests, respectively (Zar, 1996).

We tested for differences in T_a , $T_{a,max}$ and $T_{a,min}$ between seasons and experimental phases of our water restriction experiment by comparing 20 min means with a Wilcoxon matched pairs signed-rank test.

To test for differences between mean daily T_b , maximum daily T_b ($T_{b,max}$), minimum daily T_b ($T_{b,min}$) and daily variation in T_b ($T_{b,max} - T_{b,min}$) in free-ranging gazelles, we used a mixed model two-way analysis of variance [ANOVA; with season (winter/summer) and time of the day (night/day) as fixed

effects, and individuals as random factor (type III)] (Crowder and Hand, 1993). We ran *post hoc* Newman-Keuls multiple range tests to explore for statistical differences between groups. 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.

In our study on captive gazelles, we tested for differences between mean daily T_b , $T_{b,max}$, $T_{b,min}$, and $T_{b,max} - T_{b,min}$ with a two-way analysis of variance (ANOVA; with level of daily food and water allowance as a fixed effect, and individual as random factor). In addition, because we suspected that there could be an effect of the body mass on T_b , we tested for differences between mean daily T_b , $T_{b,max}$, $T_{b,min}$ and $T_{b,max} - T_{b,min}$ measured on day 3 of each treatment with a mixed model analysis of covariance (ANCOVA; with level of daily food and water allowance as a fixed effect, final body mass as covariate and individual as random factor). Though we consistently tested the interaction between final body mass and level of daily food and water allowance, we do not report results of these analyses if they were insignificant. Measurements of initial and final body mass, change in body mass and blood osmolality were compared between treatments with a repeated measures analysis of variance (RM ANOVA).

Values are reported as means \pm 1 s.d. We assumed statistical significance at $P=0.05$ (Zar, 1996).

Results

Climate

Mean daily T_a was 33.3 \pm 1.3°C in summer and 18.7 \pm 2.4°C in winter. During summer, maximum air temperature ($T_{a,max}$; mean=40.4 \pm 1.3°C) occurred between 1430 h and 1630 h, and minimum air temperature ($T_{a,min}$; mean=25.2 \pm 1.8°C) occurred at dawn between 05:00 h and 05:30 h (Fig. 1A), whereas during winter, $T_{a,max}$ (mean=25.8 \pm 3.2°C) occurred between 14:30 h and 16:30 h, and $T_{a,min}$ (mean=11.5 \pm 2.4°C) occurred at dawn (Fig. 1B). Mean diurnal T_a , $T_{a,max}$ and $T_{a,min}$ were higher in summer than in winter (Wilcoxon signed-rank test; $P < 0.001$), whereas the mean amplitude of daily T_a variation was similar in summer (14.8 \pm 1.5°C) and in winter (14.3 \pm 2.9°C) ($P=0.29$). Solar radiation peaked around noon at approximately 1050 W m⁻² in summer and 800 W m⁻² in winter.

During the water deprivation experiment, T_a averaged 33.8 \pm 0.8°C, $T_{a,max}$ 41.1 \pm 0.6°C, and $T_{a,min}$ 25.5 \pm 1.05°C. The mean amplitude of daily T_a variation (ΔT_a ; mean=15.5 \pm 0.7°C), mean T_a , $T_{a,max}$ and $T_{a,min}$ did not vary significantly between the three treatment periods ($P > 0.25$).

Body temperature in free-living gazelles

With data from summer and winter combined, T_b averaged 39.5 \pm 0.2°C; there was a significant effect of the interaction between season and time of day (day/night) on mean T_b (ANOVA type III, $F_{1,1303}=7.2$, $P=0.008$). A *post hoc* range test indicated that T_b summer/night $>$ T_b summer/day $>$ T_b winter/night $>$ T_b winter/day (Newman-Keuls; $P < 0.05$).

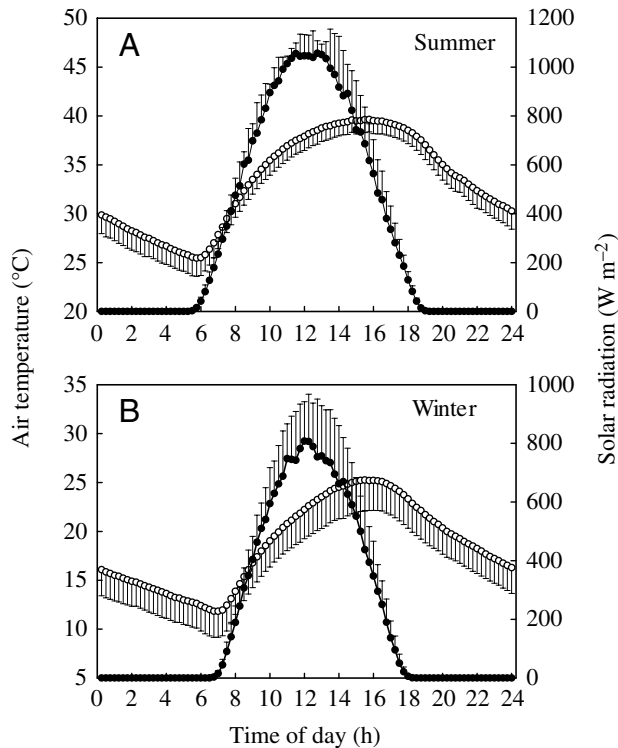


Fig. 1. Air temperature (open circles) and solar radiation (filled circles) versus time of day in Mahazat as-Sayd for (A) summer and (B) winter between January 2004 and July 2004. Values are means \pm s.d.

Combining day and night values, mean T_b during summer ($39.5 \pm 0.3^\circ\text{C}$) was significantly higher than during winter ($39.4 \pm 0.2^\circ\text{C}$) ($F_{1,1303}=83.8$, $P<0.001$), but this difference was small. The amplitude in daily variation in T_b ($T_{b,\max}-T_{b,\min}$) was significantly higher in summer ($2.6 \pm 0.8^\circ\text{C}$) than in winter ($1.7 \pm 0.3^\circ\text{C}$) ($F_{1,629}=19.7$, $P=0.01$).

During summer, $T_{b,\max}$ and $T_{b,\min}$ averaged $40.8 \pm 0.4^\circ\text{C}$ and $38.2 \pm 0.5^\circ\text{C}$, respectively. $T_{b,\min}$ occurred around 08:20 h, 02:45 h later than the minimum T_a . $T_{b,\max}$ occurred near 19:00 h, shortly before sunset, and decreased during the night (Fig. 2). Mean T_b was $39.5 \pm 0.3^\circ\text{C}$ during day and $39.6 \pm 0.2^\circ\text{C}$ during night. The largest change in T_b during one day was 5.5°C , from 36.5°C in the early morning to 42.0°C in the late afternoon in July, in a female.

During winter, mean $T_{b,\max}$ and $T_{b,\min}$ averaged $40.3 \pm 0.3^\circ\text{C}$ and $38.6 \pm 0.3^\circ\text{C}$, respectively. $T_{b,\min}$ occurred around 10:40 h, nearly 4 h later than $T_{a,\min}$. T_b increased until 18:40 h and then decreased abruptly until 20:40 h and declined monotonically during the rest of the night and early morning (Fig. 2). Mean T_b was $39.4 \pm 0.21^\circ\text{C}$ during the day, and $39.4 \pm 0.20^\circ\text{C}$ during the night. The largest change in T_b during one day was 2.8°C , from 38.8°C to 41.6°C in February, in a male.

During the summer, mean $T_{b,\max}$ was significantly higher (ANOVA type III, $F_{1,626}=10.8$, $P=0.03$), and mean $T_{b,\min}$ significantly lower ($F_{1,626}=21.6$, $P<0.01$) than during winter. There was a statistically significant correlation between mean T_a and T_b in summer ($P<0.001$, $r^2=0.24$), but not in winter.

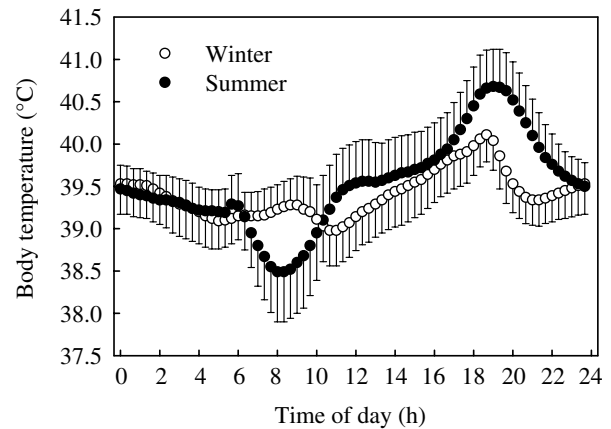


Fig. 2. Mean body temperature of six free-ranging Arabian sand gazelles in summer and winter at Mahazat as-Sayd, as a function of time of day. Values are means \pm s.d. for 60 days and 56 days in winter and summer 2004, respectively.

During summer there was a significant correlation between the total amount of heat stored and mean T_a (Fig. 3A; ANOVA, $F_{1,247}=111.1$, $P<0.001$, $r^2=0.31$), and $T_{a,\max}$ (Fig. 3B; $F_{1,247}=127.2$, $P<0.001$, $r^2=0.34$). There was no significant correlation between total amount of heat stored and $T_{a,\min}$ in summer, $T_{a,\min}$ in winter, $T_{a,\max}$ in winter and ($T_{a,\max}-T_{a,\min}$) in both seasons ($P>0.7$ in all cases).

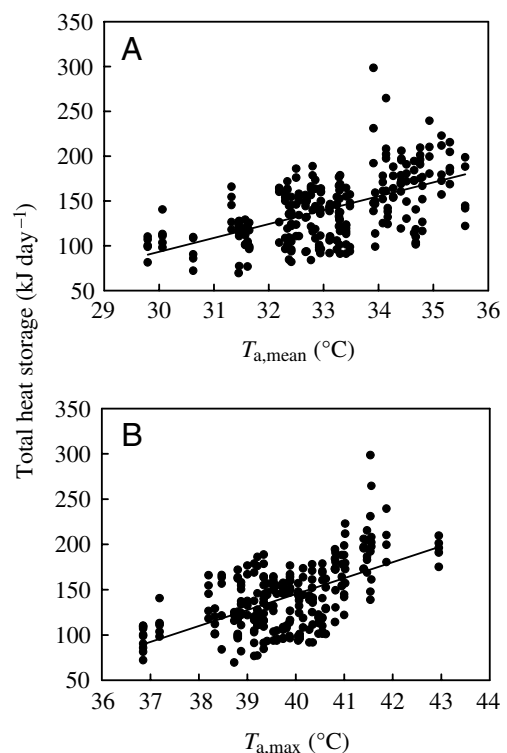


Fig. 3. Heat storage of five free-ranging Arabian sand gazelles versus (A) mean air temperature ($T_{a,\text{mean}}$) and (B) maximum air temperature ($T_{a,\text{max}}$) during the summer in Mahazat as-Sayd.

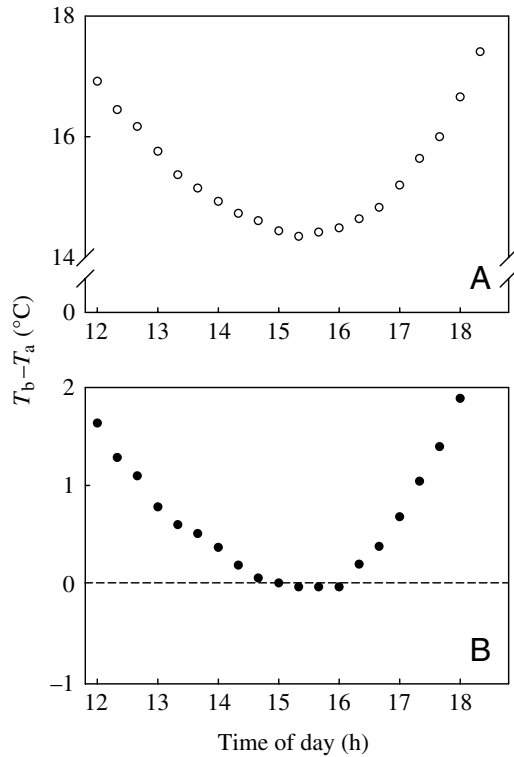


Fig. 4. Gradient between body temperature and air temperature ($T_b - T_a$) as a function of time of day in six Arabian sand gazelles during winter (A) and summer (B) in Mahazat as-Sayd.

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 winter, T_b of animals was always higher than T_a (Fig. 4A). In summer, $T_b - T_a$ was either positive or almost equal to zero. During the morning, as T_a approached T_b , the outward flow of heat declined until about 15.00 h when the gradient became slightly negative (Fig. 4B).

Assuming mean $T_b = 39.5^\circ\text{C}$ and $T_{b,\text{max}} = 40.8^\circ\text{C}$ in summer and mean $T_b = 39.4^\circ\text{C}$, and $T_{b,\text{max}} = 40.3^\circ\text{C}$ in winter and an average body mass (M) of 17.8 kg [$(M_{\text{initial}} + M_{\text{final}})/2$], heat storage was 80.5 kJ day^{-1} in summer and 55.7 kJ day^{-1} in winter. To dissipate this amount of heat by evaporation would require $33.5 \text{ ml H}_2\text{O day}^{-1}$ in summer and $23.2 \text{ ml H}_2\text{O day}^{-1}$ in winter.

Body temperature and water-deprivation

In our controlled experiment, a mixed-model ANOVA indicated that mean T_b differed significantly between treatments ($F_{2,52} = 16.0$, $P < 0.001$). Mean T_b was not different when gazelles were provided with water and food or natural food only, but was significantly higher when they were denied both drinking water and natural food (Newman-Keuls, $P < 0.05$) (Table 1). Statistical analyses confirmed a significant effect of treatments on $T_{b,\text{max}}$, $T_{b,\text{min}}$ and $(T_{b,\text{max}} - T_{b,\text{min}})$ values

Table 1. Summary data on body masses, plasma osmolality and body temperature in six captive Arabian sand gazelles exposed to three different food and water treatments in Mahazat as-Sayd, Saudi Arabia

	Food and water regimens		
	Treatment 1	Treatment 2	Treatment 3
Body mass			
Initial (kg)	16.0 \pm 1.2 ^a	16.1 \pm 1.1 ^a	16.0 \pm 1.2 ^a
Final (kg)	16.1 \pm 1.1 ^a	15.2 \pm 1.2 ^b	14.2 \pm 1.1 ^c
Change (%)	+0.1 \pm 1.1 ^a	-4.8 \pm 1.5 ^b	-11.3 \pm 1.0 ^c
Plasma osmolality (mOsm)	319.8 \pm 3.4 ^a	318.2 \pm 3.0 ^a	325.7 \pm 2.1 ^b
Body temperature ($^\circ\text{C}$)			
Mean	39.5 \pm 0.2 ^a	39.5 \pm 0.3 ^a	39.8 \pm 0.2 ^b
Maximum	40.6 \pm 0.5 ^a	40.9 \pm 0.6 ^b	41.3 \pm 0.4 ^c
Minimum	38.3 \pm 0.5 ^a	37.2 \pm 1.0 ^b	38.1 \pm 0.6 ^a
Amplitude	2.3 \pm 0.7 ^a	3.7 \pm 1.0 ^b	3.3 \pm 0.8 ^c

Treatment 1: provided with natural food and drinking water to maintenance levels for 3 days.
 Treatment 2: provided with natural food but no drinking water for 3 days.
 Treatment 3: denied natural food and drinking water for 3 days.
 Values are means \pm s.d.; values with different superscript letters differ significantly ($P < 0.05$).

($F_{2,52} > 15.8$, $P < 0.001$). $T_{b,\text{max}}$ and $(T_{b,\text{max}} - T_{b,\text{min}})$ differed significantly between treatments (Newman-Keuls, $P < 0.05$) (Table 1). $T_{b,\text{max}}$ was the highest when gazelles were deprived of drinking water and natural food, whereas the amplitude of daily T_b variation was the greatest when gazelles were only supplied with natural food. $T_{b,\text{min}}$ in the morning was the lowest when gazelles were given only natural food, but was not significantly different between the two other treatments (Newman-Keuls, $P < 0.05$) (Fig. 5).

Analyses of mean T_b , $T_{b,\text{max}}$, $T_{b,\text{min}}$ and $(T_{b,\text{max}} - T_{b,\text{min}})$ measured at day 3 of each treatment with final body mass as covariate confirmed the treatment effects described in the global analysis. In addition we found a significant effect of final body mass on variation in $T_{b,\text{min}}$ between treatments (ANCOVA; $F_{1,14} = 24.9$, $P < 0.001$). Body mass appeared to play a significant role in the decline in T_b of gazelles given only natural food (Newman-Keuls, $P < 0.05$).

Body mass and osmolality

Body masses of captive gazelles did not differ at the beginning of each treatment (RMANOVA; $F_{2,10} = 0.7$; $P = 0.49$) but were significantly different at the end ($F_{2,10} = 130.2$; $P < 0.001$). When denied drinking water or both drinking water and natural food, gazelles decreased their body mass compared with when they were given water and food (Newman-Keuls, $P < 0.05$; Table 1). Plasma osmolality of gazelles differed significantly between treatments ($F_{2,10} = 8.5$; $P = 0.007$). After 3 days of water and food deprivation, gazelles increased the osmolality of their plasma significantly, whereas plasma

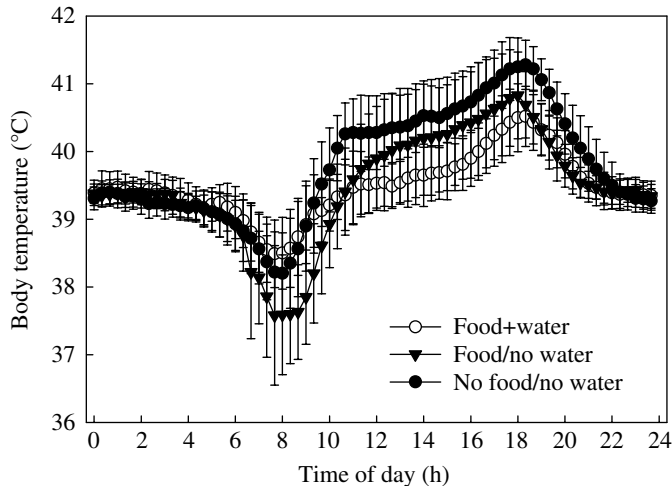


Fig. 5. Mean body temperature of six captive Arabian sand gazelles in Mahazat as-Sayd, exposed to three different food and water regimens, as a function of time of day. Values are means \pm s.d. for 3 days when food and water were provided *ad libitum*, for 3 days when water was denied, and for 3 days when both food and water were denied, in August 2004.

osmolality was not affected when gazelles were denied drinking water but were still supplied with natural food (Newman-Keuls, $P < 0.05$; Table 1).

In free-ranging gazelles, plasma osmolality was 319.2 ± 1.9 and 320.2 ± 2.3 mOsm at the beginning and end of the study, respectively, values that did not differ significantly ($P = 0.48$). Hence, we have no evidence that these gazelles were water stressed.

Discussion

We provide an unequivocal example of a small, free-living, desert ungulate utilizing heterothermy when thermal load was high, a mechanism that potentially minimizes loss of evaporative water. During summer, gazelles varied their T_b by $2.6 \pm 0.8^\circ\text{C day}^{-1}$, stored 80.5 kJ day^{-1} in their tissues, and dissipated this heat by non-evaporative means at night, findings consistent with the heterothermy hypothesis. In the early morning, T_b of gazelles continued to decline despite the fact that T_a and solar radiation were increasing, a pattern that was also observed for camels (Schmidt-Nielsen et al., 1957), Cape eland (Fuller et al., 1999) and Arabian oryx (Ostrowski et al., 2003). Allowing T_b to decrease to a lower level would presumably permit gazelles to store additional heat during the hot part of the day. Schmidt-Nielsen et al. (Schmidt-Nielsen et al., 1957) proffered the idea that this decrease in T_b in the morning was due to vasodilatation of peripheral tissues, which brings cool blood from the skin to internal body parts. In winter gazelles also increased T_b during the day, but by only $1.7 \pm 0.3^\circ\text{C}$. In winter $T_{b,\text{min}}$ was higher than in summer despite the fact that the gradient between T_b and T_a was large, suggesting that they limit the decrease in T_b during winter.

We have now two examples of the use of heterothermy during summer by free-living desert ungulates, the small sand gazelle and the much larger Arabian oryx. In response to high thermal heat load, oryx and gazelles increased their T_b during daytime, reaching similar $T_{b,\text{max}}$ values of $40.5 \pm 0.7^\circ\text{C}$ and $40.8 \pm 0.4^\circ\text{C}$, respectively (Ostrowski et al., 2003). Both species dissipated heat by non-evaporative means at night, and reached $T_{b,\text{min}}$ around 8:30 h, 2–3 h after dawn. However, whereas $T_{b,\text{min}}$ averaged $38.2 \pm 0.5^\circ\text{C}$ in gazelle, it was $36.5 \pm 1.2^\circ\text{C}$ in oryx, 1.7°C lower (Ostrowski et al., 2003). In the oryx the amplitude of T_b increase above mean T_b (38.4°C) was on average 2.1°C whereas it was only 1.3°C in the sand gazelle, suggesting that less water was saved by gazelles. Indeed, Arabian oryx in summer ($N = 6$; mean body mass = 92.9 kg) stored $627.4 \text{ kJ day}^{-1}$ and potentially saved $280 \text{ ml H}_2\text{O day}^{-1}$ (Ostrowski et al., 2003), whereas gazelles potentially saved $33.9 \text{ ml H}_2\text{O day}^{-1}$. Ideally we would compare water savings based on information about water flux of free-ranging animals, but these data are not yet available for gazelles. Alternatively, we have used, as a basis for comparison, evaporative water losses of both species measured in the laboratory at $T_a = 30^\circ\text{C}$. When we normalized evaporative water losses to body mass (kg), the water saved by sand gazelles by using heterothermy equalled $1.9 \text{ ml H}_2\text{O kg}^{-1} \text{ day}^{-1}$, or 21.6% of total evaporative water loss ($8.8 \text{ ml H}_2\text{O kg}^{-1} \text{ day}^{-1}$) (Ostrowski et al., in press). By contrast, water saved by Arabian oryx by using heterothermy was estimated to be $3.0 \text{ ml H}_2\text{O kg}^{-1} \text{ day}^{-1}$, or 29.1% of their total evaporative water loss ($10.3 \text{ ml H}_2\text{O kg}^{-1} \text{ day}^{-1}$) (Williams et al., 2001). We note that T_b measurements on the Arabian oryx were made when T_a values were higher than in the present study. In addition, during the year that we studied gazelles, more rain fell in Mahazat making preformed water more available to them in food (Noy-Meir, 1973); rainfall was 91 mm during the 7 months of this study, whereas it was $73.5 \text{ mm year}^{-1}$ during the oryx study period (Ostrowski et al., 2003). We have calculated that raising its water saving efficiency to the oryx level would require the gazelle to increase its average $T_{b,\text{max}}$ by 0.6°C , from 40.8°C to 41.4°C , a temperature that is below the maximum T_b value of 42°C recorded during this study and that could have probably been reached in circumstances of higher aridity.

The idea that heterothermy should be observed only in large desert ungulates (Fuller et al., 1999; Mitchell et al., 2002; Fuller et al., 2005) has been found wanting in this study. This supposition is based on the assumption that animals of large body mass, because of lower surface to mass ratio can store heat at proportionally slower rate than small species with high surface to mass ratio. This could allow large species to passively store heat during day and to reach $T_{b,\text{max}}$ when T_e starts declining at the end of the day, whereas small species will presumably store heat much faster and will reach a $T_{b,\text{max}}$ before T_e starts decreasing. To avoid hyperthermia, small ungulates will have to resort to evaporative cooling much earlier during the day. This scenario ignores two important facts. The heterothermy model is not based solely on the

passive process of heat storage, but it includes a mechanism whereby T_b decreases during early morning allowing greater heat storage during the day, and, animals of smaller size can exploit small micro-environments more effectively, thus decreasing exposure to heat load. We have observed that during the heat of the day in summer gazelles retreat into cooler microhabitats, such as small rock crevices, a niche inaccessible to large oryx (S.O., unpublished data).

Using implanted data loggers on springbok (20–35 kg) Fuller et al. (Fuller et al., 2005) showed that this antelope maintained core T_b within narrow limits, $\pm 1.2^\circ\text{C}$. We laud the emphasis placed by these authors on measurements of T_b of free-ranging animals to aid in our understanding of heterothermy in water savings of desert ungulates, and their usage of miniature data loggers to continuously monitor T_b , but think that they have missed the mark in their tests of the heterothermy hypothesis. Mean T_a during summer in their study was 20.2°C , a T_a for which we would also predict that animals would not employ heterothermy, as we have shown for sand gazelles during winter, when their T_b varied by only $1.7^\circ\text{C day}^{-1}$. Sand gazelles showed heterothermy in summer when mean T_a values were as much as 13°C higher than in the study of Fuller et al. (Fuller et al., 2005). Whereas it is true that ‘globe temperature’ occasionally exceeded T_b in some of their studies on arid-zone ungulates (Fuller et al., 1999; Maloney et al., 2002), we have evidence that, in full sun, globe temperature can overestimate operative temperature (T_e) (*sensu* Bakken, 1992), of a gazelle by more than 5°C (S.O., unpublished data). Finally the ungulates that they studied lived in savannah grassland habitats where annual rainfall reached as much as 700 mm (Fuller et al., 1999; Mitchell et al., 2002; Fuller et al., 2005) and, their study animals were artificially supplied with water, an unnatural situation for a desert ungulate. These conditions collectively represent an inadequate test of the heterothermy hypothesis.

The amplitude of variation in T_b in captive sand gazelles was influenced by the quantity of water available to them. When gazelles were denied drinking water but supplied with pre-formed water in food, they increased the amplitude of daily T_b variation, a pattern consistent with predictions from the heterothermy model. When gazelles were totally deprived of water, the daily amplitude of variation in T_b increased to a lesser extent. During complete water deprivation gazelles continued to display variation in T_b , but interestingly they shifted their response curve towards a higher T_b . During dehydration, domestic animals often allow their T_b to elevate, associated with a delayed onset and reduction of evaporative water loss (Taylor, 1970a; Taylor, 1970b; Finch and Robertshaw, 1979; Nijland and Baker, 1992; Jessen et al., 1998).

Fuller et al. (Fuller et al., 2004) suggested that the high T_b recorded before sunset in Arabian oryx (Ostrowski et al., 2003) could be attributed to hyperthermia induced by dehydration. There exists no evidence that free-living gazelles or oryx that used heterothermy were suffering from dehydration in either study. Free-living gazelles apparently maintained a normal state of hydration during this study as judged by their plasma

osmolality when they were recaptured. In addition, during the water deprivation experiment, gazelles that received natural food showed a daily T_b variation of 3.7°C ; close to the 4.1°C measured in free-ranging oryx, and had no increase of plasma osmolality.

One aspect of the heterothermy model suggests that dehydration will result in an increase in amplitude of T_b augmenting the savings in evaporative water (Mitchell et al., 2002). The larger daily T_b variation that we measured in gazelles supplied with natural food but denied drinking water corresponds to an estimated surplus heat storage of 78.9 kJ day^{-1} ($1.4^\circ\text{C} \times 3.48 \text{ kJ deg}^{-1} \times 16.2 \text{ kg}$) and a potential water savings of $32.8 \text{ ml H}_2\text{O day}^{-1}$.

Sand gazelles provide a clear example of a small desert ungulate employing heterothermy to reduce evaporative water losses during summer. The amplitude of T_b variation in captive gazelles was modulated by the level of water deprivation, but we found no indication that heterothermy was employed only in dehydrated animals.

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