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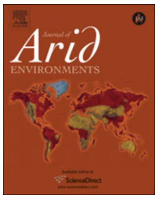

Effects of desertification on the body temperature, activity and water turnover of Angora goats

R.S. Hetem[a,*], B.A. de Witt[a], L.G. Fick[a], A. Fuller[a], S.K. Maloney[b,a], L.C.R. Meyer[a], D. Mitchell[a], G.I.H. Kerley[c]

[a] *Brain Function Research Group, School of Physiology, Medical School, University of the Witwatersrand, 7 York Road, Parktown 2193, Johannesburg, South Africa*
[b] *Physiology, School of Biomedical, Biomolecular and Chemical Science, University of Western Australia, 35 Stirling Highway, Crawley 6009, Australia*
[c] *Centre for African Conservation Ecology, Department of Zoology, P O Box 77000, Nelson Mandela Metropolitan University, Port Elizabeth 6031, South Africa*

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ABSTRACT

Globally, pastoral practices have transformed habitats, which often lead to desertification. With climate change predicted to exacerbate desertification, adaptation provides the best survival strategy for agriculturally important herbivores. We investigated body temperature, water turnover, physical activity and microclimate selection of Angora goats inhabiting transformed and intact sites in the Eastern Cape Province, South Africa. Although goats on both sites responded similarly under most environmental conditions, when goats were subjected to a thermal stress, imposed by shearing, those inhabiting the transformed site had a faster rate of rise in abdominal temperature (0.38 versus 0.31 °C h^{-1}, $P = 0.0009$), displayed an increased 24-h abdominal temperature amplitude (1.8 versus 1.6 °C, $P = 0.01$) and were generally less active (3.9 versus 5.2 activity units) compared to goats inhabiting the intact site. Post-shearing, goats inhabiting the transformed site had higher water turnover rates ($P < 0.0001$) and selected more variable microclimates ($P < 0.0001$) than goats inhabiting the intact site, despite obtaining less water from their diet ($P = 0.01$). Goats inhabiting the transformed site were more water dependent and more susceptible to thermal stresses in their environment than were those inhabiting the intact site. Coping with thermal challenges will be essential for Angora goats if the mohair industry is to thrive under future climate change scenarios.

1. Introduction

Climate change is likely to affect livestock production, both because high ambient temperatures compromise the reproductive efficiency and performance of livestock (Nardone et al., 2006; Scholes et al., 1999), and because the predicted decrease in both the quantity and quality of forage is likely to reduce the carrying capacity of rangelands (Milton and Dean, 1995; Richardson et al., 2005). Since agriculture is inherently sensitive to extreme and variable climatic conditions, it is predicted to be the economic sector most vulnerable to the risks and impact of climate change (Parry and Carter, 1989; Reilly, 1995). Agricultural production in Africa, in particular, may be compromised severely by climate change because of its heavy dependence on natural resources and a low adaptive capacity (Boko et al., 2007). Arid and semi-arid rangelands are considered to be particularly vulnerable to these effects (Schlesinger et al., 1990).

In advance of the potential threats from climate change, in the subtropical thickets of the Eastern Cape of South Africa, domestic ungulates have largely replaced indigenous herbivores since the mid 1800s (Downing, 1978), resulting in severe habitat transformation (Kerley et al., 1995). In many places, heavy browsing by goats has transformed the indigenous thicket vegetation from a dense closed canopy shrub land, frequently dominated by the highly-palatable and nutritious forage plant *Portulacaria afra*, into an open savanna-like system (Hoffman and Cowling, 1990; Kerley et al., 1995; Stuart-Hill, 1992). Such transformation of the natural flora, classified as desertification or dry-land degradation, is the result of unsustainable livestock production, and occurs worldwide (Mattison and Norris, 2005). Climate change will exacerbate desertification (Le Houerou, 1996; Robertson and Palmer, 2002), particularly because of the increased variability of climatic conditions and the frequency of extreme events, such as droughts (Boko et al., 2007; Mason and Joubert, 1997). Domestic ungulates may have to cope with, and adapt to, climatically unfavourable conditions and an increased mean annual temperature (Boko et al., 2007). Yet, we lack an understanding of the physiological capacity of mammals to cope with climate change. Most previous climate

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[*] Corresponding author. Tel.: +27 11 717 2163; fax: +27 11 643 2765.
E-mail address: robyn.hetem@wits.ac.za (R.S. Hetem).

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change assessments do not consider pre-adaptation to the expected conditions (Smit and Skinner, 2002), and especially not at the level of the herbivores affected.

Compared to other domestic ungulates, goats are well adapted to harsh, dry environments, as they have a relatively small body mass, low metabolic requirements, are able to use low-quality forage, are disease resistant and can survive long periods of water deprivation (Erasmus, 2000; Lachica and Aguilera, 2003; Silanikove, 2000). Although Angora goats are susceptible to inanition because of their high nutritional requirement for fibre production (Hart et al., 1993), they are particularly well suited to low rainfall areas, making them a good domestic ungulate model to investigate physiological responses to desertification. To test whether domestic ungulates inhabiting desertified landscapes are more susceptible to thermal stress, we employed data loggers to obtain remote and continuous measurements of the body temperature, physical activity and microclimate selection of Angora goats inhabiting transformed and intact thicket sites in the Eastern Cape. To investigate potential water stress, we also measured rate of water influx and turnover, by dilution of the stable isotope deuterium oxide, after shearing in summer.

2. Materials and methods

2.1. Study area

We conducted our research at Blaauwkrantz ranch (33°32′S 25°23′E, at an altitude of 75 m above sea level), a commercial Angora goat farm in the Kirkwood district near Port Elizabeth, in the Eastern Cape Province, South Africa. The study was conducted on two adjacent paddocks. The 40-ha paddock (transformed site) had been transformed by historical heavy browsing to form a savanna-like vegetation with scattered trees and a sparse ground cover of ephemeral grasses and forbs (Lechmere-Oertel, 2003), which provided a model of the ecological patterns and processes of a desertified landscape. The vegetation of the adjacent 50-ha paddock (intact site) was classified as Sundays Spekboomveld (Vlok et al., 2003). This dense, semi-succulent, thorny vegetation consisted primarily of perennial shrubs and trees, was largely dominated by the tree-succulent, *P. afra*, and has been shown to represent the pre-desertified state (Lechmere-Oertel, 2003).

2.2. Animals and habitat

Twenty-four neutered adult male Angora goats (*Capra aegagrus*), were captured at Blaauwkrantz ranch and underwent surgery (detailed below) in July 2005 before being randomly assigned to one of two sites. Twelve goats (body mass 39.2 ± 3.5 kg, mean ± SD) were released into the intact site and 12 goats (body mass 39.7 ± 5.9 kg) were released into the adjacent transformed site. Goats had access to water *ad libitum*, provided by water troughs, and foraged on the natural vegetation available on each site. Except for the naturally occurring trees and shrubs, no specific shelter was provided for the goats. Experimental procedures were approved by the Animal Ethics Screening Committee of the University of the Witwatersrand (protocol no. 2005/45/4).

2.3. Surgery

For implantation of data loggers, the goats were anaesthetised by intramuscular (I.M.) injection of 2.5 mg kg^{-1} ketamine hydrochloride (Anaket-V, Bayer Animal Health Pty, Isando, South Africa) and 0.04 mg kg^{-1} medetomidine hydrochloride (Domitor, Novartis, Kempton Park, South Africa). Anaesthesia was maintained with 1–4% halothane (Fluothane, Astra Zeneca, Johannesburg, South Africa) administered in 100% oxygen via a facemask. After ~10 min of halothane administration, the action of medetomidine was reversed with 0.2 mg kg^{-1} (I.M.) atipamezole hydrochloride (Antisedan, Novartis, Kempton Park, South Africa). Respiratory rate, oxygen saturation, heart rate and rectal temperature were monitored throughout the surgical procedure, which lasted ~30 min.

Implanted data loggers were covered in an inert wax (Sasol wax EXP986, Sasol, Johannesburg, South Africa) and dry-sterilized in formaldehyde vapour before implantation. A 70 mm cranial-caudal incision was made on the ventral abdomen through the skin and *linea alba* and a miniature temperature-sensitive data logger (see description below) was placed into the abdominal cavity, where it floated freely. A single goat from each group also received an implantable tracking transmitter (African Wildlife Tracking, Pretoria, South Africa) intra-abdominally, for relocation purposes. The skin and muscle layers then were sutured closed. In six of the goats from each group, after administration of a local anaesthetic (0.04 g lignocaine hydrochloride, subcutaneous (S.C.), Bayer Animal Health Pty, Isando, South Africa), an additional incision was made on the upper hind leg. A smaller temperature-sensitive data logger (see below) was inserted subcutaneously. At the same subcutaneous site, a single goat from each group also had an activity logger implanted (see below).

To prevent infection and flystrike, wounds were sprayed with a topical antiseptic spray (Necrospray, Centaur Labs, Johannesburg, South Africa) and coated with a topical tick repellent (Tickgrease, Cypermethrin 0.025% m/m, Bayer Animal Health Pty, Isando, South Africa). Each goat received a long-acting antibiotic (500 mg penicillin I.M., Peni LA Phenix, Virbac Animal Health, Centurion, South Africa), analgesic and anti-inflammatory medication (420 mg ramiphenazone I.M., Dexa-Tomanol, Centaur Labs, Johannesburg, South Africa), and a long-acting parasiticide (5 mg doramectin S.C., Dectomax, Pfizer Laboratories, Sandton, South Africa). Goats were marked individually with different coloured plastic ear tags.

Before halothane administration was terminated, a collar was fitted to a single index goat from each group. The collar supported a miniature (diameter 30 mm) black globe thermometer (miniglobe) to allow for the dynamic measurement of the microclimate the goat, and by inference its herd, chose to occupy. This technique has proven successful on other ungulate species (Hetem et al., 2007). Miniglobe temperature was measured with a small temperature-sensitive data logger, which was inserted into the centre of the matt-black hollow copper sphere (Press Spinning & Stamping co., Cape Town, South Africa).

After recovery from surgery, the goats were released into their allocated habitats where they roamed freely for a year. Within each site, the goats behaved similarly and remained as a herd, so the activity and microclimate selection of the index goats reflected that of all goats in the habitat. They were caught and weighed once a month and subjected to standard husbandry practices of parasite control. In September 2005 (austral winter, two months post-surgery) and March 2006 (austral summer, 8 months post-surgery), the goats were shorn according to the standard management practices of the farm. The diet composition and quality, and fibre productivity of these goats were measured in a parallel study (Milne, 2008; Milne and Kerley, 2009).

In August 2006, the goats once again were anaesthetised and the data loggers were removed under a surgical procedure similar to that used for the original implantation. Most of the abdominal loggers were found in the pelvic canal and were not encapsulated in adhesive tissue. After surgery the goats were returned to the resident herd on Blaauwkrantz ranch.

2.4. Temperature and activity measurements

The miniature data loggers (StowAway XTI, Onset Computer, Pocasset, USA) used to measure abdominal temperature had outside dimensions of ~50 × 45 × 20 mm and a mass of ~40 g when covered in wax. The data loggers had a storage capacity of 32 kb and measured temperatures within the range of +34 to +46 °C, at a resolution of 0.04 °C. The loggers measuring abdominal temperature were set to record at 20-min intervals. Subcutaneous and miniglobe temperatures were recorded every hour with a smaller thermometric data logger (iButton DS1922T, Maxim, Dallas Semiconductor, Texas USA), which had a diameter of ~25 mm, a height of 15 mm, and weighed about 10 g. These loggers had a resolution of 0.5 °C and a measurement range from 0 to 125 °C. All the loggers were calibrated, in an insulated water bath, against a high-accuracy thermometer (Quat 100, Heraeus, Hanau, Germany).

The activity logger (Actical, Mini-Mitter Corporation, Bend, OR, USA) recorded at 10-min intervals, had dimensions of ~40 × 40 × 15 mm, and weighed ~40 g when covered in wax. The activity logger recorded movement via a multidirectional, piezo-electric accelerometer which was sensitive to 0.05 G. To account for differences in the sensitivity of individual activity loggers we calculated activity as a percentage of the maximum reading each logger recorded, over the entire period.

2.5. Meteorological data measurements

We collected climatic data by erecting a portable weather station in the open at the transformed field site (Hobo Weather Station, Onset Computer Corporation, Pocasset, USA). We recorded wind speed ($m\ s^{-1}$), solar radiation ($W\ m^{-2}$), dry-bulb temperature (°C), relative humidity (%), standard (150 mm diameter) and miniature (30 mm diameter) black globe temperature (°C), at a height of 1 m, at hourly intervals.

2.6. Isotope analysis

We assessed water influx and water turnover rates, by dilution of the stable isotope, deuterium oxide, for seven days directly after the summer (March) shearing. Before the deuterium oxide was administered, goats were weighed and 10 ml jugular blood samples were taken to determine background concentration of deuterium oxide. Goats then received a dose of 0.04 ml kg^{-1} deuterium oxide (D_2O, I.M., 99.8 atom %, Merck & Co. Ltd. Rahway, USA). A second 10 ml blood sample was taken 4 h after injection, when we assumed that the administered deuterium oxide had equilibrated with body water. The goats' drinking water source was removed before injection of deuterium oxide. The goats were weighed and 10 ml blood samples were taken three, five and seven days after injection. Water was returned after the blood samples had been taken on the seventh day. The blood samples were collected by jugular venipuncture with Vacutainers (BD Diagnostics-preanalytical systems, Plymouth, UK), placed in ice and centrifuged (Wifug Ltd., Bradford, England) at 6000 G for 10 min. Serum and plasma were separated and stored in 2 ml vials (cryogenic vials 430489, Corning Inc., NY, USA) and frozen at −20 °C for later analysis.

Deuterium concentration of the serum was measured using a high-temperature elemental analyser (Flinnigan elemental analyser, Thermo Electron Corporation, Bremen, Germany), normalized against an international reference, namely Vienna-Standard Mean Ocean Water (V-SMOW). A log-linear regression line was fitted to establish rate constants for deuterium dilution. The y-intercept of the curve at time zero was used to estimate isotope distribution space. The total body water was calculated as the dilution space of the known dose of injected deuterium oxide, corrected for the background concentration of deuterium oxide. Water influx was determined from the average rate of deuterium oxide dilution over each 48-h period and multiplied by the total body water for that period. Water turnover was determined as the sum of water influx and the total weight loss, as all weight loss was assumed to be water loss.

2.7. Data analysis

To test how the goats in the two habitats responded to climatic extremes, before being shorn, we analysed data from the five hottest days and the five coldest days. The five hottest days were non-continuous and determined by the highest maximum globe temperatures, which averaged 47.7 ± 3.1 °C, within the two-month period before the March shearing. The five coldest days also were non-continuous and determined by the lowest night-time globe temperatures, which averaged 0.4 ± 0.5 °C, within the month before the September shearing. The mean ± SD of the mean, minimum, maximum, 24-h variability and amplitude of nychthemeral rhythm of both abdominal and subcutaneous temperatures of the goats that inhabited each site were calculated for each of these periods. We used a repeated-measures two-way analysis of variance (ANOVA) to test for differences between the goats that inhabited the two sites across hot and cold days. We tested for differences in the time of minimum and maximum abdominal temperature, as well as differences in the maximum rate of abdominal temperature rise over a 4-h interval, between the goats that inhabited the two sites. We also compared the difference between abdominal and subcutaneous temperatures, over 24 h and during the night-time period, between the goats that inhabited the two sites across hot and cold days. Newman–Keuls multiple comparisons *post-hoc* tests were used to identify sources of significant differences in ANOVAs.

To assess how the goats that inhabited the two sites responded to shearing stress, we analysed 10 days of data immediately after the summer (March) shearing, which included the seven days of water deprivation. The mean ± SD of the mean, minimum, maximum, 24-h variability and amplitude of nychthemeral rhythm of both abdominal and subcutaneous temperatures of the goats that inhabited the two sites were calculated for this post-shearing period. We then used an unpaired Student's t-test to investigate differences in the temperature profiles between the goats that inhabited the two sites post-shearing. Over the seven days during which we restricted access to water, we also performed a two-way repeated-measures analysis of variance (ANOVA) on the water influx and water turnover data to test for an interaction between the goats that inhabited the two sites across time. Newman–Keuls multiple comparisons tests were used to identify sources of significant differences in ANOVAs.

To assess whether the goats were conforming to ambient conditions or were selecting microclimates, we tested whether the slope of the regression equation, fitted to the correlation between miniglobe temperature of the microclimate selected by the index goat and weather station miniglobe temperature, was significantly different from one (the slope of the line of identity). In addition, we tested whether the slope and elevation of the regression equation was significantly different between the goats inhabiting the two sites using an analysis of co-variance (ANCOVA).

Data are expressed as mean ± SD and $P < 0.05$ was considered to be statistically significant.

3. Results

3.1. Climate

Black globe temperature peaked just after solar noon and reached a minimum just before sunrise. Solar radiation peaked between 12:00 and 13:00 and wind speed increased in the late afternoon. Environmental conditions over the three periods analysed, namely cold days, hot days and post-shearing, are presented in Table 1. Both solar radiation and wind speed were lower on the

Table 1
Environmental conditions (mean ± SD) prevailing in the open at the field site for the five hottest days, the five coldest days, and the 10-day period after summer shearing.

	Hot days	Cold days	Post-shearing
Black globe temperature (°C)			
mean	29.2 ± 1.1	14.6 ± 1.4	22.2 ± 1.4
minimum	18.3 ± 1.7	0.4 ± 0.5	12.7 ± 3.2
maximum	47.7 ± 3.1	31.1 ± 2.4	35.9 ± 3.5
Mean daily radiation (W m^{-2})	564 ± 66	376 ± 26	379 ± 159
Mean daily wind speed (m s^{-1})	2.0 ± 0.2	1.7 ± 0.3	1.6 ± 0.3

cold than on the hot days, but both maintained a similar rhythm. Rainfall totalled 402 mm over the one-year study period, which was nearly 30% higher than the long-term (1958–2005) average annual rainfall of 313 mm per annum as measured by a rain gauge on site (A. Rudman, pers. comm.). Rainfall was highest in late austral spring (110.5 mm in November 2005) and late austral autumn (90 mm in May 2006).

3.2. Response to climatic variations (hot and cold days)

3.2.1. Abdominal temperature

The abdominal temperature of the goats showed a nychthemeral (24 h) rhythm with a nadir shortly after sunrise and peak

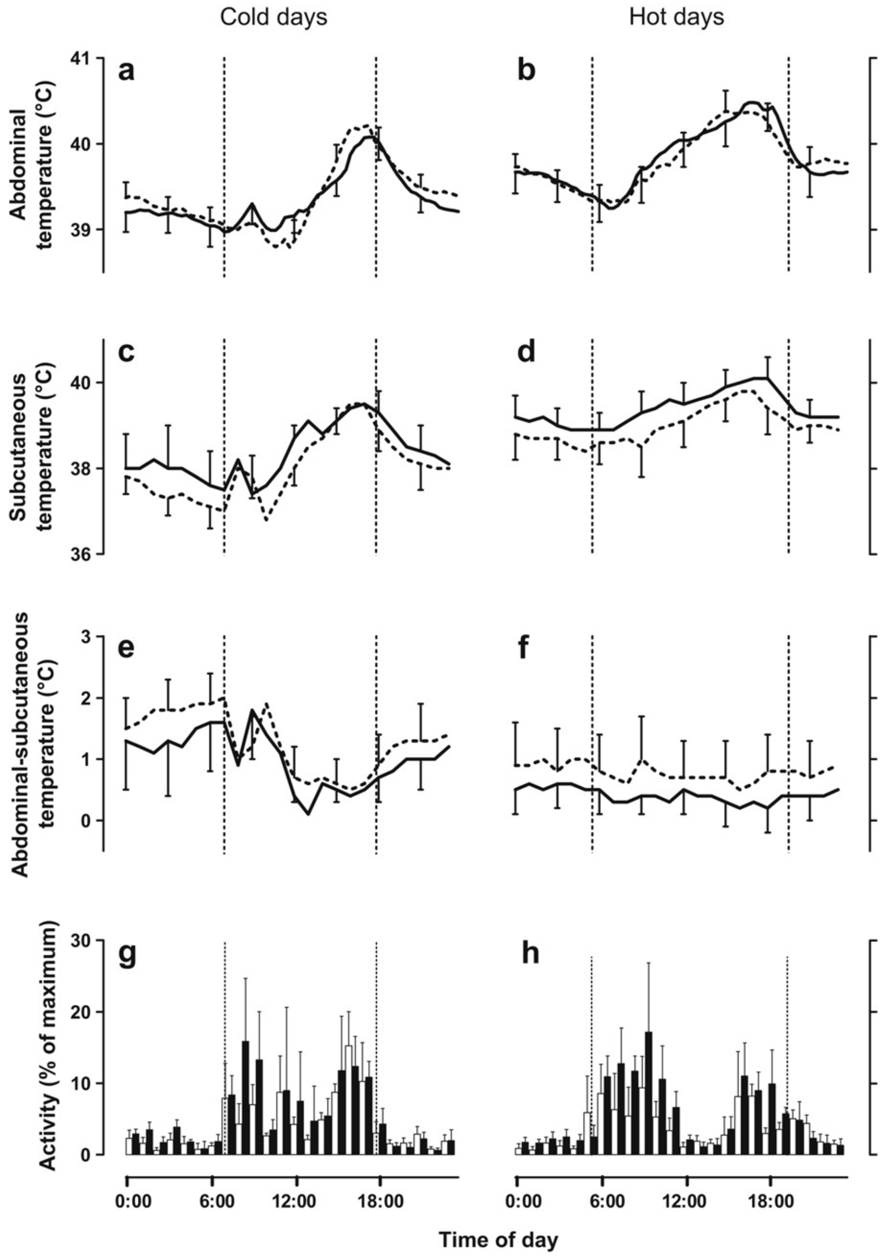

Fig. 1. Nychthemeral rhythm (mean ± SD) of abdominal temperature (upper panels), subcutaneous temperature (upper middle panels) and the difference between abdominal and subcutaneous temperatures (lower middle panels) of 12 goats that inhabited the intact site (solid line) and 12 goats that inhabited the transformed site (dotted line), as a function of time of day, over the five coldest days in winter (average minimum globe temperature of 0.4 ± 0.5 °C, left panel) and the five hottest days in summer (average maximum globe temperature of 47.7 ± 3.1 °C, right panel) of the one-year study period. The lower panel represents the nychthemeral activity rhythm (mean ± SD) of a single goat that inhabited the transformed site (white bars) and another goat that inhabited the intact site (black bars) over the same periods. Both goats displayed a biphasic activity pattern with crepuscular peaks with less activity between peaks on hot days than on cold days. The dotted horizontal lines indicate time of sunrise and sunset.

near sunset. On cold days, daily mean ($F_{1,20} = 129.5$, $P < 0.0001$), minimum ($F_{1,20} = 91.9$, $P < 0.0001$) and maximum ($F_{1,20} = 54.8$, $P < 0.0001$) abdominal temperatures of the goats were lower, but the 24-h amplitude ($F_{1,20} = 6.1$, $P = 0.02$) of abdominal temperature rhythm was higher, than on hot days (Fig. 1a and b). On hot days (Fig. 1b), goats that inhabited the intact site reached a higher maximum abdominal temperature (40.8 ± 0.3 °C versus 40.6 ± 0.3 °C, $P = 0.01$) than did goats that inhabited the transformed site. However, on cold days (Fig. 1a), goats that inhabited the transformed site displayed a higher maximum abdominal temperature (40.4 ± 0.2 °C versus 40.2 ± 0.2 °C, $P = 0.02$), a greater variability of abdominal temperature, as represented by a larger standard deviation of abdominal temperature (0.47 ± 0.05 °C versus 0.38 ± 0.04 °C, $P = 0.004$), and a higher amplitude of abdominal temperature rhythm (1.98 ± 0.24 °C versus 1.61 ± 0.19 °C, $P = 0.001$) than did goats that inhabited the intact site. Also, on cold days, goats that inhabited the transformed site reached their minimum abdominal temperatures later in the day (09:07 ± 0:39 versus 07:39 ± 1:17, $P = 0.003$), which resulted in a faster maximum rate of abdominal temperature rise during the day (0.36 ± 0.07 °C h^{-1} versus 0.24 ± 0.05 °C h^{-1}, $P = 0.0002$) than goats that inhabited the intact site.

3.2.2. Subcutaneous temperature

On cold days, the daily mean ($F_{1,9} = 150.9$, $P < 0.0001$), minimum ($F_{1,9} = 152.4$, $P < 0.0001$) and maximum ($F_{1,9} = 11.8$, $P = 0.007$) subcutaneous temperatures of the goats were lower, and had a greater amplitude ($F_{1,9} = 72.1$, $P < 0.0001$), than on the hot days (Fig. 1c and d). Daily mean subcutaneous temperatures were lower in the goats that inhabited the transformed site than in the goats that inhabited the intact site, on both hot (39.0 ± 0.5 °C versus 39.4 ± 0.4 °C, $P = 0.008$, Fig. 1d) and cold (38.0 ± 0.4 °C versus 38.4 ± 0.6 °C, $P = 0.007$, Fig. 1c) days. In addition, goats that inhabited the transformed site had a lower daily minimum (38.0 ± 0.7 °C versus 38.7 ± 0.5 °C, $P = 0.04$) and a lower daily maximum (40.0 ± 0.5 °C versus 40.4 ± 0.4 °C, $P = 0.01$) subcutaneous temperature than did goats in the intact site on hot days (Fig. 1d). These lower subcutaneous temperatures resulted in a larger difference between abdominal and subcutaneous temperatures in goats that inhabited the transformed site compared to those in the intact site, on both hot (0.79 ± 0.62 °C versus 0.40 ± 0.35 °C, $P = 0.03$, Fig. 1f) and cold (1.3 ± 0.4 °C versus 1.0 ± 0.5 °C, $P = 0.04$, Fig. 1e) days. This greater difference between abdominal and subcutaneous temperatures was likely to reflect greater vasoconstriction in goats that inhabited the transformed site. On hot days the goats remained vasodilated throughout the day and night (Fig. 1f), but on cold days goats were vasoconstricted during the cold night (Fig. 1e), as represented by a greater difference between abdominal and subcutaneous temperatures during cold nights ($F_{1,9} = 30.5$, $P < 0.0004$). Shortly after sunrise on cold days, there was a distinct rise in the subcutaneous temperature, likely to correspond to a period of vasodilation, which resulted in a reduced difference between abdominal and subcutaneous temperatures (Fig. 1c and e).

3.2.3. Activity

Fig. 1g and h shows the nychthemeral rhythm of activity for an index goat that inhabited the transformed site and another that inhabited the intact site. Whenever observed, goats, within each site, behaved similarly and remained as a herd, so the activity of the index goats reflected that of all goats in the habitat. On hot days (Fig. 1h), the goat, and, by inference, others in the herd, displayed a biphasic activity pattern with crepuscular peaks, but there was more activity between the peaks on cold days (Fig. 1g), so the goats were active throughout the daylight period. The index goat that

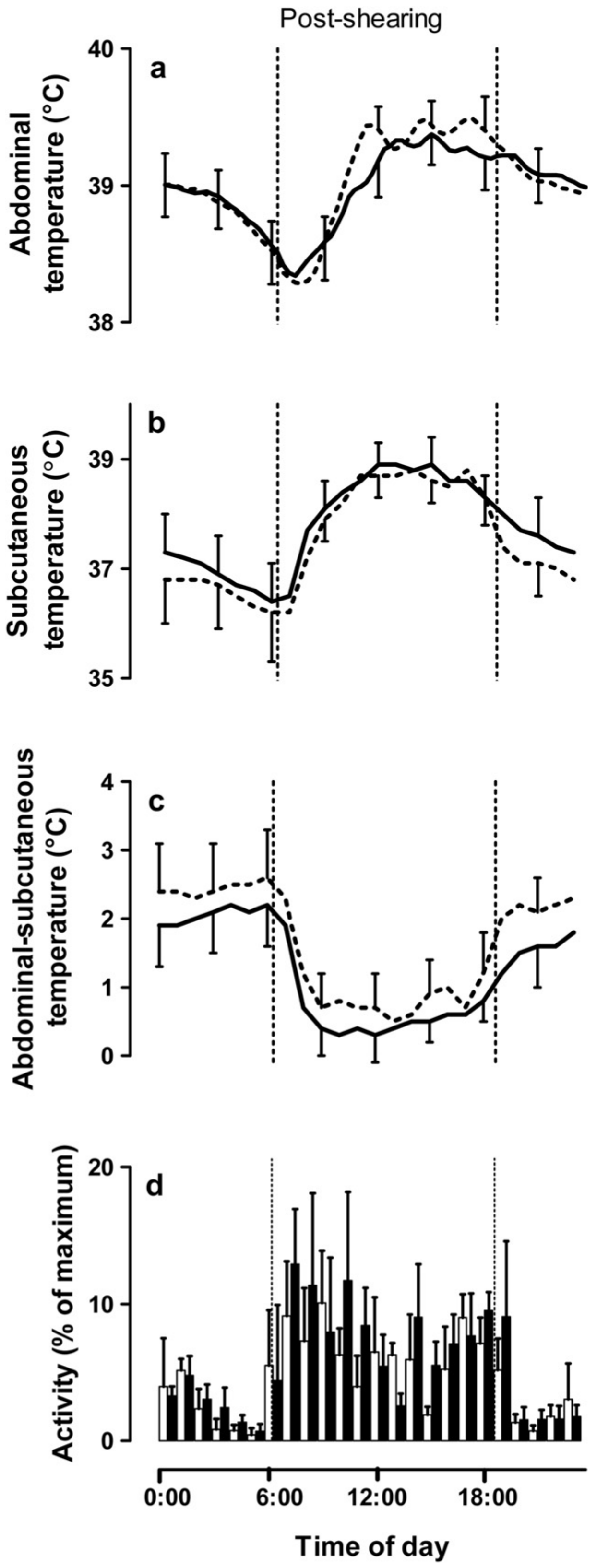

Fig. 2. Nychthemeral rhythm (mean ± SD) of abdominal temperature (a), subcutaneous temperature (b) and the difference between abdominal and subcutaneous temperatures (c) for 12 goats that inhabited the transformed site (dotted line) and 12 goats that inhabited intact site (solid line) over 10 days after summer shearing. The lowest panel (d) shows the nychthemeral rhythm of activity for a single goat that inhabited the transformed site (white bars) and another goat that inhabited the intact site (black bars) over the same 10-day period. The dotted horizontal lines indicate time of sunrise and sunset.

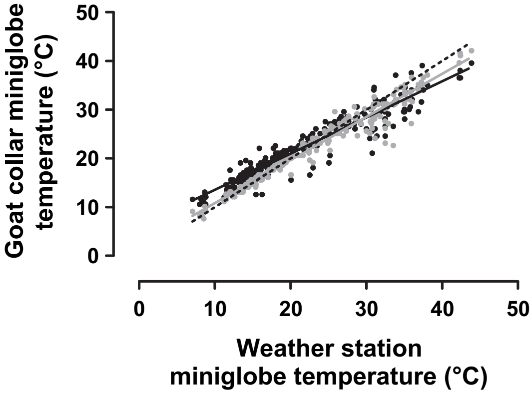

Fig. 3. Scatter diagram showing the relationship between miniglobe temperatures recorded on a single Angora goat that inhabited the transformed site (grey dots and regression line) and another goat that inhabited the intact site (black dots and regression line) plotted against miniglobe temperatures recorded at the nearby weather station, during a 10-day period post-shearing in summer. The dashed line is the line of identity. Both goats exhibited microclimate selection as shown by the slopes of the regression lines being significantly less than the slope of the line of identity. The goat, and, by inference, the herd, that inhabited the intact site selected more stable microclimates as indicated by the lower slope of the regression line ($F_{1;414} = 42.9$, $P < 0.0001$), than did the goat that inhabited the transformed site.

inhabited the transformed site appeared to be less active than the index goat that inhabited the intact site on both hot (mean activity of 3.9 ± 3.6 versus 5.2 ± 5.6 relative activity units) and cold (4.1 ± 4.2 versus 5.3 ± 5.5 relative activity units) days.

3.3. *Response to thermal stress (shearing)*

3.3.1. *Abdominal temperature*

Shearing imposed a thermal stress on the goats (Hetem et al., 2009). After summer shearing, goats that inhabited the transformed site displayed a higher 24-h variability of abdominal temperature, as represented by a greater standard deviation of abdominal temperature (0.46 ± 0.06 °C versus 0.38 ± 0.04 °C, $t_{18} = 3.7$, $P = 0.002$), and had a higher amplitude of abdominal temperature (1.8 ± 0.2 °C versus 1.6 ± 0.1 °C, $t_{18} = 2.8$, $P = 0.01$) than did goats inhabiting the intact site (Fig. 2a). Shorn goats that inhabited the transformed site showed a faster maximum rate of change of abdominal temperature than did the goats that inhabited the intact site (0.4 ± 0.05 °C h^{-1} versus 0.3 ± 0.03 °C h^{-1}, $t_{18} = 3.9$, $P = 0.0009$, Fig. 2a).

3.3.2. *Subcutaneous temperature and activity*

There was no significant difference between subcutaneous temperatures (Fig. 2b), nor the difference between abdominal and subcutaneous temperatures (Fig. 2c), for goats that inhabited the transformed site and goats that inhabited the intact site, after shearing. However, both groups of goats vasoconstricted at night (Fig. 2c), which they did not do on hot days when they were not shorn (Fig. 1f). Both groups of goats also appeared to be inactive during the night, with high levels of activity during the day (Fig. 2d), a similar pattern to that observed in unshorn goats on cold days. In general, the shorn index goat inhabiting the transformed site appeared to be less active than was the shorn index goat inhabiting the intact site (mean activity 4.6 ± 2.9 versus 5.6 ± 3.7 relative activity units).

3.3.3. *Microclimate selection*

The slopes of the regression lines between miniglobe temperatures at the sites chosen by the index goats and miniglobe temperature recorded at a nearby weather station, for 10 days after shearing were significantly less than one (Fig. 3), both for the goat that inhabited the intact site ($F_{1,414} = 223.9$, $P < 0.0001$) and the goat that inhabited the transformed site ($F_{1,414} = 73.3$, $P < 0.0001$). Both regression lines intersected the line of identity within the range of observations, implying that the goats selected microclimates cooler than the prevailing environmental conditions at high environmental heat loads (threshold miniglobe temperature 24 °C) on the intact site and on the transformed site (threshold miniglobe temperature 17 °C). The slope of the regression line was significantly lower ($F_{1,414} = 42.9$, $P < 0.0001$) for the goat that inhabited the intact site (0.74 ± 0.02) than for the goat that inhabited the transformed site (0.89 ± 0.01). Thus, goats on the intact site appeared to select more stable microclimates than did goats that inhabited the transformed site, post-shearing. The combination of lower slope and higher threshold implies that the goat that inhabited the intact site selected warmer microclimates at low environmental heat loads.

3.3.4. *Water influx and turnover*

Although there was no difference in body mass between the two groups (47.1 ± 3.6 kg versus 48.5 ± 6.5 kg, $t_{22} = 0.68$, $P = 0.50$), goats that inhabited the intact site had a significantly higher initial total body water than did goats that inhabited the transformed site (72 ± 9% versus 62 ± 7%, $t_{21} = 2.6$, $P = 0.02$). In both sites, water influx ($F_{2,40} = 82.2$, $P < 0.0001$) and water turnover rates ($F_{3,51} = 82.2$, $P < 0.0001$) of goats decreased with increasing level of dehydration (Fig. 4). Goats in the transformed site had a higher water turnover rate (Fig. 4b, $F_{1,20} = 10.7$, $P < 0.004$) despite their lower water influx (Fig. 4a, $F_{1,20} = 7.8$, $P = 0.01$). It therefore appears that goats in the transformed site were more dependent on evaporative cooling to maintain their abdominal temperature in what would appear to be a more thermally challenging environment.

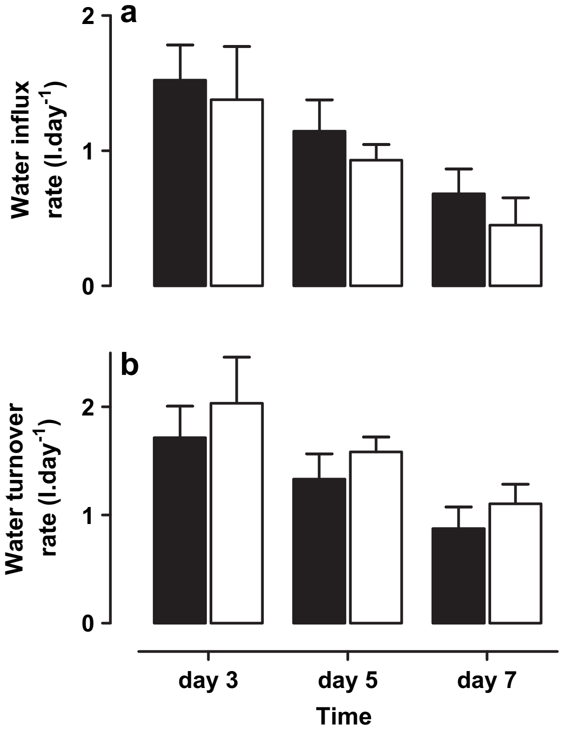

Fig. 4. Mean ± SD of water influx (upper panel) and water turnover rates (lower panel) of 12 goats that inhabited the transformed (white bars) and intact (black bars) sites, after summer shearing, over a seven day period during which the goats were denied access to water.

4. Discussion and conclusions

We have shown that the thermoregulatory responses of Angora goats, under conditions of thermal stress, depend on the habitat that they inhabit. Goats that inhabited our transformed site were more water dependent and appeared more labile thermally than were those that inhabited the intact site. Post-shearing, goats that inhabited the transformed site had higher water turnover rates and were exposed to more variable microclimates (see Lechmere-Oertel, 2003), even though they had a lower water influx, than did goats that inhabited the intact site. Both after summer shearing and on cold days, goats that inhabited the transformed site had a higher amplitude of 24-h abdominal temperature rhythm and a faster maximum rate of abdominal temperature rise, than did the goats that inhabited the intact site. In addition, goats that inhabited the transformed site were more vasoconstricted and generally less active than were goats that inhabited the intact site. Nevertheless, though statistically significant, the differences we observed were small and, under most environmental conditions, the Angora goats responded similarly, irrespective of which site they inhabited.

The physiological differences between the goats that inhabited the intact and the transformed sites may well have been anomalously small as a result of the benign conditions of high rainfall which prevailed at the study site during our study. We found no differences in mass between the goats that inhabited the two sites, and the goats did not exhibit any differences in mohair production (Milne, 2008), so any thermoregulatory differences that we did find were not likely the result of nutritional stress.

The fact that we did find thermoregulatory differences during times of thermal stress between the goats that inhabited the two sites implies that the sites provided different thermal environments. Previous studies have reported that thicket vegetation may restrict wind and create a more humid environment (Henley, 2001), resulting in a more stressful thermal environment by reducing an animals' access to convective and evaporative cooling, on hot days. The higher maximum abdominal temperature of the goats that inhabited the intact site, compared to goats that inhabited the transformed site, on hot days, may reflect those effects. Conversely, the soil of the transformed habitat reached higher maximum and lower minimum temperatures than did that of the intact thicket (Lechmere-Oertel, 2003), implying more thermal variability in the transformed environment. Indeed, goats that inhabited the transformed site displayed higher maximum, greater variability, and faster rates of rise of abdominal temperature than did goats that inhabited the intact site, on cold days. In other species, the amplitude of daily body temperature rhythm depends on habitat features and environmental temperatures, with species from more stable temperate habitats displaying smaller amplitude than do species from desert and tropical habitats, which are exposed to a much greater variability in environmental temperature (Lowe et al., 2001; Refinetti, 1999). Although our climatic variability and habitat differences were less extreme than these examples, those influences may have played out in the significant differences in the 24-h amplitude of abdominal temperature rhythm that we found between the goats that inhabited the transformed site and those that inhabited the intact site.

Despite the habitat effects, the amplitude of abdominal temperature rhythm of our goats remained within a narrow limit of 2 °C. Goats typically regulate core body temperature within narrow limits (Appleman and Delouche, 1958; Piccione et al., 2007), but Angora goats in South Africa are more labile thermally than are other livestock species in the same tropical environment (Hofmeyr et al., 1965). Such breed-specific responses may result from differences in the insulative properties of the hair coat (Bianca and Kunz, 1978), so that removal of the insulation by shearing makes the animal more susceptible to changes in environmental conditions, and the presence of a full coat may further stress Angora goats on hot days (McGregor, 1985). It was around summer shearing that thermoregulatory differences between the goats that inhabited the two sites were most apparent.

Shorn Angora goats in poor body condition are more sensitive to changes in the ambient thermal conditions than goats in good body condition (Fourie, 1984). Similarly, shorn sheep in poor condition show a lower rectal temperature (Hopkins et al., 1978; Morris et al., 1962; Parer, 1963), a greater rate of change and a greater daily amplitude in rectal temperature (Parer, 1963) than shorn sheep in good condition. These differences are similar to those reported here for our shorn goats that inhabited the transformed site compared to the intact site, despite there being no evidence for a loss of body condition of goats that inhabited the transformed site. Such differences in the abdominal temperature profile are therefore likely to be the result of differences in environmental conditions between the two sites.

While they were carrying their full fleeces, our goats remained vasodilated over both day and night (Hetem et al., 2009), as evidenced by the small difference between abdominal and subcutaneous temperatures (Fig. 1f). After summer shearing, however, the goats vasoconstricted at night, and the degree of vasoconstriction (or, at least, the difference between abdominal and subcutaneous temperatures) was greater for the goats that inhabited the transformed site, than in the goats that inhabited the intact site. Morris et al. (1962) found skin temperatures were up to 1.4 °C higher in shorn sheep stocked at high densities than in shorn sheep stocked at low densities in winter. Since high stocking densities decrease the availability of pasture and alter pasture composition and structure (McGregor, 1998), and since transformed thicket has a decreased carrying capacity (Stuart-Hill and Aucamp, 1993), one would expect stocking densities to affect vasoconstriction responses in a way similar to site transformation. The low subcutaneous temperatures of shorn sheep stocked at low densities resulted in a difference between rectal and skin temperatures of nearly 6 °C for sheep stocked at low densities, compared to only 3 °C for those stocked at high densities (Morris et al., 1962), with the latter value similar to the difference for our shorn goats on summer nights. Similarly, Sykes and Slee (1969) found skin temperatures of sheep maintained on a low plane of nutrition to be an average 1.8 °C higher than sheep maintained on a high plane of nutrition, during cold exposure. These authors attributed the failure of heat conservation in poorly nourished, and high-density, sheep to a loss of insulating fat, thinning of the skin, and reduced vasomotor tone of animals on a low plane of nutrition (Morris et al., 1962; Sykes and Slee, 1969). Since even our goats that inhabited the transformed site were not stressed nutritionally (Milne, 2008), and goats generally have less subcutaneous fat than do sheep (Owen et al., 1977), the greater vasoconstriction of our goats that inhabited the transformed site was likely the result of heat loss to the environment potentially being greater on the transformed site, particularly at night. Indeed, the transformed vegetation has been shown to have greater air movement than does intact thicket vegetation (Henley, 2001).

Climatic factors not only are important determinants of body temperature, but also affect the foraging behaviour of both goats (Askins and Turner, 1972) and sheep (Dudzinski and Arnold, 1979). Although we might have expected that goats on the transformed site would have to walk further for an adequate supply of food and water, as found for grazing ruminants in arid areas (Lachica and Aguilera, 2003; Manteca and Smith, 1994), we found that the index goat, and, by implication, the herd, that inhabited our intact site was generally more active than the counterpart that inhabited the transformed site. The higher activity levels on the intact site may be explained by foraging theory, which predicts that animals should feed more selectively when high-quality foods are more abundant (Stephens and Krebs, 1986). Indeed, Angora goats fed more selectively on natural forage, thus increasing their foraging effort and movement rates by nearly 70%, when given a high-quality supplement (Murden and Risenhoover, 1993). Similarly, sheep spent a greater portion of time grazing on pastures which had high levels of soluble carbohydrates (Birrell, 1989), which are abundant in succulent species, such as *P. afra*, as a result of their crassulacean acid metabolism (Borland et al., 2009). Herselman et al. (1999) found that Angora goats that grazed on pasture with a high content of browse had higher heat energy, grazed for longer and took more steps per unit of time spent grazing than did goats that grazed on grass pasture. Our goats on the intact site consumed a high proportion of browse and succulent species such as *P. afra* (Milne, 2008) and so may have foraged for longer, resulting in higher activity levels than goats that inhabited the transformed site.

The high proportion of grass in the diet of goats that inhabited the transformed site likely contributed to the lower water influx of our goats there. Both Angora goats and sheep grazed at high densities have higher water intake than animals grazed at low densities (Morris et al., 1962; McGregor, 1986), a difference which may be attributed to the animals grazed at low-density eating more food with a higher water content. Similarly, desert goats both acquire more water when maintained on alfalfa than on wheat straw (Brosh et al., 1986) and gain more water from pre-formed and metabolic water when maintained on a lucerne hay than on a grass hay diet (Ahmed and El Kheir, 2004). Our goats that inhabited the intact site had access to browse of high moisture content, such as *P. afra*, whereas the goats that inhabited the transformed site had a lower availability of browse and succulents (Milne, 2008), potentially making the goats that inhabited the transformed site more dependent on free water, as found for other grazing ruminants (Kay, 1997), but from which our goats were deprived during the water influx experiment.

Although our goats that inhabited the intact site had higher water influx, they had lower water turnover rates. Conversely, Morris et al. (1962) estimated summer water turnover rates for Merino sheep stocked at low densities to be 26% greater than those of sheep stocked at high densities. The authors suggested that differences in the constitution of the two pastures may have accounted for the difference in water turnover rates, but did not mention what these differences may have been. We believe that the higher water turnover rates of our goats that inhabited the transformed site were the result of differences in the microclimates selected by the goats. Goats that inhabited the transformed site were exposed to higher environmental heat loads than were the goats that inhabited the intact site, particularly during the heat of the day (Fig. 3), and would have had access to fewer microhabitat niches (Lechmere-Oertel, 2003). Since maintaining homeothermy during heat stress demands water, and water turnover rates increase with increasing ambient temperature (Maloiy, 1973), we propose that our goats that inhabited the transformed site were more reliant on evaporative cooling to dissipate their heat load, resulting in higher water turnover rates and lower total body water than those of the goats that inhabited the intact site.

In summary, goats that inhabited the transformed site appeared to be more stressed thermally, and more water dependent, than were goats that inhabited the intact site. We concede that the differences that we observed were small. The year of our study had above average rainfall, and even the goats on the transformed site maintained good body condition. Nevertheless, we demonstrate physiological changes in response to desertification, despite the relatively benign conditions of high rainfall prevalent during our study. Given that climate change is already exacerbating drought extremes (Chamaillé-Jammes et al., 2007), understanding the effects of these extremes will become increasingly important. The long-term viability and sustainability of agricultural herbivores will depend on maintaining appropriate stocking rates under changing climatic conditions (Richardson et al., 2005). The use of sophisticated physiological measurements, as we have demonstrated in our goats, will allow a better understanding of the consequences for herbivores of not only the direct thermal effects of climate change but also of habitat changes.

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