

A year in the thermal life of a free-ranging herd of springbok *Antidorcas marsupialis*

Andrea Fuller^{1,*}, Peter R. Kamerman¹, Shane K. Maloney^{1,2}, André Matthee³, Graham Mitchell^{1,4}
and Duncan Mitchell¹

¹*School of Physiology, University of the Witwatersrand Medical School, 7 York Road, Parktown 2193, South Africa,*
²*Physiology, School of Biomedical and Chemical Science, University of Western Australia, Crawley, Perth, 6009,*
Australia, ³*National Zoological Gardens Lichtenburg Game Breeding Centre, PO Box 716, Lichtenburg 2740, South*
Africa and ⁴*Department of Zoology and Physiology, University of Wyoming, Laramie, WY 82071, USA*

*Author for correspondence (e-mail: fullera@physiology.wits.ac.za)

Accepted 27 May 2005

Summary

We used miniature data loggers implanted in the abdominal cavity to measure core body temperatures at 30 min intervals in eight (three males, five females) adult free-ranging springbok *Antidorcas marsupialis* in their natural habitat, over a period of 11–13 months. The animals were subjected to a nycthemeral range of air temperature that often exceeded 20°C, with an absolute minimum temperature of –6°C and a maximum of 34°C. Abdominal temperature exhibited a low amplitude (~1.2°C) nycthemeral rhythm, with a temperature peak near sunset and a trough shortly after sunrise. The amplitude of the nycthemeral rhythm of body temperature was not correlated with the 24 h range of air temperature. Although mean 24 h body temperatures were positively correlated with corresponding air temperatures, mean daily body temperature increased, on average, by only 0.02°C per 1°C increase in air

temperature, so that it was only ~0.3°C higher in summer than in winter. Mean monthly body temperatures were strongly positively correlated with photoperiod and, in parallel with changes in the time of sunrise, the times at which the minimum and maximum body temperatures occurred were shifted ~1.2 h earlier in summer than in winter. Annual and daily variations in body temperature of springbok, like those of other free-living African ungulates, therefore appear to reflect an endogenous rhythm, entrained by the light:dark cycle, but largely independent of fluctuations in the environmental thermal load. Springbok exhibit remarkable homeothermy and do not employ adaptive heterothermy to survive in their natural environment.

Key words: springbok, *Antidorcas marsupialis*, circadian rhythm, body temperature, homeothermy, thermoregulation.

Introduction

Although the temperature regulating system usually acts to maintain mammalian core body temperature high and within narrow limits, several mammalian species are reported to allow body temperature to fluctuate widely, usually in parallel with changes in environmental heat load, as a strategy for water or energy savings. It is widely held that large mammals survive in hot arid-zone environments by allowing body temperature to rise during the day, so storing heat and reducing evaporative water loss (Louw and Seely, 1982; Willmer et al., 2000). During the subsequent night, body temperature is not maintained by the usual heat conservation or generation mechanisms, but allowed to fall to provide scope for extra heat storage the following day without elevating mean daily body temperature. This adaptation, known as adaptive heterothermy, is thus characterised by an increased amplitude of the nycthemeral body temperature rhythm (reportedly as much as 7°C) with a diurnal peak in body temperature near the end of

the peak ambient heat load followed by an unusually low body temperature at night (Louw and Seely, 1982). Adaptive heterothermy has been reported in eland *Tragelaphus oryx* (Taylor, 1969; Taylor and Lyman, 1967), water-deprived camels *Camelus dromedarius* (Schmidt-Nielsen et al., 1957), oryx *Oryx beisa* (Taylor, 1969; Taylor, 1970), giraffe *Giraffa camelopardalis* (Langman and Maloiy, 1989) and, despite their smaller size, gazelles (*Gazella granti* and *Gazella thompsonii*; Taylor, 1970). At the time these studies were carried out, however, technical limitations precluded the continuous measurement of core body temperature in unrestrained animals exposed to natural environmental stressors. The studies were therefore conducted using restrained, captive or hand-reared animals, usually in a laboratory climatic chamber or small outdoor paddock.

Although earlier studies yielded valuable insights, recent investigations employing miniature data loggers (Fuller et

al., 1999, 2000; Jessen et al., 1994; Lehmer et al., 2003; Maloney et al., 2002; Mitchell et al., 1997; Mzilikazi and Lovegrove, 2004) or radiotelemetry (Ostrowski et al., 2003; Zervanos and Salsbury, 2003) to record body temperatures in free-living mammals have demonstrated the importance of studying thermoregulatory responses in the natural environment, where animals are subjected to complex stressors that alter their behaviour and thermoregulatory mechanisms. Indeed, no African ungulate studied so far, free-living in its natural habitat, has employed adaptive heterothermy (for a review, see Mitchell et al., 2002). The ungulates had low-amplitude 24 h rhythms of body temperature (1–3°C) with mean body temperatures at night higher than those during the day. We have suggested that the absence of wide swings in body temperature can be attributed to the animals employing behavioural thermoregulation, both to maintain body temperatures at night and to escape solar radiation during the day (Fuller et al., 2004; Mitchell et al., 2002).

All the published studies on free-ranging African ungulates have been carried out over periods ranging from as little as 6 days (for one springbok, *Antidorcas marsupialis*; Mitchell et al., 1997) to 2 months, much shorter than necessary to detect seasonal changes, and the consequences of life events like births. For some species, including springbok (Mitchell et al., 1997), data were not obtained during the hot summer months, when adaptive heterothermy is most likely to be employed. In the absence of long-term studies allowing comparison of body temperature fluctuations across seasons, the finding that core body temperature of large African arid-zone ungulates is independent of environmental thermal load (Mitchell et al., 2002) may be attributed, at least in part, to limited fluctuations in nycthemeral heat load that happened to occur during the study periods. To obtain continuous and long-term data and to investigate whether heterothermy is evident in springbok, a small antelope that occupies semi-arid regions of Southern Africa, we used implanted miniature data loggers to record abdominal temperatures of free-ranging animals in their natural habitat for a period of 11–13 months.

Materials and methods

Study site and animals

The study took place in South Africa at the Lichtenburg Game Breeding Centre (26°07'S, 26°10'E), 220 km west of Johannesburg. The Centre includes a reserve for animals from African plains that extends over an area of 4500 ha, consisting mainly of grassland with scattered trees and shrubs. Eight springbok *Antidorcas marsupialis* Zimmermann were captured, in a pop-up coral system, on the reserve during July and August 1999. After capture, the animals were sedated with haloperidol (10–15 mg i.m., Kyron Laboratories, South Africa) and perphenazine (50–100 mg i.m., Kyron Laboratories, Johannesburg, South Africa) and relocated in a mass crate on a vehicle to a nearby (10 km) pen (5 m×5 m), where they were held for 3 days before surgery. The group consisted of five

adult females (females 1–5; body mass 20–35 kg) and three adult males (males 1–3; body mass 30–35 kg).

Procedures

All experimental procedures were approved by the Animal Ethics Screening Committee of the University of the Witwatersrand (protocol no. 99/28/4). On the day of surgery, springbok were herded into a mass crate, and transported to a nearby temporary surgical theatre. They were removed individually from the crate and anaesthetised with 1–2% halothane (Fluothane, Zeneca, South Africa) in oxygen, administered *via* a face mask. Using aseptic techniques, we implanted miniature thermometric data loggers into the abdominal cavity of each animal. Average duration of surgery was 6 min. Respiratory rate, heart rate and rectal temperature were monitored throughout surgery. Wounds were sutured with nylon and treated with a topical antiseptic spray (Necrospray, Centaur Labs, Pretoria, South Africa), and each animal was given prophylactic long-acting penicillin (3 ml i.m., Duplocillin, Intervet, Johannesburg, South Africa) and an analgesic and anti-inflammatory medication (1 ml s.c., Dexa-Tomanol, Centaur Labs). A coloured ear tag was fixed to each animal for identification. After recovery from anaesthesia the animals were released into a study enclosure, a 62 ha fenced section of the reserve, where they became ambulatory within 5 min, and subsequently ranged freely with other ungulate species. On the day of release two male springbok (males 2 and 3) escaped from the enclosure, into a larger section of the reserve (1470 ha), which is open to tourist vehicles. We could not readily identify these males for recapture; they returned to their original territory with a springbok population of ~250, and several other large African mammal species. All animals had access to water *ad libitum* and grazed on natural vegetation of the reserve.

The six springbok in the study enclosure were recaptured 1 year or more after surgery, by chasing them into game capture nets. Each animal was sedated with haloperidol (10 mg i.m.) before being carried to a mass crate. Data loggers were removed the following day during surgery (using the surgical and anaesthetic procedures as described above). The animals' surgical sites had healed and there were no signs of infection. After surgery, springbok (with ear tags) were released back into the main reserve; intermittent observations of the animals in the following year revealed that all animals remained healthy. All females gave birth to healthy lambs during the study period and were pregnant again at the time of logger retrieval.

Loggers from the two male springbok that escaped from the study enclosure were retrieved serendipitously after the animals were captured, more than 1 year after surgery, during routine game management practices at the centre.

Body temperature measurement

The miniature data loggers (StowAway XTI, Onset Computer Corporation, Pocasset, USA) had outside dimensions of ~50 mm×45 mm×20 mm and a mass of ~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. Before implantation, loggers were calibrated against a high-accuracy quartz thermometer (Quat 100, Heraeus, Hanau, Germany) in an insulated water bath, to an accuracy of better than 0.05°C. The scan interval of the loggers was set at 30 min, to allow recording for up to 677 days. Loggers retrieved from animals were in perfect order and all data was retrieved. However, four loggers had stopped recording after ~11 months because of premature battery failure. Recalibration of loggers revealed no calibration drift.

Climate measurement

Climatic data were obtained from a portable weather station (Mike Cotton Systems, Cape Town, South Africa) at the study site and from the nearby Lichtenburg meteorological station (South African Weather Bureau). Data on air temperature, globe temperature and wind speed are given in more detail below and in Table 1. Solar noon was between 12:00 h and 13:00 h; times of sunrise and sunset for each season are given in Table 1. Total annual rainfall was 514 mm in 1999, similar to that of previous years, but was significantly higher at 753 mm in 2000, when rainfall occurred atypically in all months of the year.

Statistical analyses

The relationship between air temperature and body temperature of each animal was assessed using Pearson's linear correlation and regression. Repeated measures analysis of variance (ANOVA), with Student–Newman–Keuls *post hoc* test, was used to determine changes in body temperature of the eight animals across seasons. For analyses of seasonal rhythms, data were grouped and averaged in four 3-month

periods (seasons). The three coldest months (May, June and July) were termed 'winter', and successive three-month periods then named 'spring' (August–October), 'summer' (November–January) and 'autumn' (February–April). Other comparisons of body temperature were made using paired or unpaired Student's *t*-tests, where appropriate. For analysis of nycthemeral patterns of body temperature, actual values of minimum body temperature and maximum body temperature, and the time they occurred, were used. A curve-fitting procedure was not used because a biphasic 24 h body temperature pattern was not always evident. Values of $P < 0.05$ are considered significant. All data are reported as means \pm S.D.

Results

Body temperature for one springbok (female 1) measured every 30 min for 13 months is shown in Fig. 1. A clear episode of fever (in April 2000), where mean body temperature was elevated by ~2°C for several days, is visible in the tracing. All but one springbok experienced at least one such episode, during which mean daily body temperature was sustained 0.5°C or more above the normal mean daily body temperature. The figure also shows several short (1–3 h) episodes of hypothermia and hyperthermia. We believe the elevations reflect exercise hyperthermia, arising from spontaneous or induced activity. Days on which animals experienced fevers – including the day before and the day after the febrile period – or exercise hyperthermia (both defined as maximum body temperature more than 0.5°C above normal maximum at that time of year) were excluded from data analyses of effects of microclimate and season on body temperature, but were examined separately (see below).

Table 1. Characteristics of the environment and of body temperatures of eight free-ranging springbok

	Aug–Oct 'Spring'	Nov–Jan 'Summer'	Feb–Apr 'Autumn'	May–Jul 'Winter'
Environment				
Air temperature (°C)	15.8 \pm 3.7	20.2 \pm 2.2	17.6 \pm 2.8	10.0 \pm 2.1
Globe temperature (°C)	17.2 \pm 4.2	24.0 \pm 2.4	20.9 \pm 2.5	no data
Wind speed (m s ⁻¹)	3.6 \pm 0.9	3.2 \pm 0.6	2.6 \pm 0.6	2.4 \pm 0.7
Rainfall (mm)	9 \pm 15	97 \pm 52	88 \pm 21	34 \pm 19
Time of sunrise (h)	06:11	05:24	06:15	06:55
Time of sunset (h)	18:08	18:58	18:29	17:36
Photoperiod (h)	11:57	13:34	12:14	10:41
Body temperature (°C)				
Mean	39.43 \pm 0.15	39.50 \pm 0.12	39.39 \pm 0.14	39.22 \pm 0.07
Minimum	38.85 \pm 0.21	38.97 \pm 0.12	38.87 \pm 0.11	38.61 \pm 0.10
Maximum	40.02 \pm 0.20	40.10 \pm 0.15	39.97 \pm 0.21	39.85 \pm 0.18
Amplitude	1.17 \pm 0.25	1.13 \pm 0.14	1.11 \pm 0.18	1.24 \pm 0.21
Time of minimum (h)	06:44 \pm 0:31	06:12 \pm 0:39	06:40 \pm 0:52	07:26 \pm 0:32
Time of maximum (h)	18:41 \pm 1:02	17:53 \pm 0:55	18:08 \pm 0:40	19:04 \pm 0:39

For air temperature, globe temperature and wind speed, values are means \pm S.D. of 24 h averages. Rainfall is mean \pm S.D. of monthly averages; time of sunrise, sunset and photoperiod are means of monthly averages. Body temperature indices were determined for each day, and then averaged over about 90 days for each animal; thereafter mean \pm S.D. was calculated for the eight animals.

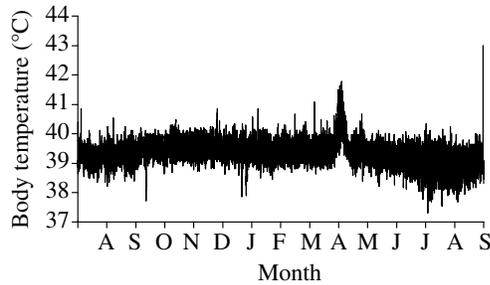


Fig. 1. Original record of 30 min readings of abdominal temperature from one springbok (female 1) over 13 months (August 1999 to September 2000). Note the apparent decrease in minimum body temperature in July–September (southern hemisphere late winter), the episode of fever in April, and the hyperthermia exceeding 43°C associated with ultimate capture of the animal.

Body temperature as a function of climate

The means of core body temperature, calculated over the entire period of recording but excluding days when animals experienced fevers or exercise hyperthermia, were $39.32 \pm 0.20^\circ\text{C}$ (female 1, 384 days), $39.51 \pm 0.21^\circ\text{C}$ (female 2, 346 days), $39.44 \pm 0.16^\circ\text{C}$ (female 3, 258 days), $39.26 \pm 0.11^\circ\text{C}$ (female 4, 334 days), $39.44 \pm 0.22^\circ\text{C}$ (female 5, 341 days), $39.26 \pm 0.16^\circ\text{C}$ (male 1, 359 days), $39.30 \pm 0.13^\circ\text{C}$ (male 2, 306 days) and $39.39 \pm 0.12^\circ\text{C}$ (male 3, 315 days). Mean body temperature of female springbok was not significantly different ($t=1.16$, $P=0.29$) to that of the males. Mean body temperature for the springbok, weighted by the reciprocal of the variance for each individual animal, was $39.34 \pm 0.003^\circ\text{C}$.

In each springbok, mean 24-h body temperature was correlated significantly with mean 24 h air temperature ($P < 0.0001$; female 1 shown in Fig. 2A). Although correlation coefficients were modest (0.3–0.7), upper and lower 95% prediction intervals (around a fitted regression line; not shown in Fig. 2A) never separated by more than 1°C . Thus, at any mean air temperature between 0 and 30°C , body temperature usually varied by no more than 0.5°C above or below the mean body temperature expected for that air temperature. Slopes of linear regression lines fitted to each animal's data ranged from 0.01 to 0.03, so that, on average, mean daily body temperature of springbok increased 0.022°C per 1°C increase of mean daily air temperature.

Minimum daily body temperature was also correlated significantly with minimum air temperature ($P < 0.0001$ for all animals, $r=0.3$ –0.7). However, the relationship between daily maximum body temperature and maximum air temperature was less robust. Correlation coefficients, although significant ($P < 0.05$), were low ($r=0.1$ –0.4), and for one animal (male 3) there was no statistically significant relationship between its maximum body temperature and the maximum air temperature. Similarly, there was no clear linear relationship between 24 h range of air temperature and the amplitude of the animal's 24 h body temperature rhythm. In two animals (females 4 and 5) there was a significant negative correlation between daily range of air temperature and the nycthemeral amplitude of body

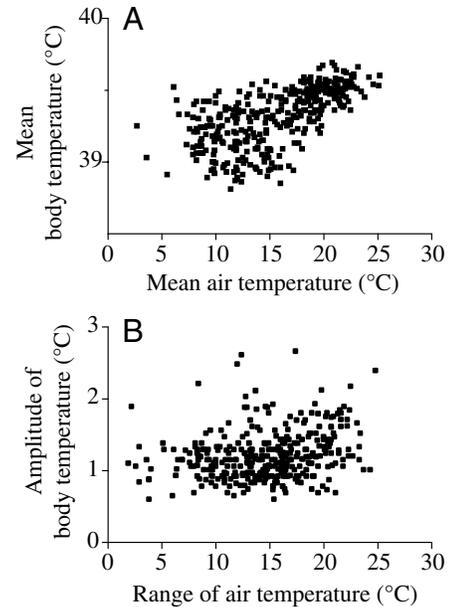


Fig. 2. 24 h mean of body temperature plotted against 24 h mean of air temperature (A), and 24 h amplitude of body temperature plotted against 24 h range of air temperature (B), for one springbok (female 1, 353 days data).

temperature ($r=-0.13$, $P < 0.05$), in one animal (male 3) no linear relationship was evident ($P=0.89$), and in five animals there was a positive correlation ($r=0.2$ to 0.3 , $P < 0.0001$). Despite this significant correlation for the five animals, there was considerable scatter of data. For example, female 1 ($r=0.24$; Fig. 2B), on a day when the range of air temperature was only 2.2°C , had an amplitude of body temperature rhythm of 1.9°C , while on another day when air temperature varied by 24.3°C , her amplitude was 1°C . Prediction intervals around a fitted linear regression line (not shown in Fig. 2) separated by 1.3°C , so that, at the mean 24 h range of air temperature (14.8°C) experienced by the animal, the amplitude of her 24 h body temperature rhythm could vary, according to the regression analyses, from 0.57 to 1.87°C .

The association of body temperature with air temperature is depicted in another way in Fig. 3, which shows, as a function of time of day, mean air temperature (Fig. 3A) and mean body temperature for all springbok (Fig. 3B) over 1 month with high air temperatures (November) and 1 month with low air temperatures (June). The parallel downward shift in air temperature at all times of day in June was accompanied by an almost parallel downward shift in body temperature. For both months, body temperature was at its lowest in the early morning after sunrise, and started to rise about 2 h after the morning rise in air temperature to reach a maximum in the early evening, several hours after air temperature had peaked. Despite large fluctuations (more than 10°C) in mean air temperature over the 24 h, the mean nycthemeral amplitude of body temperature usually was no more than 1.2°C (see also Table 1).

Relationships between black globe temperature and body

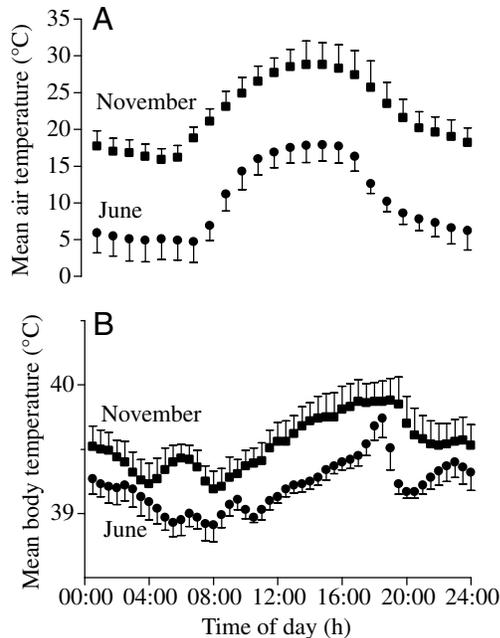


Fig. 3. Mean (\pm S.D.) air temperature and body temperature ($N=8$ animals) as a function of time of day for 1 month with high air temperatures (November) and 1 month with low air temperatures (June).

temperature were similar in pattern to those between air temperature and body temperature. There was no statistically significant association between wind speed and body temperature; wind speeds were usually low by global standards, rarely exceeding 4 m s^{-1} . Examination of body temperatures over periods when rainfall events were recorded revealed no significant effect of rain on body temperature; the heaviest rainfall occurred in summer when air temperature and globe temperature were highest.

Seasonal variations in body temperature

Table 1 shows mean (\pm S.D.) daily air temperature, globe temperature and wind speed, and mean (\pm S.D.) monthly rainfall, during each season. Air temperature, as measured each hour, reached a maximum of 34°C (in November) and dropped as low as -6°C (in July). The average 24 h range of air temperature was about 16°C in autumn and winter, and 12°C in summer and spring. Peak black globe temperature was 54°C (in November); globe temperatures were not obtained in winter because of equipment failure. Air temperatures were unusually low in January because of anomalously high rainfall (154 mm, compared to annual January average of ~ 50 mm).

Mean daily body temperature, maximum and minimum body temperature, and mean amplitude of daily body temperature for the eight springbok over each 3-month period are also shown in Table 1. Mean daily body temperature in winter was significantly lower ($F=19.39$, $P<0.0001$, $N=8$) than it was in summer (by 0.28°C ; $P<0.001$), spring (0.21°C , $P<0.001$) and autumn (0.17°C , $P<0.001$), and was lower in autumn than in summer (by 0.11°C , $P<0.05$). These seasonal

reductions in mean body temperature were accompanied by decreases of similar magnitude in both minimum daily body temperature and maximum daily body temperature, so that the mean nycthemeral amplitude of body temperature did not differ across the four seasons ($F=1.48$, $P=0.25$).

The times at which the minimum body temperature and the maximum body temperature (acrophase) occurred in each season also are given in Table 1. The time at which body temperature reached a minimum was significantly later in winter ($F=6.57$, $P=0.003$) than in summer (by 1.2 h; $P<0.01$) and autumn (by 0.8 h; $P<0.05$). Similar shifts in the acrophase occurred ($F=6.49$, $P=0.003$); in winter it occurred 1.2 h later than in summer ($P<0.01$), and in autumn it was delayed by 0.9 h ($P<0.05$). Because both phases of the nycthemeral cycle were shifted in the same direction and by similar amounts, there was no significant change in the time elapsed between the minimum and maximum body temperature, over seasons.

The shifts in the phases of the nycthemeral rhythm across seasons were coincident with changes in the time of sunrise. Time of sunrise was 1 h later in autumn, and 1.5 h later in winter, than it was in summer (Table 1). Time of sunrise was significantly correlated with the time at which body temperature reached a minimum ($r=0.98$, $P=0.02$, $N=12$). Time of sunset was earliest in winter and latest in summer (Table 1), resulting in a photoperiod (length of day light) that was shortest in the winter months (by an average of 2 h and 53 min, compared to summer; Table 1). Comparisons of mean body temperature for each month of the year with the mean photoperiod for that month revealed that mean body temperature was very tightly correlated with photoperiod ($r=0.9$, $P<0.0001$, $N=12$; Fig. 4).

Natural fevers

Conspicuous sustained but episodic elevations in body temperature were evident in the recordings obtained from seven of the springbok (for example, see Fig. 1). We believe that these elevations reflect spontaneous fevers; body temperatures were unusually high (mean maximum temperature $41.3\pm 0.3^\circ\text{C}$, compared with the typical summer maximum of $40.1\pm 0.2^\circ\text{C}$), were not associated with changes in climate, were maintained for more than 24 h and, on one occasion, developed consecutively in different animals in the

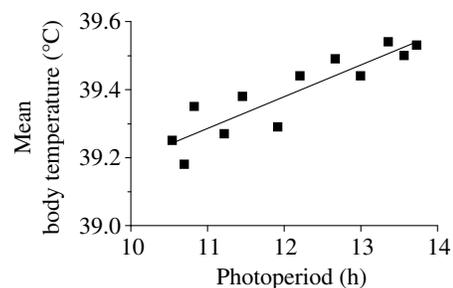


Fig. 4. Mean monthly body temperature for the eight springbok plotted against mean monthly photoperiod, with linear regression line ($r=0.9$, $P<0.0001$).

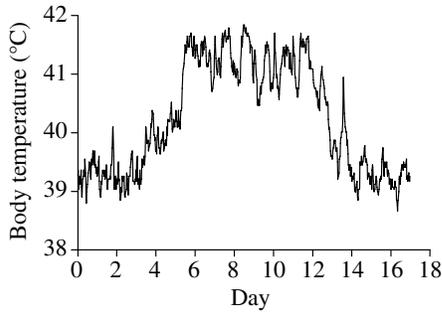


Fig. 5. Original record of 30 min readings of abdominal temperature from one springbok (female 3) over 17 days, illustrating a period of fever.

herd. Some springbok displayed more than one febrile episode, with each episode lasting between 1 and 12 days.

Fig. 5 shows the body temperature of one springbok (female 3) over 17 days with a typical sustained elevation in body temperature. Mean body temperature was elevated by more than 1°C during the febrile period, but the nycthemeral variation of body temperature was unaffected. Comparisons of body temperatures on febrile days and on non-febrile days (preceding each febrile episode) showed that there were no significant changes in the amplitude of the 24 h body temperature rhythm ($t=1.71$, $P=0.13$, $N=8$), and that the time of day at which the peak ($t=1.25$, $P=0.25$) and trough ($t=1.06$, $P=0.33$) of body temperature occurred did not differ. During fevers, therefore, body temperature was shifted above normal levels at all times of day but subject to the same nycthemeral rhythm. Although, by design, we did not monitor the behaviour of the animals routinely, at no stage did any animal that we happened to observe demonstrate visible sickness behaviour (Dantzer, 2004).

Exercise-induced hyperthermia

In addition to the fevers, which lasted days, the springbok also sporadically experienced short-duration episodes of elevated body temperature (for example, see Fig. 1). Fig. 6 shows the body temperature of one springbok (male 2) on 2 days in December. On one occasion on day 1, and two on day

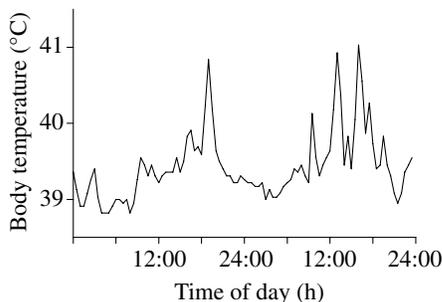


Fig. 6. Original record of 30 min readings of abdominal temperature from one springbok (male 2) on 2 days, illustrating hyperthermias likely to have been associated with exercise.

2, body temperature rose by more than 1°C within 1 h, reaching a level of ~41°C. The high body temperatures resolved rapidly. These elevations of body temperature probably reflect episodes of moderate to intense activity. Elevations were not always evident in the records of all animals at the same time and no unusual climatic conditions prevailed. Short-duration episodes of elevated body temperature were evident at any time, but particularly during the night.

What we presume to be exercise episodes may have been spontaneous or induced by a disturbance of which we were unaware. The animal shown in Fig. 6 was one of the males resident in the main reserve and may have fled from vehicles (during the day), or from predation by a resident population of jackals *Canis mesomelas* at night, or may have been involved in territorial disputes with other males. Both those males (males 2 and 3) were members of small bachelor herds at the time of their capture. Indeed, episodes of elevated body temperature occurred much more frequently in these two springbok in the main reserve than in any animal housed in the study enclosure, including one male animal, where the animals were disturbed less often and where there were no other males.

Examination of our records revealed that our occasional observations (by vehicle) of animals in the study enclosure indeed elicited moderate hyperthermia of short duration (less than 1 h), typically in all animals in the herd. However, attempts to catch the animals at the end of the study period using capture nets erected in the enclosure invoked much higher elevations in body temperature. Fig. 7 shows the body temperatures of three female springbok, the abdominal loggers of which still were recording at the time, during attempted capture by high-intensity chasing with two vehicles (for ~45 min). During and after the chase, body temperature rose precipitously, reaching 43°C, a level much higher than that measured at any other time during the year of recording (see Fig. 1, for example). The hyperthermia, however, resolved rapidly after the unsuccessful capture attempt, with no apparent sequelae for the animals.

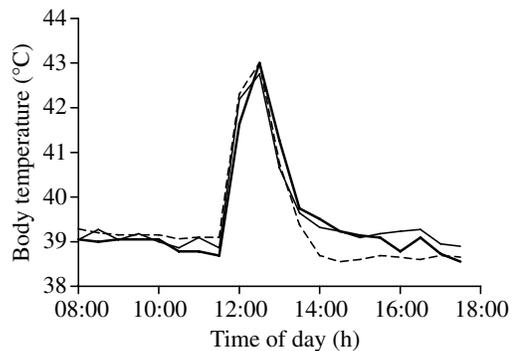


Fig. 7. Original record of 30 min readings of abdominal temperatures from three female springbok over 10 h, illustrating hyperthermia reaching 43°C during an unsuccessful capture attempt (chased by vehicle).

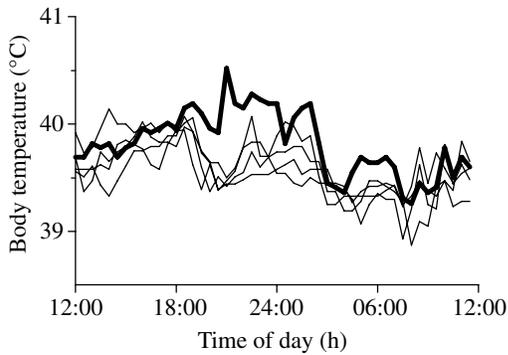


Fig. 8. Original record of 30 min readings of abdominal temperatures of five female springbok over 24 h, illustrating the hyperthermia likely to reflect labour and birth, in one animal (bold line) between 20:00 h and 24:00 h.

Parturition and lactation

All females gave birth to healthy lambs between 24 October and 28 December 1999, 12–20 weeks after surgery (gestation period ~25 weeks; Skinner and Louw, 1996). Fig. 8 shows body temperatures of all females over a selected 24 h period. At 20:30 h, the body temperature of female 3 (bold tracing in figure) rose rapidly from 39.9 to 40.5°C, exceeding that of the other females by about 1°C. The animal's body temperature remained elevated above that of the other females until after dawn the following day; the duration was longer than the hyperthermia of presumed exercise but shorter than the fevers. We suspect that this rise in body temperature, which occurred at a time when body temperature usually was stable, reflected the hyperthermia experienced during the final stages of labour (Laburn et al., 1994), a suspicion supported by the sighting of a lamb with female 3, 2 days later. The remaining females all gave birth in the following 2 months, but we could find no discernible differences in body temperatures, which we could attribute to labour. Gestational hypothermia, a regulated decrease in body temperature in the last trimester of pregnancy (Kozak, 1997), also was not evident. Similarly, there were no obvious changes in body temperature during the four-month lactation periods (Skinner and Louw, 1996) and temperatures of females in the expected periods of lactation were not different to those of males at the same time.

Discussion

Our study provides the first continuous, accurate measurements of core body temperature in an undisturbed free-ranging ungulate species in its natural habitat for a 1 year period, and also is the first to record body temperatures of all individual animals in a social group. Our results show that, in the face of many endogenous and external stressors, including pregnancy, lactation, social interactions, and changes in microclimate and vegetation, springbok maintain their core body temperatures within narrow 24 h limits of ~1.2°C. Although body temperatures, measured at 30 min intervals for 1 year, were correlated positively with corresponding air

temperatures and were higher statistically in summer than in winter, mean body temperature varied by only about 0.3°C across seasons and, at any air temperature, by no more than 1°C around its mean. Mean body temperatures over each month were correlated positively with average photoperiod for that month. Remarkably, there was no seasonal variation in the amplitude of the nycthemeral body temperature rhythm, or in the time between the minimum and maximum body temperature. However, in parallel with a change in time of sunrise, all the phases of the 24 h cycle of body temperature were shifted ~1.2 h later in winter than in summer.

Although our springbok exhibited extraordinary homeothermy from week to week, and month to month, there were sporadic episodes when body temperature deviated outside of its normal range, sometimes exceeding 41°C or dropping below 38°C (for example, see Fig. 1). The hyperthermic episodes presumably were associated with animals engaging in exercise or, when sustained over days, developing spontaneous fevers. We previously have observed similar sustained elevations in body temperature with maintenance of the normal circadian rhythm in free-ranging impala (Kammerman et al., 2001). There also was a period when springbok in the herd, like the impala, developed fevers consecutively, possibly reflecting the spread of a contagious pathogen. Body temperature also rose precipitously during capture, consistent with previous findings that springbok reach rectal temperatures in excess of 42°C in response to capture stress (Gericke et al., 1978). Rapid decrements of abdominal temperature, which occurred sporadically, were not associated with unusually cold climate, and typically occurred at different times for each animal, may reflect drinking (Mitchell et al., 1997). Because we deliberately wanted to limit human interactions with the animals we did not observe behavioural patterns, except on rare occasions when we entered the study enclosure. Further studies with other remote-sensing miniature devices (Cooke et al., 2004) to record, for example, activity, heart rate or skin temperature, are necessary to discover what thermoregulatory mechanisms unrestrained animals exhibiting voluntary behaviour in the absence of human observers actually employ. Further studies are also needed to investigate if patterns of thermoregulation differ in detail between genders, age classes and animals in different social groups. In our study, episodes of hyperthermia occurred more often in the two males that escaped from the study enclosure into the main reserve. Whether the higher incidence of these increments in body temperature was associated with reproductive behaviour, with more frequent disturbances by tourists, or with the animals being housed in a much larger area, is unknown.

The short-duration episodes of hyperthermia, in which body temperature increased by more than 1°C h⁻¹ and then decreased at a similar rate, are likely to reflect high-intensity activity. Springbok, reported to run at speeds up to 88 km h⁻¹ to avoid predation (Skinner and Louw, 1996), generate a peak metabolic rate at least 10 times that of basal metabolic rate (Mitchell et al., 1997). Their pelage, which is thinner and has a higher conductance than expected for an antelope of similar

size (Hofmeyr and Louw, 1987), together with evaporative cooling from both the skin and respiratory tract (Hofmeyr and Louw, 1987), facilitate rapid heat loss at cessation of exercise. Although the pelage offers the advantage of off-loading excess heat rapidly, its properties carry the disadvantages of the animals losing heat rapidly even at moderately low ambient temperatures, and gaining substantial heat under conditions of high ambient temperature or solar radiation (Hofmeyr and Louw, 1987). In the face of air temperatures that often varied by more than 20°C on a single day, and minimum and maximum air temperatures that differed by as much as 40°C across the year, springbok in our study therefore maintained body temperature within a remarkably narrow range.

The homeothermy of the springbok in the face of substantial nychthemeral variation in environmental heat load, though remarkable, was not unexpected. We previously have shown, in a short-term study, that the amplitude of the 24 h rhythm of arterial blood temperature in free-ranging springbok during winter and spring in similar climatic conditions was less than 1°C, and that core body temperature was unaffected by day-to-day changes of environmental thermal loads (Mitchell et al., 1997). Also, unrestrained springbok in a 4 ha paddock maintained abdominal temperature between 37.5 and 41.0°C, despite being subjected to summer air temperatures varying between 16 and 39°C and high solar radiation, and water deprivation for 17 days (Hofmeyr and Louw, 1987). The amplitude of the nychthemeral rhythm of body temperature of other free-ranging African ungulates, including black wildebeest *Connochaetes gnou* (Jessen et al., 1994), eland (Fuller et al., 1999), zebra *Equus burchelli* (Fuller et al., 2000) and oryx *Oryx gazella* (Maloney et al., 2002), was also not related to environmental thermal load. In other words, none of these African ungulates exhibited the wide swings in body temperature characterising adaptive heterothermy, an adaptation widely considered to be crucial for the survival of ungulates in arid-zone habitats.

Although adaptive heterothermy, which relies on thermal inertia, typically is ascribed to animals of large body mass, it has been reported in Thompson's gazelle *Gazella thompsonii* and Grant's gazelle *Gazella granti*, antelope species that are similar in size and closely related phylogenetically to springbok. During water deprivation in a simulated desert environment, rectal temperature of the gazelles fluctuated by between 2.5 and 3.5°C between morning and evening (Taylor, 1970). Anomalously, the increased amplitude of the nychthemeral body temperature rhythm in dehydrated, compared to hydrated, animals, a feature considered a hallmark of adaptive heterothermy, was greater in the Thompson's gazelle than in the larger eland and oryx (Taylor, 1970). We have argued, however, that the wide nychthemeral swings in body temperature in captive animals, like those described above, arise mainly from experimental protocols that deprive the animals of their natural microclimate and access to behavioural thermoregulation (Fuller et al., 1999, 2004; Mitchell et al., 2002) and do not imply that the same species will employ adaptive heterothermy when living free. Free-

ranging eland, for example, sought shade during the hottest part of the day and defended body temperature at night, possibly by interactions with conspecifics (Fuller et al., 1999), thermoregulatory behaviour denied to captive animals.

Ostrowski et al. (2003) have argued recently that our studies on eland (Fuller et al., 1999) and springbok (Mitchell et al., 1997) failed to demonstrate adaptive heterothermy because they were conducted over short periods when air temperatures were moderate. Their intermittent and opportunistic measurements of abdominal temperatures of free-living Arabian oryx *Oryx leucoryx* exposed to severe heat (mean maximum air temperature of 44°C) and water deprivation in summer, revealed that body temperature fluctuated daily by more than 4°C in summer, but by less than 2°C in winter. However, the relationship between 24 h fluctuations in air temperature and body temperature was weak; only 17% of the variation in heat storage of oryx in summer could be attributed to variation in air temperature. Only three other comparable studies have investigated seasonal patterns of body temperature in unrestrained ungulates. Jessen and Kuhnen (1996) showed that the 24 h amplitude of arterial blood temperature of goats was greater in summer than in winter; however, even in summer the amplitude was small (2°C). In contrast, the 24 h fluctuation of body temperatures of six free-ranging mule deer *Odocoileus hemionus* (Sargeant et al., 1994) and of one unrestrained sheep (Bligh et al., 1965), like that of our springbok, did not vary across seasons.

The key to springbok thermoregulation, in the face of nychthemeral and seasonal changes of ambient temperature, appears to lie not in adaptive heterothermy but in their ability to employ behavioural thermoregulation. Although we did not observe our animals' behaviour, Hofmeyr and Louw (1987) have reported that springbok counter high intensity solar radiation by seeking shade or, if not available, by reducing the body surface area exposed to solar radiation by orienting the long axis of the body parallel to the rays of the sun. Springbok also exploit the colouration of their pelage, by presenting the white rump, which has a high reflectance, towards the incident radiation. During cold nights, when the properties of the pelage make the animals vulnerable to rapid heat loss, we believe that springbok avoid hypothermia primarily by a combination of locomotor activity (Mitchell et al., 1997) and peripheral vasoconstriction. Indeed, activity, measured with an omnidirectional mercury switch attached to a logger on a collar, was greater overnight for a free-ranging springbok exposed to cold winter nights than for another springbok exposed to a warmer period in spring (Mitchell et al., 1997). Seasonal patterns in locomotor activity of springbok have not been investigated. However, time spent foraging increases in winter months, at the cost of other activities (Davies and Skinner, 1986).

Even though the primary thermal problem facing arid-zone ungulates would conventionally be considered to be that of heat, winter cold may present a formidable challenge too. One way in which mammals, particularly those of low body mass (<2 kg), respond to the predictable decrease in food

availability and energetically challenging demands of winter is by reducing body temperature (for example, Wollnik and Schmidt, 1995; Lehmer et al., 2003). The lowering of body temperature is not simply a passive response to a fall in air temperature. Hamsters, for example, housed at a constant 23°C, exhibited a 0.7°C decrease of mean body temperature, without a change in the nycthemeral amplitude of body temperature, in response to photoperiod being reduced from 16 h to 8 h (Heldmaier et al., 1989). Similarly, and surprisingly, considering their substantial body mass, we found that mean body temperatures of our springbok were correlated strongly with monthly changes in photoperiod. Mean body temperature in winter, when photoperiod was shorter by almost 3 h, was ~0.3°C lower than that in summer. Although mean 24 h body temperatures were correlated with mean 24 h air temperatures, we do not believe that the lowering of body temperature in winter reflected a failure of thermoregulatory ability. Rather, we think it represented a regulated, downward shift in the set-point level around which body temperature was maintained (Heldmaier et al., 1989). Nycthemeral fluctuations in body temperature, which do not vary in amplitude over the year, are superimposed on that set-point. The primary environmental cue responsible for triggering the change in set-point appears to be photoperiod. Seasonal changes in air temperature do not provide a reliable signal for lowering of body temperature (Heldmaier et al., 1989). Our finding that the times of daily minimum and maximum body temperatures of springbok were also shifted in parallel with a change in time of sunrise provides further evidence for the importance of the light:dark cycle in thermoregulation of springbok. A similar 1–2 h seasonal shift in the phases of the nycthemeral body temperature rhythm also has been reported for mule deer (Sargeant et al., 1994).

The downward shift in mean body temperature that we observed in springbok amounted to ~0.3°C, an amount similar to that previously reported for unrestrained goats (Jessen and Kuhnen, 1996) and somewhat less than the 0.6 to 0.8°C reported for sheep (Bligh et al., 1965; da Silva and Minomo, 1995). The energy saving provided by a 0.3°C lowering of body temperature in winter may be a critical adaptation for springbok exposed to food scarcity and cold. We have observed that nutritional stress in African antelope was associated with an increased 24 h amplitude of body temperature, and episodes where core body temperatures fell below 36°C (S. A. Leisegang, D. Mitchell, and A. Fuller, unpublished). Though springbok undoubtedly encounter nutritional stress in their natural habitats, it is unlikely that our experimental animals were subjected to significant nutritional stress during our study; rainfall, the primary determinant of forage availability, was unusually high in 2000 (753 mm; typical annual mean ~450 mm) and rain fell in all months of the study. All female springbok gave birth to healthy lambs 3–5 months after implant surgery and were pregnant again, with foetuses of late-gestational age, at surgery to remove loggers, 13 months after implant surgery. Such a pattern, where a 6-month gestation period is followed by 4 months of

lactational anoestrus and then another pregnancy, is characteristic of the springbok reproductive cycle under favourable conditions (Skinner and Louw, 1996). Winter hypothermia of the springbok may well have been more marked in less favourable conditions.

Another hypothermia, which we expected to observe but did not, was gestational hypothermia. At least in rodents, a fall in body temperature of ~0.5°C is evident in the third trimester of gestation (Kozak, 1997). Remarkably, with the exception of a possible lambing event in one female, we were unable to detect any obvious changes in body temperature patterns of females during the approximate periods of pregnancy and lactation. In rats, body temperature is elevated ~0.5°C higher during the energetically expensive period of lactation as a consequence of increased metabolic heat load and reduced heat dissipation (Eliason and Fewell, 1997). If springbok had been faced with inadequate resources, we predict that they may have forgone precise maintenance of body temperature in favour of meeting their energetic needs, and those of their offspring.

We cannot rule out that some degree of adaptive heterothermy may be evident in springbok had they been subjected to food shortage, or indeed to water deprivation. Water deprivation may also elicit diurnal dehydration hyperthermia, a consequence of reduced evaporative water loss, which is a well-characterised phenomenon in dehydrated animals exposed to heat (Mitchell et al., 2002). Our animals did not exhibit those phenomena. They maintained body temperature within extraordinarily narrow limits while being subjected to a wide variety of stressors over the year. Although springbok exhibited sporadic episodes of uncontrolled hyperthermia, for example during presumed exercise and during capture, such episodes resolved quickly. Annual and daily variations in body temperature, like those of other free-living antelope (see Mitchell et al., 2002), appeared to reflect an endogenous rhythm rather than a reaction to environmental thermal load. Our long-term study of body temperatures of springbok, like others using remote-sensing technology, illustrates once more the importance of studying thermoregulatory mechanisms in free-living animals with access to their natural habitat, to conspecifics and to behavioural thermoregulation.

We thank Dr Ferdi Schoeman and the National Zoological Gardens of South Africa for allowing us access to their property and resources, and the staff of the Lichtenburg Game Breeding Centre for excellent support in animal capture and management. We thank the South African Department of Environmental Affairs and Tourism for generous provision of weather data for the study period. We also thank Tammy Cartmell, Raymond Cherry, Mary-Ann Costello, Peter Costello, Alida Faurie and Linda Reid for assistance with experimental procedures. This work was funded by University Research Committee and Medical Faculty Research Endowment Fund grants, from the University of the Witwatersrand, and by the National Research Foundation, South Africa.

References

- Bligh, J., Ingram, D. L., Keynes, R. D. and Robinson, S. G.** (1965). The deep body temperature of an unrestrained Welsh Mountain sheep recorded by a radiotelemetric technique during a 12-month period. *J. Physiol.* **176**, 136-144.
- Cooke, S. J., Hinch, S. G., Wikelski, M., Andrews, R. D., Kuchel, L. J., Wolcott, T. G. and Butler, P. J.** (2004). Biotelemetry: a mechanistic approach to ecology. *Trends Ecol. Evol.* **19**, 334-343.
- Dantzer, R.** (2004). Cytokine-induced sickness behaviour: a neuroimmune response to activation of innate immunity. *Eur. J. Pharmacol.* **500**, 399-411.
- da Silva, R. G. and Minomo, F. R.** (1995). Circadian and seasonal variation of the body temperature of sheep in a tropical environment. *Int. J. Biometeorol.* **39**, 69-73.
- Davies, R. A. G. and Skinner, J. D.** (1986). Temporal activity patterns of springbok *Antidorcas marsupialis* and merino sheep *Ovis aries* during a Karoo drought. *Trans. R. Soc. S. Afr.* **46**, 133-147.
- Eliason, H. L. and Fewell, J. E.** (1997). Thermoregulatory control during pregnancy and lactation in rats. *J. Appl. Physiol.* **83**, 837-844.
- Fuller, A., Moss, D. G., Skinner, J. D., Jessen, P. T., Mitchell, G. and Mitchell, D.** (1999). Brain, abdominal and arterial blood temperatures of free-ranging eland in their natural habitat. *Pflügers Arch.* **438**, 671-680.
- Fuller, A., Maloney, S. K., Kamerman, P. R., Mitchell, G. and Mitchell, D.** (2000). Absence of selective brain cooling in free-ranging zebras in their natural habitat. *Exp. Physiol.* **85**, 209-217.
- Fuller, A., Maloney, S. K., Mitchell, G. and Mitchell, D.** (2004). The eland and the oryx revisited: body and brain temperatures of free-living animals. *Int. Conf. Ser.* **1275**, 275-282.
- Gericke, M. D., Hofmeyr, J. M. and Louw, G. N.** (1978). The effect of capture stress and haloperidol therapy on the physiology and blood chemistry of springbok, *Antidorcas marsupialis*. *Madoqua* **11**, 5-18.
- Heldmaier, G., Steinlechner, S., Ruf, T., Wiesinger, H. and Klingenspor, M.** (1989). Photoperiod and thermoregulation in vertebrates: body temperature rhythms and thermogenic acclimation. *J. Biol. Rhythm.* **4**, 251-265.
- Hofmeyr, M. D. and Louw, G. N.** (1987). Thermoregulation, pelage conductance and renal function in the desert adapted springbok, *Antidorcas marsupialis*. *J. Arid Environ.* **13**, 137-141.
- Jensen, C. and Kuhnen, G.** (1996). Seasonal variations of body temperature in goats living in an outdoor environment. *J. Therm. Biol.* **21**, 197-204.
- Jessen, C., Laburn, H. P., Knight, M. H., Kuhnen, G., Goelst, K. and Mitchell, D.** (1994). Blood and brain temperatures of free-ranging black wildebeest in their natural environment. *Am. J. Physiol.* **267**, R1528-R1536.
- Kamerman, P. R., Fuller, A., Fauries, A. S., Mitchell, G. and Mitchell, D.** (2001). Body temperature patterns during natural fevers in a herd of free-ranging impala (*Aepyceros melampus*). *Vet. Rec.* **149**, 26-27.
- Kozak, W.** (1997). Regulated decreases in body temperature. In *Fever: Basic Mechanisms and Management* (ed. P. A. Mackowiak), pp. 467-478. Philadelphia: Lippincott-Raven Publishers.
- Laburn, H. P., Goelst, K. and Mitchell, D.** (1994). Body temperatures of lambs and their mothers measured by radio-telemetry during parturition. *Experientia* **50**, 708-711.
- Langman, V. A. and Maloiy, G. M. O.** (1989). Passive obligatory heterothermy of the giraffe. *J. Physiol.* **415**, 89P.
- Lehmer, E. M., Bossenbroek, J. M. and van Horne, B.** (2003). The influence of environment, sex, and innate timing mechanisms on body temperature patterns in free-ranging black-tailed prairie dogs. *Physiol. Biochem. Zool.* **76**, 72-83.
- Louw, G. and Seely, M.** (1982). *Ecology of Desert Organisms*. London: Longman.
- Maloney, S. K., Fuller, A., Mitchell, G. and Mitchell, D.** (2002). Brain and arterial blood temperatures of free-ranging oryx (*Oryx gazella*). *Pflügers Arch.* **443**, 437-445.
- Mitchell, D., Maloney, S. K., Laburn, H. P., Knight, M. H. and Jessen, C.** (1997). Activity, blood temperature and brain temperature of free-ranging springbok. *J. Comp. Physiol. B* **167**, 335-343.
- Mitchell, D., Maloney, S. K., Jessen, C., Laburn, H. P., Kamerman, P. R., Mitchell, G. and Fuller, A.** (2002). Adaptive heterothermy and selective brain cooling in arid-zone mammals. *Comp. Biochem. Physiol.* **131B**, 571-585.
- Mzilikazi, N. and Lovegrove, B.** (2004). Daily torpor in free-ranging rock elephant shrews, *Elephantulus myurus*: a year-long study. *Physiol. Biochem. Zool.* **77**, 285-296.
- Ostrowski, S., Williams, J. B. and Ismael, K.** (2003). Heterothermy and the water economy of the free-living Arabian oryx (*Oryx leucoryx*). *J. Exp. Biol.* **206**, 1471-1478.
- Sargeant, G. A., Eberhardt, L. E. and Peek, J. M.** (1994). Thermoregulation by mule deer (*Odocoileus hemionus*) in arid rangelands of southcentral Washington. *J. Mammal.* **75**, 536-537.
- Schmidt-Nielsen, K. B., Schmidt-Nielsen, B., Jarnum, S. A. and Houpt, T. R.** (1957). Body temperature of the camel and its relation to water economy. *Am. J. Physiol.* **188**, 103-112.
- Skinner, J. D. and Louw, G. N.** (1996). The Springbok: *Antidorcas marsupialis* (Zimmerman, 1970). Pretoria: Transvaal Museum.
- Taylor, C. R.** (1969). The eland and the oryx. *Sci. Am.* **220**, 88-97.
- Taylor, C. R.** (1970). Strategies of temperature regulation: effect on evaporation in East African ungulates. *Am. J. Physiol.* **219**, 1131-1135.
- Taylor, C. R. and Lyman, C. P.** (1967). A comparative study of the environmental physiology of an East African antelope, the eland, and the Hereford steer. *Physiol. Zool.* **40**, 280-295.
- Willmer, P., Stone, G. and Johnston, I.** (2000). *Environmental Physiology of Animals*. Oxford: Blackwell Science.
- Wollnik, F. and Schmidt, B.** (1995). Seasonal and daily rhythms of body temperature in the European hamster (*Cricetus cricetus*) under semi-natural conditions. *J. Comp. Physiol.* **165B**, 171-182.
- Zervanos, S. M. and Salsbury, C. M.** (2003). Seasonal body temperature fluctuations and energetic strategies in free-ranging Eastern woodchucks (*Marmota monax*). *J. Mammal.* **84**, 299-310.