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Validation of a Biotelemetric Technique, Using Ambulatory Miniature Black Globe Thermometers, to Quantify Thermoregulatory Behaviour in Ungulates

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ABSTRACT Behavioural thermoregulation is an animal's primary defence against changes in the thermal environment. We aimed to validate a remote technique to quantify the thermal environment behaviourally selected by free-ranging ungulates. First, we demonstrated that the temperature of miniature, 30 mm diameter, black globes (miniglobes) could be converted to standard, 150 mm diameter, black globe temperatures. Miniglobe temperature sensors subsequently were fitted to collars on three free-ranging ungulates, namely blue wildebeest (*Connochaetes taurinus*), impala (*Aepyceros melampus*) and horse (*Equus caballus*). Behavioural observations were reflected in animal miniglobe temperatures which differed from those recorded by an identical miniglobe on a nearby exposed weather station. The wildebeest often selected sites protected from the wind, whereas the impala and the horse sheltered from the sun. Nested analysis of variances revealed that the impala and horse selected significantly less variable environments than those recorded at the weather station ($P < 0.001$) over a 20-min time interval, whereas, the microclimates selected by wildebeest tended to be more variable ($P = 0.08$). Correlation of animal miniglobe against weather station miniglobe temperature resulted in regression slopes significantly less than one ($P < 0.001$) for all species studied, implying that, overall, the animals selected cooler microclimate s at high environmental heat loads and/or warmer microclimates at low environmental heat loads. We, therefore, have developed an ambulatory device, which can be attached to free-ranging animals, to remotely quantify thermoregulatory behaviour and selected microclimates. *J. Exp. Zool. 307A:342–356, 2007.*

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Free-living terrestrial animals employ a suite of thermoregulatory behaviours in thermally heterogeneous habitats, thus selecting their microclimate (Bartholomew, '64, '87; Huey, '91). While estimating the consequences of implementing an autonomic effector, such as panting or shivering, on an animal's thermal balance is relatively straightforward, estimating how behaviour affects thermal balance is not. The heat exchange characteristics of a specific microenvironment have been assessed using hollow models (Bakken et al., 1985, Huey, '91, Hertz et al., '93), but the animal's selection of different microenvironments is more difficult to ascertain.

Often, when microclimates are assessed, the only variable measured is ambient dry-bulb

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temperature (Kinahan et al., 2007). The rate of heat exchange of an animal depends not only on dry-bulb temperature but also on wind velocity, solar radiation, long wave radiation and ambient water vapour pressure. Vernon ('30) proposed the use of the temperature of a hollow, 150 mm diameter, copper globe painted matt black, to derive the mean radiant temperature (Vernon '32; Bedford and Warner, '34; Kerslake, '72) in an attempt to assess the radiant component of the human microclimate. The temperature of the globe reaches equilibrium when radiant heat exchange is equal and opposite to convective heat exchange, which, in turn, depends on both dry-bulb temperature and wind speed. Although the temperature of the globe is not affected by ambient water vapour pressure, it is affected by three of the four factors which influence the animal's thermal balance. Hence, though it was not Vernon's original intention, users of his globe began to employ globe temperature, rather than mean radiant or dry-bulb temperatures, as a physiologically more-appropriate index of the microclimate.

While the globe thermometer was developed to assess the human microclimate, enterprising comparative physiologists saw its potential for estimating the thermal load on other species (Bond and Kelly, '55; Schmidt-Nielsen et al., '56; Kuehn et al., '70). Though it seemed implausible that a simple black globe could be useful in assessing thermal balance of animals of widely varying mass and appearance, it has been established that animal size, colour and morphology may be only minor confounders of the thermal load experienced (Walsberg and Weathers, '86; Vitt and Sartorius, '99). Thus, for many investigations, the 150 mm globe thermometer has supplanted the traditional species-specific hollow-body models as an estimate of operative environmental temperature (Huey, '91) and has been used successfully to assess the microclimates of animals, ranging from cattle, through lizards, to bees (Seely et al., '90; Thiagarajan and Thomas, '92; Corbet et al., '93).

Conventionally, when globe thermometers have been used to assess thermal load, they have been attached to fixed weather stations exposed to full radiant heat load and prevailing wind. If measurement of the microclimate selected by a free-living animal in a thermally heterogeneous habitat is needed, multiple weather stations are required in numerous habitats (Huey, '91; Kinahan et al., 2007). We suggested an alternative approach; attach the globe thermometer to the animal (Fuller et al., '99). In recent years biotelemetric collars have been successfully used to monitor a range of parameters, including GPS position, body movement and air temperature (Cooke et al., 2004; Brosh et al., 2006; Kinahan et al., 2007). Collars therefore provide the ideal location for the attachment of an ambulatory globe thermometer.

But attaching a 150 mm diameter globe to an animal's collar is impractical for all but the largest species. Smaller globes have been designed for commercially available human heat stress monitors. We know that these small globes do not reach the same equilibrium temperature as 150 mm globes in the same thermal environment, because their heat transfer coefficients for both radiant and convective heat transfer are different (Bond and Kelly, '55; Graves, '74). Many of the commercially available personal heat stress monitors appear not to address the issue of globe diameter. When globes of smaller diameters (''miniglobes'') are employed, it is desirable to standardise the measurements to what the temperature attained by a standard 150 mm globe would be, otherwise comparisons between studies would be meaningless. Hey ('68) proposed a linear approximation for converting temperatures measured by miniglobes to standard globe temperatures. Later, Peters et al. ('76) proposed the manipulation of heat transfer equations as a more accurate approach to convert miniglobe to standard globe temperature, for use in personal heat stress monitors. However, neither study tested the accuracy of their conversion. We address this issue by exposing globes of different sizes to varying temperature, radiation and convection environments in a climatic chamber. Moreover, we also developed and tested a new algorithm for the conversion of miniglobe to standard globe temperature.

After successfully converting miniglobe to standard globe temperatures, we then validated an ambulatory technique to assess the microclimates selected by a free-living terrestrial animal in a thermally heterogeneous habitat. We attached 30 mm-diameter miniglobes to collars on three animals of different ungulate species (blue wildebeest (*Connochaetes taurinus*), impala (*Aepyceros melampus*) and horse (*Equus caballus*)) and measured miniglobe temperatures continually as the animals exhibited their normal behaviour undisturbed. We correlated miniglobe temperature with observed behaviour, over simultaneous time periods. To the best of our knowledge, no one has attempted to validate ambulatory globe thermometers, attached to an animal, as a means to quantify thermoregulatory behaviour.

MATERIALS AND METHODS

Agreement between miniglobe and standard globe temperatures

Estimating standard globe temperatures from miniglobe temperatures

A globe thermometer will reach thermal equilibrium when the rate at which it exchanges heat through convection with its environment is equal and opposite to the rate it exchanges heat through radiation (Kerslake, '72):

$$\sigma\epsilon(T_{\mathrm{r}}^4 - T_{\mathrm{g}}^4) = h_{\mathrm{cg}}(T_{\mathrm{g}} - T_{\mathrm{a}}),$$

where σ is a Stefan–Boltzmann constant ($5.67 \times 10^{-8}\,\mathrm{W\,m^{-2}\,K^{-4}}$), ϵ is the emissivity of the globe surface, T_{r} the mean environmental radiant temperature (K), T_{g} the globe temperature (K), T_{a} the ambient dry-bulb temperature (K) and h_{cg} the convective heat transfer coefficient of the globe ($\mathrm{W\,m^{-2}\,K^{-1}}$). If the globe has a non-reflecting black coating, ϵ is approximately equal to 1. Setting $\epsilon = 1$, the thermal equilibrium equation can be rearranged as:

$$T_{\mathrm{r}}^4 = \frac{h_{\mathrm{cg}}(T_{\mathrm{g}} - T_{\mathrm{a}})}{\sigma} + T_{\mathrm{g}}^4.$$

For spheres with diameters of the order of 100 mm, the convective heat transfer coefficient is inversely proportional to the 0.4th power of diameter (Kerslake, '72), so that, comparing a miniglobe to a standard globe:

$$\frac{h_{\mathrm{cmg}}}{h_{\mathrm{csg}}} = \left(\frac{L_{\mathrm{mg}}}{L_{\mathrm{sg}}}\right)^{-0.4},$$

where h_{c} is the convective heat transfer coefficient ($\mathrm{W\,m^{-2}\,K^{-1}}$), L the globe diameter (mm) and sg or mg refer to values for the standard (150 mm diameter) or miniglobe, respectively.

Convective heat transfer coefficients are dependent not only on diameter, but also on the prevailing wind speed and air pressure (Whillier and Mitchell, '68; Mitchell, '74). At sea level atmospheric pressure and air temperature of 20°C, the convective coefficient of the standard globe (Kerslake, '72) is:

$$h_{\mathrm{cg}} = 14.1 \times V^{0.6},$$

where V is the wind speed ($\mathrm{m\,s^{-1}}$). This convective coefficient constant remains relatively stable over a wide range of air temperatures, but not over the range of atmospheric pressures likely to be encountered by terrestrial animals at different altitudes (Mitchell, '74). Kerslake ('72) did not explicitly take account of atmospheric pressure. The convective heat transfer coefficient of a non-standard globe can be derived from the above formula by incorporating corrections for atmospheric pressure and differences in diameter, giving:

$$h_{\mathrm{cmg}} = 14.1\left(\frac{P}{101.3}\right)^{-0.6}\left(\frac{\mathrm{Lmg}}{150}\right)^{-0.4}V^{0.6},$$

where P is the barometric pressure (kPa).

Since the environmental mean radiant temperature is the same for globes of different diameters in the same environment, it can be calculated from their respective thermal equilibrium equations that:

$$\frac{h_{\mathrm{cmg}}(T_{\mathrm{mg}} - T_{\mathrm{a}})}{\sigma} + T_{\mathrm{mg}}^4 = \frac{h_{\mathrm{csg}}(T_{\mathrm{sg}} - T_{\mathrm{a}})}{\sigma} + T_{\mathrm{sg}}^4,$$

where T_{mg} is the equilibrium temperature of the miniglobe (K) and T_{sg} the equilibrium temperature of the standard globe (K).

Solving for the standard globe temperature gives:

$$T_{\mathrm{sg}} = \left[\frac{\left(T_{\mathrm{mg}}^3 + \frac{h_{\mathrm{cmg}}}{\sigma}\right)T_{\mathrm{mg}} - \left(\frac{h_{\mathrm{cmg}} - h_{\mathrm{csg}}}{\sigma}\right)T_{\mathrm{a}}}{\left(T_{\mathrm{sg}}^3 + \frac{h_{\mathrm{csg}}}{\sigma}\right)}\right].$$

As a quartic equation, the equation cannot be solved easily by algebraic procedures, but by using modern computing power it can be solved by successive approximation. Thus, what the standard globe temperatures would have been, can be calculated from the temperature measured by a miniglobe of known diameter, dry-bulb temperature and wind speed, at a known barometric pressure. We wrote a software program to apply the heat transfer equations and to execute successive approximations, terminating when two successive approximations differed by less than 0.1 K, so as to calculate standard globe temperatures from that of a miniglobe of any diameter.[1]

Testing of the conversion algorithm

We conducted a laboratory study to compare the temperatures obtained from a single standard (150 mm diameter) black globe to the concurrently measured temperature of a single 30 mm diameter miniglobe, in the same environment. We assessed three methods to approximate standard globe

[1]The software was written as a macro in Microsoft Excel using the Microsoft Visual Basic Programming System and is freely available from the authors.

temperature from miniglobe temperature; (1) our algorithm as described above, (2) Hey ('68) approximation and (3) a conversion formula apparently used in commercially available personal heat stress monitors (Peters et al., '76).

Our 150 mm standard globes consisted of hollow, thin-walled copper spheres and the 30 mm miniglobes were hollow thin-walled bronze spheres (Press Spinning & Stamping Co., Cape Town, South Africa). Both globes were painted matt black and had a fine thermocouple suspended in the centre. The thermocouple voltage was referenced against an electronic ice point cell (Omega Engineering Inc., Stamford, USA) and recorded on a data logger (Hewlett-Packard data acquisition/control unit, HP 75000 series B). Each thermocouple was calibrated by water immersion against a precision thermometer (Quat 100, Heraeus, Hanau, Germany) to an accuracy of better than 0.1°C. The globes were mounted on a polyvinyl chloride base and placed along side each other in the centre of a 3 m × 3 m × 3 m climatic chamber, in which we could vary and control ambient dry-bulb temperature, wind speed and humidity. Ambient dry-bulb temperature was measured by an array of fine-tipped thermocouples placed in the free-stream environment above the globes, but not exposed to radiation. Wind speed was varied by changing the speed of a fan, and measured using a portable thermo-anemometer (Alnor GGA-65, Turku, Finland). Solar radiation was simulated using 500 W halogen lamps (Cixi Zhongfa lamps co., Ltd, Ningbo, China) placed such that both globes were irradiated equally. Net heat flow under radiation was measured at the globe surface using a calibrated Heat Flux Transducer (HA 12-18-5-P, Thermonetics corp, CA, USA) connected to a Fluke 8800A digital multimeter (Fluke Corporation, WA, USA).

A range of conditions were tested, with dry-bulb temperature (15–35°C), wind speed (0–4 $m\,s^{-1}$) and radiation (90–1,200 $W\,m^{-2}$) being varied systematically to simulate the range of conditions prevailing historically, during the summer months, at the field site where our animals were resident. The globes were allowed to stabilise to 0.1°C at a fixed combination of ambient dry-bulb temperature, wind speed and radiant temperature and then one of these variables was altered while the others kept constant. Globe temperatures were recorded for half an hour after an ambient variable was changed (''dynamic conditions''), and then for a further half an hour (''static conditions''). We also conducted a single test in an extreme condition unlikely to occur in the natural environment, but designed to challenge the validity of the algorithm, namely high wind speed (3.5 $m\,s^{-1}$), high radiation (1,148 $W\,m^{-2}$) and low dry-bulb temperature (6°C). In addition, we measured the response times of both the standard globe and miniglobe by initially allowing them to stabilise at 23°C dry-bulb and radiant temperature and then moving them simultaneously and quickly into a cold environment (dry-bulb and mean radiant temperature of 5°C) and, on a separate occasion, a hot environment (dry-bulb and mean radiant temperature of 35°C) and measuring the standard globe and miniglobe temperatures every 30 s. We set the wind speeds in the new environment at 0.3 and 35 $m\,s^{-1}$, on separate occasions. Time constants were calculated assuming an exponential approach to equilibrium.

Data analysis

The 95% limits of agreement (Bland and Altman, '86) for differences between actual miniglobe temperature and standard globe temperature were calculated, as well as between standard globe temperature and the standard globe estimates derived from Hey ('68) approximation, a conversion formula derived by the US National Institute for Occupational Safely and Health and apparently used in commercially available personal heat stress monitors (Peters et al., '76), and our algorithm and software.

Use of miniglobes to investigate thermoregulatory behaviour

Field site and animals used

The field test was performed in September 2003 (southern hemisphere spring) at the National Zoological Gardens Game Breeding Centre in Lichtenburg (26°07′S, 26°10′E, with an altitude of 1,450 m), 220 km west of Johannesburg, South Africa. We used an impala ewe (*Aepyceros melampus*, Lichenstein), a blue wildebeest bull (*Connochaetes taurinus*, Burchell) and a semi-domesticated female horse (*Equus caballus*, Linnaeus). All the animals were released into a 62 ha fenced enclosure, which consisted predominantly of flat and open grassland with a few scattered trees and shrubs.

To attach the equipment, the impala was chemically immobilised with 1 mg etorphine (M99, Logos Agvet, Johannesburg, South Africa) and 40 mg azaperone (Kyron Laboratories, Johannesburg, South Africa), and the wildebeest was chemically immobilised with 4 mg etorphine (M99, Logos Agvet) and 100 mg azaperone (Kyron Laboratories). Collars holding a 30 mm miniglobe and tracking telemeter (Africa Wildlife Tracking, Pretoria, South Africa) were fitted to each animal (Fig. 1). Each collar was custom designed to weigh less than 1% of the animals' body mass and have a width of 30–50 mm. A weight at the base of the collar ensured that the miniglobe remained over the dorsum of the neck and could not be shaded by the animal. The effect of the etorphine then was reversed using 2 mg diprenorphine (M5050, Logos Agvet, Johannesburg, South Africa) for the impala and 8 mg diprenorphine (M5050, Logos Agvet) for the wildebeest. The animals became mobile within about 10 min. They were released into an enclosure, where they joined conspecifics to form herds of approximately ten individuals. The horse mare was restrained without sedation, collared and released into the same enclosure. All animals were recaptured after 1 month, using the same immobilisation procedure, the equipment removed and the animals released to rejoin their herds. The Animal Ethics Screening Committee of the University of the Witwatersrand approved the experimental procedures (clearance no. 2003/20/4).

The temperature of each miniglobe was measured with an uncoated bead thermistor (bead diameter 1.5 mm; 27–10K4A801, Onset Computer Corporation, Pocasset, MA, USA), positioned at the centre of the globe. The globe was attached to a 10 mm diameter, polyvinyl chloride rod, which in turn was attached to the outer surface of the collar. The rod provided thermal insulation of the miniglobe from the collar, and also housed the leads from the thermistor. Dental acrylic added strength to attachment points. The thermistor was connected to a miniature thermometric data logger (StowAway, Onset Computer Corporation), with a temperature range of -39 to $+122°C$, an intrinsic accuracy of 0.4°C and a mass of approximately 50 g, which was moulded into the collar (Fig. 1). All temperature sensors were calibrated against a certified precision thermometer (Quat 100, Heraeus, Hanau, Germany) in an insulated water bath. Globe temperatures were recorded every 5 min for the wildebeest and horse, and, because some of our loggers had a lower memory capacity, every 10 min for the impala, for a minimum of 2 weeks.

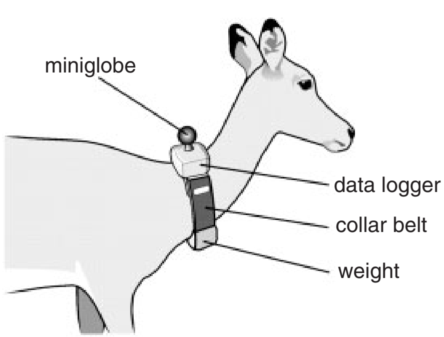

Fig. 1. Miniglobe thermometer attached to a collar and fitted on an impala.

We collected climatic data by erecting a portable weather station at the site (Hobo Weather Station, Onset Computer Corporation). We monitored wind speed, photosynthetically active radiation (PAR), dry-bulb temperature, relative humidity and standard (150 mm diameter) globe temperature, 1 m above the ground. In addition, we attached a miniglobe, identical to those on the collars, connected to a separate data logger (StowAway, Onset Computer Corporation), 1 m above the ground. Both globes on the weather station were situated on the northern side of the weather station so that they were never shaded by the remaining equipment. As wind speed can vary over short distances, an additional wind speed measurement was made in the vicinity of the animal, with a portable thermo-anemometer (Alnor GGA-65, Turku, Finland), to coincide with behavioural observations.

Behavioural observations

As the Game Breeding Centre was open to the public confined to slow-moving vehicles, the animals were accustomed to vehicle activity, so we could make behavioural observations from a vehicle, without impacting adversely on the animals' natural behavioural patterns. The herds were observed from inside a stationary vehicle parked between 10 and 250 m (typically 100 m) away, with binoculars (Nikon Travelite III 8×23CF). Behavioural data were collected by one observer (RSH) using instantaneous sampling methods (Altmann, '74), identifying the behaviour of the instrumented animals every 5 min, synchronously with the temperature measurement on the data loggers.

Behaviour was assigned to a sub-category within various categories, with each sub-category being mutually exclusive. The categories defined the animal's exposure to the sun (sun or shade), body posture (standing upright or lying recumbent), activity type (grazing with snout to ground;

walking, which was classified as moving with snout above ground; or little/no activity, which included time spent ruminating), and finally we defined wind exposure subjectively (exposed to or protected from the wind). Measurements for each individual were made for a minimum of 12 h, divided into 4-h sampling sessions. The timing of these behavioural sampling sessions was based on animal activity periods reported by Estes ('97) and Smithers ('83), to cover a variety of potential behaviours.

Data analysis

Miniglobe temperatures on the collars were compared to concurrent miniglobe temperatures from the nearby weather station and the animals' observed behaviour. We extracted the upper and lower quartile ranges of the miniglobe temperatures on the animal and the weather station and compared them using an Unpaired Student's *t*-tests. We also used the χ^2 test to test for associations between the likelihood of an observed behavioural category occurring when miniglobe temperature on the animal was both higher and lower than the stationary miniglobe on the nearby weather station.

We correlated weather station and animal miniglobe temperatures using linear Pearson procedures. Thereafter, we tested whether the slope of the regression equation was significantly different from one (the slope of the line of identity), to assess whether the globe temperature measured on the animals was the same as that measured at the exposed weather station, and so whether the animals were tracking ambient conditions or were selecting micro-environments. A nested analysis of variance (ANOVA) was used to test variability between the weather station and collar miniglobe temperatures on different time scales (Maloney et al., 2002). The analysis was performed over the following time scales: over all days for which data were obtained, over each day, over 4-h intervals, over each hour and at 20-min intervals. In all statistical tests values of $P<0.05$ were considered significant.

RESULTS

Agreement between miniglobe and standard globe temperatures

Miniglobe temperatures were consistently lower than standard globe temperatures measured concurrently in the climatic chamber environment, in which dry bulb temperature, wind speed and radiation intensity were independently varied over a range of environmental conditions (Fig. 2A). Miniglobe temperatures converted to standard globe temperature by our algorithm cluster around the line of identity under both dynamic and stable conditions (Fig. 2B and C), indicating the potential for the converted miniglobe temperatures to predict actual standard globe temperatures without bias. However, the scatter around the line of identity was greater under dynamic (Fig. 2B) compared to stable conditions (Fig. 2C).

A plausible explanation for the less favourable agreement between actual standard globe temperature and those estimated from miniglobe temperature shortly after a change in conditions would be that the smaller-diameter globe responded more quickly to the changing environmental conditions. The miniglobe indeed did exhibit shorter response times (Fig. 3), with times to equilibration ($5\times$ the time constant τ, i.e. the time taken to reach 99% of final temperature) being faster at high wind speeds. The time to equilibration of the standard globe placed at $0.3\,\mathrm{m\,s^{-1}}$ wind speed was 25-min, compared to 20-min for the miniglobe, whereas at $3.5\,\mathrm{m\,s^{-1}}$ wind speed, the equivalent times to equilibrium were 10 and 7.5-min, respectively. While we attribute most of the difference in time constant between the globes to the effect of size, we cannot rule out the possibility that the different thermal properties of the brass miniglobe compared to the copper standard globe had a small effect.

The accuracy of the different conversion algorithms proposed to estimate standard globe temperatures from miniglobe temperatures were assessed using the limits of agreement analysis (Bland and Altman, '86) (Table 1). The average difference between measured standard globe and the converted miniglobe temperatures was smaller under dynamic compared to static conditions, but the variability from environment to environment was much greater under dynamic conditions. All converted miniglobe temperatures reflected standard globe temperatures more accurately than did the raw miniglobe temperature. Under most environmental conditions, standard globe temperatures estimated with our algorithm were very similar to those achieved with Hey ('68) estimation, and closer to actual standard globe temperature than the algorithm of Peters et al. ('76). However, under extreme conditions of high radiation ($1{,}148\,\mathrm{W\,m^{-2}}$) and wind speeds ($3.5\,\mathrm{m\,s^{-1}}$)

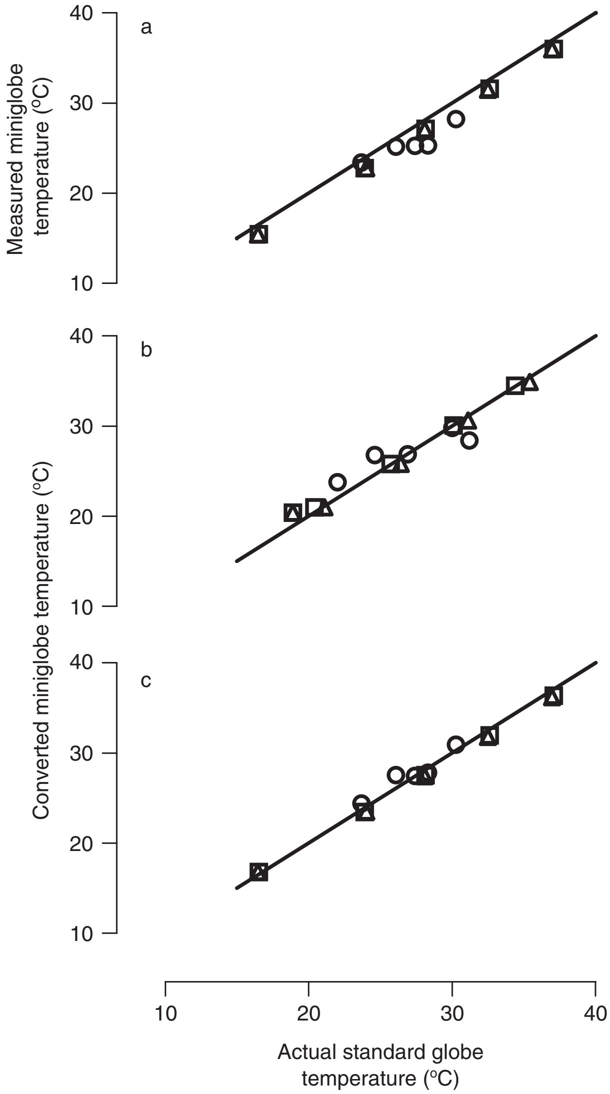

Fig. 2. Correlation between measured standard (150 mm diameter) globe temperature and measured miniglobe (30 mm diameter) temperatures (**a**), and between measured standard globe temperature and standard globe temperature estimated from miniglobe temperatures by our analysis of the heat transfer equations under dynamic conditions (**b**) (first half hour after changing ambient conditions) and under static conditions (**c**) (second half hour of measurements after a change in ambient conditions). Both globes were placed under the same environmental conditions in a climatic chamber and their temperatures measured while we independently varied dry-bulb temperature between 15 and 35°C (□), wind speed between 0 and 4 m s^{-1} (△) and radiation between 90 and 1,200 W m^{-2} (○). The solid lines are lines of identity ($y = x$).

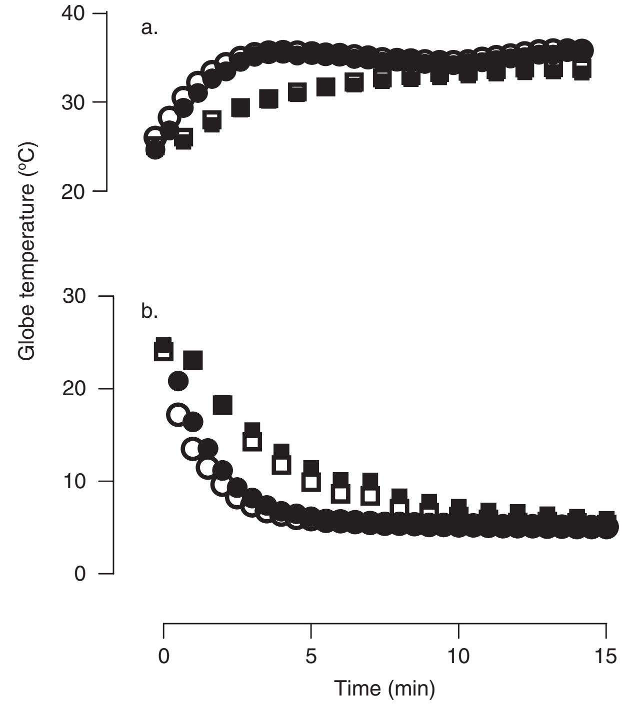

Fig. 3. Temperatures indicated by the standard globe (closed symbols) and miniglobe (open symbols) after their rapid transfer from a 23°C environment to a 35°C environment (**a**) and from a 23°C environment to a 5°C environment (b) on two occasions, with low wind speeds (0.3 m s^{-1} ■ and □) and high wind speed (3.5 m s^{-1} ● and ○). At low wind speed, calculated time constants were 6 and 7 min in the hot environment (upper panel), and 10 and 13 min in the cold environment (lower panel), for miniglobes and standard globes, respectively. At the high wind speed, time constants were reduced to 2 and 2.5 min in the hot environment (**a**), and 4 and 4.5 min in the cold environment (**b**), for miniglobes and standard globes, respectively.

accompanied by low temperatures (6°C), Hey ('68) estimation overestimated standard globe temperature by nearly 4°C, compared to only 1.8°C by our conversion algorithm. Under these extreme conditions and conditions of high radiation Peters et al. ('76) algorithm performed the best.

Use of miniglobes to investigate thermoregulatory behaviour

Field site environment

For the 1-month study period, average wind speed, dry-bulb air temperature and solar radiation varied as a function of time of day at the study site (Fig. 4). Wind speed was highest in the mid-morning, decreased progressively throughout the afternoon, but remained higher during the day than during the night. Solar radiation showed the expected bell-shaped distribution, with a mean peak of approximately 1,800 uE at 13:00, and a maximum exceeding 2,000 uE. The low standard deviations of solar radiation measurements were the consequence of predominantly cloudless skies. Hourly mean dry-bulb temperature ranged between 10 and 27°C, reaching an absolute

TABLE 1. Summary of the 95% limits of agreement (mean ± 1.96 SD) for the difference between standard globe temperatures and the raw miniglobe temperatures measured concurrently in the same environment, as well as standard globe temperatures estimated from miniglobe temperatures according to Hey ('68) approximation, Peters et al. ('76) conversion and our algorithm and software

	Raw miniglobe		Hey ('68) approximation		Peters et al. ('76) formula		Our algorithm and software	
	Static	Dynamic	Static	Dynamic	Static	Dynamic	Static	Dynamic
Temperature variation (15–35°C)	−1.04±0.05	−0.82±0.24	−0.42±0.41	−0.12±0.90	−0.59±0.48	−0.39±0.93	−0.42±0.42	−0.11±0.91
Wind variation (0–4 $m\,s^{-1}$)	−1.06±0.07	−0.82±0.31	−0.46±0.45	−0.12±0.87	−0.63±0.48	−0.35±0.83	−0.45±0.46	−0.11±0.88
Radiation variation (90–1,200 $W\,m^{-2}$)	−1.70±1.10	−1.59±1.16	0.67±0.82	0.27±0.91	0.48±0.82	0.05±0.91	0.73±0.95	0.31±0.92
Extreme conditions (6°C, 3.5 $m\,s^{-1}$, 1,150 $W\,m^{-2}$)	−2.27±0.58		3.80±0.35		1.45±0.42		1.77±0.35	

We independently varied each of the three environmental variables under both static and dynamic conditions. Dynamic measurements were made at times 0, 10 and 20 min after the change in environmental conditions, whereas static conditions were averaged over 30–60 min following a change in environment.

minimum and maximum of 1 and 35°C, respectively. Hourly mean standard (150 mm diameter) black globe temperatures varied between 9 and 38°C, reaching an absolute minimum of 0°C and an absolute maximum of 45°C.

Ambulatory miniglobes on animals

Figure 5 shows typical examples of temperatures measured by identical miniglobes on the collar of an animal and on the fixed weather station, for the three species studied, together with records of behaviour made by direct observation. For all three species, ambulatory miniglobe temperature deviated from the miniglobe temperature on the fixed weather station for at least part of the day or night. On the days of observation, the temperature of the wildebeest's miniglobe was usually within 1°C of that recorded at the weather station (Fig. 5A). That agreement is reflected in the behavioural observations, with the wildebeest seeking shade only on two brief occasions and spending the majority of the day grazing in the sun. In the morning, however, the temperature of the miniglobe on the wildebeest exceeded that of the miniglobe on the weather station by up to 10°C just after 9:00 (see Fig. 5A). At this time the animal was protected from strong winds by assuming a lying down posture or taking refuge behind bushes. All periods when collar miniglobe temperatures exceeded the weather station miniglobe by more than 10°C were associated with high wind speeds at the weather station ($3.0 \pm 0.1\,m\,s^{-1}$). The mean standard globe temperatures of the microclimate selected in these circumstances was calculated, from the animal's miniglobe temperature, to be 31.7 ± 2.5°C, at a time when standard globe temperature on the exposed weather station averaged 22.3 ± 3.0°C.

The impala did not remain in any particular microclimate for long, however, even these transient changes in the behaviourally selected microclimate were reflected in corresponding changes in the animal's miniglobe temperatures (Fig. 5B). For example, impala miniglobe temperature decreased abruptly when the animal entered shade shortly after noon. The calculated standard globe temperature of the microclimate selected in the periods when collar miniglobe temperature was more than 5°C below the miniglobe at the weather station averaged 24.7 ± 0.8°C; the standard globe temperature on the weather station averaged 31.4 ± 1.3°C over the same time. The horse also entered shade on occasions. Fig. 5C shows a

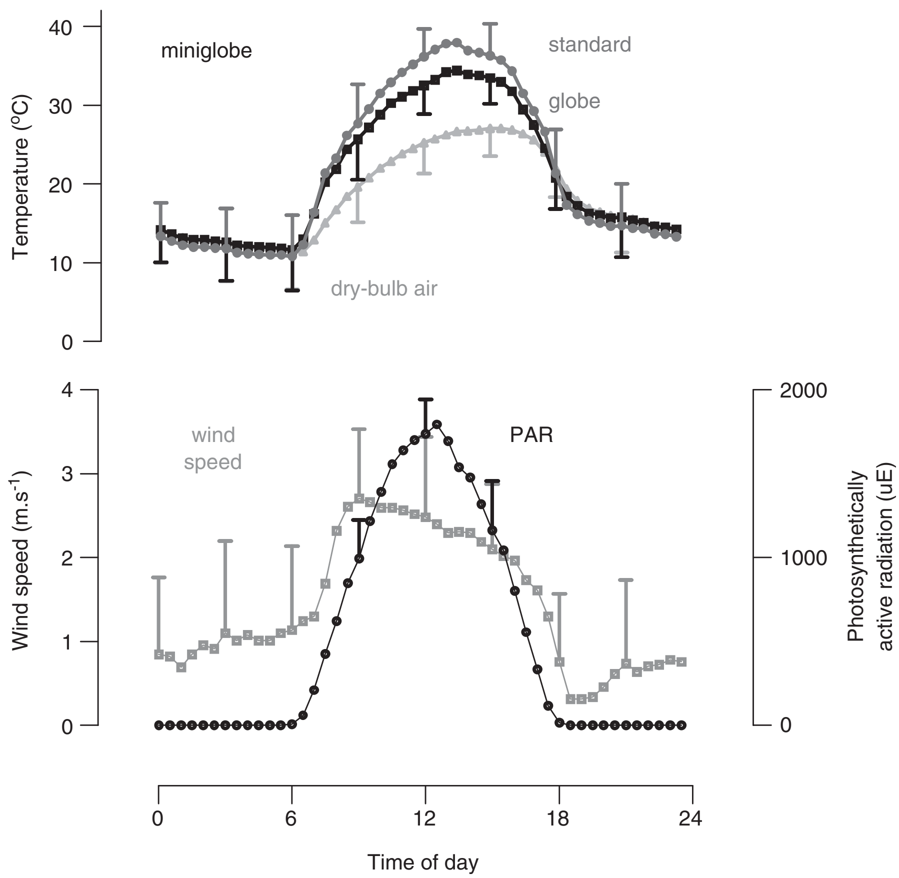

Fig. 4. Field site weather station data, showing the miniglobe, standard globe and air temperatures (upper panel), as well as photosynthetically active radiation and wind speed (lower panel), as a function of time of day, as mean and SD for the 1-month study period.

decrease of nearly 10°C in horse miniglobe temperatures, compared to the weather station miniglobe temperatures, on one such occasion when the animal entered shade at 12:25. The calculated standard globe temperature to which the horse was exposed just before shade seeking was 37°C, which decreased to 23.3°C on entering shade.

The examples shown in Fig. 5 reveal the potential for the use of the collar miniglobe as a biotelemetric measure of thermoregulatory behaviour. To confirm that potential quantitatively we plotted every measurement of collar miniglobe temperature against the weather station miniglobe temperature prevailing at the time and fitted regression lines to the data. The scatter of data around the lines of identity indicate how the animal miniglobe temperatures differed from those at the weather station. At low environmental temperatures, during the night, both impala and wildebeest scattergrams show an upward shift, consistent with the animals selecting microclimates warmer than that at the exposed weather station. During the heat of the day, the impala and horse often reduced their environmental heat load by seeking shade. This thermoregulatory behaviour was associated with a downward shift of the scattergram at the high environmental heat loads (Fig. 6B and C). Conversely, wildebeest miniglobe temperatures were higher, generally, than the weather station miniglobe temperatures throughout the day, and sometimes exceeded weather station miniglobe temperatures by more than 10°C (Fig. 6A). These shifts were consistent with our observation that the wildebeest sought protection from strong winds, and did not seek shade.

If animals use modification of their thermal environment to aid homeostasis, and if collar miniglobe temperatures reflect such a response, then the animal's miniglobe temperatures should be higher than the weather station miniglobe temperatures at low environmental heat loads, and/or lower than the weather station miniglobe temperatures at high environmental heat loads.

Such an outcome would be reflected in the slope of a regression line relating collar miniglobe to weather station miniglobe being significantly less than one. For all three animals studied, that proved to be the case ($F_{1,3240} = 10.18$, $P = 0.001$ for the wildebeest, $F_{1,1736} = 140.64$, $P < 0.0001$ for the impala, $F_{1,7616} = 588.30$, $P < 0.0001$ for the horse). However, such analysis provides no information on the elevation of the slope and further analysis may be necessary for a more complete understanding of thermoregulatory behaviour.

For the second quantitative analysis of collar miniglobe temperatures, as indices of thermoregulatory behaviour, we targeted the circumstances in which the environment of each animal was particularly hot, or particularly cold, by extracting the upper and lower quartiles of the weather station miniglobe temperatures, and then investigated whether there was a statistically significant difference between collar miniglobe temperature and weather station miniglobe temperature at that time. Upper quartile temperatures tended to occur around solar noon, and lower quartile temperatures at night. The temperature of the miniglobes on the collar of the wildebeest, impala, and horse all were significantly higher than that of the weather station miniglobe at the lower quartile range ($t_{760} = 12.26$, $P < 0.0001$, $t_{726} = 8.32$, $P < 0.0001$, $t_{1735} = 3.78$, $P = 0.0002$, respectively). These results are consistent with the animals selecting warmer environments, from amongst those accessible, at night. We were not able to observe the horse or impala at night, but observed the wildebeest lying close to the vegetation at night.

Although analysis of the lower quartiles yielded similar results between the species, interesting differences in the thermoregulatory behaviour observed were picked up by analysis of the upper quartile ranges. The wildebeest miniglobe temperatures were higher than those recorded at the weather station within the upper quartile ranges ($t_{793} = 10.74$, $P < 0.0001$), a result consistent with

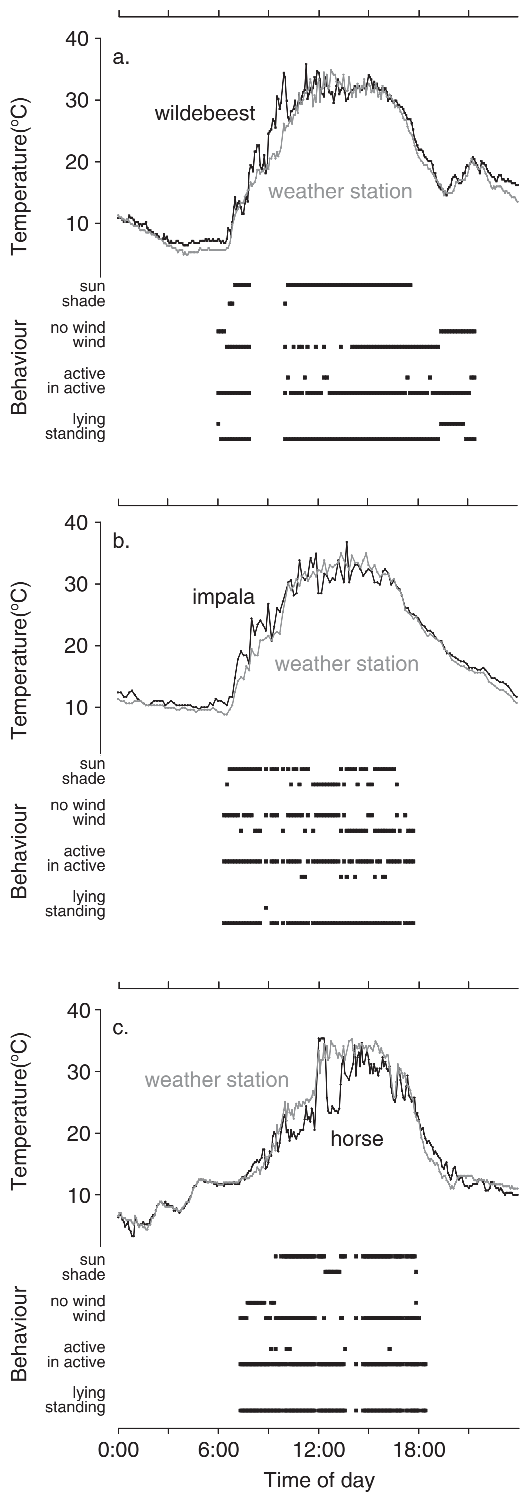

Fig. 5. Temperatures of miniglobe on the collar of a wildebeest (**a**), impala (**b**) and horse (**c**) and an identical miniglobe on the weather station over a 24-h period, together with a record, obtained by direct observation, of potential thermoregulatory behaviours (sheltering from the sun or wind, level of activity and posture). Gaps in behaviour bars represent periods when either the animal was not visible or the behavioural category was invalid, e.g. when the sun set or the wind was not blowing. Note that the wildebeest (**a**) did not seek shade, and instead avoided wind, in the hottest part of the day reflected in a collar miniglobe temperature higher than that of the weather station. Conversely, both the impala (**b**) and horse (**c**) sought shade for about 2 h shortly after noon but the observed decrease in collar miniglobe temperature associated with shade-seeking behaviour was far more dramatic for the horse who also remained exposed to the prevailing wind.

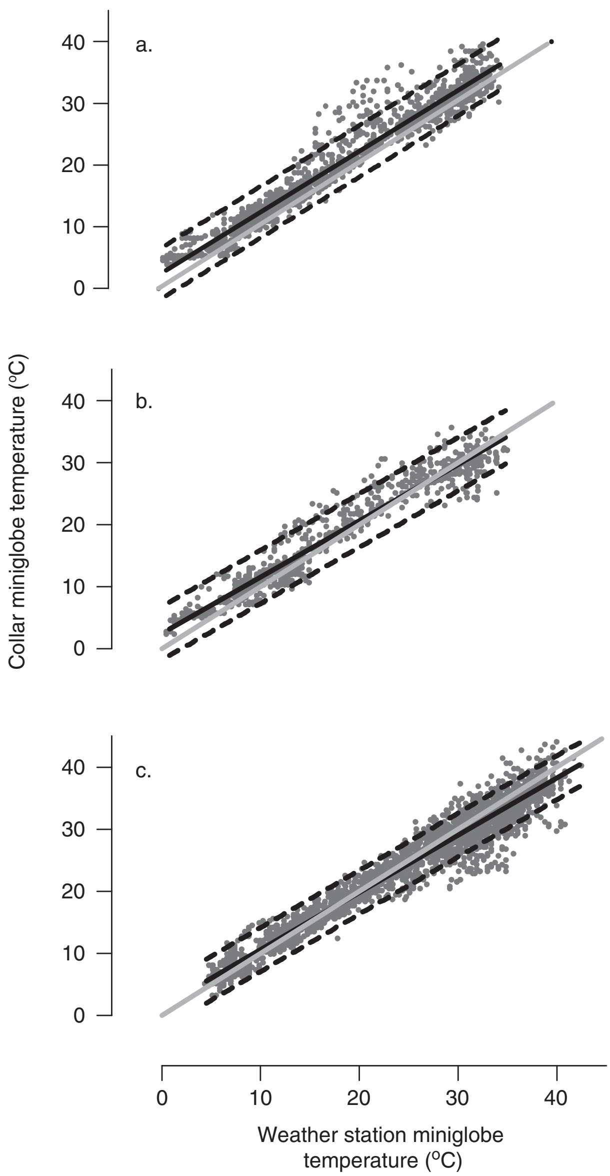

Fig. 6. Scatter diagram showing the relationship between miniglobe temperatures on the collars and that of an identical miniglobe on the weather station for wildebeest (**a**), impala (**b**) and horse (**c**). The solid grey lines are lines of identity, solid black lines are linear regressions and the dashed lines are the 95% prediction bands of the regression lines. A regression slope significantly less than one (the line of identity) was observed in all three species and implies thermoregulatory behaviour, that is the animal selecting cooler microclimates at high environmental temperatures and warmer microclimates at low environmental temperatures. For each animal, measurements were made within a 1-month period, at intervals of 5 min (wildebeest and horse) and 10 min (impala). Regression equations: wildebeest $y = 0.981x+2.13$, $F_{1,3240} = 10.18$, $P = 0.001$, $r^2 = 0.94$; impala $y = 0.907x+2.50$, $F_{1,1736} = 140.64$, $P<0.0001$, $r^2 = 0.94$ horse $y = 0.922x+1.39$, $F_{1,7616} = 588.30$, $P<0.0001$, $r^2 = 0.96$.

the wildebeest seeking warmer microclimates from amongst those accessible. The impala miniglobe temperatures within the upper quartile range were not significantly different from weather station miniglobe temperatures ($t_{400} = 1.35$, $P = 0.17$), probably because of frequent transient changes in the impala's thermoregulatory behaviour. Nevertheless, a contingency analysis showed a significantly higher frequency of collar miniglobe temperatures below weather station miniglobe temperatures when the animal was in the shade ($\chi^2 = 13.43$, $P = 0.0002$). The horse miniglobe temperatures were significantly lower than the weather station miniglobe temperatures in the upper quartile range ($t_{1745} = 7.39$, $P<0.0001$), a result consistent with the horse selecting cooler environments in the heat of the day. However, unlike the impala, which appeared to reduce its thermal load by seeking shade, the horse did not attain its cooler microclimate by consistently seeking shade ($\chi^2 = 2.35$, $P = 0.13$). Instead, the horse exhibited miniglobe temperatures lower than the weather station miniglobe temperatures significantly more often when it was exposed to the wind ($\chi^2 = 13.93$, $P = 0.0002$).

For the third quantitative analysis, we used nested ANOVAs to compare variability of collar miniglobe temperatures to that of weather station miniglobe temperatures. We found no difference in variability between collar miniglobe and weather station miniglobe temperatures overall for the wildebeest ($F_{1151,1151} = 1.01$, $P = 0.45$) or impala ($F_{575,575} = 0.88$, $P = 0.94$). However, the horse's collar miniglobe as a whole was significantly less variable than the weather station miniglobe temperature ($F_{2879,2879} = 1.08$, $P = 0.01$). As the horse sought protection from both wind and sun, this result supports the notion of behavioural thermoregulation through the selection of more stable microclimates. Further analysis into the variability over different time scales revealed no difference between collar and weather station miniglobe variability over the period of days ($F_{3,3} = 1.30$, $P = 0.42$; $F_{3,3} = 1.39$, $P = 0.40$ and $F_{9,9} = 1.14$, $P = 0.42$ for the wildebeest, impala and horse, respectively) or even 4 h intervals ($F_{20,20} = 1.01$, $P = 0.49$; $F_{20,20} = 1.17$, $P = 0.37$; $F_{50,50} = 1.00$, $P = 0.50$ for the wildebeest, impala and horse, respectively). All collar miniglobe temperatures, however, were significantly less variable than the weather station miniglobe over the shorter time interval of hours ($F_{72,72} = 1.57$, $P = 0.03$; $F_{72,72} = 1.65$, $P = 0.02$; $F_{180,180} = 1.34$, $P = 0.02$ for the wildebeest, impala and horse, respectively) implying that factors with a time course shorter than daily weather and circadian variation contributed to the variance. Over the shortest epoch we analysed, 20 min, the variability manifested by the miniglobe on the collar of the horse ($F_{480,480} = 1.51$, $P < 0.0001$) and impala ($F_{192,192} = 1.56$, $P = 0.001$), was less variable than the miniglobe temperatures on the weather station, while those of the wildebeest tended to be more variable ($F_{192,192} = 1.23$, $P = 0.08$).

DISCUSSION

Our study had two objectives. The first objective was to test whether we could successfully predict standard (150 mm diameter) globe temperature from miniglobe temperature, using an algorithm derived from heat transfer equations for spheres of different diameters. The correlations in Fig. 2, together with the 95% limits of agreement in Table 1, demonstrate that the algorithm was successful, with an average accuracy better than 1°C over a wide range of environmental conditions, and often better than 0.5°C. Although others (e.g. Peters et al., '76) had compared predicted and actual globe temperatures previously, no-one had explored a comprehensive range of ambient conditions previously, and no-one had deliberately manipulated several environmental variables systematically. The accuracy of our conversion algorithm and that of the earlier approximation of Hey ('68) should be sufficient for most research purposes. Under extreme conditions of high radiation and wind speeds accompanied by low dry-bulb temperatures, some limitations in Hey ('68) approximation were revealed (Table 1). The algorithm of Peter's et al. ('76) proved less accurate overall than either of the other conversion routines, but was better than the others under extreme conditions (Table 1). We know that Peters et al. ('76) corrected their convective heat transfer coefficient for changes in air temperature, whereas we corrected for changes in barometric pressure, because we wanted our algorithm to be applicable at different altitudes. We have not been able to determine whether commercially available human heat stress monitors, that use globes of non-standard diameter, correct for that parameter.

The reason that we, and others, derived conversion algorithms for the miniglobe was to allow comparisons between the temperatures of a miniglobe and those of the standard globe, with which many researchers are familiar. The experiments which we conducted, in a climatic chamber, to check the accuracy of the algorithm, revealed why commercial instruments may be reasonably accurate despite not correcting for differences in diameter. In most circumstances the average temperature indicated by a 30 mm diameter globe was within 2°C of the 150 mm diameter globe.

Although the miniglobe exhibited a slightly shorter response time compared to the standard globe (Fig. 3), both globes were relatively slow to reach equilibrium. These time constants, however, were similar to those found after improvements were made to globe thermometers in the middle of the last century and further reductions in the thickness of the globe is unlikely to improve the time constant (Hellon and Crockford, '59). Although a slow response time for the globe may mean that short-term changes in the thermal environment are not recorded, the thermal inertia of the animal is much larger than that of the globe, reducing the overall impact of such short-term microclimate selection on the animal's heat balance.

Our second objective was to test whether miniglobes could be attached to an animal to provide a quantitative measure of thermoregulatory behaviour, in the form of microclimate selection. For that purpose we compared the temperature of the miniglobe on the collar with that of an identical miniglobe on a nearby exposed weather station. Thus, a lower miniglobe temperature on the animal during the day would result if the animal behaviourally reduced its radiation exposure by seeking shelter from direct solar radiation. A higher miniglobe temperature on the animal would result if the animal sought shelter from strong winds, while remaining in the sun. Fig. 5 graphically represents how differences between the weather station and animals' miniglobe temperatures correspond to various behavioural observations. Further quantitative analysis revealed the capacity of the miniglobe to reflect thermoregulatory behaviour.

The elevation in the slope of the collar versus weather station miniglobe correlation in the wildebeest (Fig. 6A) and the greater variability over 20-min epochs, revealed that the animal selected microclimates warmer than the weather station in both hot and cold environments. The impala's transient shade-seeking behaviour was reflected in rapid changes in miniglobe temperatures (Fig. 5B) with a significantly higher frequency of collar miniglobe temperatures dipping below weather station miniglobe temperatures when the animal was in the shade. The downward shift in the correlation graph at high environmental heat loads (Fig. 6B), together with a slope significantly less than one, provides further support for observations of the impala seeking cooler microclimates at high environmental heat loads. For the horse, the selection of cooler microclimates at high environmental heat loads was revealed through the horse's selection of a significantly cooler microclimate during the heat of the day, defined by the upper quartile range, and a regression slope significantly less than one (Fig. 6C). The horse, like the impala, was seen to seek shade.

Miniglobes thus appear to detect changes in the selected microclimate, consistent with the behaviour we observed during the day, for example, when the animals entered shade or were protected from wind. We were unable to observe the animals throughout the night, but comparison of lower quartile temperatures revealed that all three species selected warmer microclimates than the free-stream environment at night. This warmer microclimate may have arisen from high infrared thermal radiation from vegetation or by close association with conspecifics. Recumbency is an additional behavioural adjustment which can provide a warmer microclimate by allowing an animal to exploit the boundary layer of the ground, thus reducing convective heat loss due to the increased air temperature and decreased wind temperature closer to the ground (Bakken '92; Bustamante et al., 2002; Maloney et al., 2005a).

Although it may be beneficial for the animal to reduce convective heat loss at night by seeking protection from wind, such behaviour would not be reflected by an increase in collar miniglobe temperature if the animal were exposed to a clear night sky. The situation becomes complex because the radiation temperature of the night sky can be as low as $-30°C$. Exposed to such low radiation temperatures, a low wind speed would result in globe temperature close to the cold radiation temperature of the night sky, while increases in wind speed would increase globe temperature closer to the dry-bulb temperature. Thus the effect of changes in wind speed on globe temperature varies depending if radiation temperature is higher or lower than dry-bulb temperature.

While we have identified that miniglobe temperatures on an animal can indicate thermoregulatory behaviours, a major shortcoming of the technique is that a globe thermometer provides no measure of the ambient water vapour pressure, which is the main determinant of the gradient for evaporative cooling. In addition, a single miniglobe, attached to collars, provides no measure of thermoregulatory behaviours such as postural adjustments, nor the animal's orientation to wind or sun, which may profoundly affect radiant heat absorption (Mitchell et al., '97; Maloney et al., 2005b). Miniglobe temperatures also cannot reflect changes in surface areas in contact with a heat source or heat sink. For example, a standing animal exposes a greater surface area to the wind, and would lose heat more rapidly, than would a recumbent animal (Fuller et al., '99), but neither choice would be reflected in a change in miniglobe temperature.

Although miniglobes may have some shortcomings, the method provides the first, to our knowledge, data using an ambulatory technique to quantify thermoregulatory behaviour in free-living animals. A similar method was previously attempted by Fuller et al. ('99), but in that study the miniglobes were attached to the horns of eland (*Tragelaphus oryx*). The globes were dislodged from horns after only 10 days. Attaching the miniglobes to collars therefore appears to provide a more durable alternative. In both this study and that of Fuller et al. ('99), miniglobe temperatures at night regularly exceeded those recorded at a nearby weather station. However, unlike the results obtained in this study, Fuller et al. ('99) found globe temperatures on the animals to be consistently lower than that of a nearby weather station between 10:00 and 17:00. The arid-adapted eland may be more dependent on thermoregulatory behaviour as the cost of water loss through evaporative cooling mechanisms is high in their extreme thermal environments. Quantifying such differences in thermoregulatory behaviour between species and environments is a valuable future objective.

Traditionally, the study of behavioural thermoregulation in free-living animals has relied on observational studies. In many instances the presence of an observer can disrupt normal animal behaviour (Recarte et al., '98). In addition, the thermoregulatory importance of behaviour may easily be misinterpreted because temperature regulation is not the only objective of postural adjustments. A good example is that the stereotypic postures of the lizard (*Angolosaurus skoogi*), were initially attributed to thermoregulatory behaviour, but later found to serve the purpose of urination and defecation (Seely et al., '88). Huddling behaviours often have been associated with increased heat load through increased infrared thermal radiation (Finch, '72), however, this clustering may instead represent an anti-predatory defence, in which individuals use each other as living shields for protection, termed ''selfish herd'' theory (Alcock, '98). It is therefore essential to develop a method that is remote and provides a quantitative measure of the heat load in the animal's microclimate, to accurately define the thermoregulatory benefit of each behaviour.

In summary, using miniature globe thermometers, attached to free-ranging ungulates, we were able to remotely quantify the thermal environment of an animal. Shade-seeking behaviour and the selection of wind-protected sites was reflected in animal miniglobe temperatures lower or higher, respectively, than those recorded at a nearby weather station. We also used a new algorithm to successfully predict standard globe temperature from miniglobe temperature. Although the difference between the measured miniature and standard globes usually was small (less than 2°C), converting miniglobe temperatures using our algorithm, to standard globe temperatures, allows for accurate comparative studies. We believe that the miniglobe provides an important advance towards developing a complete miniature weather station, which can be attached to free-ranging animals to assess their behaviourally selected microclimates. With current advances in technology, we may ultimately be able to incorporate miniature anemometers and humidity sensors to provide a more complete measure of all the physical components of the environment that influence an animals' heat balance and how thermoregulatory behaviour influences heat balance via the microhabitat an animal chooses to occupy.

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