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Brain and arterial blood temperatures of free-ranging oryx (*Oryx gazella*)

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Abstract We used implanted miniature data loggers to measure brain and arterial blood temperatures every 5 min for up to 15 days in four free-ranging oryx (*Oryx gazella*) in their natural habitat. Globe temperatures exceeded 45°C and average peak radiant heat load was 800 W·m⁻². Arterial blood temperature exhibited a moderate amplitude nychthemeral rhythm of 1.8±0.3°C (mean ±SD). The amplitude of the nychthemeral rhythm was not influenced by variations in ambient heat load. Average brain temperature exceeded carotid arterial blood temperature by 0.29°C but there was a range of body temperatures over which the brain could be up to 0.4°C cooler or 0.5°C warmer than arterial blood. At high body temperatures (>39.5°C) at rest, three of the animals tended to maintain the brain cooler than arterial blood. During exercise the brain was always warmer than arterial blood. The slope of the regression line relating brain temperature to carotid blood temperature was less than one. At short time scales of 5–20 min, brain temperature varied significantly more than did carotid blood temperature. We attribute part of the variability in brain temperature to transient stress responses and the influence of sympathetic activation attenuating selective brain cooling. We conclude that, contrary to the widely cited postulate, the carotid rete does not protect the brain during hyperthermia. Oryx also do not show adaptive heterothermy and, over short time intervals, have a brain temperature more variable than carotid blood temperature.

Keywords Antelope · Body temperature · Circadian rhythm · Selective brain cooling · Thermoregulation

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Introduction

The oryx is often cited in scientific literature as the epitome of large animal arid adaptation. Its ability to thrive in deserts, reputedly without drinking, and aspects of the species' thermal physiology were brought to prominence by several studies last century [23, 24, 25]. Two major physiological strategies were considered to assist these animals in coping with heat and aridity. Taylor [25] presented evidence of adaptive heterothermy in captive oryx wherein the nychthemeral amplitude of body temperature increased when the nychthemeral amplitude of ambient heat load increased. Such a strategy reduces water use because the animal stores heat that would otherwise need to be evaporated and it creates a temperature gradient for dry heat exchange. Additionally, on the basis of studies that had described selective brain cooling (SBC) in other artiodactyl species [2, 22], Taylor [24] argued SBC would protect the oryx's brain during the hyperthermia associated with adaptive heterothermy and so the two strategies would be mutually beneficial.

The idea that SBC protects the brain against thermal damage is not supported by available data. The greatest hyperthermia experienced by free-ranging animals occurs when they are chased, and when they are chased they do not use SBC [6, 11, 17]. An alternative role for SBC in mammalian thermoregulation is that it modifies an animal's effector response to a thermal load by adjusting input from hypothalamic neurones in thermoregulatory pathways [9]. Under this hypothesis an animal in which SBC has been initiated will have a lower evaporative response at a given trunk temperature because there is less stimulus for heat loss provided by the hypothalamus. However, during emergency situations, when potentially lethal general-body overheating is likely, SBC can be inhibited resulting in an increased brain temperature and larger heat loss responses [9]. The advantages to the animal of this mechanism is an economy in water use for thermoregulation when the animal does not require evaporative heat loss to survive and exaggerated heat loss responses during exercise.

The degree of SBC in an animal is also influenced by non-thermal inputs. We recently reported that brain temperature in heat-exposed sheep oscillated over short time scales in response to external stimuli [16]. At high temperatures the sheep tended to use SBC, but brain temperature rose rapidly and exceeded arterial blood temperature when an investigator entered the climate chamber. We attributed this short-term variability in brain temperature to the effect of sympathetic activation on the SBC mechanism wherein stressful stimuli inhibit SBC. Given the many and varied stimuli that free-ranging animals experience, including that of a chase, a logical prediction is that brain temperature in free-ranging animals should vary more over short time scales than arterial blood temperature. Since arterial blood temperature reflects the thermal status of the body [5] it should change only slowly in a large animal. Here we use a nested hierarchical analysis of variance to determine the time scale of changes in brain and arterial blood temperatures over several weeks in free-ranging oryx.

Based on the original conjecture of Taylor [24] many textbooks describe SBC in the oryx as a crucial adaptation to life in arid environments, some claiming that the rete is capable of cooling arterial blood by up to 3°C [15]. But measurements of brain temperature actually never have been made in oryx. Here we report measurements of brain and arterial blood temperatures in free-ranging oryx to determine if SBC is present in the species and, if so, whether its magnitude and utilization differ from that in other large mammals.

Materials and methods

Animals and habitat

The experiments took place in November 1998 and December 1999 (southern hemisphere summer) at the Lichtenburg Game Breeding Centre (26° 07' S, 26° 10' E), 220 km west of Johannesburg, South Africa, and in the historical natural habitat of the species *Oryx gazella*. The Centre extends over an area of 4500 ha, consisting mainly of grassland with scattered trees and shrubs, and maintains breeding stocks of several large mammal species, including *Oryx gazella*, which range freely in a large (approx. 1500 ha) camp. Our experimental oryx were captured in that camp and subsequently released into a 62-ha enclosure. Two females and one male (masses estimated at 120, 150 and 180 kg respectively) were instrumented initially, and a year later one male oryx (estimated mass 150 kg) was instrumented and added to that herd. The oryx shared the enclosure with a small number of other mammals.

Body temperature measurement

For surgery, the oryx were darted with 5–7 mg etorphine hydrochloride (M99, Logos Agvet, Johannesburg) and transported to a nearby temporary theatre. The animals were placed in sternal recumbency and anaesthetized with 1–2% halothane (Fluothane, Zeneca) in oxygen, administered via a facemask. Approximately 5 min after the start of halothane administration, the etorphine was reversed with 12–14 mg diprenorphine hydrochloride (M5050, Logos Agvet). Respiratory rate, heart rate and rectal temperature were monitored throughout surgery.

Using aseptic surgical procedures we implanted miniature data loggers with thermistor sensors for temperature measurement. A

thermistor in a blind-ended and thin-walled polytetrafluoroethylene (PTFE) tube (OD 0.9 mm; Straight Aortic Flush 4F Catheter, Cordis, The Netherlands) was advanced 100 mm into the left common carotid artery, and secured in position with a purse-string suture. Outside the artery, the PTFE tube was connected to silicone rubber tube (length \approx 150 mm, OD 3 mm) covering the leads from the thermistor to a temperature logger (see below). The logger was covered with an inert wax (paraffin wax/Elvax, Mini-Mitter, Sunriver, USA) and was implanted near the artery within a pocket made in muscle layers of the neck. A second temperature logger connected to a brain thermistor probe was also positioned in the muscle layers of each animal's neck just behind the left ear. Its silicone rubber tube conveying the thermistor leads was advanced subcutaneously over the nuchal crest to the parietal skull, where it was connected to a head plate and guide tube. The guide tube, constructed from cellulose acetate butyrate tubing (OD 3.2 mm, ID 1.6 mm; World Precision Instruments, Sarasota, USA) with a steel tip, was positioned between the parieto-frontal suture and the parietal crest, such that the tip lay deep in the brain tissue near the hypothalamus. Correct positioning was established using sectioned heads of oryx of similar size. The brain guide tube was connected to a subcutaneous polyvinyl chloride headplate (20×20×5 mm) secured to the skull by two bone screws. There were no external components to any of the equipment.

A 50-mg enrofloxacin tablet (Baytril, Bayer, Johannesburg) was inserted into each surgical site and the skin suture line sealed with topical antiseptic spray (Necrospray, Centaur Labs, Johannesburg). The animals also received long-acting antibiotic (20 ml i.m. Duplocillin, Intervet, Johannesburg) and an analgesic and anti-inflammatory medication (15 ml s.c. Dexa-Tomanol, Centaur Labs, Johannesburg). After surgery, animals were transported to the fenced 62-ha enclosure, where they became mobile within 5 min of withdrawal of the halothane.

The miniature temperature loggers (StowAway XTI, Onset Computer, Pocasset, USA) had outside dimensions of \approx 50×45×20 mm and a mass of \approx 40 g when covered in wax. These loggers were custom-modified for us to have a storage capacity of 32 kb, a measurement range from +34 to +46°C, and a resolution of 0.04°C. We replaced the standard thermistors with fine ruggedized glass-coated bead thermistors with insulated extension leads (bead diameter 0.3 mm; AB0E3-BR11KA103 N, Thermometrics, Edison, USA). The loggers with their thermistors were calibrated against a high-accuracy certified quartz thermometer (Quat 100, Heraeus, Hanau, Germany) in an insulated water bath and proved to have an accuracy of one sampling step of the logger (0.04°C). The scan interval of the loggers was set at 5 min.

Animals were redarted and anaesthetized about 2 months after surgery using the same procedures as described above. The data loggers and thermistors were removed but the headplates left in place. The implanted loggers were in perfect order, the animals' wounds had healed and there were no signs of infection. In all animals, however, at least one of the thermistor/logger combinations had failed, generally as a result of thermistor breakage between 7 and 16 days after surgery. In vivo examination of the carotid arteries after the month revealed no occlusion or clotting along the length of the intravascular guide tube, that is, the thermistors measured the temperature of free-flowing blood. At the end of the experiment the oryx were released back into the study enclosure and remain healthy (now more than 2 years later).

Meteorological data measurement

Meteorological data were obtained from a portable weather station (MCS, Cape Town, South Africa) at the study site, but for technical reasons some days of data were missing. Vapour pressure of the air was 1.31 ± 0.24 kPa (mean \pm SD) during the first study period and 1.48 ± 0.14 kPa during the second. Rainfall was 68 mm and 86 mm. Wind direction in the first study period was easterly during the morning (01:00 to 06:00 hours) and southeasterly thereafter, while in the second the prevailing winds were northerly. Data on air temperature, globe temperature, solar radiation and wind speed are given in more detail below. Solar noon was at 12:00 hours.

Data analysis

The animals were slightly hypothermic immediately post-anaesthesia but warmed rapidly during the first night after release. The following day mean body temperatures did not differ from those recorded for the remainder of the data collection period for each animal. To avoid introducing a circadian bias to body temperature analysis, the analysed data for each animal consist of the data from midnight on the day following surgery to the midnight before equipment failure. Analysed data consists of 9 days (male 1), 6 days (male 2), 7 days (female 1) and 15 days (female 2).

Since the total time of body temperature data collection varied between animals and some meteorological data were missing, the average meteorological data were obtained by compiling available data for each hour for each animal over the period of body temperature measurement. The hourly means for each variable were then calculated. The hourly maximum and minimum of each variable were also calculated for each animal and then averaged for the four animals. The analysed meteorological data consist of 6 days (male 1), 6 days (male 2), 7 days (female 1) and 10 days (female 2).

Body temperatures were analysed in several ways. The original 5-min recordings were used to find the daily mean, SD, minimum, maximum and range of carotid blood temperature (T_{car}) and hypothalamic temperature (T_{hyp}) for each animal. These data were also used to analyse for the effects of meteorological variables on body temperatures by correlation and regression analysis. The original 5-min records were used to regress T_{hyp} on T_{car} and the threshold for SBC was calculated as the intersection of that line with the line of identity. The relationship between T_{car} and T_{hyp} was analysed by calculating the frequency of occurrence of each 0.1°C category of T_{car} and the mean, SD, minimum and maximum T_{hyp} for each T_{car} category. Hourly means for T_{car} and T_{hyp} , as well as the difference between T_{car} and T_{hyp} , were calculated for each animal over the data collection period.

To analyse further the variations in body temperatures we performed a nested (hierarchical) analysis of variance on T_{car} and T_{hyp} [21]. We used six randomly chosen days from each animal to avoid bias in favour of the animals with larger data sets. The analysis was performed on the following time scales: over the full 6 days, over each day, over each hour, at 20-min intervals and at 5-min intervals. Total variability was equal to the variability of the 5-min readings. A hierarchical analysis calculates the amount of variability introduced at each step up the hierarchy (for example if the average daily T_{car} for the animals was the same each day there would be no extra variance introduced at the level of "days in animals"). Since the variance for each subsequent level of the hierarchy includes the variance present in the lower level, the "added variance" component was calculated by subtraction for each level of the analysis. The significance of the added variance at each step compared to the level below was determined using a variance ratio (F) test.

We compared T_{car} and T_{hyp} at each level of the hierarchy to determine whether the two temperatures varied in parallel or if the introduction of variability at each level differed. We normalized the overall total sum of squares (so that the proportion of the total variability introduced at each level was compared) for T_{car} and T_{hyp} and compared the resulting introduced variance at each level with an F ratio test.

The Animal Ethics Screening Committee of the University of the Witwatersrand (clearance no. 96-115-5) approved all experimental procedures.

Results

Environmental effects on body temperature

During the period of body temperature measurement the ambient dry-bulb temperature varied from an average of 15°C at night to $25\text{--}30^\circ\text{C}$ during the day (Fig. 1).

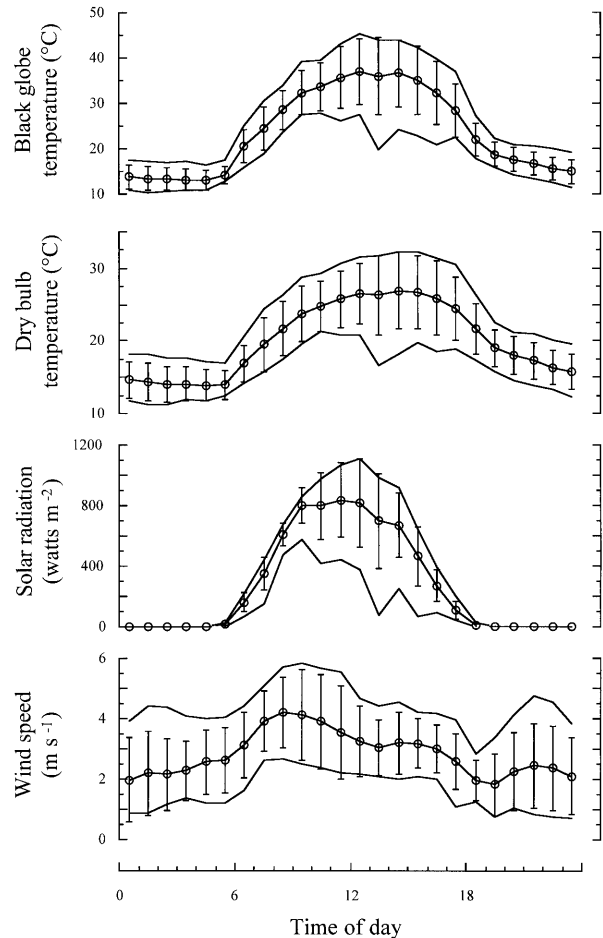


Fig. 1 Mean hourly meteorological data during collection of body temperatures in four adult oryx. Points show mean \pm SD and the outer lines show the average minimum and maximum of each variable

The highest solar radiation values recorded exceeded $1000\text{ watts}\cdot\text{m}^{-2}$ at midday with average solar radiation levels peaking at $800\text{ watts}\cdot\text{m}^{-2}$. Wind speed was highest mid-morning, dropped consistently in the afternoon and was never greater than $6\text{ m}\cdot\text{s}^{-1}$. Black globe temperature varied from 10 to 15°C at night to an average of 35°C during the day. Maximum black globe temperatures during the experiments exceeded 45°C and there was at least one day for each animal when black globe temperature exceeded 40°C for 5 h or more.

Brain and blood temperatures of the oryx exhibited a nycthemeral variation with a nadir at approximately 07:00 hours and a peak around sunset at 18:00 hours (Fig. 2). Peak body temperatures therefore did not coincide with peak environmental heat load, but in general body temperatures increased during the day and decreased during the night. The average nycthemeral T_{car} range, calculated as the maximum recorded T_{car} minus the minimum recorded T_{car} each day, did not exceed 2.2°C (Table 1). We tested for a gender difference using an analysis of variance with gender as a "between" factor, and the different number of days for each animal nested

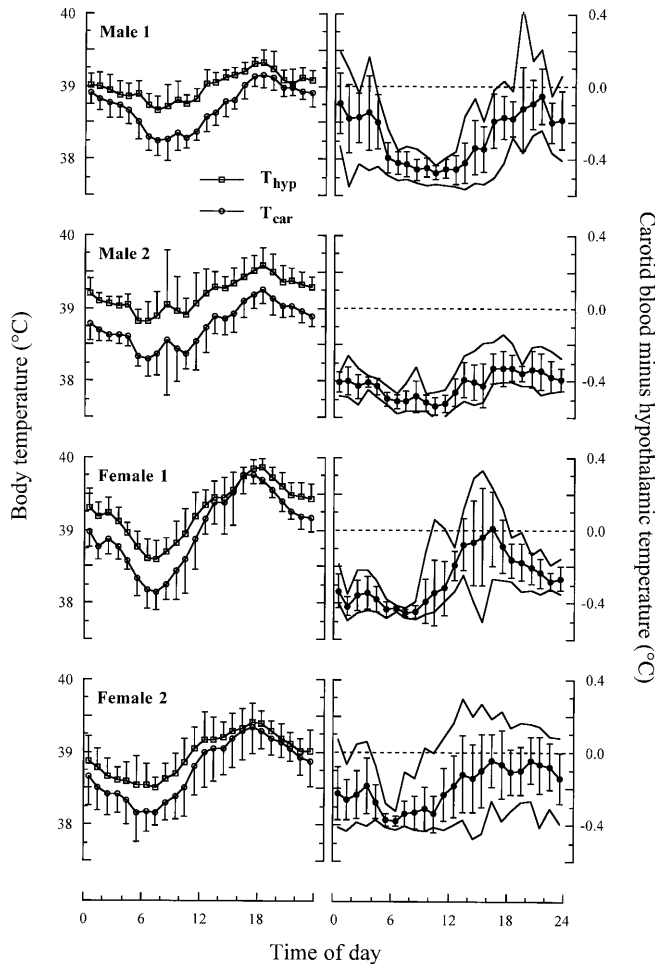


Fig. 2 Mean hourly hypothalamic and carotid blood temperatures (*left*) and the mean hourly difference between carotid blood and hypothalamic temperatures (*right*) in two male and two female oryx recorded for time periods ranging from 6 to 15 days. Points show mean \pm SD. The *outer lines* on the right plots show the minimum and maximum recorded difference for each hour. The *dashed lines* mark the point where carotid blood and hypothalamic temperatures were equal. A positive value indicates selective brain cooling

within an “individual” factor. Both T_{car} and T_{hyp} had a significantly greater range in the females than males ($F_{1,33}=8.3$, $P=0.007$ and $F_{1,33}=4.0$, $P=0.05$ respectively). While this result has some interesting implications and is worthy of further study, being based on only two animals

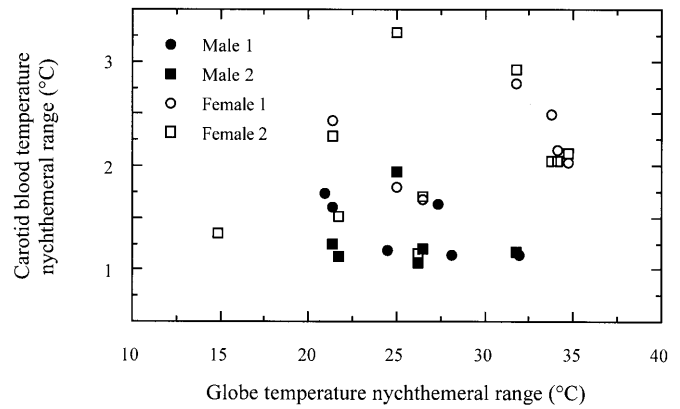


Fig. 3 Daily range of carotid blood temperature (maximum–minimum recorded temperatures logged every 5 min over the nychthemeral period) plotted against daily range of black globe temperature (maximum–minimum recorded temperatures logged every hour over the nychthemeral period) for four oryx over 6–10 days. There was no significant relationship between the two variables for any animal

per gender, the result is considered tentative and will not be discussed further here. For each individual carotid blood temperature had a larger daily range than T_{hyp} (Table 1).

Exploration of the effects of meteorological changes on body temperatures failed to find any significant influence of minimum, maximum, or range of ambient dry bulb temperature or black globe temperature on the minimum, maximum, or range of either T_{car} or T_{hyp} . Figure 3 shows the relationship between range of T_{car} and range of black globe temperature for the four animals and illustrates the lack of influence of changes in environmental heat load on body temperature.

The relationship between T_{car} and T_{hyp}

The relationship between T_{car} and T_{hyp} varied as a function of time of day (Fig. 2) and also as a function of body temperatures (Fig. 4). For the majority of the time T_{hyp} exceeded T_{car} . Episodes of T_{hyp} cooler than T_{car} (indicative of SBC) were observed routinely in three of the animals, but very rarely in Male 2. These episodes occurred mostly in the afternoon and evenings when body temperatures were highest, and the animals were inactive. Of the total

Table 1 Mean daily average and range of brain and blood temperatures recorded every 5 min, selective brain cooling threshold, and minimum T_{car} at which selective brain cooling was observed in two male and two female oryx. Data are mean \pm SD

| | Mean temperature | | Temperature range | | Significance of range ^a | Threshold for SBC (°C) | Minimum T_{car} for SBC (°C) |
|----------|------------------|------------------|-------------------|-----------------|------------------------------------|------------------------|--------------------------------|
| | T_{car} (°C) | T_{hyp} (°C) | T_{car} (°C) | T_{hyp} (°C) | | | |
| Male 1 | 38.72 \pm 0.35 | 38.99 \pm 0.27 | 1.41 \pm 0.24 | 1.13 \pm 0.24 | 6 \times 10 ⁻⁴ | 39.4 | 38.4 |
| Male 2 | 38.76 \pm 0.40 | 39.18 \pm 0.36 | 1.75 \pm 0.67 | 1.59 \pm 0.68 | 3 \times 10 ⁻³ | 40.2 | 39.0 |
| Female 1 | 39.00 \pm 0.57 | 39.27 \pm 0.44 | 2.19 \pm 0.40 | 1.72 \pm 0.36 | 1 \times 10 ⁻³ | 40.0 | 39.0 |
| Female 2 | 38.76 \pm 0.52 | 38.95 \pm 0.41 | 1.98 \pm 0.58 | 1.66 \pm 0.52 | 5 \times 10 ⁻⁶ | 39.5 | 38.5 |

^a Probability result of paired *t*-test for T_{car} versus T_{hyp} over days within each individual

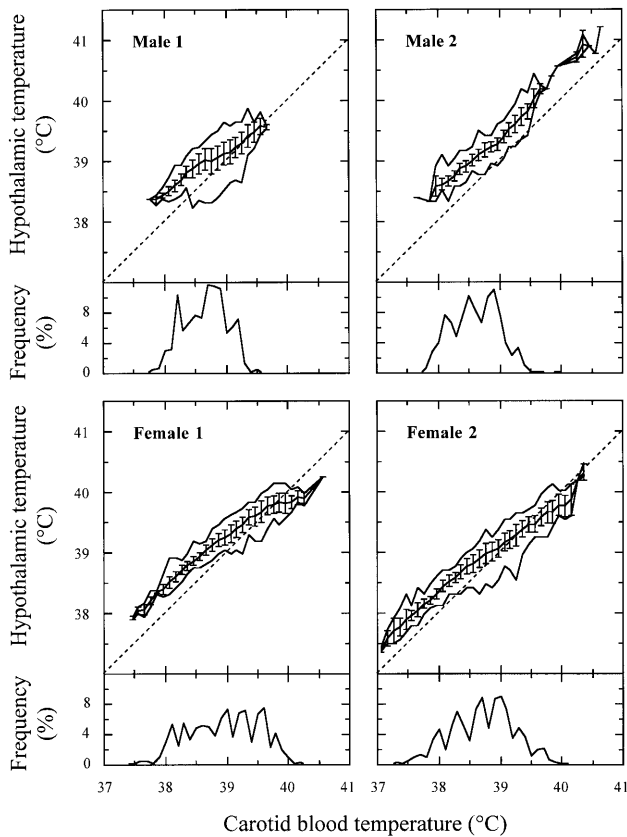


Fig. 4 Mean hypothalamic temperature at each 0.1°C category of carotid blood temperature (*upper panel* for each individual) and the relative frequency of occurrence of each category of carotid blood temperature (*lower panel* for each individual) for four oryx over time periods ranging from 6 to 15 days. Each point shows mean \pm SD. The *lines* directly above and below the data points denote the maximum and minimum, respectively, recorded hypothalamic temperature for each category of carotid blood temperature. The *dashed diagonal line* marks the line of identity between carotid blood and hypothalamic temperatures. The saw-tooth pattern of the frequency plots reflects the sampling interval of the loggers (0.04°C) in that some 0.1°C classes of T_{car} contained three steps of resolution and some only two

recording period, the SBC episodes occupied 12.8% (male 1), 0.4% (male 2), 11.2% (female 1) and 35.3% (female 2) of the recording period.

The SBC that did occur tended to happen when the animals had a high body temperature, but high body temperatures were not always accompanied by SBC. Around the mode of arterial blood temperature (between 38.5 and 39.0°C for the four animals), T_{hyp} could be up to 0.4°C cooler or 0.5°C warmer than T_{car} (Fig. 4). As a consequence the “threshold” for SBC was more than a degree higher than the minimum T_{car} at which SBC could occur (Fig. 4; data in Table 1). Although departures from linearity were evident, linear regression lines relating T_{hyp} to T_{car} were significant for each individual ($P < 10^{-20}$) and were: Male 1, $T_{hyp} = 0.60 \times T_{car} + 15.7$, $r^2 = 0.61$; Male 2, $T_{hyp} = 0.86 \times T_{car} + 5.9$, $r^2 = 0.90$; Female 1, $T_{hyp} = 0.73 \times T_{car} + 10.7$, $r^2 = 0.92$; Female 2, $T_{hyp} = 0.74 \times T_{car} + 10.5$, $r^2 = 0.88$. The slope of each regression was significantly less than

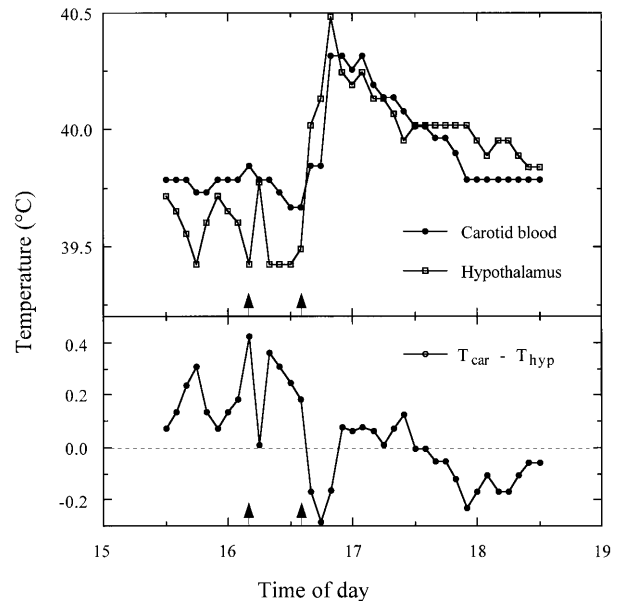


Fig. 5 Body temperatures of a female oryx recorded every 5 min over several hours on one day when we disturbed the herd. *Arrows* indicate times of disturbance. Details given in the text. (T_{car} Carotid temperature, T_{hyp} hypothalamic temperature)

1 (t -test, $P < 10^{-6}$ in each case), implying that hypothalamic temperature did not change as much as carotid blood temperature did. The correlation coefficients imply that between 60% and 90% of the variability in brain temperature can be attributed to variability in blood temperature.

Figure 5 shows several hours of T_{car} and T_{hyp} from one animal measured every 5 min on a day on which we disturbed the animals and observed them as they ran approximately 2 km at speed. Our vehicle entered the camp at approximately 16:00 hours and encountered the animals at approximately 16:35 hours. At 16:35 hours there was an immediate increase of T_{hyp} of 0.53°C in 5 min, while T_{car} increased by only 0.18°C, as the disturbed animals ran approximately 2 km. Over the following 20 min, which included the run, T_{car} rose by 0.65°C while T_{hyp} rose by another 0.57°C for a total increase of 1.1°C. During the next hour both temperatures fell gradually, presumably as the animal activated cooling mechanisms. We interpret this chain of events as suppression of the prevailing SBC by increased sympathetic nervous system activity associated with the “flight” reaction.

The data to the top right of the plot for Male 2 (Fig. 4) were from isolated incidents resulting from the combination of two factors (note that T_{car} above 39.5°C does not register on the frequency plot). This large, aggressive bull was very flighty and ever vigilant, and ran away at high speed when we entered the camp to check the animals on the days following surgery. These bouts of exercise account for the high body temperatures represented by the data points at the top right of his figure. Removing these exercise-induced excursions from the data results

Table 2 Results of hierarchical nested analysis of variance on body temperature data of four oryx. The first four columns show the variance ratio and significance (** $P < 0.001$) of each level of the hierarchy for the two body temperatures. The last two columns

| Source of variation | Variance ratio | | | | T_{car} versus T_{hyp} | |
|--------------------------------------|------------------|-----|------------------|-----|--|-------------|
| | T_{car} | | T_{hyp} | | | |
| Between animals | 12.6 | *** | 11.1 | *** | T_{hyp} | NS |
| Between days within animals | 1.1 | NS | 2.9 | *** | T_{hyp} | $P = 0.05$ |
| Between hours within days | 39.2 | *** | 27.1 | *** | T_{car} | $P = 0.03$ |
| Between 20-min blocks within hours | 9.2 | *** | 8.0 | *** | T_{hyp} | $P < 0.001$ |
| Between 5-min readings within 20 min | 1 | | 1 | | T_{hyp} | $P < 0.001$ |

in the linear regression equation $T_{\text{hyp}} = 0.74 \times T_{\text{car}} + 10.5$, $r^2 = 0.86$. The slope of the regression was significantly less than 1 (t -test, $P < 10^{-6}$) and was similar to that reported earlier for the other three animals. The threshold for SBC presented in Table 1 for this animal is based on the reduced data set. In the absence of exercise induced by us, T_{car} did not exceed 39.5°C . Similarly, for Male 1 there were only two data points where T_{car} exceeded 39.5°C . Female 1 and Female 2 spent 24% and 7%, respectively, of the data collection period with T_{car} above 39.5°C .

Hierarchical analysis results

Table 2 shows the results of the hierarchical nested analysis of variance. For both T_{car} and T_{hyp} significant variability was introduced at each level of the hierarchy, except for T_{car} at the level of “Days within animals”, indicating that the mean daily T_{car} for each animal did not differ much over the recording period. Mean daily T_{hyp} , however, did vary significantly. Most of the variability in each temperature was introduced at the level of “Hours within days”, presumably as a result of the nychthemeral rhythm depicted in Fig. 2. T_{car} was significantly more variable overall than was T_{hyp} ($F_{6911,6911} = 1.46$, $P < 10^{-50}$) which accords with the larger range of T_{car} than T_{hyp} reported earlier for each animal. Analysing the hierarchy with standardized total sums of squares revealed some differences in the time frames of variability in T_{hyp} and T_{car} . At the shortest time scales (“5 min within 20 min”, and “20 min within an hour”) there was significantly more variation in T_{hyp} than T_{car} , or conversely T_{car} was relatively constant compared to T_{hyp} . At the longer time scale (“Hours within days”) there was significantly more variation in T_{car} . At the level of “Days within animals” significantly more variation occurred in T_{hyp} than in T_{car} , confirming the relative stability of T_{car} from day to day. There was no difference between T_{hyp} and T_{car} in the variation added at the level of “Between animals”, indicating that the variability between overall means of the animals was similar for the two temperatures.

In summary these analyses of variability reveal that the two body temperatures of the oryx varied across time scales ranging from minutes to days. T_{car} was relatively

show the temperature to which most variability was added at each level and the P value for the significance of the difference between the amount of variability added to each temperature

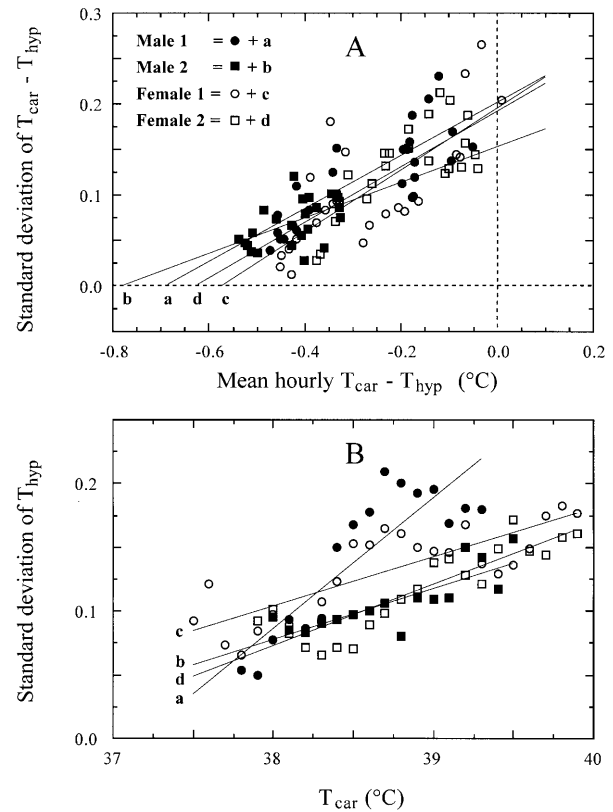


Fig. 6 **A** Hourly standard deviation of the ($T_{\text{car}} - T_{\text{hyp}}$) difference plotted against the mean hourly value of ($T_{\text{car}} - T_{\text{hyp}}$) for four oryx recorded over time periods ranging from 6 to 15 days. Linear regression equations fitted to the data for each individual were all significant and are denoted by the letters on the abscissa and referred to individuals in the legend. The vertical dashed line marks $T_{\text{car}} - T_{\text{hyp}} = 0$ and the horizontal dashed line marks $\text{SD} = 0$. **B** Standard deviation of mean T_{hyp} at each 0.1°C category of T_{car} recorded over the duration of the study. Data are taken from the SD bars on Fig. 4. Legend same as **A**

stable across days within individual animals and between animals. T_{hyp} , however, varied between days. Over minute time scales, T_{hyp} varied significantly more than T_{car} while over the hour time scales T_{car} varied more than T_{hyp} .

A noticeable feature of Fig. 2 is that as mean $T_{\text{car}} - T_{\text{hyp}}$ became less negative the variability about the mean

became larger. Analysis of this observation was done by plotting hourly mean $T_{\text{car}} - T_{\text{hyp}}$ versus the standard deviation of that mean (Fig. 6A). Each of the regression lines is significant ($P=0.007$ for male 2, $P<10^{-5}$ for the other animals). The regression lines predict that the variation in ($T_{\text{car}} - T_{\text{hyp}}$) will become zero when T_{hyp} exceeds T_{car} by 0.6 to 0.8°C. The least negative mean values for $T_{\text{car}} - T_{\text{hyp}}$ in each animal tended to occur at times when the body temperature was highest (Fig. 2). Thus, as body temperature increased the variability of T_{hyp} increased. Figure 6B shows the standard deviation of T_{hyp} at each 0.1°C category of T_{car} . Each of the regression lines is significant ($P<10^{-4}$). The slopes of the regression lines range from 0.04 to 0.10, indicating that the variability in T_{hyp} nearly tripled for a 2°C increase in T_{car} . So the hotter the animal, the less likely it was to sustain brain homeothermy.

Discussion

Ours are the first measurements of brain and arterial blood temperatures in oryx and the first reports on the thermal physiology of the species under free-ranging conditions. Free-ranging oryx maintained body temperatures within a range of approximately 2°C despite exposure to ambient temperature fluctuations of up to 20°C and 1000 W·m⁻² of incident solar radiation. The animals tended to implement SBC at high body temperatures but its implementation was not obligatory. The pattern of SBC implementation was not very different from that reported previously in African antelope except that the calculated threshold was higher. T_{hyp} varied more over short time scales than did T_{car} . T_{car} was very stable across days for individuals, and between individuals, indicating the relatively tight homeothermy in the face of large changes in environmental conditions. The variability of T_{hyp} between days for individuals presumably arose because on some days the animals used SBC often and other days seldom, if at all.

The effect of ambient conditions on body temperatures

In a previous study on a related sub-species, then known as *Oryx beisa* but now recognized as *O. gazella beisa* [20], and several other African antelope Taylor [23] identified adaptive heterothermy as an important mechanism when these animals were exposed to environmental heat stress. In that study captive oryx displayed a rectal temperature range of over 2.5°C when exposed to simulated desert conditions, compared to a range of approximately 1°C at constant 22°C ambient conditions. These responses were assigned adaptive significance in that storage of heat reduces the demand for evaporative cooling and creates a temperature gradient for dry heat exchange to the environment [25]. However, free-ranging eland [6] exposed to similar fluctuations in ambient conditions as captive eland [25] exhibit much smaller nychthemeral

body temperature ranges, an outcome which Fuller et al. [6] ascribe to the inhibition of behavioural strategies in captive animals, especially interactions with conspecifics. A similar situation may exist with the oryx, since we found that ambient conditions spanning globe temperature ranges from 15 to 35°C had no effect on the body temperature range of free-ranging oryx (Fig. 3).

The magnitude of the nychthemeral range in oryx body temperature was similar to that observed in zebras at the same location [7], and in eland exposed to similar conditions [6], but greater than that measured in free-ranging black wildebeest [11], springbok [17], or goats living outdoors unrestrained [10]. Thus an intuitive supposition that larger mammals have smaller nychthemeral rhythms because of thermal inertia does not hold for the species studied to date. Together with previous data [4, 19], our results are congruent with the proposition that body mass does not influence the amplitude of the nychthemeral temperature rhythms of mammals.

Since the gain of the thermoregulatory system is not infinite, ambient and body temperature ranges should be related [8]. Some studies using larger data sets collected from other artiodactyls have identified a small effect of ambient conditions on the nychthemeral body temperature range [10]. However, there are now several lines of evidence suggesting that adaptive heterothermy is an experimental artefact in virtually all artiodactyl species studied, and that the strategy is not employed by free-ranging animals in their natural habitats [18]. Our data suggest that as nychthemeral range is relatively independent of body mass and ambient conditions, its major cause must be an endogenous rhythm.

The relationship between T_{car} and T_{hyp}

SBC was evident in free-ranging oryx, but it occurred sporadically and was of small magnitude (less than 0.5°C). Although our experimental animals were out of human contact for most of the study period, we disturbed them on several occasions. Figure 5 presents the data from one such episode. Similar episodes were recorded in each animal and all had one common feature: the increase in body temperature during flight was never accompanied by SBC. These episodes of exercise generated the highest body temperatures we recorded. As is the case for other free-ranging ungulates [18] therefore, SBC does not occur during exertional hyperthermia in free-ranging oryx.

Resting oryx tended to exhibit SBC when their body temperatures were high. However, we found no evidence that the use of SBC was enhanced in the arid-adapted oryx compared to other artiodactyls studied to date, namely the black wildebeest [11], goats [10], springbok [17], or eland [6]. In fact the calculated threshold for SBC in oryx of over 39.5°C is somewhat higher than that observed in other artiodactyl species [16]. A higher threshold for SBC in a more arid-adapted species may seem counterintuitive, but the threshold needs to be

interpreted in the light of several factors. The threshold as we calculated it does not separate the effects of thermal from those of non-thermal factors influencing SBC, and will always be higher than a threshold driven exclusively by thermal stimuli [16]. Animals continually stressed or vigilant and so with continuous sympathetic nervous system activation presumably would never implement SBC. On the other hand, an unstressed tame animal in familiar surroundings should implement SBC at a thermally driven threshold. The minimum T_{car} at which SBC is observed may provide a better index of the animal's normal physiological responses to heat. For the oryx the minimum T_{car} at which SBC was observed was similar to the minima observed in other free-ranging artiodactyls (38–38.5°C). Thus a higher than normal threshold for SBC may not have anything to do with the intrinsic thermal biology of the species, but may be related to vigilance and sympathetic tone.

Hydrated oryx implement evaporative cooling (panting and sweating) at a rectal temperature of approximately 39°C [24], which corresponds to a central blood temperature of around 38.7°C if there is a similar relationship between rectal and carotid blood temperature as that which exists in sheep [16]. The arterial blood temperature at which SBC was first observed in the oryx that did use SBC was just below this value, at around 38.5°C. In goats, the only other species for which data are available, the same general pattern holds. Goats first implement SBC at an arterial blood temperature of approximately 38.6°C [14] and evaporative cooling occurs at approximately 39.0°C [13, 14]. Thus SBC is initiated below the threshold needed to increase evaporation. Two important inferences can be drawn from these observations: first, that enhanced respiratory evaporation is not a prerequisite for SBC to occur [13], and second, that the threshold for SBC places it into the realm where the modulation of evaporative responses is possible [12].

Variability in T_{car} and T_{hyp}

In all free-ranging artiodactyls studied to date, the slope of the line relating T_{hyp} to T_{car} has been less than one and so, overall, the range of T_{hyp} is smaller than T_{car} [6, 10, 11, 17]. However, the gross conclusions drawn from regression analyses obscure subtleties in control mechanisms, because the variation of each of the temperatures differed at different time scales. T_{car} reflects the general thermal status of the body [5] and its relative stability over short time periods is consistent with the thermal inertia of a large animal. The fact that at short time scales T_{hyp} varied more than T_{car} may reflect the dynamic control of the SBC effector mechanism. The supply of cool venous blood to the cavernous sinus is under sympathetic control [3] and probably is altered dynamically as the animals respond to stimuli in their environment, both thermal and non-thermal [16]. The data in Fig. 6 accord with such a scenario. There is a thermal drive for SBC that increases above a threshold T_{hyp} . Overlain on

that thermal drive is the effect of sympathetic activation. If sympathetic activation is low SBC is implemented in accord with thermal drive, and if sympathetic activation is high then SBC is attenuated regardless of the thermal drive. The pattern that we see emerges because, as T_{car} increases, the thermal drive for SBC increases and the magnitude of SBC can vary between zero and the thermally driven maximum. Since the range of available T_{hyp} increases as T_{car} increases, the influence of transient sympathetic activation results in an increase in T_{hyp} variability as T_{car} increases.

A recent study of reindeer also raises the possibility that the amount of SBC may be influenced by the proportion of minute volume that traverses the nasopharynx [1]. Since SBC depends on the cooling of blood in the nasal mucosa, open mouth panting will potentially reduce SBC capacity compared to closed mouth nasal panting. If this possibility is confirmed, then part of the variability in brain temperature that we measured may have resulted from alterations in ventilatory mode.

Conclusion

We have made the first measurements of brain and body (carotid artery) temperature in oryx and confirm that these animals do use SBC when at rest and near the acrophase of an endogenous nychthemeral rhythm of body temperature. The amplitude of the endogenous nychthemeral rhythm was not influenced by the nychthemeral amplitude of ambient dry bulb or black globe temperature. Oryx implement SBC as part of their normal thermoregulation and the style of their use of SBC was not very different to that observed in other artiodactyls, with the magnitude of the $T_{\text{car}}-T_{\text{hyp}}$ difference and time spent using SBC similar to those observed in free-ranging black wildebeest, goats, springbok and eland. Therefore, enhanced SBC usage does not appear to have accompanied arid adaptation in this species. We found T_{hyp} to be more variable than T_{car} at short time scales and attribute that extra variability to the dynamic nature of SBC and the effect of sympathetic tone on its status. As with other free-ranging artiodactyls, SBC was abolished during exertional hyperthermia, so oryx do not use SBC to protect the brain from thermal damage during exercise. Rather, SBC in free-ranging artiodactyls appears to be a component of routine thermoregulation concerned with the modulation of evaporative heat loss.

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