RESEARCH ARTICLE

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

Robin C. Dunkin[1],*, Dinah Wilson[2], Nicolas Way[3], Kari Johnson[4] and Terrie M. Williams[1]

[1]Department of Ecology and Evolutionary Biology, University of California, Santa Cruz, Santa Cruz, CA, USA, [2]Wildlife Safari, Winston, OR, USA, [3]Six Flags Discovery Kingdom, Vallejo, CA, USA and [4]Have 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 kg; six Asian, 3834±498 kg) 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 Asian elephants and 0.26 and 6.5 g min^{-1} m^{-2} for African elephants. Simulated thermal and water budgets using climate data from Port Elizabeth, South Africa, and Okaukuejo, Namibia, suggested that the 24-h evaporative cooling water debt incurred in warm climates can be more than 4.5 times that incurred in mesic 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

(Wright and Luck, 1984), a result of a relatively high integumental permeability relative to other animals (Dunkin, 2012). Therefore, water-dependent thermoregulation has the potential to be a critical driver of differential landscape use across populations from the diverse climate regions inhabited by elephants.

The objective of this study was to characterize the interaction between climate, thermal balance and water use in elephants to understand the potential impact of these factors in dictating landscape use by these animals. Based on the classification of elephants as water dependent and on previous measures of evaporative water loss, we hypothesized that evaporative cooling will constitute a significant portion of the thermal and water budget for both elephant species and that this contribution will be positively related to ambient temperature. To test these hypotheses we developed empirical relationships between air temperature, thermal balance and water use for elephants across a range of air temperatures and used these relationships to assess the degree to which elephants are obligated to use evaporative cooling in different climates or seasons. We carried out these measurements in both African [*Loxodonta africana* (Blumenbach 1797)] and Asian (*Elephas maximus* Linnaeus 1758) elephants to evaluate species-specific differences given the disparate climates (temperature, humidity) in which each group has evolved.

MATERIALS AND METHODS
Approach

To determine the relative contribution of evaporative cooling to the thermal budgets of African and Asian elephants across a range of air temperatures, we measured skin surface temperatures (T_{ss}) 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 (REWL) and resting heat production using open flow respirometry to estimate the contribution of respiration to total heat and water balance and to determine heat production for the individuals in this study.

Animals and facilities

We used 13 elephants in this study – seven adult African (six 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 climate 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 examine the range of variation in the thermal response to changes in air temperature across the surface of the body, measurements were taken at five body sites as detailed in Fig. 1. For consistency, care was taken to avoid sites directly over large blood vessels when measuring the ears. The surface area of the body and legs of each elephant (six Asian and five African) was estimated by collecting a series of morphometric measurements as detailed in Fig. 1. These measurements were used to model the body and legs of the elephant as individual cylinders (Williams, 1990) from which surface area could then be estimated. Ear surface area for each individual was measured from digital photographs taken of the front surface of one ear. A metric was photographed in the same plane as the ear and the total surface area was measured using National Institutes of Health ImageJ software (Rasband, 1997-2009) (Fig. 1).

Body mass was periodically measured (±5 kg) throughout the study for each individual as part of the normal husbandry procedures at each facility. For the metabolic measurements (described below), mass-specific calculations used the body mass measured within 1 month of the metabolic measurements. All other mass measurements are presented as the mean of the measurements taken over the course of the study.

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 (T_{air}) and relative humidity (RH) were measured at elephant shoulder height, within 1.8 m of where the elephant was standing [7400 Perception II, Davis Instruments, Hayward, CA, USA, temperature (±0.5°C) and RH (±5%) sensors], and water vapor pressure was calculated using the Arden–Buck equation (Buck, 1981; Buck, 1996). The T_{air} 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. T_{air} 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
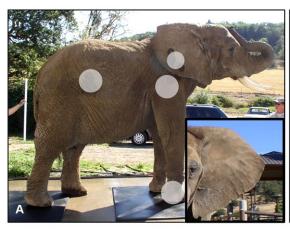
Fig. 1. An African (A) and an Asian elephant (B) with corresponding ear surfaces and location of measurements on body. Cutaneous evaporative water loss (CEWL) and skin surface temperature were measured at five body sites including: the outer margin of the (1) anterior and (2) posterior ear surfaces, (3) the shoulder just ventral to the lower margin of the ear when the ear was flat against the body, (4) the lateral flank near the widest point of the body, and (5) the front right or left foot just dorsal to the toenails. The surface area of the animals was calculated by modeling the body and legs as cylinders using morphometric measurements, including the length of the torso (from the insertion of the back of the ear to the base of the tail), the circumference of the animal at the widest part of the belly, the height of the front and rear leg measured from the axilla to the ground, the circumference of the front and rear leg at the knee, and the circumference of the front and rear foot when pressed to the ground.

minimum T_{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_{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_{air} and RH (measured as above) were recorded at the same time as each individual measurement of T_{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 $N=518$ measurements including all body sites).

Radiant, convective and conductive heat loss were calculated according to Williams (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):

$$\text{Radiant heat exchange} = \sigma\varepsilon\left(T_{ss}^4 - T_{air}^4\right) \times 0.85A, \quad (1)$$

where σ is the Stephan–Boltzmann constant, $5.7 \times 10^{-8}\,\text{W m}^{-2}\,\text{K}^{-4}$; ε is the emissivity of the skin, 0.98 (Clark and Edholm, 1985; Williams, 1990); T_{ss} and T_{air} are the temperature of the skin and air, respectively (K); A is surface area (m²); 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; $\text{W m}^{-2}\,°\text{C}^{-1}$) 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):

$$\text{Convective heat exchange} = h_c A(T_{ss} - T_{air}). \quad (2)$$

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:

$$\text{Conductive heat exchange} = kA(T_{ss} - T_{floor}) / b, \quad (3)$$

where k is the thermal conductivity of the tissue [0.19 for Asian elephant and $0.23\,\text{W m}^{-1}\,°\text{C}^{-1}$ for African elephants; measured in a

concurrent study (Dunkin, 2012)] and *b* is the foot thickness across which heat is transferred (0.05 m) (Williams, 1990).

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.
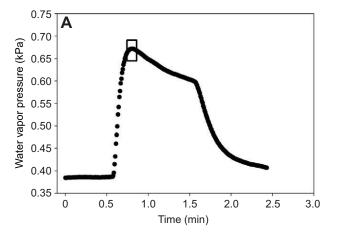
The ventilated capsule technique relies upon low velocity airflow (mean ± s.d. STDP flow rate=0.79±0.281 min^{-1}) across the skin, and thus error resulting from changes in the water vapor pressure directly above the skin and convective effects due to higher velocity air flow across the skin are minimized (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):

$$CEWL = \frac{\dot{V}\left(\frac{p_{out}-p_{in}}{T_{air} \times R}\right)}{A}, \qquad (4)$$

where CEWL (g min^{-1} m^{-2}) was determined from the STPD-corrected flow rate of the inlet air ($\dot{V}$; 1 min^{-1}), the water vapor pressure (Pa) of the outlet and inlet air stream (p_{out} and p_{in}), the air temperature, T_{air} (K), the gas constant for water vapor, 461.5 J K^{-1} kg^{-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
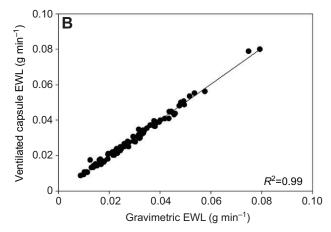

Fig. 2. Sample raw data of cutaneous evaporative water loss (CEWL) measurement from an African elephant (A) and the relationship between gravimetric and ventilated capsule measurement techniques across three temperatures and three flow rates for calibration of the evaporative water loss system used to measure CEWL (B). Box in A indicates the area where the maximum CEWL value was calculated.

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 min^{-1} m^{-2} 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 (WVPSD; kPa). The WVPSD was determined by first

calculating the saturated water vapor pressure at the measured T_{ss}. 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±0.3, 22.8±0.6 and 27.6±0.2°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±0.021 min^{-1}), medium (mean 0.79±0.011 min^{-1}) and high (mean 0.96±0.041 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 ±0.0001 g (Model 1712, Sartorious, 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±5.2%. 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±4.4, −7.8±4.3 and −9.8±3.7% 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:

$$CEWL = \left[\left(\frac{CEWL_R \times \left((-8.5538) + (0.5387 \times T_{air}) + (4.8819 \times F) \right)}{100} \right) + CEWL_R \right], \quad (5)$$

where CEWL is the temperature- and flow-corrected rate of evaporative water loss (g min^{-1}), $CEWL_R$ is the raw rate of CEWL in the same units, T_{air} is the air temperature (°C), and F is the flow rate (1 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±4.4% (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 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

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.

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 incurrent 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 $20.1\,kJ\,l^{-1}\,O_2$.

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 T_{ss} 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 or WVPSD and to determine whether there were differences between species. In all REML analyses, facility was included as a random effect to account for potential variation between the three facilities.

A subset of the T_{ss} 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 T_{ss} changed with T_{air}. Similar to the CEWL analysis, we constructed separate relationships for the body and ears and before and after simulated 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 Eqns 1–3 and T_{ss} 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 with 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

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

Table 1. Relationships between skin surface temperature (T_{ss}) and air temperature (T_{air}) for Asian and African elephants

Species	Body region	Wet/dry skin	Regression equation	d.f.	F	P	R^2
Elephas maximus	Body	Dry	$T_{ss}=16.59+0.55T_{air}$	70,1	82.4	<0.0001	0.54
	Ears	Dry	$T_{ss}=-4.05+1.49-0.10(T_{air}-20.9)^2$	45,2	158.4	<0.0001	0.87
	Body	Wet	$T_{ss}=9.71+0.76T_{air}$	70,1	168.0	<0.0001	0.71
	Ears	Wet	$T_{ss}=-5.26+1.31T_{air}$	46,1	142.5	<0.0001	0.76
Loxodonta africana	Body	Dry	$T_{ss}=19.35+0.39T_{air}$	99,1	144.8	<0.0001	0.60
	Ears	Dry	$T_{ss}=9.36+0.67T_{air}$	66,1	176.7	<0.0001	0.73
	Body	Wet	$T_{ss}=16.91+0.36T_{air}$	97,1	199.7	<0.0001	0.67
	Ears	Wet	$T_{ss}=9.51+0.57T_{air}$	64,1	123.5	<0.0001	0.66

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.
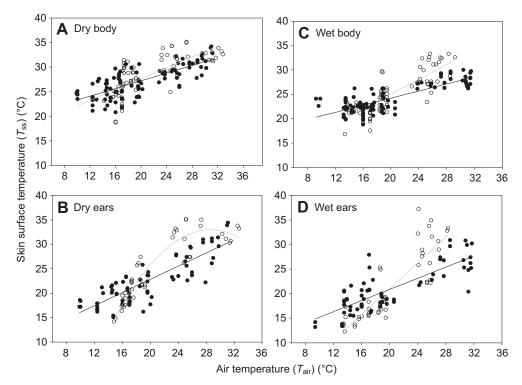
Fig. 4. Skin surface temperature (T_{ss}) in relation to air temperature (T_{air}) for African (filled symbols) and Asian (open symbols) elephants. Measurements were performed on three sites on the body and two sites on the ears when dry (A,B) or wet (C,D). Solid black (African) and gray lines (Asian) represent the best-fit equation for each species (see Table 1 for complete equations and statistics).

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
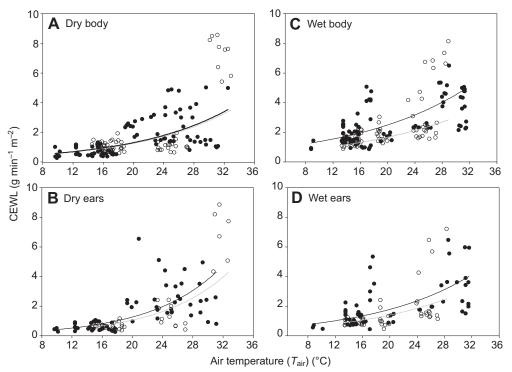

Fig. 5. Cutaneous evaporative water loss (CEWL) in relation to air temperature (T_{air}) for African (filled symbols) and Asian (open symbols) elephants. Measurements were performed on three sites on the body and two sites on the ears when dry (A,B) and wet (C,D). Solid black (African) and gray lines (Asian) represent the best-fit equation determined from a REML analysis (see Table 2 for complete equations and statistics).

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 g min^{-1} m^{-2} from all body sites of dry Asian elephants and ranged between 0.26 and 6.5 g min^{-1} 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 × T_{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_{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_{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 W 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 l H$_2$O 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

Table 2. Relationships between CEWL and air temperature (T_{air}) or water vapor pressure saturation deficit (WVPSD) for Asian and African elephants

	Body region	Wet/dry skin	E. maximus	L. africana	N	Terms*	F	P	R^2
CEWL vs T_{air}	Body	Dry	e^(−1.36−0.02+T_{air}×0.08)	e^(−1.36+0.02+T_{air}×0.08)	159	Species / T_{air}	0.09 / 169.7	0.77 / <0.0001	0.60
	Ears	Dry	e^(−2.05+0.11×T_{air}−0.09)	e^(−2.05+0.11×T_{air}+0.09)	107	Species / T_{air}	1.29 / 168.1	0.26 / <0.0001	0.66
	Body	Wet	e^(−0.45−0.04+0.06×T_{air}−20.2×0.01)	e^(−0.45+0.04+0.06×T_{air}−20.2×−0.01)	152	Species × T_{air} / Species / T_{air}	5.44 / 1.04 / 143.89	0.02 / 0.31 / <0.0001	0.56
	Ears	Wet	e^(−0.94+0.07×T_{air}−0.12)	e^(−0.94+0.07×T_{air}+0.12)	100	Species / T_{air}	3.18 / 92.4	0.08 / <0.0001	0.54
CEWL vs WVPSD	Body	Dry	e^(−0.17+0.23×WVPSD−0.05)	e^(−0.17+0.23×WVPSD+0.05)	159	Species / WVPSD	0.31 / 14.57	0.58 / 0.0002	0.24
	Ears	Dry	e^(−0.35+0.37×WVPSD−0.17)	e^(−0.35+0.37×WVPSD+0.17)	107	Species / WVPSD	2.60 / 36.3	0.11 / <0.0001	0.33
	Body	Wet	e^(0.22+0.42×WVPSD−0.12+WVPSD−1.43×−0.13)	e^(0.22+0.42×WVPSD+0.12+WVPSD−1.43×0.13)	152	Species × WVPSD / Species / WVPSD	4.71 / 4.41 / 46.23	0.03 / 0.04 / <0.0001	0.32
	Ears	Wet	e^(0.096+0.38×WVPSD−0.23+WVPSD−0.98×−0.14)	e^(0.096+0.38×WVPSD+0.23+WVPSD−0.98×0.14)	98	Species × WVPSD / Species / WVPSD	4.86 / 7.47 / 37.97	0.03 / 0.009 / <0.0001	0.38

*All statistics in this table are the result of REML analyses with facility included as a random effect. If the interaction term is not listed it was not significant and was discarded.
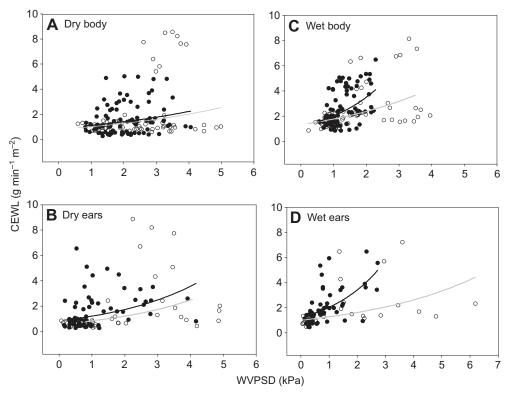
Fig. 6. Cutaneous evaporative water loss (CEWL) in relation to water vapor pressure saturation deficit (WVPSD) for African (filled symbols) and Asian (open symbols) elephants. Measurements were performed on three sites on the body and two sites on the ears when dry (A,B) and wet (C,D). Solid black (African) and gray lines (Asian) represent the best-fit equation determined from a REML analysis (see Table 2 for complete equations and statistics).

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
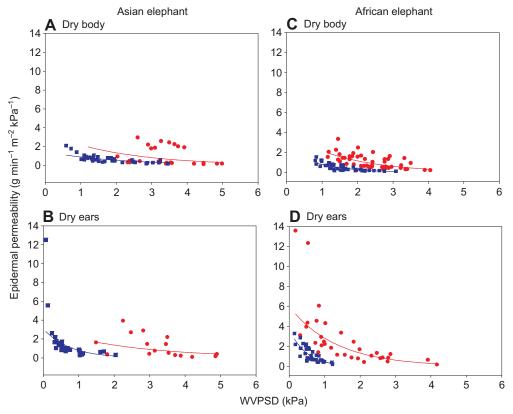

Fig. 7. Epidermal permeability in relation to water vapor pressure saturation deficit (WVPSD) for the body (A,C) and ears (B,D) of Asian and African elephants in summer (red) and winter (blue). Lines represent the best-fit equation determined through a REML analysis (see Table 3 for complete equations and statistics). All values are for dry skin only.

Table 3. Relationships between epidermal permeability and WVPSD across seasons for Asian and African elephants

Species	Body region	Season	E. maximus	N	Terms*	F	P	R^2
E. maximus	Body	Summer	e^(0.82–0.48×WVPSD+0.44)	65	Season	25.2	<0.0001	0.59
		Winter	e^(0.82–0.48×WVPSD–0.44)		WVPSD	36.7	<0.0001	
	Ears	Summer	e^(1.13–0.89×WVPSD+0.86–1.78×0.47)	43	Season × WVPSD	15.27	0.0004	0.74
		Winter	e^(1.13–0.89×WVPSD–0.86–1.78×–0.47)		Season	27.86	<0.0001	
					WVPSD	54.49	<0.0001	
L. africana	Body	Summer	e^(1.12–0.83×WVPSD+0.70)+[(WVPSD–1.99)×0.21]	94	Season × WVPSD	6.79	0.011	0.69
					Season	150.05	<0.0001	
		Winter	e^(1.12–0.83×WVPSD–0.70)+[(WVPSD–1.99)×–0.21]		WVPSD	120.15	<0.0001	
	Ears	Summer	e^(1.56–1.44×WVPSD+1.00)+[(WVPSD–1.13)×0.68]	64	Season × WVPSD	18.6	<0.0001	0.74
					Season	106.7	<0.0001	
		Winter	e^(1.56–1.44×WVPSD–1.00)+[(WVPSD–1.13)×–0.68]		WVPSD	83.1	<0.0001	

*All statistics in this table are the result of REML analyses with facility included as a random effect. If the interaction term is not listed it was not significant and was discarded.

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 5.6 l (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.
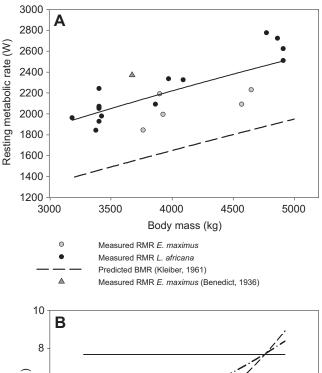
Our results also demonstrate species-specific differences in the response of skin surface temperature to increasing air temperature. Over the body, Asian elephant skin surface temperature tended to be only slightly higher at any given air temperature compared with African elephants, but there was a marked 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 Asian 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 elephants may need to maintain a larger gradient between skin and air temperature to facilitate adequate heat loss through the ears. As air temperature rises, Asian elephants may shunt blood away from the ears to avoid heat gain, which may explain the slight decrease in ear surface temperature as air temperature exceeds 28°C.

The overall influence of bathing on skin temperature of African elephants was as expected; skin temperatures were generally lower after bathing. The most pronounced effect of bathing on Asian elephants was that ear skin temperature continued to increase with T_{air} rather than plateau (Fig. 4B,D). Asian elephants also maintained a higher skin temperature in relation to air after bathing compared with African elephants. Not surprisingly, CEWL, which after bathing included both endogenous and exogenous water, was higher from the body and ears of both species over all measured temperatures. Our results support the idea that wallowing has a clear thermoregulatory function through not only the increased heat loss that occurs while submerged in water but also through enhanced evaporative cooling after leaving the waterhole. The suggested functions of mud and dust bathing range from sun protection to protection from insects to thermoregulatory benefits (Rees, 2002; Sikes, 1971). Lillywhite and Stein (Lillywhite and Stein, 1987) found that the highly sculptured surface of the skin enhances the adherence of mud and water for up to 26 h and hypothesized that water and mud would protect the skin from solar radiation and enhance evaporative cooling. 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
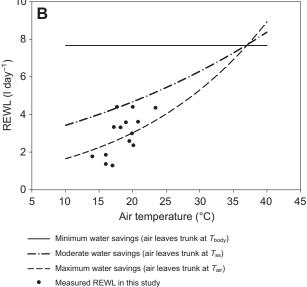
Fig. 8. (A) Resting metabolic rate and (B) respiratory evaporative water loss (REWL) measured for African and Asian elephants. Animals were not fasted prior to measurements to better predict resting heat production for animals in a field environment. Kleiber's (Kleiber, 1961) prediction of basal metabolic 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$^{0.58}$, 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.
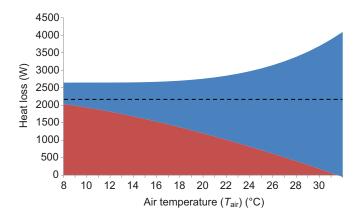

Fig. 9. The estimated amount of heat dissipated through non-evaporative (red) and evaporative (blue) routes across the temperature range measured in this study for African elephants. The black dashed line indicates the resting metabolic rate for a 3800 kg African elephant based on measurements in this 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 24 h 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
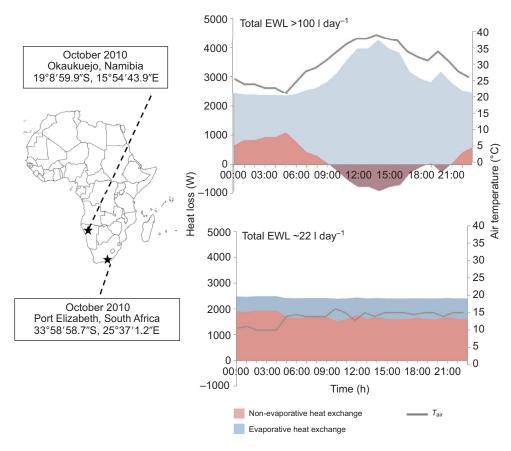
Fig. 10. Hourly temperature data from weather stations near Etosha National Park, Namibia (top), and in Port Elizabeth, South Africa, near Addo Elephant Park (bottom), were used to construct a model of heat exchange and total water lost to evaporative cooling (EWL) for a representative African elephant 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.

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 24 h 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 rely upon evaporative cooling throughout the day, yet they would incur a water debt of only ~22 l over 24 h. This is in marked contrast with elephants in Okaukuejo, Namibia, who were predicted to incur a water debt of over 100 l day^{-1}. The 24 h period chosen for this exercise was not an especially extreme day in Namibia; the maximum temperature reached only 38.8°C, significantly less than the temperatures of 45°C or greater that occur in this region (Loarie et al., 2009). Previous reported values for water requirements for African elephants are between 150 and 200 l day^{-1} (reviewed in Fowler and Mikota, 2006; Sikes, 1971). Thus, in hot climates, well over one half to three quarters of the daily water debt may result from evaporative cooling. Although some of this water debt will be reclaimed through food intake and metabolic water production, most will require the animal to visit a water hole, thereby effectively tethering the animal to a water source.

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. 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	area (m^2)
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_c	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_{air}	air temperature (°C)
T_{floor}	floor temperature (°C)
T_{ss}	skin surface temperature (°C)
$\dot{V}$	STPD-corrected flow rate of air ($l\,min^{-1}$)
WVPSD	water vapor pressure saturation deficit (kPa)
ε	emissivity of skin (decimal fraction)
ρ	water vapor pressure (Pa)
σ	Stephan–Boltzmann constant ($W\,m^{-2}\,K^{-4}$)

AUTHOR CONTRIBUTIONS

R.C.D. conceived of the question and design, carried out the measurements, analyzed the data and wrote the manuscript. D.W., N.W. and K.J. contributed to the design of the study, made possible the execution of the study by providing access to and training of the animals in this study, and provided feedback on the manuscript. T.M.W. contributed to the design, assisted with the execution and contributed to the writing of the manuscript.

COMPETING INTERESTS

No competing interests declared.

REFERENCES

Anderson, D. (1936). Relative humidity or vapor pressure deficit. *Ecology* **17**, 277-282.

Bakken, G. S. (1976). A heat transfer analysis of animals: unifying concepts and the application of metabolism chamber data to field ecology. *J. Theor. Biol.* **60**, 337-384.

Benedict, F. G. (1936). *The Physiology of the Elephant*. Washington, DC: Carnegie Institute.

Buck, A. L. (1981). New equations for computing vapor pressure and enhancement factor. *J. Appl. Meteorol.* **20**, 1527-1532.

Buck, A. L. (1996). *Buck Research CR-1A User's Manual*. Boulder, CO, USA: Buck Research Instruments.

Buss, I. O. and Estes, J. A. (1971). The functional significance of movements and positions of the pinnae of the African elephant, Loxodonta africana. *J. Mammal.* **52**, 21-27.

Chamaillé-Jammes, S. and Fritz, M. V. H. (2007). Managing heterogeneity in elephant distribution: interactions between elephant population density and surface-water availability. *J. Appl. Ecol.* **44**, 625-633.

Chamaillé-Jammes, S., Valeix, M. and Fritz, H. (2007). Elephant management: why can't we throw out the babies with the artificial bathwater? *Divers. Distrib.* **13**, 663-665.

Clark, R. P. and Edholm, O. G. (1985). *Man And His Thermal Environment.* London: Edward Arnold.

de Beer, Y. and van Aarde, R. J. (2008). Do landscape heterogeneity and water distribution explain aspects of elephant home range in southern Africa's arid savannas? *J. Arid Environ.* **72**, 2017-2025.

Dunkin, R. C. (2012). From tissues to landscapes: how thermal physiology, water use, and climate influence patterns of landscape use in elephants. PhD dissertation, University of California, Santa Cruz.

Elias, P. M. (1991). Epidermal barrier function: intercellular lamellar lipid structures, origin, composition and metabolism. *J. Control. Release* **15**, 199-208.

Epaphras, A. M., Gereta, E., Lejora, I. A., Meing'ataki, G. E. O., Ng'umbi, G., Kiwango, Y., Mwangomo, E., Semanini, F., Vitalis, L., Balozi, J. et al. (2008). Wildlife water utilization and importance of artificial waterholes during dry season at Ruaha National Park, Tanzania. *Wetlands Ecol. Manage.* **16**, 183-188.

Fedak, M. A., Rome, L. and Seeherman, H. J. (1981). One-step N$_2$-dilution technique for calibrating open-circuit V_{O_2} measuring systems. *J. Appl. Physiol.* **51**, 772-776.

Fowler, M. E. and Mikota, S. K. (2006). *Biology, Medicine, and Surgery of Elephants*. Ames, IA: Blackwell Publishing.

Gates, D. M. (1980). *Biophysical Ecology*. New York, NY: Springer-Verlag.

Gaylard, A., Owen-Smith, N. and Redfern, J. (2003). Surface water availability: implications for heterogeneity and ecosystem processes. In *The Kruger Experience* (ed. J. T. D. Toit, K. Rogers and H. Biggs), p. 519. Washington, DC: Island Press.

Gibbs, A. G. (2011). Thermodynamics of cuticular transpiration. *J. Insect Physiol.* **57**, 1066-1069.

Hiley, P. G. (1977). The thermoregulatory response of the rhinoceros *Diceros bicornis* and *Ceratotherium simum* and the zebra *Equus burchelli* to diurnal temperature change. *East Afr. J. Ecol.* **15**, 337.

Horstmann, E. (1966). Die epidermis des elefanten. *Cell Tissue Res.* **75**, 146-159.

Jenkinson, D. M. (1973). Comparative physiology of sweating. *Br. J. Dermatol.* **88**, 397-406.

Kinahan, A. A., Inge-moller, R., Bateman, P. W., Kotze, A. and Scantlebury, M. (2007). Body temperature daily rhythm adaptations in African savanna elephants (*Loxodonta africana*). *Physiol. Behav.* **92**, 560-565.

Kleiber, M. (1947). Body size and metabolic rate. *Physiol. Rev.* **27**, 511-541.

Kleiber, M. (1961). *The Fire of Life*, 456 pp. New York: Wiley.

Langman, V. A., Maloiy, G. M. O., Schmidt-Nielsen, K. and Schroter, R. C. (1979). Nasal heat exchange in the giraffe and other large mammals. *Respir. Physiol.* **37**, 325-333.

Langman, V. A., Roberts, T. J., Black, J., Maloiy, G. M. O., Heglund, N. C., Weber, J. M., Kram, R. and Taylor, C. R. (1995). Moving cheaply: energetics of walking in the African elephant. *J. Exp. Biol.* **198**, 629-632.

Lester, C. W. and Costa, D. P. (2006). Water conservation in fasting northern elephant seals (*Mirounga angustirostris*). *J. Exp. Biol.* **209**, 4283-4294.

Lighton, J. and Feener, D. (1989). Water loss and cuticular permeability in foragers of the desert ant, *Pogonomyrmex rugosus*. *Physiol. Zool.* **62**, 1232-1256.

Lillywhite, H. B. (2006). Water relations of tetrapod integument. *J. Exp. Biol.* **209**, 202-226.

Lillywhite, H. B. and Stein, B. R. (1987). Surface sculpturing and water retention of elephant skin. *J. Zool.* **211**, 727-734.

Loarie, S. R., Aarde, R. J. V. and Pimm, S. L. (2009). Fences and artificial water affect African savannah elephant movement patterns. *Biol. Conserv.* **142**, 3086-3098.

Luck, C. P. and Wright, P. G. (1964). Aspects of the anatomy and physiology of the skin of the hippopotamus (*H. amphibius*). *Q. J. Exp. Physiol. Cogn. Med. Sci.* **49**, 1-14.

Maloiy, G. M. O. (1973). The water metabolism of a small East African antelope: the dik-dik. *Proc. R. Soc. B* **184**, 167-178.

Maloiy, G. M. O. and Hopcraft, D. (1971). Thermoregulation and water relations of two East African antelopes: the hartebeest and impala. *Comp. Biochem. Physiol.* **38A**, 525-534.

Myhrvold, C. L., Stone, H. A. and Bou-Zeid, E. (2012). What is the use of elephant hair? *PLoS ONE* **7**, e47018.

Owen-Smith, N., Kerley, G. I. H., Page, B., Slotow, R. and van Aarde, R. J. (2006). A scientific perspective on the management of elephants in the Kruger National Park and elsewhere. *S. Afr. J. Sci.* **102**, 389-394.

Parker, K. L. and Robbins, C. T. (1984). Thermoregulation in mule deer and elk. *Can. J. Zool.* **62**, 1409-1422.

Phillips, P. K. and Heath, J. E. (1992). Heat exchange by the pinna of the African elephant (*Loxodonta africana*). *Comp. Biochem. Physiol.* **101A**, 693-699.

Pinnagoda, J., Tupkek, R. A., Agner, T. and Serup, J. (1990). Guidelines for transepidermal water loss (TEWL) measurement. *Contact Dermatitis* **22**, 164-178.

Rasband, W. S. (1997-2009). *ImageJ, (NIH).* Bethesda, MD.

Redfern, J. V., Grant, R., Biggs, H. and Getz, W. M. (2003). Surface water constraints on herbivore foraging in the Kruger National Park, South Africa. *Ecology* **84**, 2092-2107.

Redfern, J. V., Grant, C. C., Gaylard, A. and Getz, W. M. (2005). Surface water availability and the management of herbivore distributions in an African savanna ecosystem. *J. Arid Environ.* **63**, 406-424.

Rees, P. A. (2002). Asian elephants (*Elephas maximus*) dust bathe in response to an increase in environmental temperature. *J. Therm. Biol.* **27**, 353-358.

Saikawa, Y., Hashimoto, K., Nakata, M., Yoshihara, M., Nagai, K., Ida, M. and Komiya, T. (2004). Pigment chemistry: the red sweat of the hippopotamus. *Nature* **429**, 363-363.

Schmidt-Nielsen, K. (1997). *Animal Physiology: Adaptation and Environment*. New York, NY: Cambridge University Press.

Schmidt-Nielsen, B., Schmidt-Nielsen, K., Houpt, T. R. and Jarnum, S. A. (1956). Water balance of the camel. *Am. J. Physiol.* **185**, 185-194.

Schmidt-Nielsen, K., Schroter, R. C. and Shkolnik, A. (1981). Desaturation of exhaled air in camels. *Proc. R. Soc. Lond.* **211**, 305-319.

Shannon, G., Matthews, W. S., Page, B. R., Parker, G. E. and Smith, R. J. (2009). The affects of artificial water availability on large herbivore ranging patterns in savanna habitats: a new approach based on modelling elephant path distributions. *Divers. Distrib.* **15**, 776-783.

Sikes, S. K. (1971). *The Natural History of the African Elephant*. New York, NY: Elsevier.

Smallwood, R. H. and Thomas, S. E. (1985). An inexpensive portable monitor for measuring evaporative water loss. *Clin. Phys. Physiol. Meas.* **6**, 147-154.

Smit, I. P. J., Grant, C. C. and Whyte, I. J. (2007). Elephants and water provision: what are the management links? *Divers. Distrib.* **13**, 666-669.

Smith, F. (1890). Histology of the skin of the elephant. *J. Anat. Physiol.* **24**, 493-503.

Spearman, R. I. C. (1970). The epidermis and its keratinization in the African elephant (*Loxodonta africana*). *Zool. Africana* **5**, 327-338.

Spotila, J. R. and Berman, E. N. (1976). Determination of skin resistance and the role of the skin in controlling water loss in amphibians and reptiles. *Comp. Biochem. Physiol.* **55**A, 407-411.

Sukumar, R. (2003). *The Living Elephants*. New York, NY: Oxford University Press.

Taylor, C. R. (1970). Dehydration and heat: effects on temperature regulation of East African ungulates. *Am. J. Physiol.* **219**, 1136-1139.

Taylor, C. R., Spinage, C. A. and Lyman, C. P. (1969). Water relations of the waterbuck, an East African antelope. *Am. J. Physiol.* **217**, 630-634.

Webster, M. D. and Bernstein, M. H. (1987). Ventilated capsule measurements of cutaneous evaporation in mourning doves. *Condor* **89**, 863-868.

Weissenböck, N., Arnold, W. and Ruf, T. (2011). Taking the heat: thermoregulation in Asian elephants under different climatic conditions. *J. Comp. Physiol. B* **182**, 311-319.

Western, D. (1975). Water availability and its influence on the structure and dynamics of a savanna large mammal community. *Afr. J. Ecol.* **13**, 265-286.

Western, D. and Lindsay, W. K. (1984). Seasonal herd dynamics of a savanna elephant population. *Afr. J. Ecol.* **22**, 229-244.

Williams, T. M. (1990). Heat transfer in elephants: thermal partitioning based on skin temperature profiles. *J. Zool.* **222**, 235-245.

Withers, P. C. (1977). Measurement of V_{O_2}, V_{CO_2}, and evaporative water loss with a flow-through mask. *J. Appl. Physiol.* **42**, 120-123.

Wright, P. G. (1984). Why do elephants (*Loxodonta africana*) flap their ears? *S. Afr. J. Zool.* **19**, 267-269.

Wright, P. G. and Luck, C. P. (1984). Do elephants (*Loxodonta africana*) need to sweat? *S. Afr. J. Zool.* **19**, 270-274.