RESEARCH ARTICLE

Climate influences thermal balance and water use in African and Asian elephants: physiology can predict drivers of elephant distribution

Robin C. Dunkin1,*, Dinah Wilson2, Nicolas Way3, Kari Johnson4 and Terrie M. Williams1

1Department of Ecology and Evolutionary Biology, University of California, Santa Cruz, Santa Cruz, CA, USA, 2Wildlife Safari, Winston, OR, USA, 3Six Flags Discovery Kingdom, Vallejo, CA, USA and 4Have Trunk Will Travel, Perris, CA, USA

*Author for correspondence (dunkin@biology.ucsc.edu)

SUMMARY

Elephant movement patterns in relation to surface water demonstrate that they are a water-dependent species. Thus, there has been interest in using surface water management to mitigate problems associated with localized elephant overabundance. However, the physiological mechanisms underlying the elephant’s water dependence remain unclear. Although thermoregulation is likely an important driver, the relationship between thermoregulation, water use and climate has not been quantified. We measured skin surface temperature of and cutaneous water loss from 13 elephants (seven African, 3768±642 g and six Asian, 3834±498 g) and determined the contribution of evaporative cooling to their thermal and water budgets across a range of air temperatures (8–33°C). We also measured respiratory evaporative water loss and resting metabolic heat production on a subset of elephants (N=7). The rate of cutaneous evaporative water loss ranged between 0.31 and 8.9 g min⁻¹ m⁻² for African elephants and 0.26 and 6.5 g min⁻¹ m⁻² for Asian elephants. Simulated thermal and water budgets using climate data from Port Elizabeth, South Africa, and Okaauejo, Namibia, suggested that the 24-h evaporative cooling water debt incurred in warm climates can be more than 4.5 times that incurred in mesci climates. This study confirms elephants are obligate evaporative coolers but suggests that classification of elephants as water dependent is insufficient given the importance of climate in determining the magnitude of this dependence. These data highlight the potential for a physiological modeling approach to predicting the utility of surface water management for specific populations.

INTRODUCTION

Because of their marked impact on vegetation, there is significant interest in determining the factors that most strongly influence the use of landscape by elephants (Chamaillé-Jammes and Fritz, 2007; Epaphras et al., 2008; Owen-Smith et al., 2006; Shannon et al., 2009). The influence of surface water in particular has received marked attention (Chamaillé-Jammes and Fritz, 2007; de Beer and van Aarde, 2008; Epaphras et al., 2008; Gaylard et al., 2003; Redfern et al., 2003; Shannon et al., 2009; Smit et al., 2007) because elephants are recognized as water dependent (Western, 1975; Western and Lindsay, 1984); therefore, surface water management may be a powerful tool for mitigating problems associated with localized overabundance of elephants, particularly in small reserves (Chamaillé-Jammes and Fritz, 2007; Chamaillé-Jammes et al., 2007; Smit et al., 2007). Heat dissipation has long been recognized as a challenge for these large mammals (Benedict, 1936; Lillywhite and Stein, 1987; Phillips and Heath, 1992; Williams, 1990; Wright, 1984; Wright and Luck, 1984) and reliance on evaporative cooling is hypothesized to contribute to the elephant’s dependence on water (Wright and Luck, 1984). Thus, the interaction between two abiotic factors, temperature and the distribution of surface water, is likely an important driver of landscape use by elephants. Despite this, there has been little work to quantify the influence of climate on water use in elephants.

Elephants are able to dissipate heat using a variety of non-evaporative strategies, including ears that are adapted for maximum heat transfer (Buss and Estes, 1971; Phillips and Heath, 1992; Wright, 1984), and a low surface density of hair, which likely enhances heat loss especially at low wind speeds (Myhrvold et al., 2012), and through behavioral strategies such as shade seeking (Sikes, 1971; Sukumar, 2003). However, while heat transfer from the body surface via conduction, convection and radiation may sufficiently dissipate heat at mild temperatures, the effectiveness of these strategies diminishes and reverses to heat gain once air temperature surpasses skin surface temperature (Gates, 1980). At higher air temperatures, heat storage or evaporative cooling are the only mechanisms that an animal can employ to dissipate excess metabolic heat. The extent to which elephants use heat storage remains unclear, but based on recent work in both African (Kinahan et al., 2007) and Asian elephants (Weissenböck et al., 2011), heat storage appears to play a relatively minor role in thermal balance for these species, though measurements at very high air temperature or under water stress have not been made. Thus, evaporative cooling may in fact be obligatory above a threshold air temperature depending upon activity state and climatic conditions. Despite lacking sweat glands (Horstmann, 1966; Smith, 1890; Spearman, 1970), elephants do have significant rates of insensible water loss across the skin.
of respiration to total heat and water balance and to determine heat production using open flow respirometry to estimate the contribution of respiratory evaporative water loss (REWL) and resting heat production to the thermal balance of elephants. On a subset of animals, we simultaneously measured cutaneous evaporative water loss (CEWL) from dry skin of trained females, one male; mean ± s.d. body mass=3768±642 kg) and six adult Asian (six females; mean ± s.d. body mass=3834±498 kg) elephants housed at three facilities (Wildlife Safari in Winston, OR, USA; Six Flags Discovery Kingdom in Vallejo, CA, USA; and Have Trunk Will Travel in Perris, CA, USA). These facilities were chosen for their access to trained animals and for the range of climatic conditions under which measurements could be made between seasons. All animals had been at each facility for greater than 1 year and were acclimated to the environmental conditions under which the measurements were made. Though air temperature was the main factor that varied between measurements, we controlled other aspects of climate such as solar radiation, and thus we use the term climate to collectively refer to air temperature, humidity and radiation. Collection of data from animals acclimated to a wide range of climates (achieved by collection of data at three facilities at differing latitudes and across seasons) allowed us to evaluate the generalized response for broad application to elephants inhabiting different thermal environments. Not all measurements were carried out on all animals because of training constraints and movement of animals during the course of the study. Sample sizes for each set of measurements are specified in the text.

Data were collected between February 2005 and September 2010. At all facilities, elephants had daytime and nighttime access to both indoor and outdoor enclosures throughout the year. If air temperatures were too cold (generally <4–7°C), elephants were housed in a heated barn. All elephants had free access to water and were maintained on their normal diets consisting primarily of pellets, alfalfa or other hay, and smaller amounts of fresh fruits and vegetables. Research was conducted under the approval of the University of California Santa Cruz Institutional Animal Care and Use Committee and each facility’s own animal use protocols.

**Body sites, surface area and body mass**

To determine the relative contribution of evaporative cooling to the thermal balance of elephants across a range of air temperatures, we measured skin surface temperatures (Ts) and cutaneous evaporative water loss (CEWL) from dry skin of trained elephants across a nearly 25°C span of air temperatures. We also made these measurements on wet skin after the animals had been fully bathed to simulate how wallowing may influence the thermal and water budgets of these animals. We then used data from skin surface temperature measurements and measured surface areas to calculate non-evaporative heat loss via radiation, conduction and convection across the range of air temperatures measured in this study. On a subset of animals, we simultaneously measured respiratory evaporative water loss (REW) and resting heat production using open flow respirometry to estimate the contribution of respiration to the thermal balance.

**Facility climatic conditions**

To investigate the widest possible range of air temperatures and maximize the number of measurements taken for each individual, data were collected across seasons as well as in the morning and afternoon at all facilities. Air temperature (Ta) and relative humidity (RH) were measured at elephant shoulder height, within 1.8 m of the elephant. Ta ranged between 8.7 and 32.9°C (overall mean ± s.d.: 20.2±6.1°C) while water vapor pressure ranged between 0.54 and 1.99 kPa (overall mean ± s.d.: 1.15±0.30 kPa). To assess differences in the annual climate experienced by individuals at the three facilities, daily maximum, mean and minimum air temperatures were calculated for each month at each facility for a single year. The Physitemp Bat-5 and RH sensors were calibrated prior to each measurement session using a precision thermometer (Physitemp Bat-5, Clifton, NJ, USA) and an external water vapor analyzer (RH-100 or RH-300, Sable Systems, Las Vegas, NV, USA), respectively. The Physitemp Bat-5 and RH 100 or 300 were each calibrated in the laboratory prior to departure for a trip to each zoo. The Physitemp Bat-5 was calibrated against a National Institute of Standards and Technology (NIST) traceable mercury thermometer in a water bath. The RH 100 or 300 water vapor analyzer was calibrated prior to each trip as described in detail below. Ta ranged between 8.7 and 32.9°C (overall mean ± s.d.: 20.2±6.1°C) while water vapor pressure ranged between 0.54 and 1.99 kPa (overall mean ± s.d.: 1.15±0.30 kPa).
minimum $T_{\text{air}}$ and RH values were obtained for nearby weather stations for each facility (METAR reports) for the years during which data were collected as well as for 1 year prior to the start of data collection (supplementary material Table S1). Water vapor pressure was then calculated from these measurements as described above. The southernmost facility (Perris, CA) experienced significantly warmer temperatures and lower water vapor pressures compared with those of the other facilities (ANOVA, all $P<0.0001$). There were significant but smaller differences in climate between the central (Vallejo, CA) and northern (Winston, OR) facilities (supplementary material Table S1), but these differences were less than 1.1°C and 0.1 kPa. To minimize the variable effects of solar radiation, all data were collected inside large elephant barns at each facility.

**Simulation of wallowing behavior**

The effects of wallowing on thermal status and CEWL were determined by collecting data prior to and after the animal was given a full body bath. Animals were bathed by the trainer with cool water from a hose and each bath lasted ~15 to 20 min. Care was taken to ensure that all body surfaces were thoroughly soaked; post-bathing data were collected immediately upon completion of the bath (usually within 8–10 min) to simulate the rates of water loss likely experienced soon after an animal emerges from a water hole. The body site order was varied randomly to ensure there were no systematic differences associated with the time since completion of bathing. Skin surface temperatures and CEWL were collected under four conditions: morning/pre-bathing, morning/post-bathing, afternoon/pre-bathing and afternoon/post-bathing.

**Skin surface temperatures and non-evaporative heat exchange**

$T_{\text{ss}}$ values were measured using an infrared thermometer (Raynger PM4L5, Raytec, Santa Cruz, CA, USA) held 7–10 cm from the skin surface. The infrared thermometer was periodically calibrated against an ice water bath. Ambient conditions including $T_{\text{air}}$ and RH (measured as above) were recorded at the same time as each individual measurement of $T_{\text{ss}}$ at each body site and used to calculate water vapor pressure as described above. Measurements were performed at least once on all 13 elephants (total 518 measurements including all body sites).

Radiant, convective and conductive heat loss were calculated according to Williams (1990). Briefly, standard equations for the three non-evaporative routes of heat dissipation have been previously developed and tested in humans and in various animals and plants (Clark and Edholm, 1985; Gates, 1980). Radiant heat loss was calculated using the modified form of Christensen’s equation as derived in Clark and Edholm (Clark and Edholm, 1985):

$$\text{Radiant heat exchange} = \sigma (T_{\text{sk}}^4 - T_{\text{air}}^4) \times 0.85 A,$$

where $\sigma$ is the Stephan–Boltzmann constant, 5.7×10$^{-8}$ W m$^{-2}$ K$^{-4}$; $\varepsilon$ is the emissivity of the skin, 0.98 (Clark and Edholm, 1985; Williams, 1990); $T_{\text{sk}}$ and $T_{\text{air}}$ are the temperature of the skin and air, respectively (K); $A$ is surface area ($\text{m}^2$); and 0.85 is a correction factor to account for the radiant heat exchange between body surfaces (legs) in near contact (Clark and Edholm, 1985; Williams, 1990).

Clark and Edholm (Clark and Edholm, 1985) also developed equations for estimating convective heat loss (natural and forced) from animals where the value of the convective coefficient ($h_c$; W m$^{-2}$ °C$^{-1}$) varies with the shape and orientation to the ground of the body area. We modeled the torso and legs of the elephant as horizontal and vertical cylinders, respectively, and the ear as a vertical flat plate and used the following equation with the corresponding convective coefficient as given by Clark and Edholm (Clark and Edholm, 1985):

$$\text{Convective heat exchange} = h_c A (T_{\text{ss}} - T_{\text{air}}).$$

We elected to use $h_c$ values for free convection given that measurements were made in large buildings with minimal air flow (Williams, 1990).

Conductive heat loss from the animal’s feet was calculated as:

$$\text{Conductive heat exchange} = k A (T_{\text{ss}} - T_{\text{floor}})/b,$$

where $k$ is the thermal conductivity of the tissue [0.19 for Asian elephant and 0.23 W m$^{-1}$°C$^{-1}$ for African elephants; measured in a...
Cutaneous evaporative water loss and evaporative heat loss

CEWL was measured using the ventilated capsule technique adapted from Webster and Bernstein (Webster and Bernstein, 1987) and Smallwood and Thomas (Smallwood and Thomas, 1985). In this method, an air stream was dried to achieve a stable, low water vapor pressure (mean ± s.d. = 0.61 ± 0.22 kPa) by combining an ambient and dry airstream. The air was then directed to a factory calibrated ball flow meter (Cole-Palmer EW-03229-17, Vernon Hills, IL, USA, ±2% accuracy) and the rate of flow was adjusted and recorded. The airstream was then passed over the skin of the animal via a PVC capsule (5 cm diameter) fitted with a neoprene gasket. The humidified air was directed from the capsule through a second calibrated ball flow meter (used to ensure a good seal) and then to a water vapor analyzer (RH-100 or RH-300, Sable Systems). The data were recorded using Expedata software (Sable Systems). The water vapor analyzer was calibrated before each week of data collection according to the manufacturer’s instructions by setting the zero using dry nitrogen gas and the span using a fully saturated airstream with a precisely measured temperature (NIST traceable mercury thermometer calibrated with a stable water bath). Low-permeability tubing was used throughout to reduce exchange of water vapor within the system (Bev-a-Line, Thermoplastic Processes, Georgetown, DE, USA).

To make the CEWL measurements, a neoprene gasket on the PVC capsule was coated in a thin layer of petroleum jelly to create a seal between the capsule and the elephant’s skin. The capsule was then pressed against the skin of the elephant until the slope of the rising water vapor pressure of the outlet airstream reached an inflection point and began to level or decline (0.5–3 min) (Fig. 2A). If any contamination of the skin with petroleum jelly was found to have occurred upon removal of the capsule, the measurement was discarded.

The ventilated capsule technique relies upon low velocity airflow (mean ± s.d. STPD flow rate = 0.79 ± 0.28 l min−1) across the skin, and thus error resulting from changes in the water vapor pressure directly above the skin and convective effects due to higher velocity air flow across the skin are minimized (Smallwood and Thomas, 1985). In addition, dehydration effects on the skin that may occur during the course of the measurement, which can be problematic in ventilated capsule measurements, are minimized by taking the maximum rate of water loss initially achieved (Fig. 2A) (Smallwood and Thomas, 1985).

The amount of water lost through evaporation was then calculated using the following equation (modified from Webster and Bernstein, 1987):

\[
\text{CEWL} = \frac{\dot{V} \left( p_{\text{out}} - p_{\text{in}} \right)}{A},
\]

where CEWL (g min−1 m−2) was determined from the STPD-corrected flow rate of the inlet air (\(\dot{V} ; 1 \text{ min}^{-1}\)), the water vapor pressure (Pa) of the outlet and inlet air stream (\(p_{\text{out}} \text{ and } p_{\text{in}}\)), the air temperature, \(T_{\text{air}} \) (K), the gas constant for water vapor, 461.5 KJ kg\(^{-1}\) K\(^{-1}\), and the contact area of the cup, \(A \) (m\(^2\)); cup area = 0.00196 m\(^2\)). The rate of CEWL was converted to evaporative heat loss using the latent heat of vaporization for water (2.43 × 10\(^6\) J kg\(^{-1}\) H\(_2\)O at 30°C).

CEWL is governed by properties of the integument as well as environmental factors. Changes in blood flow in the dermis as well as the composition and structure of the stratum corneum, the rate-limiting barrier to water loss in the integument (Elias, 1991), can influence the rate of CEWL in the short and long term (Lillywhite, 2006). The difference between the water vapor pressure within the animal and in the environment above the integument provides the driving force for evaporation (Anderson, 1936; Spotila and Berman, 1976). Because the capacity for air to hold water vapor increases exponentially with temperature, the driving force for evaporation is greater at higher temperatures than at lower temperatures (Anderson, 1936). Thus, both air temperature and the saturation of the air above the skin play a major role in determining the rate of CEWL. If the integument is playing a passive role in controlling CEWL, then CEWL should increase exponentially with air temperature. To examine how the integument alone may influence CEWL across a range of air temperatures, we computed epidermal permeability (g m\(^{-1}\) m\(^{-2}\) min\(^{-1}\) kPa\(^{-1}\)), which is analogous to the cuticular permeability often reported for insects (Gibbs, 2011; Lighton and Feener, 1989). Epidermal permeability refers to how readily water is able to diffuse from the dermis, across the epidermis (and specifically the stratum corneum), and evaporate from the integument surface. Epidermal permeability was calculated by dividing the rate of CEWL by the water vapor pressure saturation deficit (WVPD; kPa). The WVPD was determined by first

**Fig. 2.** Sample raw data of cutaneous evaporative water loss (CEWL) measurement from an African elephant (A) and the relationship between gravimetric and ventilated capsule measurement techniques across three temperatures and three flow rates for calibration of the evaporative water loss system used to measure CEWL (B). Box in A indicates the area where the maximum CEWL value was calculated.
calculating the saturated water vapor pressure at the measured $T_{av}$. The actual water vapor pressure of the air was determined from the baseline value of the air passing through the cup before being applied to the skin (Fig. 2A) and the WVPSD was then calculated by subtracting the actual water vapor pressure from the saturated water vapor pressure at skin temperature (Webster and Bernstein, 1987).

**Calibration of evaporative water loss device**

The evaporative water loss device described above was calibrated to determine both its accuracy and precision at three temperatures and three flow rates. Measurements were performed in a temperature-controlled room in which the mean temperature and standard deviation for the low, moderate and high temperature trials were $13.9\pm0.3$, $22.8\pm0.6$ and $27.6\pm0.2°C$, respectively (7400 Perception II, Davis Instruments). These temperatures represented the lower, middle and upper end of the conditions under which actual evaporative water loss was measured in this study. At each temperature, 10 trials were performed at low (mean $0.58\pm0.02$ min$^{-1}$), medium (mean $0.79\pm0.01$ min$^{-1}$) and high (mean $0.96\pm0.04$ min$^{-1}$) flow rates representative of those used in the actual experiments.

For these measurements, the cup of the CEWL device was modified to screw onto a PVC base into which a wetted cotton ball was placed. The PVC base and wetted cotton ball were weighed to $\pm0.0001$ g (Model 1712, Sartorius, Goettingen, Germany) and then immediately screwed to the cup of the CEWL device. The flow was then directed through the cup and water was allowed to evaporate from the cotton ball for between 2 and 27 min. Upon completion of the trial the flow was directed to bypass the cup, the base was immediately unscrewed, and the base and cotton ball were again weighed together to gravimetrically determine the mass of water lost during the trial. Data were collected and analyzed using Sable Systems Expedata software.

**Calibration results**

The mean ± s.d. error for all calibration trials was $6.7\pm5.2\%$. A multiple stepwise linear regression was performed to determine whether there were any systematic errors associated with the temperature or flow rate. There was no significant interaction between temperature and flow rate ($P=0.92$) and this term was discarded. The flow rate was only marginally significant in explaining the occurrence of systematic error ($P=0.08$); however, there was a strong positive correlation between air temperature and occurrence of systematic error ($P<0.0001$) such that higher temperature trials had greater error than low temperature trials (overall model $P=0.001, F=17.21, d.f.=3,87$). The mean ± s.d. error was $-2.5\pm4.4$, $-7.8\pm4.3$ and $-9.8\pm3.7\%$ for the low, medium and high temperature trials, respectively. To remove the systematic error associated with temperature, the raw data were corrected using the equation:

$$CEWL = \left[ \frac{CEWL_{L}(0.8538+0.5387\times T_{av}+4.8819\times F)}{100} \right] + CEWL_{R},$$

where $CEWL$ is the temperature- and flow-corrected rate of evaporative water loss (g min$^{-1}$), $CEWL_{L}$ is the raw rate of CEWL in the same units, $T_{av}$ is the air temperature (°C), and $F$ is the flow rate (min$^{-1}$). Although flow was only marginally significant ($P=0.08$) it was included to account for the maximum variation possible in the correction.

After correcting for the systematic temperature effect, the overall error of the system was $-0.55\pm4.4\%$ (Fig. 2B) and there was no effect of temperature ($P=0.49, F=0.71, d.f.=2,88$) on the measurements. All raw data collected for this study were subsequently corrected using Eqn.5.

**Heat production and respiratory evaporative water loss**

Resting heat production, measured as the rate of oxygen consumption per unit time, and REWL were measured simultaneously using open flow respirometry on a subset of animals (Asian=three female, African=three female, one male, total $N$ for all trials=20). Resting is defined in this study as standing quietly but alert. To facilitate training and to best approximate a true ‘resting rate’, elephants were not fasted before measurements because elephants typically eat almost continuously.

Elephants were trained, using positive reinforcement, over a period of several months to keep their mouth closed and place their trunk in a specially designed mask adapted from Langman et al. (Langman et al., 1995) (Fig. 3) through which a vacuum pump (Flow Kit 500H, Sable Systems) drew air at a rate of $4401\text{min}^{-1}$. A subsample stream of the expired air was diverted and directed through a water vapor analyzer (RH-100 or RH-300, Sable Systems), and then scrubbed of water and CO$_2$ with alternating tubes of Drierite (Drierite, Hammond Drierite, Xenia, OH, USA) and Sodasorb (Sodasorb, Chemetron, St Louis, MO, USA). The airstream was then directed through an oxygen analyzer (model FC-1B, Sable Systems). The RH, $T_{air}$ and fractional concentration of oxygen in the expired air were continuously recorded (Expedata, Sable Systems). The water vapor analyzer was calibrated before each set of measurements as described above for the measurement of CEWL. The oxygen analyzer was calibrated before each measurement.

**THE JOURNAL OF EXPERIMENTAL BIOLOGY**

![Fig. 3. Flow-through respirometry chamber that was used to measure resting metabolic heat production and respiratory evaporative water loss. Photo credit: T. M. Williams.](image)
measurement using dry air (20.95% oxygen) and the system was checked for leaks before each trial using dry nitrogen gas (Fedak et al., 1981). Bev-A-Line tubing was used in the connection between the excurrent flow tube and the water vapor analyzer to minimize condensation and water vapor exchange.

The rate of REWL was calculated from the difference between the absolute humidity of the incoming and excurrent air stream and the rate of total flow through the system (440 l min⁻¹) (Lester and Costa, 2006). Oxygen consumption was calculated using eqn 4B from Withers (Withers, 1977) and a respiratory quotient of 0.83 for herbivores (Schmidt-Nielsen, 1997). The rate of oxygen consumption was converted to heat production using a conversion factor of 20.1 kJ l⁻¹ O₂.

Analysis

The main objective of this work was to determine how important evaporative cooling is to the thermal and water budgets of an elephant as air temperature increases. Thus, we analyzed the data to determine the relationship between 𝑇𝑠𝑠 or CEWL and air temperature. As stated above, however, WVPSD is ultimately the driving force for evaporation and takes into account both air temperature and the relative saturation of the air with water vapor. Thus, we also analyzed the relationship between CEWL and WVPSD. Restricted maximum likelihood analysis (REML) was used to construct regressions for log-transformed CEWL using air temperature and species as main effects as well as the two-way interaction term. A second REML analysis was used to construct regressions for log-transformed CEWL versus WVPSD. Separate REML models were constructed for the dry/body, dry/ears, wet/body and wet/ears to examine just the effects of air temperature and species as well as body site, as factors. We included season because we hypothesized that elephants undergo seasonal acclimation to ambient conditions of temperature and humidity. Epidermal permeability was hypothesized to vary within and between species and body region (ears, body) and only examined dry skin. All analyses were performed using the REML analyses, facility was included as a random effect to account for potential variation between the three facilities.

A subset of the 𝑇𝑠𝑠 data set did not meet the linearity assumptions of the REML analysis and could not be transformed, and thus separate linear or non-linear regressions were calculated to understand how 𝑇𝑠𝑠 changed with 𝑇𝑎𝑖𝑟. Similar to the CEWL analysis, we constructed separate relationships for the body and ears and before and after stimulated wallowing for each species. To determine the degree to which elephants are obligated to use evaporative cooling at different air temperatures, we computed heat loss via both non-evaporative and evaporative routes over the range of temperatures under which measurements were made. Non-evaporative heat exchange was computed separately for the body and ears using Eqs 1–3 and 𝑇𝑖𝑛 𝑇𝑎𝑖𝑟 was computed using the regression equations developed as described above. Non-evaporative heat loss via conduction, convection and radiation was then summed for the whole body to yield a total non-evaporative rate of heat exchange over the measured range of air temperatures.

CEWL was computed over the measured range of air temperatures using the regressions constructed through the REML analyses. Respiratory evaporative water loss could only be measured at a subset of temperatures. Thus, to validate our measurements and predict a likely relationship between REWL and air temperature, we calculated three theoretical rates of REWL corresponding to minimum, moderate or maximum water saving strategies. The strategy that saved the least amount of water (minimum water saving strategy) assumed air was exhaled at core body temperature, the moderate water saving strategy assumed air was exhaled at skin surface temperature, and the maximum water saving strategy assumed air was exhaled at air temperature. Other large animals, including the giraffe (Giraffa camelopardalis), have been found to save significant water through cooling of exhaled air (Langman et al., 1979; Schmidt-Nielsen et al., 1981), although the absolute water savings varies across species. We chose the strategy (minimum, moderate or maximum) that best fit our measured data and then summed the calculated rate of REWL with the rate of CEWL to yield a total rate of evaporative water loss across air temperatures. The total water evaporated was converted to heat loss using the latent heat of vaporization of water as described above. The total rates of non-evaporative and evaporative heat loss for each species were then plotted against air temperature to determine the temperatures at which evaporative heat loss exceeded non-evaporative heat loss and to compare these values with the resting rate of heat production.

To determine whether elephants have the ability to control evaporative water loss, we also calculated epidermal permeability. We were primarily interested in evaluating whether epidermal permeability is altered with increasing WVPSD. Thus, like the prior analyses, we used a REML approach and used WVPSD and season, as well as body site, as factors. We included season because we hypothesized that elephants undergo seasonal acclimation to ambient conditions of temperature and humidity. Epidermal permeability was log transformed and facility was again included as a random factor. We ran separate models for each species and body region (ears, body) and only examined dry skin. All analyses were performed using JMP 9.0 (SAS Institute, Cary, NC, USA). Data are presented as means ± s.e.m. unless otherwise indicated.

RESULTS

Skin surface temperature versus air temperature

𝑇𝑠𝑠 of the ears and body increased significantly with 𝑇𝑎𝑖𝑟 in both Asian and African elephants (all 𝑃<0.0001; Table 1). In all cases, the 𝑇𝑠𝑠 of the Asian elephants rose more rapidly with increasing air temperature than in African elephants (Fig. 4). The two species differed in how the 𝑇𝑠𝑠 of the dry ears changed with air temperature.

<table>
<thead>
<tr>
<th>Species</th>
<th>Body region</th>
<th>Wet/dry skin</th>
<th>Regression equation</th>
<th>d.f.</th>
<th>F</th>
<th>P</th>
<th>𝑅²</th>
</tr>
</thead>
<tbody>
<tr>
<td>Elephas maximus</td>
<td>Body</td>
<td>Dry</td>
<td>𝑇𝑠𝑠=6.59+0.557𝑇𝑎𝑖𝑟</td>
<td>70.1</td>
<td>82.4</td>
<td>&lt;0.0001</td>
<td>0.54</td>
</tr>
<tr>
<td></td>
<td>Ears</td>
<td>Dry</td>
<td>𝑇𝑠𝑠=−4.05+1.49−0.10(𝑇𝑎𝑖𝑟–20.9)^2</td>
<td>45.2</td>
<td>158.4</td>
<td>&lt;0.0001</td>
<td>0.87</td>
</tr>
<tr>
<td></td>
<td>Body</td>
<td>Wet</td>
<td>𝑇𝑠𝑠=9.71+0.767𝑇𝑎𝑖𝑟</td>
<td>70.1</td>
<td>168.0</td>
<td>&lt;0.0001</td>
<td>0.71</td>
</tr>
<tr>
<td></td>
<td>Ears</td>
<td>Wet</td>
<td>𝑇𝑠𝑠=−5.26+1.31𝑇𝑎𝑖𝑟</td>
<td>46.1</td>
<td>142.5</td>
<td>&lt;0.0001</td>
<td>0.76</td>
</tr>
<tr>
<td>Loxodonta africana</td>
<td>Body</td>
<td>Dry</td>
<td>𝑇𝑠𝑠=19.35+0.397𝑇𝑎𝑖𝑟</td>
<td>99.1</td>
<td>144.8</td>
<td>&lt;0.0001</td>
<td>0.60</td>
</tr>
<tr>
<td></td>
<td>Ears</td>
<td>Dry</td>
<td>𝑇𝑠𝑠=9.36+0.677𝑇𝑎𝑖𝑟</td>
<td>66.1</td>
<td>176.7</td>
<td>&lt;0.0001</td>
<td>0.73</td>
</tr>
<tr>
<td></td>
<td>Body</td>
<td>Wet</td>
<td>𝑇𝑠𝑠=16.91+0.367𝑇𝑎𝑖𝑟</td>
<td>97.1</td>
<td>199.7</td>
<td>&lt;0.0001</td>
<td>0.67</td>
</tr>
<tr>
<td></td>
<td>Ears</td>
<td>Wet</td>
<td>𝑇𝑠𝑠=9.51+0.57𝑇𝑎𝑖𝑟</td>
<td>64.1</td>
<td>123.5</td>
<td>&lt;0.0001</td>
<td>0.66</td>
</tr>
</tbody>
</table>

Statistics in this table are the result of individual linear regressions. A subset of the data did not meet the linearity requirements of a REML and could not be transformed.
The $T_{ss}$ of the dry Asian elephant ears rose rapidly between $T_{air}$=15 and 24°C but then slowed and reached a plateau as $T_{air}$ approached ~26°C (Fig. 4B). In contrast, the $T_{ss}$ of the African elephant ears rose steadily with $T_{air}$. Wet skin heightened the difference between species such that the $T_{ss}$ of both the wet body and ears of the Asian elephants rose more steeply than in the African elephant (Fig. 4C,D).

Non-evaporative heat loss depends upon the differential between $T_{ss}$ and $T_{air}$ (Eqns 1–3). As $T_{ss}$–$T_{air}$ approaches 0, heat loss via non-evaporative mechanisms becomes reduced until the animal begins to gain heat as $T_{air}$ surpasses $T_{ss}$. The $T_{air}$ at which the differential is equal to 0°C is therefore an important physiological metric for determining when an animal becomes fully dependent on evaporative heat loss or heat storage mechanisms to maintain thermal balance. We found that the $T_{air}$ at which the differential approached 0 ranged between 29 and 32°C for the dry skin of the body and ears of each species.

Cutaneous evaporative water loss and epidermal permeability

CEWL increased exponentially with increasing air temperature across the body and ears in both species ($P<0.0001$ for reduced
models for dry/body and dry/ears, all \( R^2 > 0.54 \) but there was no significant difference in this relationship between species (Fig. 5, Table 2). CEWL ranged between 0.31 and 8.9 \( \text{g} \text{min}^{-1} \text{m}^{-2} \) from all body sites of dry Asian elephants and ranged between 0.26 and 6.5 \( \text{g} \text{min}^{-1} \text{m}^{-2} \) from dry African elephants. CEWL was generally greater from wet than dry skin in both species but the rate of CEWL from the body rose more steeply with air temperature in Asian elephants compared with African elephants (species \( \times T_{\text{air}} \) interaction \( P = 0.02 \)).

CEWL from dry and wet skin and from the body and ears also increased exponentially with increasing WVPSD in both species (Fig. 6, Table 2). In general, the relationship between CEWL and WVPSD was more variable than between CEWL and \( T_{\text{air}} \) (\( R^2 = 0.24–0.38 \) for all models; Table 2). When the skin was dry, there was no difference between species and no interaction between species and WVPSD; however, when the skin was wet, there was a significant interaction between species and WVPSD (body \( P = 0.03 \), ears \( P = 0.03 \)). In both cases, CEWL was similar at low WVPSD; however, as WVPSD increased, CEWL from African elephants increased more quickly than from Asian elephants (Fig. 6C, D).

Epidermal permeability corrects for the changing WVPSD and represents the response of the integument alone to changing air temperature. If the exponential relationship between CEWL and \( T_{\text{air}} \) or WVPSD was due only to the increasing WVPSD, epidermal permeability should remain similar as WVPSD increases. We instead found a significant decrease in epidermal permeability with increasing WVPSD as well as an effect of season (Fig. 7, Table 3). Epidermal permeability tended to be greater in summer in both species, and the effect was most pronounced from the ears (Fig. 7B, D). There was also a significant interaction between season and WVPSD for the ears of the Asian elephants and the ears and body of the African elephants such that the seasonal difference in epidermal permeability tended to be greater at lower WVPSDs (all \( P < 0.011 \); Table 3).

### Metabolic heat production and respiratory evaporative water loss

The mean resting metabolic heat production for Asian and African elephants was 0.50±0.02 and 0.58±0.01 \( \text{W} \text{kg}^{-1} \), respectively (Fig. 8A). As expected, these values were greater than those predicted by Kleiber (Kleiber, 1947) given that the animals were not post-absorptive. Of the three water saving strategies that were evaluated against the measured rates of REWL in this study, elephants appeared to most closely follow the maximum water saving strategy, even under conditions of no water stress (Fig. 8B). This strategy corresponds to the amount of water that would be lost if the exhaled air approximated air temperature. Thus, a 3800 kg elephant would lose between 0.07 and 0.26 \( \text{g} \text{H}_2\text{O} \text{h}^{-1} \) at temperatures ranging between 10 and 33°C, respectively.

### DISCUSSION

We found that both the absolute and surface-area-specific rate of CEWL from African and Asian elephants is the highest of that measured for a variety of arid-dwelling herbivores (supplementary material Table S2). Previous investigations have recognized the importance of behavioral thermoregulation such as shade seeking and dust bathing (Rees, 2002; Sikes, 1971), as well as the potential role for heat storage or heterothermy (Kinahan et al., 2007; Weissenböck et al., 2011), to how elephants maintain thermal balance in warm climates. Wright and Luck (Wright and Luck, 1984 and Lillywhite and Stein (Lillywhite and Stein, 1987) also recognized that evaporative cooling may be an important component
of the overall thermal budget for elephants despite the absence of sweat glands in these species. Our results extend these previous investigations by demonstrating that across a broad range of air temperatures, evaporative cooling is not only a large component of the overall thermal budget, it is obligatory above air temperatures as low as 10–12°C (Fig. 9).

The only other mechanism for dealing with heat at high air temperatures, aside from changes in behavior, is heterothermy. Weissenböck et al. (Weissenböck et al., 2011) investigated heterothermy in Asian elephants housed in Thailand and Germany and found that these animals did undergo daily fluctuations in core body temperature of ~1.15 and 0.51°C, respectively. Based on these
results as well as the temporal pattern of core body temperature change in relation to air temperature, these authors concluded that heterothermy, or heat storage, can be an important component of the thermal budget for Asian elephants. We find that while elephants may use heterothermy to some extent, evaporative cooling is likely to be more significant to the overall thermal budget of both African and Asian elephants. For example, the median body mass of the elephants measured by Weissenböck et al. (Weissenböck et al., 2011) was ~3365 kg, thus a rise of 1.15°C over a 12 h period represents a rate of heat storage of ~313 W (total of 13,466 kJ) (Clark and Edholm, 1985) or ~15.5% of resting metabolic heat production with an approximate water savings of 5.61 (2.8–3.7% of estimated daily water intake) (Fowler and Mikota, 2006; Sikes, 1971). In contrast, under similar air temperatures (~30°C), evaporative cooling dissipated ~157% of resting heat production for Asian elephants in this study (Fig. 9). Although approximate, these calculations illustrate that both elephant species appear to rely extensively on evaporative cooling as air temperature rises. However, the role of heterothermy under conditions of severe water stress or extremely high air temperatures, when it would be most useful, remains uninvestigated in these species.

Our results also demonstrate species-specific differences in the response of skin surface temperature to increasing air temperature. Over the body, Asian elephant skin surface temperature tended to be only slightly higher at any given air temperature compared with African elephants, but there was a marked difference in skin temperature of the ears between species. Based on the rise in ear surface temperature, Asian elephants appeared to rapidly perfuse the dermal capillaries of the ear with blood above 16°C while African elephants seemed to perfuse the ears steadily as air temperature increased (Fig. 4B). The parabolic shape of the Asian elephant’s ear surface temperature in relation to air temperature may be related to the smaller surface area of African elephant ears compared with African elephants. The mean African elephant ear surface area in this study was more than twice that of the Asian elephants. Asian ears seemed to perfuse the ears steadily as air temperature increased (~3°C) while African ears perfused ~157% of resting heat production for Asian elephants in water intake) (Fowler and Mikota, 2006; Sikes, 1971). Lillywhite and Stein (Lillywhite and Stein, 1987) also noted that African elephants, who are larger and generally live in more arid conditions, seemed to have more significant sculpturing compared with Asian elephants, which may further enhance adherence of surface water and evaporative cooling in this species. Our results support this hypothesis because CEWL rates of African elephants were generally greater than those of Asian elephants after bathing (Fig. 5, Fig. 6C,D).

The skin and control of CEWL

Of the megaherbivores, only the elephant and the hippopotamus do not have sweat glands (supplementary material Table S2). The hippopotamus secretes a modified sweat-type substance from subdermal glands that functionally acts as sweat but which also provides sun protection and has antibacterial properties (Luck and Wright, 1964; Saikawa et al., 2004). In contrast, elephant integument is more permeable to water relative to other mammalian species (Dunkin, 2012). A critical difference, though, between elephants and animals with sweat glands, or functionally similar glands such as in the hippopotamus, is the lack of fine neuroendocrine control over CEWL. In animals with sweat glands, control of sweating is mediated through a variety of sympathetic pathways including direct innervation of the sweat glands and via hormonal control depending on the species (Jenkinson, 1973). Neuroendocrine control permits the integration of the animal’s thermal and water needs in...
Thermal and water balance in elephants 2949

Fig. 8. (A) Resting metabolic rate and (B) respiratory evaporative water loss (REWL) measured for African and Asian elephants. Animals were not fasted prior to measurements to better predict resting heat production for animals in a field environment. Kleiber’s (Kleiber, 1961) prediction of basal metabolic rate in relation to body mass is shown for reference (dashed line). Metabolic heat production scaled with body mass according to the equation metabolic rate=18.16*mass^{0.78}, where metabolic rate is in watts and mass is in kilograms ($R^2=0.84$). In B, predicted minimum, moderate and maximum water saving strategies calculated with three potential temperatures for air leaving the trunk are shown in relation to measured rates of REWL measured in this study.

determination of the onset and magnitude of the sweat response. For example, many desert ungulates significantly reduce the rate of cutaneous and respiratory water loss when dehydrated (Maloiy, 1973; Schmidt-Nielsen et al., 1956), indicating that neuroendocrine integration is used to balance heat and water loss.

We found that elephants are able to modulate water loss when evaporation potential is greatest (high WVPSD) (Fig. 7). Interestingly though, we found that epidermal permeability is greater in summer than in winter in both elephant species, indicating seasonal acclimation, resulting in greater rates of evaporative cooling when air temperatures are highest. In addition, among Asian elephants, this effect was somewhat greater for animals housed at the southern California facility where summer temperatures were on average 7.4°C higher than the other two facilities. Thus, within a season, epidermal permeability is lower at high WVPSDs, yet between seasons, epidermal permeability is greater in summer for all WVPSDs (Fig. 7). This pattern reinforces the idea that adequate heat dissipation, rather than water conservation, is the greater challenge for these animals despite their frequent occupation of arid, water-scarce habitats.

Control of peripheral blood flow as well as structural and compositional changes in the skin are likely mechanisms influencing changes in epidermal permeability and the rate of CEWL in elephants. Peripheral blood flow to the dermis will influence the skin surface temperature and the hydration status of the deep epidermis, both of which will influence CEWL and epidermal permeability (Lillywhite, 2006). Longer-term acclimatization on the order of days to weeks is possibly the result of changes in lipid composition in the stratum corneum, the rate-limiting barrier to water loss in mammals and birds (Lillywhite, 2006) and suggests an area of future work.

The role of climate in influencing water use

Ultimately, the elephant’s reliance on evaporative cooling will translate into patterns of habitat use as the water requirements of these large mammals directly influences both their foraging distance from water and their frequency of return to water holes. Our results suggest that the effects of this shuttle-type life history on the landscape may be highly variable and depend significantly on climate. To illustrate the impact of climate on water use for thermoregulation we calculated theoretical thermal status and water lost to evaporative cooling (CEWL and REWL) for a representative African elephant (3800 kg). We did these calculations for a 24h period for an animal exposed to two different climates (Fig. 10). We used hourly climate data (NOAA, National Climate Data Center) from October 2010 from Port Elizabeth, South Africa (33°58'58.7"S, 25°37'1.2"E) and Okaukuejo, Namibia (19°8'59.9"S, 15°54'43.9"E). Both of these regions support large African elephant populations which experience very different climatic conditions that broadly represent two climate extremes experienced by this species. We used...
the measured relationships between skin surface temperature and air temperature (Table 1, Fig. 4) to calculate non-evaporative (radiation, conduction and convection) heat loss at each hour over the 24h period. For simplicity, we assumed that the elephant was standing still in the shade and was not flapping its ears, so direct solar radiation was absent and forced convection from either wind or ear flapping was minimal. CEWL was calculated at each hour based on the measured relationships in Table 3 and REWL was assumed to follow the maximum water saving strategy detailed above (Fig. 8B). The total amount of water lost through evaporation was then converted to heat loss (W) and the sum of non-evaporative and evaporative heat loss was plotted against time along with the corresponding air temperature.

The results of this back-of-the-envelope calculation demonstrate that climate may be the single most important factor influencing the need for surface water in elephants. In this simulation, elephants in the mild climate of the Port Elizabeth region were predicted to incur a water debt of only ~22 l day$^{-1}$. In contrast, elephants in Okaukuejo, Namibia, who were predicted to incur a water debt of over 100 l day$^{-1}$, had significantly less temperature (Table 2) to calculate non-evaporative (radiation, conduction and convection) heat loss at each hour over the 24h period. For simplicity, we assumed that the elephant was standing still in the shade and was not flapping its ears, so direct solar radiation was absent and forced convection from either wind or ear flapping was minimal. CEWL was calculated at each hour based on the measured relationships in Table 3 and REWL was assumed to follow the maximum water saving strategy detailed above (Fig. 8B). The total amount of water lost through evaporation was then converted to heat loss (W) and the sum of non-evaporative and evaporative heat loss was plotted against time along with the corresponding air temperature.

These results reflect several assumptions that will most certainly alter the amount of water lost through evaporative cooling as well as the relative contribution of non-evaporative cooling, including the absence of solar radiation and the lack of forced convection that would occur from ear flapping or walking against a wind. A more detailed biophysical model incorporating operative temperature (Bakken, 1976) would certainly offer further insight into field thermal and water budgets. However, this simple model does serve to illustrate the magnitude of the influence that climate can have on water requirements. African elephants have been classified as water dependent (Western, 1975), a classification based on their mean ranging distance and population density relative to water during the dry season. While there is significant variation among populations, most undergo a dry season range contraction around water (Loarie et al., 2009; Western, 1975). Our results demonstrate that an elephant’s water dependence is likely to be strongly habitat and climate specific. In addition to surface water, a number of factors influence home range size of elephants and other large herbivores, including, most importantly, the quality and quantity of food (Redfern et al., 2003; Redfern et al., 2005). We propose that the interaction between climate and water use may be as important as food quality or abundance and that this interaction should be considered in modeling landscape use and habitat selection by elephants and other large herbivores. Future physiological work to quantify thermal and water budgets of elephants under varying microclimates such as under different wind speeds and at higher air temperatures would facilitate the use of these data for ecological modeling purposes.

Our results provide a potential mechanistic link between climate-influenced physiological processes and ecosystem-level patterns of landscape use in relation to surface water in African and Asian elephants.

**Figure 10.** Hourly temperature data from weather stations near Etosha National Park, Namibia (top), and in Port Elizabeth, South Africa, near Addo Elephant Park (bottom), were used to construct a model of heat exchange and total water lost to evaporative cooling (EWL) for a representative African elephant in different climate regions. The red area indicates heat exchanged via conduction, convection and radiation while blue indicates heat exchange via cutaneous and respiratory evaporative heat loss. The gray line represents the ambient air temperature.
elephants. As the largest terrestrial mammals, elephants represent a physiological extreme. This study provides evidence that large body size has a thermoregulatory consequence that results in an obligation to use evaporative cooling and thus translates into a climate-dependent tether to surface water.

**LIST OF SYMBOLS AND ABBREVIATIONS**

- \( A \): arca (m²)
- \( b \): foot thickness (m)
- \( CEWL \): cutaneous evaporative water loss (g min⁻¹ m⁻²)
- \( CEWL_R \): raw rate of cutaneous evaporative water loss (g min⁻¹ m⁻²)
- \( F \): flow rate for calibration experiments (l min⁻¹)
- \( h_g \): convection coefficient (W m⁻²°C⁻¹)
- \( k \): thermal conductivity (W m⁻¹°C⁻¹)
- \( R \): gas constant for water vapor (J K⁻¹ kg⁻¹)
- \( REML \): restricted maximum likelihood analysis
- \( REWL \): respiratory evaporative water loss (l day⁻¹)
- \( T_a \): air temperature (°C)
- \( T_s \): soil surface temperature (°C)
- \( V \): STPD-corrected flow rate of air (l min⁻¹)
- \( W_{VPSD} \): water vapor pressure saturation deficit (kPa)
- \( \varepsilon \): emissivity of skin (decimal fraction)
- \( \rho \): water vapor pressure (Pa)
- \( \sigma \): Stefan-Boltzmann constant (W m⁻² K⁻⁴)

**ACKNOWLEDGEMENTS**

We thank the staff at Wildlife Safari, Six Flags Discovery Kingdom and Have Trunk Will Travel for their assistance in training and collection of these data. We also thank Gena Bentall, Christine Alfano, Traci Kendall and Beau Richter for their assistance in training and collection of these data. We thank the staff at Wildlife Safari, Six Flags Discovery Kingdom and Have Trunk Will Travel for their assistance in training and collection of these data. We thank Gena Bentall, Christine Alfano, Traci Kendall and Beau Richter for their assistance in training and collection of these data. We thank the staff at Wildlife Safari, Six Flags Discovery Kingdom and Have Trunk Will Travel for their assistance in training and collection of these data. We thank the staff at Wildlife Safari, Six Flags Discovery Kingdom and Have Trunk Will Travel for their assistance in training and collection of these data. We thank the staff at Wildlife Safari, Six Flags Discovery Kingdom and Have Trunk Will Travel for their assistance in training and collection of these data. We thank the staff at Wildlife Safari, Six Flags Discovery Kingdom and Have Trunk Will Travel for their assistance in training and collection of these data. We thank the staff at Wildlife Safari, Six Flags Discovery Kingdom and Have Trunk Will Travel for their assistance in training and collection of these data. We thank the staff at Wildlife Safari, Six Flags Discovery Kingdom and Have Trunk Will Travel for their assistance in training and collection of these data. We thank the staff at Wildlife Safari, Six Flags Discovery Kingdom and Have Trunk Will Travel for their assistance in training and collection of these data. We thank the staff at Wildlife Safari, Six Flags Discovery Kingdom and Have Trunk Will Travel for their assistance in training and collection of these data. We thank the staff at Wildlife Safari, Six Flags Discovery Kingdom and Have Trunk Will Travel for their assistance in training and collection of these data. We thank the staff at Wildlife Safari, Six Flags Discovery Kingdom and Have Trunk Will Travel for their assistance in training and collection of these data. We thank the staff at Wildlife Safari, Six Flags Discovery Kingdom and Have Trunk Will Travel for their assistance in training and collection of these data. We thank the staff at Wildlife Safari, Six Flags Discovery Kingdom and Have Trunk Will Travel for their assistance in training and collection of these data. We thank the staff at Wildlife Safari, Six Flags Discovery Kingdom and Have Trunk Will Travel for their assistance in training and collection of these data. We thank the staff at Wildlife Safari, Six Flags Discovery Kingdom and Have Trunk Will Travel for their assistance in training and collection of these data. We thank the staff at Wildlife Safari, Six Flags Discovery Kingdom and Have Trunk Will Travel for their assistance in training and collection of these data. We thank the staff at Wildlife Safari, Six Flags Discovery Kingdom and Have Trunk Will Travel for their assistance in training and collection of these data. We thank the staff at Wildlife Safari, Six Flags Discovery Kingdom and Have Trunk Will Travel for their assistance in training and collection of these data. We thank the staff at Wildlife Safari, Six Flags Discovery Kingdom and Have Trunk Will Travel for their assistance in training and collection of these data. We thank the staff at Wildlife Safari, Six Flags Discovery Kingdom and Have Trunk Will Travel for their assistance in training and collection of these data. We thank the staff at Wildlife Safari, Six Flags Discovery Kingdom and Have Trunk Will Travel for their assistance in training and collection of these data. We thank the staff at Wildlife Safari, Six Flags Discovery Kingdom and Have Trunk Will Travel for their assistance in training and collection of these data. We thank the staff at Wildlife Safari, Six Flags Discovery Kingdom and Have Trunk Will Travel for their assistance in training and collection of these data. We thank the staff at Wildlife Safari, Six Flags Discovery Kingdom and Have Trunk Will Travel for their assistance in training and collection of these data. We thank the staff at Wildlife Safari, Six Flags Discovery Kingdom and Have Trunk Will Travel for their assistance in training and collection of these data. We thank the staff at Wildlife Safari, Six Flags Discovery Kingdom and Have Trunk Will Travel for their assistance in training and collection of these data. We thank the staff at Wildlife Safari, Six Flags Discovery Kingdom and Have Trunk Will Travel for their assistance in training and collection of these data. We thank the staff at Wildlife Safari, Six Flags Discovery Kingdom and Have Trunk Will Travel for their assistance in training and collection of these data. We thank the staff at Wildlife Safari, Six Flags Discovery Kingdom and Have Trunk Will Travel for their assistance in training and collection of these data. We thank the staff at Wildlife Safari, Six Flags Discovery Kingdom and Have Trunk Will Travel for their assistance in training and collection of these data. We thank the staff at Wildlife Safari, Six Flags Discovery Kingdom and Have Trunk Will Travel for their assistance in training and collection of these data. We thank the staff at Wildlife Safari, Six Flags Discovery Kingdom and Have Trunk Will Travel for their assistance in training and collection of these data. We thank the staff at Wildlife Safari, Six Flags Discovery Kingdom and Have Trunk Will Travel for their assistance in training and collection of these data. We thank the staff at Wildlife Safari, Six Flags Discovery Kingdom and Have Trunk Will Travel for their assistance in training and collection of these data. We thank the staff at Wildlife Safari, Six Flags Discovery Kingdom and Have Trunk Will Travel for their assistance in training and collection of these data. We thank the staff at Wildlife Safari, Six Flags Discovery Kingdom and Have Trunk Will Travel for their assistance in training and collection of these data. We thank the staff at Wildlife Safari, Six Flags Discovery Kingdom and Have Trunk Will Travel for their assistance in training and collection of these data. We thank the staff at Wildlife Safari, Six Flags Discovery Kingdom and Have Trunk Will Travel for their assistance in training and collection of these data. We thank the staff at Wildlife Safari, Six Flags Discovery Kingdom and Have Trunk Will Travel for their assistance in training and collection of these data. We thank the staff at Wildlife Safari, Six Flags Discovery Kingdom and Have Trunk Will Travel for their assistance in training and collection of these data. We thank the staff at Wildlife Safari, Six Flags Discovery Kingdom and Have Trunk Will Travel for their assistance in training and collection of these data. We thank the staff at Wildlife Safari, Six Flags Discovery Kingdom and Have Trunk Will Travel for their assistance in training and collection of these data. We thank the staff at Wildlife Safari, Six Flags Discovery Kingdom and Have Trunk Will Travel for their assistance in training and collection of these data. We thank the staff at Wildlife Safari, Six Flags Discovery Kingdom and Have Trunk Will Travel for their assistance in training and collection of these data. We thank the staff at Wildlife Safari, Six Flags Discovery Kingdom and Have Trunk Will Travel for their assistance in training and collection of these data. We thank the staff at Wildlife Safari, Six Flags Discovery Kingdom and Have Trunk Will Travel for their assistance in training and collection of these data. We thank the staff at Wildlife Safari, Six Flags Discovery Kingdom and Have Trunk Will Travel for their assistance in training and collection of these data. We thank the staff at Wildlife Safari, Six Flags Discovery Kingdom and Have Trunk Will Travel for their assistance in training and collection of these data. We thank the staff at Wildlife Safari, Six Flags Discovery Kingdom and Have Trunk Will Travel for their assistance in training and collection of these data.


Table S1. Minimum, mean and maximum air temperature ($T_{\text{air}}$) and relative humidity (RH) values for the three facilities where measurements were collected

<table>
<thead>
<tr>
<th>Facility</th>
<th>$T_{\text{air}}$</th>
<th>RH</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Minimum</td>
<td>Mean</td>
</tr>
<tr>
<td>Have Trunk Will Travel (Perris, CA)</td>
<td>8.1±6.0$^a$</td>
<td>16.9±6.5$^a$</td>
</tr>
<tr>
<td>Six Flags Discovery Kingdom (Vallejo, CA)</td>
<td>6.6±4.7$^b$</td>
<td>13.6±4.9$^b$</td>
</tr>
<tr>
<td>Wildlife Safari (Winston, OR)</td>
<td>7.0±5.2$^c$</td>
<td>12.8±6.7$^c$</td>
</tr>
</tbody>
</table>

Data are means ± s.d. Values with the same superscripted letters in a column are not significantly different from one another.
<table>
<thead>
<tr>
<th>Common name (species)</th>
<th>Body mass (kg)</th>
<th>$T_{av}$ °C</th>
<th>CEWL (g m$^{-2}$ h$^{-1}$)*</th>
<th>Comments</th>
<th>Citation</th>
<th>Classification of water dependence</th>
</tr>
</thead>
<tbody>
<tr>
<td>Dik-dik (R. kirkii &amp; guentheri)</td>
<td>2–6</td>
<td>20–45</td>
<td>10–20</td>
<td>Low density of sweat glands</td>
<td>Maloiy, 1973</td>
<td>Water independent</td>
</tr>
<tr>
<td>Thompson’s gazelle (G. thomsonii)</td>
<td>14–15</td>
<td>20–50</td>
<td>50**</td>
<td>Sweat glands present</td>
<td>Taylor, 1970</td>
<td>Water dependent</td>
</tr>
<tr>
<td>Grant’s gazelle (G. granti)</td>
<td>26–34</td>
<td>20–50</td>
<td>75**</td>
<td>Sweat glands present</td>
<td>Taylor, 1970</td>
<td>Water independent</td>
</tr>
<tr>
<td>Mule deer (O. h. hemionus)</td>
<td>28–78</td>
<td>10–30</td>
<td>0–80</td>
<td>Minimal sweating</td>
<td>Parker and Robbins, 1984</td>
<td>NA</td>
</tr>
<tr>
<td>Impala (A. melampus)</td>
<td>55–75</td>
<td>22–50</td>
<td>10–65</td>
<td>Sweat glands present</td>
<td>Maloiy and Hopcroft, 1971</td>
<td>NA</td>
</tr>
<tr>
<td>Oryx (O. beisa)</td>
<td>104–121</td>
<td>20–50</td>
<td>25–130</td>
<td>Sweat glands present</td>
<td>Taylor, 1970</td>
<td>Water independent</td>
</tr>
<tr>
<td>Hartebeest (A. buscelaphus)</td>
<td>80–130</td>
<td>22–50</td>
<td>5–60</td>
<td>Sweat glands present</td>
<td>Maloiy and Hopcroft, 1971</td>
<td>Water dependent</td>
</tr>
<tr>
<td>Elk (C. e. nelsoni)</td>
<td>76–186</td>
<td>14–30</td>
<td>0–320</td>
<td>Sweat glands present</td>
<td>Parker and Robbins, 1984</td>
<td>NA</td>
</tr>
<tr>
<td>Waterbuck (K. d. ugandae)</td>
<td>95–105</td>
<td>25–45</td>
<td>50–125</td>
<td>Sweat glands present</td>
<td>Taylor et al., 1969</td>
<td>Water dependent</td>
</tr>
<tr>
<td>Wildebeest (C. taurinus)</td>
<td>138–158</td>
<td>20–50</td>
<td>50**</td>
<td>Sweat glands present</td>
<td>Taylor, 1970</td>
<td>Water dependent</td>
</tr>
<tr>
<td>Zebra (E. burchelli)</td>
<td>275–420**</td>
<td>29.9</td>
<td>90–291</td>
<td>Sweat glands present</td>
<td>Hiley, 1977</td>
<td>Water dependent</td>
</tr>
<tr>
<td>Hippopotamus (H. amphibious)</td>
<td>1500</td>
<td>32–39</td>
<td>86.4–268.8</td>
<td>Subdermal glands present</td>
<td>Luck and Wright, 1964; Saikawa et al., 2004</td>
<td>Water dependent</td>
</tr>
<tr>
<td>Rhinoceros (white &amp; black)</td>
<td>1000–3000**</td>
<td>29.9</td>
<td>210–310</td>
<td>Sweat glands present</td>
<td>Hiley, 1977</td>
<td>NA</td>
</tr>
<tr>
<td>(C. bicornis &amp; D. bicornis)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Asian elephant (E. maximus)</td>
<td>3834±498</td>
<td>8–33</td>
<td>18.6–534</td>
<td>Insensible</td>
<td>Present study</td>
<td>Water dependent</td>
</tr>
<tr>
<td>African elephant (L. africana)</td>
<td>3768±642</td>
<td>8–33</td>
<td>15.6–390</td>
<td>Insensible</td>
<td>Present study</td>
<td>Water dependent</td>
</tr>
<tr>
<td>African elephant (L. africana)</td>
<td>3000–6000**</td>
<td>25.0</td>
<td>192–493 (means)</td>
<td>Insensible, range is for different body sites</td>
<td>Wright and Luck, 1984</td>
<td>Water dependent</td>
</tr>
<tr>
<td>Human (H. sapiens)</td>
<td>70–90**</td>
<td>19–28</td>
<td>2.8–37.4 (means)</td>
<td>Sweat glands present, means from several studies &amp; body sites</td>
<td>Pinnagoda et al., 1990</td>
<td>NA</td>
</tr>
</tbody>
</table>

*CEWL ranges represent the values at the low and high end of the ambient temperatures that were measured unless otherwise noted.

**Body mass not given in paper. Commonly reported ranges are given instead.

*Values are estimated from fig. 3 in Taylor (Taylor, 1970) for hydrated animals. Rates were nearly constant across range of $T_{av}$.