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UNIVERSITY OF CALIFORNIA
SANTA CRUZ

**FROM TISSUES TO LANDSCAPES: HOW THERMAL PHYSIOLOGY,
WATER USE, AND CLIMATE INFLUENCE PATTERNS OF LANDSCAPE
USE IN ELEPHANTS**

A dissertation submitted in partial satisfaction
of the requirements for the degree of

DOCTOR OF PHILOSOPHY

in

ECOLOGY AND EVOLUTIONARY BIOLOGY

by

Robin C. Dunkin

March 2012

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ABSTRACT

In the following chapters the interaction between large body size and climate and the resulting influence of this interaction at the level of the tissue, the whole body, and at the landscape level are investigated. In chapter one, tissue level adaptations of Asian (*Elephas maximus*) and African (*Loxodonta africana*) elephant integument facilitating non-evaporative and evaporative heat loss were measured. In chapter two, whole body measurements of skin surface temperature and cutaneous and respiratory evaporative water loss across a 25°C range of ambient temperatures were used to construct climate dependant thermal and water budgets. In chapter three, these budgets were used to construct a coupled biophysical and dynamic programming model to investigate how climate together with thermal, water, and energy demands, interact to produce landscape level patterns of habitat use. At the tissue level, the integument of elephants has a high water and low lipid content and its thermal conductivity (0.19 ± 0.01 to 0.23 ± 0.13 W m⁻¹°C) approaches the upper limit of previously measured mammalian values. The integument's resistance to water loss is also low and is comparable to or less than that of some amphibians. At the whole body level, low integumental resistance results in high rates of cutaneous evaporative water loss (E.m.: 0.31 and 8.9 g min⁻¹m⁻²; L.a.: 0.26 and 6.5 g min⁻¹m⁻²) and at temperatures between 28-30°C, elephants are fully dependent on evaporative cooling to dissipate heat produced from resting metabolism. At the landscape level, simulations under six combinations of climate and primary productivity demonstrated

that under cool and moderate climates, primary productivity was the strongest determinate of home range size, however, at temperatures above 24-27°C, ambient temperature was limiting as elephants were more tightly tethered to water with less access to food. Climate appears to have a non-linear influence on landscape use because evaporative cooling increases exponentially with ambient temperature. Although the drivers of landscape use by large herbivores are complex, the results of this work demonstrate the importance of interactions between body size and climate spanning three levels of biological organization, in setting the fundamental spatial and temporal patterns of landscape use reported for elephants.

DEDICATION

This work is dedicated to my husband Ross who has offered his unwavering support through every step of this process and who been an enthusiastic supporter, colleague, editor, research partner, friend, and husband along the way.

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Finally, I would like to thank my family for their support during this process. My parents, sister and brother-in-law have been patient and enthusiastic supporters and encouraged me to keep going even when things were particularly challenging. Most of all, my husband Ross has been by my side for nearly my whole graduate experience. He has encouraged me, worked beside me, helped me see the big picture when I needed it, has listened to countless hours of elephant related biology, been a willing and enthusiastic research partner (and subject), and has generally kept me sane throughout this process.

INTRODUCTION

The Asian (*Elephas maximus*) and African (*Loxodonta africana*) elephant are the largest extant terrestrial vertebrates. At a maximum, the male African elephant is six orders of magnitude larger than the smallest terrestrial mammal, the Etruscan shrew (*Suncus etruscus*). Across this extreme range of body masses, the fundamentals of mammalian physiology remain the same, yet a simple but key relationship, the surface to volume ratio, dramatically changes. As an animal increases in size, surface area increases to the square while volume increases to the cube. Thus, large animals have a much smaller surface to volume ratio relative to small animals. Because the surface of the animal is the primary site of biophysical exchange (e.g. heat and water) with the environment, this straightforward physical relationship has a cascade of effects. Most important for this work is the impact that a decreased surface to volume ratio has on the thermal and water balance of an elephant and this idea is a central theme in each of the following chapters. A second major theme of this work is the value of physiological data and methodology in predicting landscape level effects which stem from interactions between whole animal physiological and biophysical processes and the abiotic and biotic environment.

These themes are discussed in the context of the complex management challenges presented by elephants. Although officially listed as vulnerable by the IUCN, historical management practices of African elephants for example, have lead

to the sequestration of elephant populations into numerous small to medium sized reserves or into otherwise fragmented landscapes. The result is that in many of these areas, high local elephant densities and their resulting impacts are detrimental to biodiversity and lead to increased incidence of human-elephant conflict (Owen-Smith, Kerley, Page *et al.* 2006). The recognition that elephant distribution is significantly influenced by surface water availability has led to support for surface water management, a more ethically appealing and sustainable form of population regulation relative to culling or translocation. Although surface water management has gained support, its implementation has been challenged by an inability to adequately predict the outcomes and likely success of surface water management plans for particular populations. With this context in mind the overarching objective of this work was to identify and measure the physiological basis for the elephant's dependence on surface water and then use these data to develop a quantitative and predictive framework with which to examine the influence of surface water and interacting factors on the elephant's use of landscape.

The primary organ system responsible for the biophysical exchange of heat and water is the integument, which lies at the interface between the animal's internal environment and the outside world. Thus, in chapter 1, the hypothesis that the thermal and water barrier properties of the integument are adapted to maximize non-evaporative and evaporative heat exchange is tested. This chapter specifically addresses the tissue level mechanism for relatively high rates of water loss observed at the whole organism level in both this and previous investigations.

In chapter 2, the foundation for a predictive framework is laid by quantifying the relationships between an abiotic variable, ambient temperature, and thermal and water balance at the whole animal level. From this work, the contribution of evaporative cooling to an elephant's overall thermal balance as well as the nature of the relationship between ambient temperature and water use were determined. This chapter specifically addresses the whole animal level mechanism of the elephant's water dependence by quantifying the exchange of heat and water in relation to an environmental variable, thus determining the physiological demand for water at an ecologically relevant temporal scale.

Finally, in chapter 3, the relationships between thermal and water balance and ambient temperature are used to develop a biophysical model coupled with a stochastic dynamic programming model. This modeling framework was used to investigate the separate and combined effects of climate, thermal and water balance, and food availability in determining landscape level patterns of habitat use and habitat impact.

Body size was one of the earliest and most useful predictors of ecological patterns, yet as Peters (1983) points out, the so called body size relations are so ubiquitous that they risk being viewed as trivial. He notes though that body size relations "*ought not be seen as ends but as starting points*" in the pursuit of a quantitative and predictive understanding of the natural world (Peters 1983). The work that follows does indeed use body size as a starting point to pursue a more

predictive understanding of the drivers of elephant use of landscape. This goal is particularly important in light of a changing climate and ever increasing anthropogenic threats to landscapes, habitats, and individual species. Response to these threats requires a fundamental, mechanistic understanding of how animals respond to change.

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

Peters, R.H. (1983) *The ecological implications of body size*. Cambridge University Press, Cambridge [Cambridgeshire] ; New York .

**CHAPTER 1: ADAPTATIONS OF ELEPHANT SKIN FOR NON-
EVAPORATIVE AND EVAPORATIVE HEAT LOSS**

ABSTRACT

Elephants face a challenge of heat dissipation as a result of their large body size and occupation of hot, arid environments. They maintain thermal balance by relying extensively on evaporative cooling, despite an absence of sweat glands in their integument. Because the integument is the organ primarily responsible for both heat loss and water conservation we hypothesized that the thermal or water barrier properties of elephant integument may be adapted to maximize non-evaporative and/or evaporative heat loss. We measured thermal conductivity ($\text{W m}^{-1} \text{ } ^\circ\text{C}^{-1}$) and conductance ($\text{W m}^{-2} \text{ } ^\circ\text{C}^{-1}$) of integument from Asian ($n = 4$) and African ($n = 2$) elephants when dry and under conditions simulating wallowing (wet) and mud bathing (muddy). We also measured cutaneous evaporative water loss (CWL, $\text{mg cm}^{-2} \text{ hr}^{-1}$) and calculated resistance (s cm^{-1}) of the integument at three water vapor pressure deficits. Lipid and water content of the epidermis and full depth integument were also measured and the surface topography and morphology of the integumental surface were characterized across species. A close relative of the elephant, the manatee ($n = 5$) and another hairless mammal lacking sweat glands, the domestic pig ($n = 5$) were included for comparison with the elephants. We found that thermal conductivity of Asian ($0.19 \pm 0.01 \text{ W m}^{-1} \text{ } ^\circ\text{C}^{-1}$) and African elephant (0.23 ± 0.13) integument approached the upper limit of previously measured values across many species as a result of high water and low lipid content. Across species, thicker integument had higher thermal conductivity values as a result of higher water content but water content reached a plateau at 65%. Despite high conductivity values, thick

integument resulted in elephants and manatees having relatively lower thermal conductance values relative to pigs. CWL was significantly greater ($p < 0.0001$, $F = 54.21$) and resistance significantly lower ($p < 0.0001$, $F = 35.11$) in both the elephant and manatee integument relative to that of the pig at all three measured temperatures. However, all four species demonstrated a significant increase in resistance to water loss at the highest ambient temperature treatment (39.74°C). This increased resistance was most pronounced in the elephants and manatees and is likely associated with the transition temperature of lipids in the stratum corneum. We found significant inter and intra-species variation in the size and pattern of the raised epidermal pillars in the elephants and manatee. Across species, manatees had epidermal pillars that were more conical in shape while that of the elephants were similar to a truncated cone. The two African elephant individuals had very different integumental morphology which also corresponded to differences in the thermal and water barrier properties. The thermal conductance of both African and Asian elephant integument is at the high end of the range of values measured across a diverse range of species. The integument of both species also loses water at rates that are comparable to or greater than that of some amphibians. Thus, the integument of African and Asian elephants is adapted to maximize both non-evaporative and evaporative heat loss.

INTRODUCTION

As the largest terrestrial animal, elephants face a challenge of adequate heat dissipation imposed by their low surface to volume ratio and inability to escape extreme thermal conditions through burrowing or other avoidance behaviors. Although elephants have adaptations for increasing heat loss via radiation and convection, particularly through their large, highly vascularized ears (Wright 1984; Williams 1990; Phillips & Heath 1992) they are also highly dependent upon evaporative cooling (Wright & Luck 1984; Dunkin 2012). Elephants also often occupy habitats with ambient temperatures that regularly exceed body temperature and with seasonally low water availability. Thus, elephants face a tradeoff between heat dissipation and water conservation. Because the skin functions both as the primary thermoregulatory organ and as the primary barrier to water loss in terrestrial mammals (Montagna 1961), this tradeoff between heat loss and water conservation is likely to manifest in adaptations of the integument.

In many mammals, the tradeoff between heat dissipation and water economy has been circumvented through the development and regulation of sweat glands. The presence of sweat glands allows for low rates of water loss when the animal is in thermally neutral conditions but permits enhanced evaporative cooling when ambient conditions are hot or an exercise-generated thermal load must be dissipated. Elephants and pigs among others however, lack such a mechanism (Ingram 1965; Horstmann 1966; Spearman 1970) and instead must rely upon insensible water loss (passive water loss across the integument in the absence of sweating) or evaporation

of externally derived water to facilitate evaporative cooling. Indeed, prior work has found rates of evaporative water loss from the surface of elephant skin are relatively high (Wright & Luck 1984; Dunkin 2012). Although the importance of evaporative cooling for elephant thermoregulation has been recognized (Wright & Luck 1984; Lillywhite & Stein 1987; Dunkin 2012), there has been no work to determine how the conflicting functions to dissipate heat and conserve water may have influenced the thermal or water barrier properties of the integument. The relative contribution to evaporative cooling of internally versus externally derived water also remains unclear but has implications for the overall water budgets of elephants.

There are three main properties of the integument that describe how easily heat and water move across the body of an animal and upon which selection for heat dissipation or water conservation operate. Heat loss is influenced by the thermal properties *thermal conductivity*, k , ($\text{Wm}^{-1}\text{C}^{-1}$), a measure of how well heat moves through a material independent of its thickness, and *thermal conductance*, C , ($\text{W}^{\circ}\text{C}^{-1}\text{m}^{-2}$) which is dependent upon both the conductivity and the thickness of the material (reviewed in McNab 2002; Dunkin, McLellan, Blum *et al.* 2005). The rate of cutaneous evaporative water loss (CWL) across the integument is influenced by the *total resistance*, R_t , (s cm^{-1}) to water loss, which is the sum of the resistance of the integument (R_i) and the resistance imposed by the boundary layer (R_b) of air just above the skin surface (Anderson 1936; Spotila & Berman 1976; Lillywhite 2006). Each of these functional properties is of course directly related to the structure and composition of the integument. Thermal conductivity, for example, has been found

to be inversely related to the amount of lipid and positively related to the water content of the integument in marine mammals (Worthy & Edwards 1990; Dunkin *et al.* 2005). Similarly, the resistance of the integument and thus, rate of cutaneous evaporative water loss (CWL), is a function of the structure, composition, and thickness of the stratum corneum, the most superficial layer of the epidermis in mammals which provides the rate limiting barrier to water loss (Montagna 1961; Elias & Friend 1975; Lillywhite 2006).

The unique structure of elephant integument has been of interest as far back as 1712 (Leeuwenhoek 1712) and has been subsequently described by several others (Smith 1890; Horstmann 1966; Spearman 1970). Of particular interest is the significant thickness of the dermis, the prominent primary and secondary dermal papillae, as well as the remarkable thickness and topographic structure of the keratinized stratum corneum in some regions (Fig. 1A-C). The dermis, as described by Smith (1890), is very thick and composed primarily of fibrous tissue. The primary papillae are raised, arch-like sections of dermis that protrude up into the unkeratinized region of the epidermis (Fig. 1A-C) and the secondary papillae are thinner protrusions that extend off of the primary papillae (visualized at higher magnification). Such complex dermal papillae have also been described in other taxa including the hippopotamus, and in the Sirenia (Fig. 1G) and Cetacea (Luck & Wright 1964; Wright & Luck 1984).

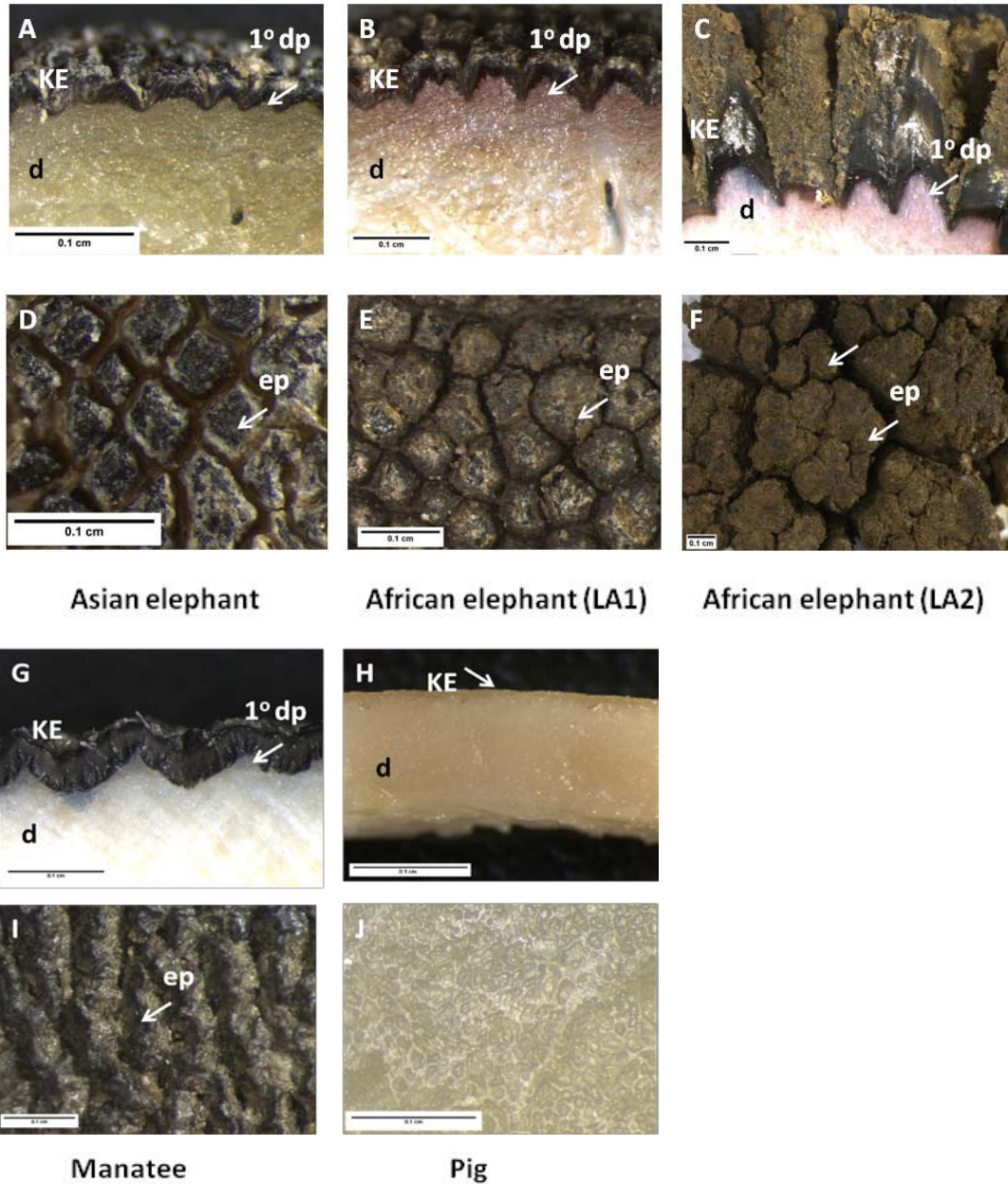


Figure 1: Morphological views of the integument of Asian and African elephant, manatee, and pig. Lateral views of the dermis (d), epidermis and keratinized epidermis (KE) of a representative Asian elephant and both African elephants in this study (A-C). The primary dermal papillae (1° dp) form arches resulting in raised pillars along the surface (D-F). Similar dermal papillae are observed in the lateral image of the manatee (G) but are absent in the pig. The epidermal pillars on the manatee dorsal surface (I) form elongated rows.

Superficial to the unkeratinized epidermis is the stratum corneum which varies regionally across the body in thickness and morphology (Smith 1890; Horstmann 1966; Spearman 1970). In most areas the keratinized epidermis forms thick polygonal columns (also referred to as epidermal pillars) traversed by deep flexural crevices (Horstmann 1966) (Fig. 1 A-C), a morphology that helps increase the adherence of water and mud to the elephant's body (Lillywhite & Stein 1987) and likely facilitates evaporation of externally derived water from the surface. The functional significance of the other features described above however, remain unknown but based on work in humans and other animals may significantly alter the rate of heat and water loss through the integument of elephants.

In this study, we tested the hypotheses that elephant integument is adapted to maximize non-evaporative heat loss through enhanced thermal properties (e.g. higher thermal conductivity, conductance) and that two behaviors commonly employed by elephants, wallowing and mud bathing, may enhance the *effective* thermal properties of the integument. We also hypothesized that elephant integument has a reduced barrier to cutaneous water loss (CWL) relative to other mammals, facilitating insensible evaporative cooling. We measured the thermal properties of the integument under three treatments (dry, wet, with surface mud). In addition, we determined the total resistance of the epidermis across three water vapor pressure saturation deficits. Finally, to understand the role of integumental composition on the thermal and water barrier properties of the integument, we measured lipid and water content of the epidermis and the full depth integument. These measurements were

performed with integument from African (*Loxodonta africana*, Blumenbach, 1797) and Asian (*Elephas maximus*, Linnaeus, 1758) elephants as well from a close relative of the elephant, the manatee (*Trichechus manatus*, Harlan, 1824), and on another hairless mammal also lacking the capacity to sweat, the domestic pig (*S. scrofa domestica*, Linnaeus, 1758).

METHODS

Tissue Samples

Samples of full depth integument (dermis and epidermis) from African (n = 2) and Asian (n = 4) elephants were obtained from U.S. zoos through the elephant research and tissue request protocol followed by U.S. zoological facilities in the event of an elephant death. Manatee integument samples (n = 5) were obtained with permission from the Florida Fish and Wildlife Department from the Marine Mammal Pathobiology Lab, St. Petersburg, FL, USA. Pig integument samples (n = 5) were purchased from a local butcher shop (Corralitos, CA, USA). All integument samples except the pig were obtained from a mid-thoracic site just caudal to the front limb for all species and ranged in size between 10x10 and 30x30cm². Pig samples were taken from a mid-thoracic site near the rear limb. All samples were wrapped in plastic wrap, sealed in two airtight plastic bags, and stored at -20°C until analysis. When it was necessary to subsample the tissues, the sample either remained frozen and was cut, or was only minimally thawed to permit cutting.

Samples were obtained with varying amounts of subcutaneous fat attached to the sample. To standardize across all species, any subcutaneous fat attached to the

deep dermal surface was carefully removed with a scalpel. Most measurements, unless specified otherwise, were performed on the remaining epidermis and dermis subsequently referred to as the full depth integument.

The samples from the two African elephants differed significantly in their morphology. LA1 had flatter, less defined epidermal pillars while LA2 had very tall pillars with deep flexural crevices traversing the surface (Fig. 1B,C and E,F). When significant differences were observed between these individuals they are reported separately in the text.

Morphology

The histochemistry and basic morphology of elephant skin has been previously described by several authors (Leeuwenhoek 1712; Smith 1890; Luck & Wright 1964; Spearman 1970) however, detailed morphological comparisons of the topographic surface and pillar morphology of Asian versus African elephant integument has not been completed. Differences in the arrangement and size of the pillars could influence the adherence of mud and liquid water as well as influence the effective surface area (ESA) (Fig 1A-H). To estimate the effective surface area and explore differences in the surface topography of each species two approaches were employed. The first approach was a modeling technique that was dependant upon the measurement of lateral and dorsal view morphological features. We also examined the surface and estimated the ESA of the integument using 3D profilometry (Commander model, B&H Machine Co., Roberts, WI, USA), a technique that has

been used recently in the study of human skin (Jacobi, Chen, Frankowski *et al.* 2004; Smalls, Lee, Whitestone *et al.* 2005).

The modeling approach relied upon several features measured from lateral and dorsal images of the integument. These measurements allowed individual pillars of the Asian and African elephant and manatee epidermis to be modeled as one of several appropriate shapes. The epidermal pillars of most elephants were modeled as a truncated cone (Fig 2A,B), a shape which most closely approximated that of the individual pillars. However, the epidermal pillars of one elephant, LA2 were exceptionally large and were more closely approximated by cylinders rather than truncated cones. Examination of the dorsal surface of manatee integument suggested that the dermal pillars were more conical in shape (Fig. G, I). Morphological features were examined under a dissecting microscope with integrated camera system (Leica DFC295, Leica Microsystems, Buffalo Grove, IL, USA) at magnifications ranging from 12.5 to 40X. Sections for lateral (approximately 2-3 cm wide) and dorsal viewing (approximately 3x3cm) were cut from frozen-thawed samples. Digital images of each sample were analyzed for the morphological features described below using NIH ImageJ software (Rasband 1997-2009).

The features examined in a lateral view of the sample included the *width of the pillar base* measured from the lowest point of the trough on each side of the pillar as well as the *slant height* of the pillar as measured from the end point of the width measurement in the trough as described above to the most superficial edge surface of the cone (Fig 2A, B). Only pillars that appeared bisected through the middle of the

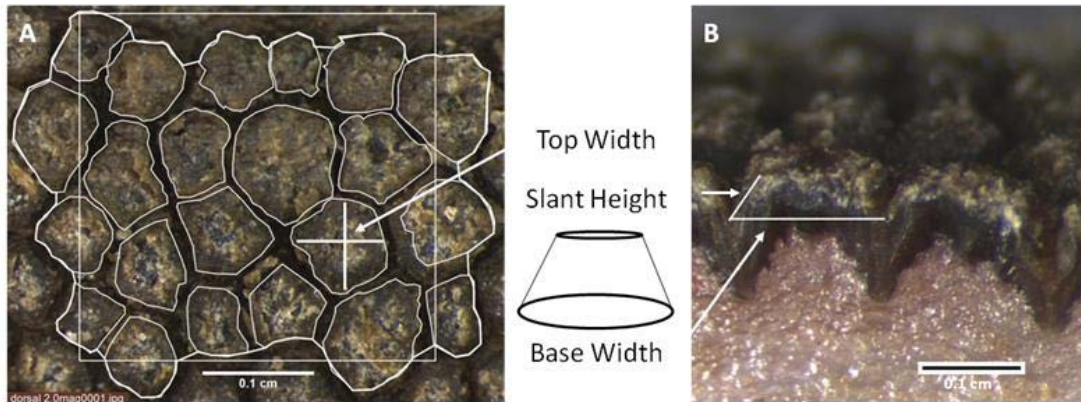


Figure 2: Calculation of the effective surface area of the integument using the modeling technique. The effective surface area (ESA) was measured by modeling the epidermal surface pillars as truncated cones in the elephants or cones in the manatee. Photographs of the dorsal surface (A) were used to derive the radius of the top of the cone from measurement of the mean width of the individual pillar surface. The total number of pillars cm^{-2} was also computed from the dorsal images. The white square represents a reference square and all pillars within or touching the square that were fully in the photographic frame were analyzed. The thick white line around the perimeter of the group of measured pillars is the actual area used in the calculation. The radius of the cone base and the slant height of the cone were measured in lateral photographs (B). Similar measurements were performed for the manatee but a cone rather than truncated cone was used to model the surface.

pillar were analyzed. Features examined in the dorsal view included the mean *surface area of the top of the epidermal pillars*, the *number of pillars per unit area* (cm^2), and two measurements of the *width of the pillar* (Fig 2A,B). Lateral measurements were made for 10 pillars and dorsal measurements were made for at least 16 to 24 pillars per individual. For each individual, the mean of all pillars for each measurement (width of pillar base, slant height, etc.) was determined and used in the calculation of the effective surface area of a typical pillar for that individual. To calculate the total ESA the mean ESA per pillar was computed for each individual and then multiplied by the mean pillar density (pillars cm^{-2}) for that individual.

The second method employed for measurement of the effective surface area was 3D non-contact profilometry. In this method, a low intensity laser is passed over the surface of the integument and a 3D representation is rendered from which the developed interfacial area ratio (S_{dr}) (%) is computed (TrueMap 5, TrueGage Surface Metrology, North Huntingdon, PA, USA). The S_{dr} is calculated as the difference between the textured surface area and the cross sectional surface area divided by the cross sectional surface area and multiplied by 100. A perfectly flat surface has an S_{dr} of 0%. The 3D profilometry method provided a validation of the modeling approach to estimate the ESA as well as provided visualization of the surface that allowed for better detection of surface patterns.

Lipid Content

Epidermal lipid content as well as full depth integument lipid content were obtained with a modified Folch extraction using 2:1 chloroform:methanol (Folch, Lees & Sloane-Stanley 1957; Koopman, Iverson & Gaskin 1996). Epidermal samples (2-3 grams) were removed from the dermis using a scalpel and with extreme care to exclude any dermal tissue, and weighed precisely to the nearest 0.0001g (Sartorius, 1712 V94, Goettingen, Germany). The epidermal samples were soaked in a 2:1 solution of chloroform:methanol overnight, manually extracted and the excess solvent evaporated off with nitrogen, and then reweighed. For determination of full depth lipid content, an approximately 3-4g full-depth integument sample (including the epidermis) was weighed to the nearest 0.0001g, macerated, and dried in an oven for approximately 6-8 hours. The lipid was then extracted using an accelerated solvent extractor (Dionex ASE 200, Salt Lake City, UT, USA), the excess solvent was evaporated and the extracted lipid then reweighed to the nearest 0.0001g.

Water Content

Water content of the epidermis and full depth integument was determined in duplicate for each individual of all four species. A subsample of either epidermis alone or full depth integument was precisely weighed to the nearest 0.0001g (Sartorius, 1712 V94, Goettingen, Germany) and then immediately placed in a freeze dryer (Labconco 4.5L, Kansas City, MO, USA) and allowed to dry for a period of 4 days. Prior trials had determined that this was a sufficient period to completely dry

the samples. After drying was complete, the samples were reweighed and the water content determined from the difference between the start and end mass of each sample.

Thermal Material Properties

Thermal conductivity was measured using the standard material method according to the protocols described in Dunkin *et al.* (2005) and Kvadsheim *et al.* (1994). Briefly, measurements were conducted in a dual compartment heat flux chamber (68 quart, Coleman Cooler, Albany, NY, USA) with a lower, highly insulated compartment, and an upper, chilled compartment, which were separated by a wood platform (Fig 3A). Integument samples were placed in series with a heat source and a standard material of known thermal conductivity (k) (Plastisol vinyl elastomer, Carolina Biological Supply, Burlington, NC, USA) ($k = 0.109 \pm 0.01 \text{ W m}^{-1} \text{ } ^\circ\text{C}^{-1}$). Copper-constantan thermocouples (9 total) were placed between the heat source and the standard material, between the standard material and the deep surface of the integument, and were secured to the superficial surface of the integument. The heat source was maintained at a constant temperature approximating the muscle-deep integument interface (30°C) while the upper chamber was cooled to a constant 15°C with ice packs. All nine thermocouples were connected to a Fluke Hydra data logger (model 2625A, Fluke Inc., Everett, WA, USA) and the outputs in $^\circ\text{C}$ were recorded at 1 minute intervals.

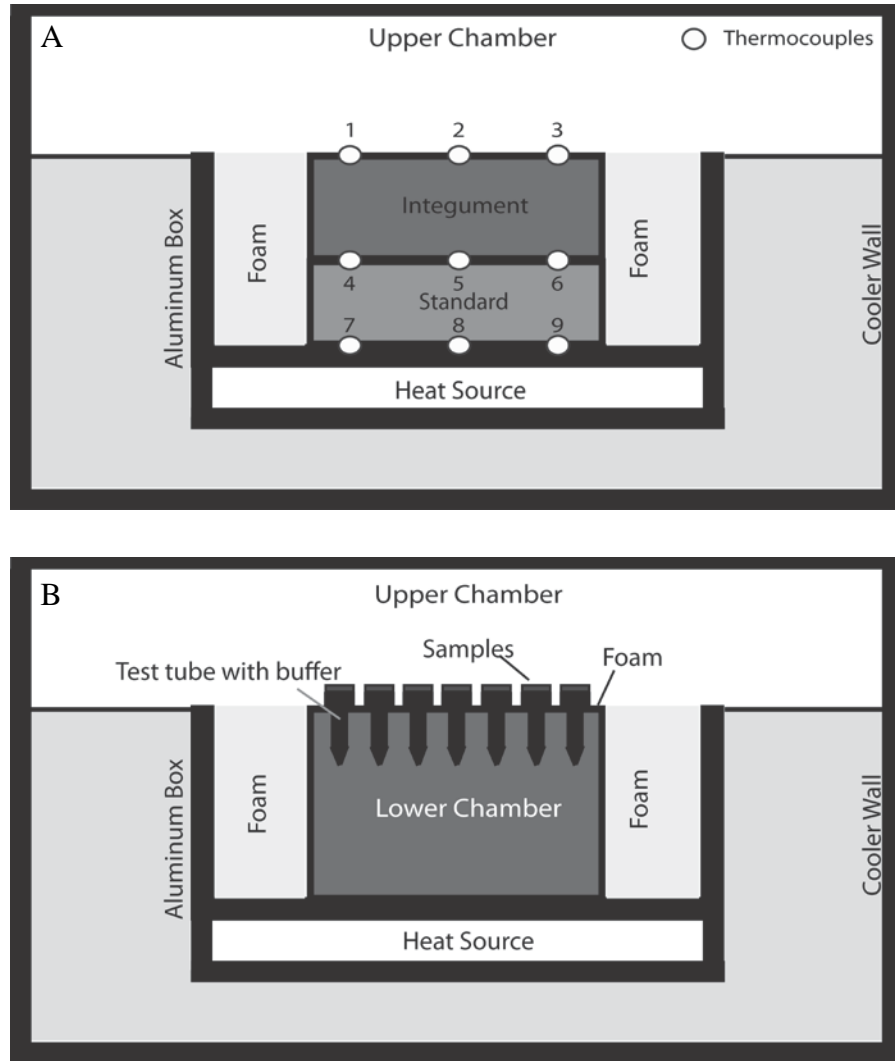


Figure 3: Experimental set-up for measuring thermal conductivity of full depth integument from Dunkin *et al.* 2005 (A) and permeability of epidermis (B). The temperatures in the upper and lower chambers are denoted in the text as T_U and T_L respectively.

Conductivity was calculated using the Fourier equation:

$$(I) \quad k = \frac{dQ}{A(T_2 - T_1)}$$

where d is the thickness of the integument (m), Q is the rate of heat transfer in Watts (W), A is the surface area across which heat flows (m^2), and $(T_2 - T_1)$ is the temperature difference ($^{\circ}C$) across the thickness of the integument (Kvadshiem, Folkow & Blix 1994; Schmidt-Nielsen 1997). Once the system reaches steady state, the heat flow rate through the standard material and the integument is equal (Kreith 1958; Kvadshiem *et al.* 1994) and Equation I was used to calculate the thermal conductivity of the integument by setting equal the heat flow through the standard material and integument sample.

Thermal conductivity was measured under one or more of three treatments: 1) dry, 2) after soaking the superficial surface in fresh water for 10 minutes, and 3) after a thin layer of mud was applied to the superficial surface. The mud was a mixture of approximately 2 parts sandy soil to 1 part water and mixed to the consistency of a wet paste. The thickness of the mud layer applied to the integumental surface ranged between 0.2 and 0.3cm and the thickness of the integument plus added mud layer was used in the conductivity calculation for this treatment. African and Asian elephant and the pig samples were measured under all three treatments to simulate the influence of their natural behaviors of water and mud bathing on their integument. Manatee integument was run under the dry treatment only.

Cutaneous Water Loss and Epidermal Resistance

To estimate the rate of water movement through the epidermis in the absence of blood flow and physiological control of skin temperature, a protocol similar to that originally developed by Blank (1952) and modified in Munoz-Garcia and Williams (2005) was developed. From each integument sample, a 1.3cm diameter leather punch was used to produce a round core of full depth integument. A scalpel was then used to carefully dissect the epidermis from the dermis. It was not possible to completely remove all dermal tissue from these samples. However, because it is well established that the rate limiting barrier to water loss lies in the stratum corneum (reviewed in Lillywhite 2006), presence of some dermal tissue should not have influenced the minimum water loss rate. The round epidermal sample was then fastened with cyanoacrylate glue to a 14mL vial filled 2/3 full with phosphate-buffered saline (PBS, $\text{Na}_2\text{HPO}_4 \cdot 7\text{H}_2\text{O}$, $\text{NaH}_2\text{PO}_4 \cdot \text{H}_2\text{O}$ monobasic, and NaCl in deionized water). The sample was allowed to set and was then inverted to check for leaks. The vial, PBS buffer, and sample were then precisely weighed to the nearest 0.0001g (Sartorius, 1712 V94, Goettingen, Germany). Duplicate open vials filled with PBS buffer were run in tandem with the tissue samples as a measure of the rate of loss from a free water surface in this system.

Weighed vials with attached samples were placed in a dual compartment insulated chamber such that the lower portion of the vial was submerged in a heated closed space set to approximate a likely maximum physiological temperature at the deep epidermal surface (35°C) while the top of the vial with attached epidermal plug was exposed to the controlled temperature of the upper chamber (Fig. 3B). The upper

chamber environmental temperature was varied using a thermostat-controlled heating pad or chilled with ice packs. A low water vapor pressure was achieved across all temperatures by placing a desiccant (drierite) in the upper chamber. The temperature of both the lower (T_L) and upper chamber (T_U) as well as the relative humidity of the upper chamber were continuously sampled and recorded every 1 minute (OM-EL-USB-2 Logger, Omega Engineering, Inc, Stamford, CT, USA) and then downloaded to a laptop computer after each trial. Samples were reweighed at approximately 2, 4, 6, 8, 11, 17, and 26 hours after the start of the trial and were concluded when the rate of water loss had stabilized. CWL was calculated by dividing the amount of water loss (mg) by the surface area of the sample and total time between mass measurements once the rate had stabilized. To compare these measurements with measurements from prior studies, we used the cross sectional area to compute the per area rate of CWL from the integument (1.33 cm^2).

The total resistance (R_t) (s cm^{-1}) to water loss was calculated as:

$$(II) \quad R_t = \frac{[WVD_s - (RH * WVD_a)]}{CWL}$$

where WVD_s (g cm^{-3}) is the water vapor density at skin temperature, RH (decimal percent) is the relative humidity of ambient air in the upper chamber, WVD_a (g cm^{-3}) is the water vapor density of the air in the upper chamber, and CWL ($\text{g cm}^{-2} \text{ s}^{-1}$) is the rate of cutaneous water loss measured for each sample (Spotila & Berman 1976; Lillywhite, Menon, Menon *et al.* 2009). Rates of CWL and resistance were plotted

against both the temperature of the upper chamber as well as the water vapor pressure saturation deficit (WVPSD, Kpa). The WVPSD was determined by first calculating the saturated water vapor pressure using the measured temperature in the vials which is the simulated maximum temperature at the deep epidermal surface. The actual water vapor pressure was calculated using the measured temperature and relative humidity in the upper chamber and was then subtracted from the saturation water vapor pressure to give the WVPSD in Kpa (Buck 1981). The rate of water loss and the total resistance of duplicate samples from each individual were measured under three environmental conditions: cool (mean \pm SE: $T_L = 31.86 \pm 0.02$ °C, $T_U = 18.59 \pm 0.63$ °C; WVPSD = 4.1435 Kpa), moderate ($T_L = 34.13 \pm 0.02$ °C, $T_U = 28.32 \pm 0.32$ °C; WVPSD = 4.6605 Kpa); and hot ($T_L = 35.13 \pm 0.02$ °C, $T_U = 39.74 \pm 0.82$ °C; WVPSD = 5.0518 Kpa).

To ensure that the water vapor pressure inside each vial did not differ significantly between trials, u-tube manometers were designed to measure the pressure inside the vial of a subset of samples (total n = 8 per trial). The manometer was constructed by bending a 1mL glass pipette over a flame into a u shape and filling the u-tube with colored water. A small PVC hose fitting was attached with epoxy into the side of the vial and the glass u-tube manometer was then connected with plastic tubing to the hose fitting. Each vial-manometer was checked for leaks by sealing the vial with a cap, placing the apparatus in the warm environmental chamber and monitoring the pressure over a period of one hour. With this system, changes in pressure as low as 0.009 Kpa were detectable. Two samples from each species

mounted on the vial-manometers were run in tandem with the rest of the samples in each temperature trial. The pressure inside each vial did not differ significantly between trials (maximum difference between trials = 0.86Kpa) and the observed variation was less than the variation observed in the atmospheric pressure during the period of the measurements (max difference in atmospheric pressure = 0.88Kpa).

Previous studies have found there to be little difference in permeability to water between fresh and frozen-thawed human and pig skin even up to 1 year after freezing (Harrison, Barry & Dugard 1984; Lynggaard, Knudsen & Jemec 2009). To confirm this result for this study, fresh pig skin (n = 5) was obtained and each sample divided and placed into two groups: fresh and frozen. The fresh samples were stored between moistened paper towels and sealed inside two airtight plastic storage bags and then refrigerated for up to 4 days. Frozen samples were wrapped in plastic wrap and stored inside two airtight plastic bags and then frozen for up to 4 days. Duplicate samples from each individual from each treatment group (fresh or frozen) were run under two temperatures (cold: 11.35 ± 1.86 °C; warm: 33.08 ± 1.17 °C). A one-way ANOVA was used to test for differences in the rate of water loss between fresh and frozen tissue at each temperature. As reported previously, no significant difference was found between fresh and frozen tissue under either temperature (cold p = 0.6771, F = 0.1867, df = 1,8; warm p = 0.4315, F = 0.6862, df = 1,8). Although fresh tissue was not available for the manatee or either species of elephant, these results suggest that results using frozen tissue are comparable to those from fresh samples.

Statistical Analysis

Across-species differences in thermal conductivity and thermal conductance were evaluated with one-way analysis of variance (ANOVA, $P = 0.05$). When a significant difference was detected between groups, a Tukey-HSD test was performed to determine which group(s) were significantly different. Least squares multiple regression was used to evaluate the relationship between lipid and water content and thermal conductivity and between temperature, species and CWL or resistance (Jmp In 8.0, SAS Institute Inc., Cary, NC, USA). All data were checked for normality and log transformed if necessary. All data are reported as the mean \pm standard error. Due to small sample size, data from the two African elephants are not included in the statistical analyses but the mean and standard error are reported for this group.

RESULTS

Morphology

As expected, primary dermal papillae and epidermal pillars were present in both species of elephant as well as the manatee but absent from the pig. There were significant differences in the morphological features of the pillars between species. The epidermal pillars of the manatee surface were significantly wider (Fig. 4A) and taller (Fig. 4B) than the pillars of the Asian elephant (width: $p < 0.0001$, $F = 50.16$, $DF = 1,88$; slant height: $p < 0.0001$, $F = 42.33$, $DF = 1,88$). The width and slant height of

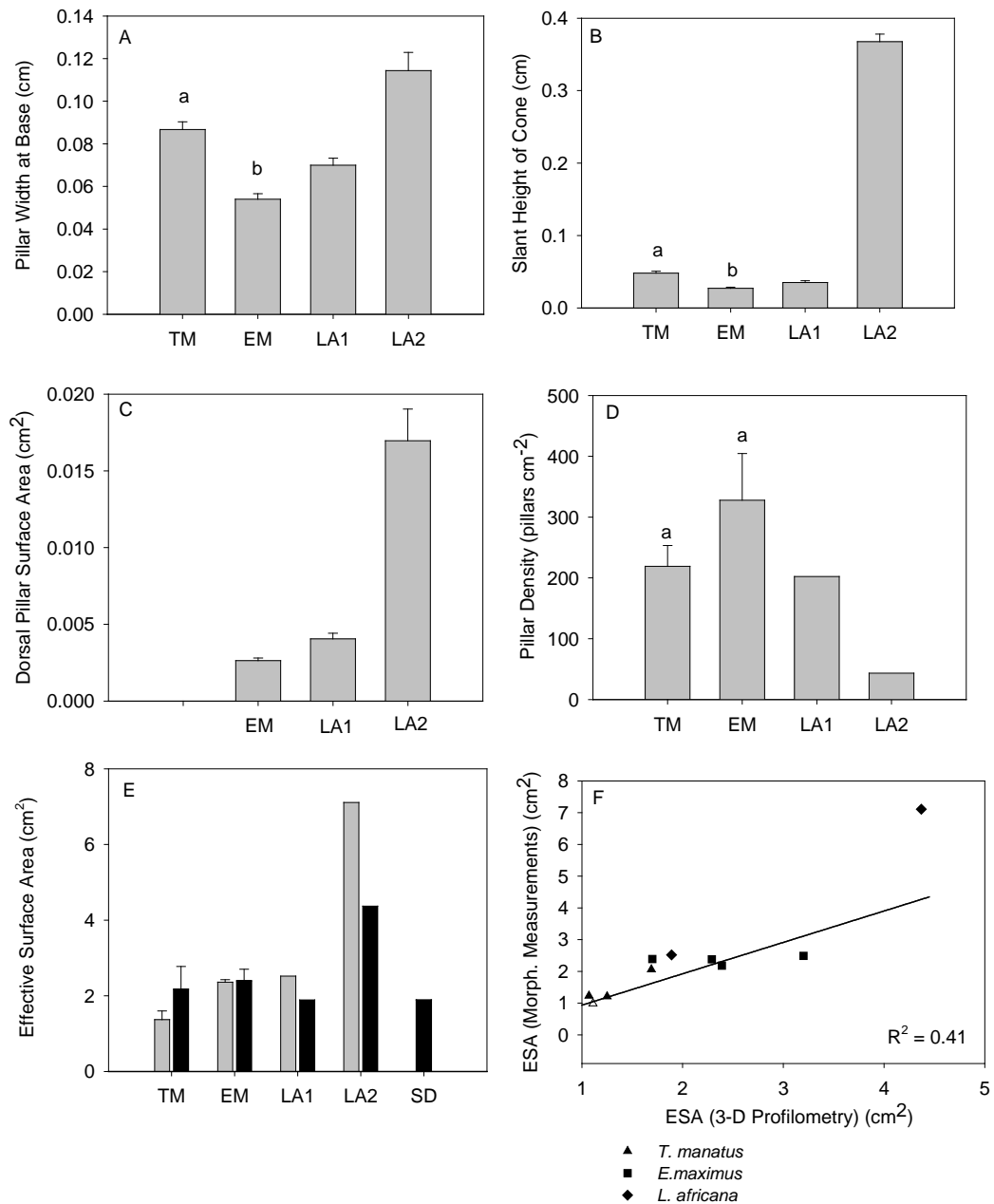


Figure 4: Morphological features and effective surface area of the superficial integument in manatee (TM), Asian elephant (EM), and African elephant (LA1, LA2). LA1 and LA2 represent the two individual African elephants which differed significantly in their epidermal morphology. The width of the pillar base (A) and the slant height (B) were measured from lateral images. The dorsal pillar surface area (C) and the pillar density (D) were measured from dorsal images. The ESA (E, F) estimated morphometrically (gray bars) and from 3D profilometry (black bars). Species with differing letters indicate significantly different groups.

African elephant LA1 were intermediate between that of the Asian elephant and the manatee while LA2 had pillars that were both wider and taller than that of the other species. The epidermal pillars of LA2 had an exaggerated slant height that was an order of magnitude larger than LA1 (mean pillar slant height = $0.13 \pm 0.012\text{cm}$).

Due to the more conical shape of the manatee pillars relative to that of either species of elephant (truncated cone or cylinder for LA2), dorsal pillar surface area was not measured for this species. While the Asian elephant and African elephant, LA1, had similar dorsal pillar surface areas, the surface area of the individual pillars in LA2 was an order of magnitude larger (E.m.: $0.003 \pm 0.0002\text{cm}^2$; LA1: $0.004 \pm 0.0004\text{cm}^2$; LA2: $0.017 \pm 0.002\text{cm}^2$) (Fig. 4C). Additionally, the pillars of LA2 tended to aggregate into larger pillars, giving the surface an additional layer of structure (Fig. 1F). The mean superficial surface area of the aggregated pillars was $0.105 \pm 0.016\text{cm}^2$.

The mean number of pillars per square centimeter (pillar density) was nearly 50% greater in the Asian elephant relative to the manatee. However, there was significant variation in pillar density among individuals of both species and thus, there was no significant difference between Asian elephants and manatees in this parameter (pillar density: $p = 0.24$, $F = 1.67$, $DF 1,6$) (Fig. 4D). One manatee sample was excluded from the dorsal measurements (TM0805) because of a significantly different morphological surface in which individual pillars were nearly indistinguishable. Although pillars were observed in the lateral view, the trough regions appeared partially or fully filled in by thickened keratinized epidermis. The

pillar density of the African elephant LA1 was similar to that of the manatee while that of LA2 was significantly lower than all other species (43.33 pillars cm^{-2}). The density of the aggregated pillars of LA2 was 9.39 pillars cm^{-2} .

The effective surface area as determined from the modeling technique resulted in a mean ESA for Asian elephants that was significantly greater than that of the manatee (mean ESA E.m.: 2.36 ± 0.07 ; T.m.: 1.37 ± 0.024 cm^2 , $p = 0.01$, $F = 16.34$, $DF = 1,6$; note manatee 805 excluded see explanation above). The ESA of African elephant LA1 was similar to the ESA of the Asian elephants while that of African elephant LA2 was more than three times as large as that of LA1 and the Asian elephant (Fig. 4E). In general, the ESA was 1.3 to 2.4 times the cross sectional surface area however, the large epidermal pillars of African elephant LA2 contributed to an ESA that was more than 7 times the cross sectional area (Fig. 4E,F).

There was a marginally significant correlation between the ESA values measured morphologically and those measured with 3D profilometry (Fig. 4F) ($p = 0.045$, $F = 4.46$, $DF = 1,9$). 3D profilometry revealed more individual variation in the textured surface area than was detected from the morphological measurements. There was not a significant difference between the Asian elephant and manatee ESA measured with 3D profilometry (mean ESA: T.m. = 2.18 ± 0.59 ; E.m. = 2.40 ± 0.31 cm^2 , $p = 0.77$, $F = 0.089$, $DF = 1,7$). However one manatee (0929) had a much higher ESA relative to the other manatees which largely drove this pattern. Surprisingly, pig integument had significant textural structure yielding an ESA value (1.89, $n = 1$) that was similar to some of the manatees and to one of the African elephants (LA1). The

pig skin had a large number of very small topographic peaks which ultimately yielded a higher textural surface area than expected (Fig. 4E, 5A).

The 3D profile scans also revealed the epidermal pillars of the Asian and African elephants as being relatively flat on their dorsal surface and thus, were consistent with the characterization of the pillars of these species as truncated cones or cylinders (LA2) (Fig. 5). The epidermal pillars of the manatee were also notably rounded and more closely approximated cones arranged in parallel ridges (Fig. 5 B). There were significant differences between individuals in the height of the epidermal pillars. The ten point height is a standard metric in profilometry calculated from the absolute heights of the five highest peaks and depth of five lowest valleys of the sample area (TrueMap 5, TrueGage Surface Metrology, North Huntingdon, PA, USA) and is used to quantify the highest areas of a surface. The mean ten point height of the Asian elephants was approximately 55% greater than that of the manatees and more than four times that of the pig (mean ten point height: S.d. 0.419 mm; E.m. 2.12 ± 0.28 mm; T.m. 1.36 ± 0.34 mm) but this was not a statistically significant difference ($p = 0.14$, $F = 2.85$, $DF = 1,7$). The ten point height of LA1 was shorter than that of LA2. However, because the valleys between the tall pillars of LA2 were not as deep, the ten point height was not as high as might be expected based on the modeling results of the slant height (LA1 1.28 mm, LA2 2.20 mm). The ten point height was also positively correlated with the ESA measured with 3D profilometry ($p = 0.012$, $F = 9.47$, $R^2 = 0.49$) indicating that there is a significant increase in surface area with taller pillars.

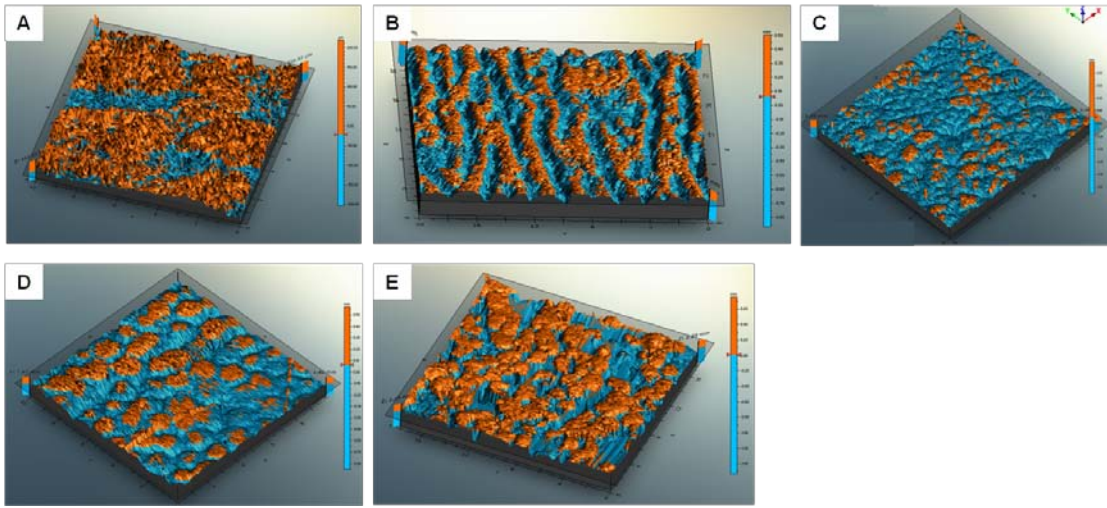


Figure 5: 3D profilometry profiles of the epidermal surface of pig (A), manatee (B), Asian elephant (C), and two African elephants with significantly different epidermal surfaces. LA 1 had shorter epidermal pillars (D) while LA2 had very tall pronounced pillars (E).

Lipid and Water Content

There were significant species-specific differences in the lipid content of the epidermis ($p = 0.014$, $F = 6.44$, $df = 2,11$) (Fig. 6A) and full depth ($p = 0.0076$, $F = 7.84$, $df = 2,11$) (Fig. 6 B) integument samples. Manatee epidermis had nearly twice the lipid content ($7.36 \pm 1.03\%$ g wet weight⁻¹) of pig epidermis ($3.86 \pm 1.44\%$ g wet weight⁻¹) and three times more lipid than either Asian or African elephant epidermis (1.70 ± 0.12 and $1.73 \pm 0.08\%$ g wet weight⁻¹ respectively). This epidermal pattern was different than that of the full depth integument. Manatee, Asian, and African elephant full depth integument all had exceptionally low and similar lipid content values (means ranged between 0.39 and 0.42% g wet weight⁻¹) while lipid content of the pig full depth integument was $6.14 \pm 1.92\%$ g wet weight⁻¹ (Fig. 6B).

The water content of the epidermis was similar between species ($p = 0.055$, $F = 3.82$, $df = 2,11$) (Fig. 6C) but that of the full depth integument differed significantly ($p = 0.0005$, $F = 16.27$, $df = 2,11$) (Fig. 6D) with the pig having significantly lower water content ($53.88 \pm 1.73\%$ g⁻¹ wet weight) relative to the manatee or Asian elephant. There was also a large difference in the epidermal water content between the two African elephants. LA1, with flatter epidermal pillars, had an epidermal water content (50.8% g⁻¹ wet weight) similar to that of the Asian elephants while LA2 with taller epidermal pillars had a much lower epidermal water content (33.28% g wet weight⁻¹) (Fig. 6C).

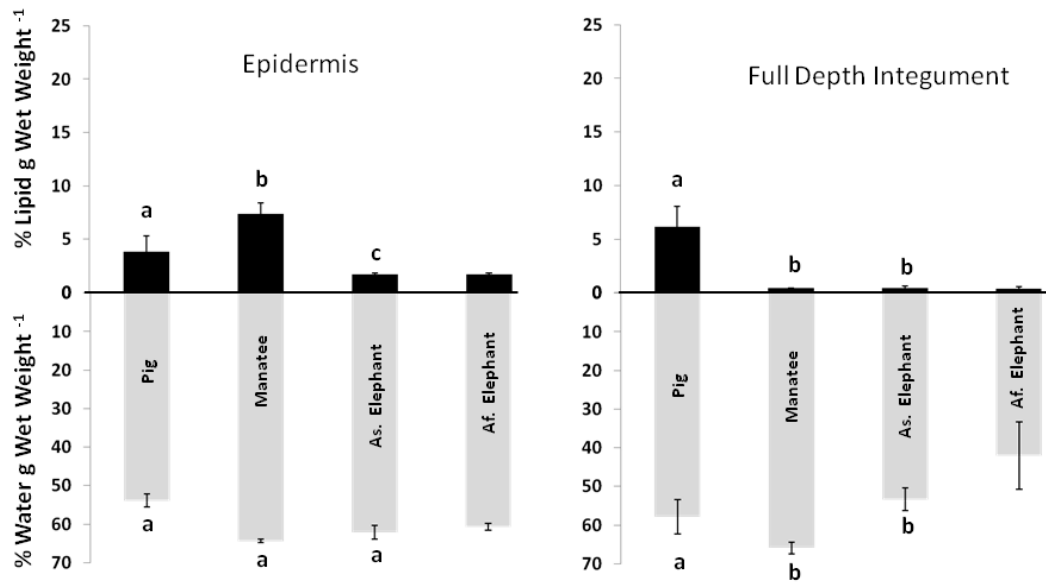


Figure 6: Lipid and water content of the epidermis and full depth integument (epidermis + dermis) for domestic pig, manatee, Asian elephant and African elephant. Categories with different letters denote significant differences between groups. African elephants (n = 2) were excluded from statistical analyses. All data represent the mean \pm standard error.

Thermal Properties

There were significant differences between species in the thermal conductivity of dry skin ($p < 0.0001$, $F = 33.37$, $df = 2, 11$) (Fig. 7, Table 1). The dry skin of the manatee and Asian elephant were 1.3 times greater and the African elephant 1.8 times greater than that of the pig (Fig. 7, Table 1). The conductivity of the pig integument was similar to that measured for temperate terrestrial mammals but was higher than previously reported for pig integument ($0.03 \text{ W/m}^\circ\text{C}$, Tregear 1965) (Table 1). Treatment of the skin of the pig and Asian elephant with water did not significantly increase the thermal conductivity. However, the addition of mud to the skin of the pig more than doubled the thermal conductivity of the skin in this species ($p < 0.0001$, $F = 36.26$, $df = 2, 12$; mean k pig dry = 0.084 ± 0.01 , with mud = $0.184 \pm 0.01 \text{ W m}^{-1}^\circ\text{C}^{-1}$). The addition of mud to the skin of the Asian elephant also increased the conductivity in this species by 24.2%. However, this increase did not result in a conductivity value that was significantly different from that of wet or dry skin ($p = 0.070$, $F = 3.59$, $df = 2, 9$) (Fig. 8, Table 1).

Small sample size precluded quantitative assessment of within-species relationships between thermal conductivity and lipid or water content, however, across species, water content of full depth integument best predicted thermal conductivity and was described by the equation $y = -0.3521 + (0.00859 * \text{water content})$ ($p = 0.0074$, $F = 9.8$, $R^2 = 0.41$, $df = 1, 14$) (Fig. 9A). Water content was also greater in thicker integument but reached a plateau at approximately 65% water g wet weight⁻¹ (Fig. 10). There was also a significant but weaker negative relationship

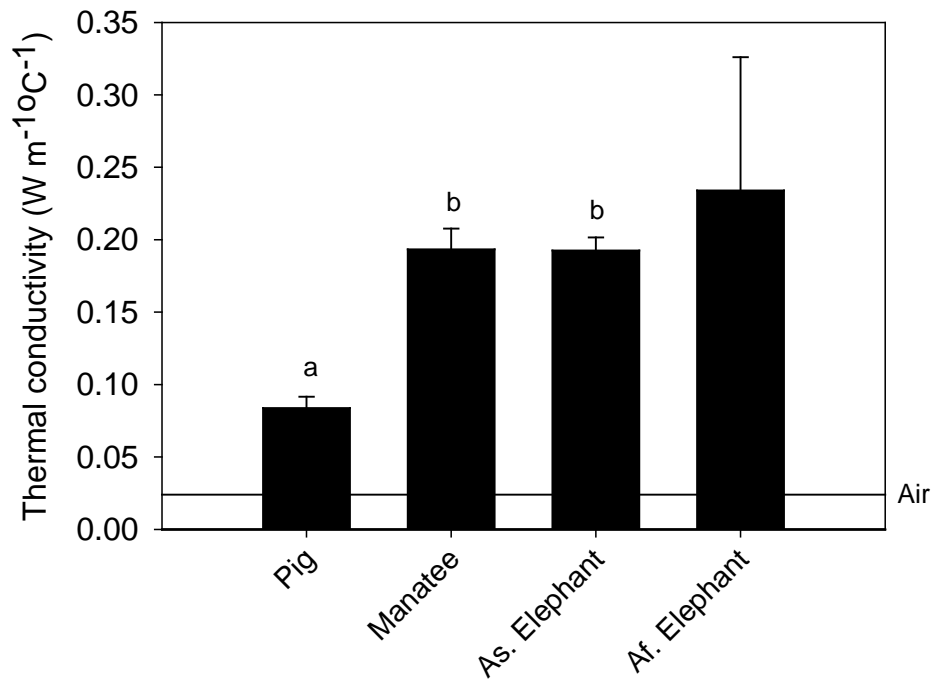


Figure 7: Thermal conductivity (k) of dry skin from pig ($n = 5$), manatee ($n = 5$), Asian (As.) elephant ($n = 4$), and African (Af.) elephant ($n = 2$). Columns with different letters denote groups that were significantly different ($p < 0.05$). Bars represent the mean \pm standard error. Due to low sample size, the African elephant was not included in the statistical analysis.

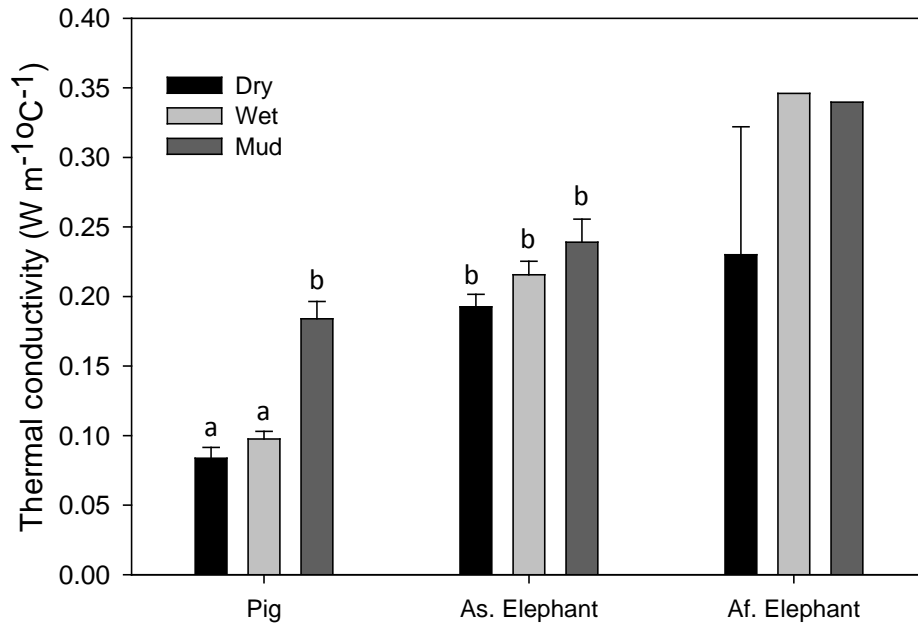


Figure 8: Thermal conductivity values for pig (n = 5), Asian (As.) elephant (n = 4), and African (Af.) elephant (n = 2 for dry, 1 for wet and mud) when the skin is dry and under treatments simulating wallowing and mud bathing behaviors. Columns with different letters denote groups that were significantly different (p<0.05). Bars represent the mean \pm standard error. Due to low sample size, the African elephant was not included in the statistical analysis.

Table 1: Measured thermal conductivity and calculated insulation and conductance values for pig, manatee, Asian, and African elephants.

Species	Common Name	Treatment(n)	K ($\text{W m}^{-1}\text{C}^{-1}$)	R ($\text{m}^2\text{C W}^{-1}$)	C ($\text{W m}^{-2}\text{C}^{-1}$)	Notes
<i>S. domesticus</i>	Pig	Dry (5)	0.08 ± 0.01	0.03 ± 0.00	37.83 ± 3.04	Flank near rump Epidermis + dermis only
		Wet (5)	0.10 ± 0.01	0.02 ± 0.00	45.04 ± 4.84	
		Mud (5)	0.18 ± 0.01	0.03 ± 0.00	40.15 ± 1.97	
<i>T. manatus</i>	Manatee	Dry (5)	0.19 ± 0.01	0.09 ± 0.01	10.78 ± 0.67	Flank, caudal to shoulder
<i>E. maximus</i>	Asian elephant	Dry (4)	0.19 ± 0.01	0.12 ± 0.04	10.07 ± 2.71	Flank, caudal to shoulder
		Wet (4)	0.22 ± 0.01	0.11 ± 0.04	11.69 ± 3.80	
		Mud (4)	0.24 ± 0.02	0.11 ± 0.04	10.24 ± 2.28	
<i>L. africana</i>	African elephant	Dry (2)	0.23 ± 0.13	0.10 ± 0.00	9.6 ± 0.21	Flank, caudal to shoulder
		Wet (1-LA2)	0.35	0.10	9.96	
		Mud (1-LA2)	0.34	0.11	9.28	

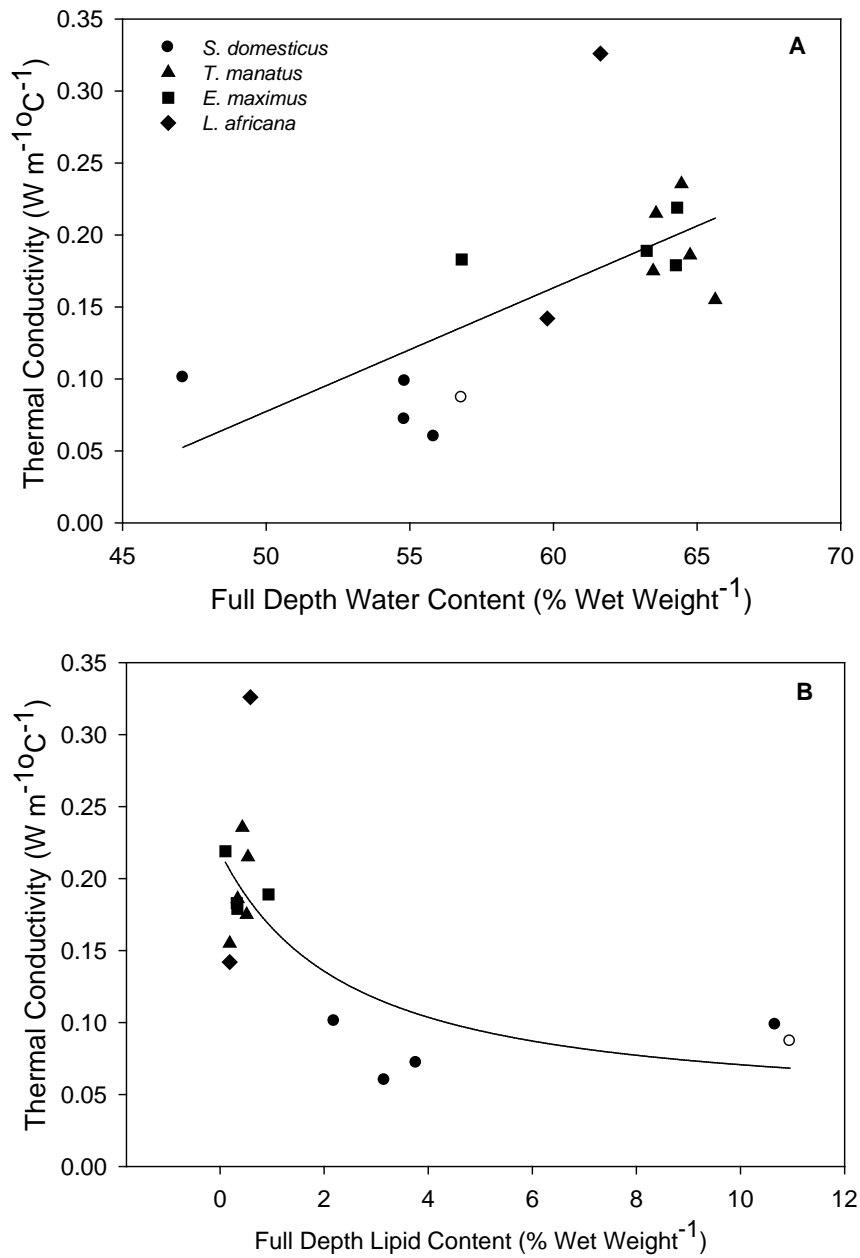


Figure 9: Lipid content (A) and water content (B) in relation to the thermal conductivity of dry skin from pig (*S. domesticus*), manatee (*T. manatus*), and Asian and African elephant (*E. maximus* and *L. africana* respectively) of the full depth (epidermis + dermis) integument. Lipid content versus conductivity equation: $y = 0.0393^{(8.93/(\text{lipid content} + 5.203))}$ ($p = 0.013$, $R^2 = 0.49$). Water content versus conductivity equation: $y = -0.3521 + 0.00859 * \text{water content}$ ($p = 0.0074$, $R^2 = 0.41$).

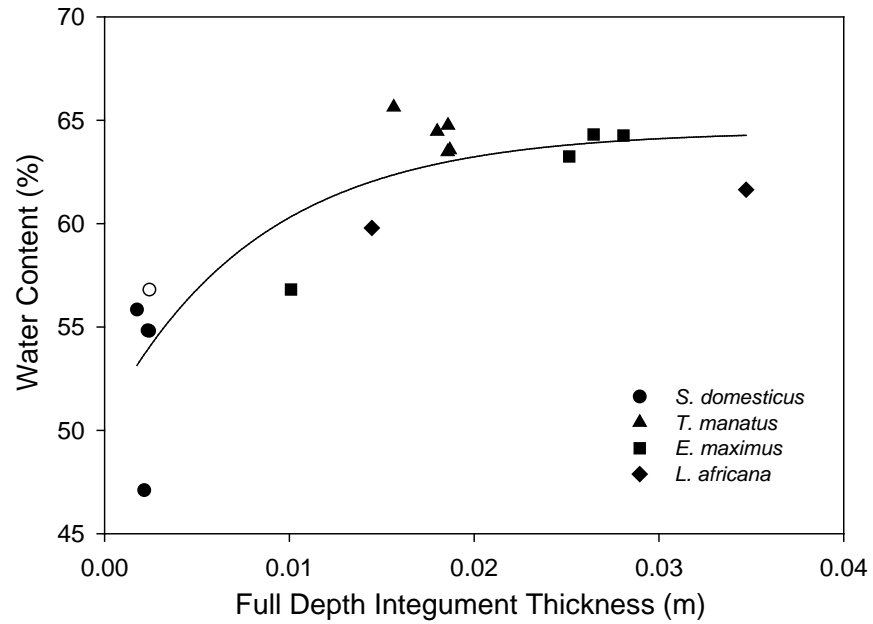


Figure 10: The integument thickness (depth) versus the percent composition of water of the full depth integument. This relationship is described by the equation $y = 50.46 + 14.02 \cdot (1 - e^{-120.67 \cdot d})$ ($p = 0.0001$, $F = 19.57$, $DF = 3, 13$, $R^2 = 0.75$).

between thermal conductivity of dry skin and lipid content of the full depth integument across species which was best described by the equation $y = 0.0393^{(8.93 \div (\text{lipid content} + 5.203))}$ ($p = 0.013$, $R^2 = 0.49$, $df = 3,13$) (Fig. 9B).

Thermal conductance also varied significantly between species ($p < 0.0001$, $F = 46.88$, $df = 2,11$). Despite a lower thermal conductivity, the much thinner pig integument was more than 3 times as conductive as that of the manatee, Asian or African elephant (Table 1). The addition of water or mud to the surface of the integument of the pig, Asian and African elephant increased the conductance of the integument in all cases, but these differences were not statistically significant (all $P > 0.36$) (Table 1). Rather, the addition of water alone tended to have the biggest thermal impact on thermal conductance in all species.

Minimum Epidermal Water Loss, Total Resistance, and ESA

Significant species-specific differences were found in the rate of CWL across all three temperature treatments (Table 2, Fig 11 A). The rates of water loss from the Asian elephant and manatee integument were significantly different from that of the pig at each temperature (overall model = $p < 0.0001$, $F = 54.21$, $DF = 4,37$, $R^2 = 0.85$) and were found to have rates of water loss more than 2 times greater than that of the pig (Table 2, Fig. 11A). Rates of water loss from all species were significantly less than the loss of water from a free water surface run in tandem with the samples [range of water loss from FWS = (cold) 9.25 ± 0.02 – (hot) 10.61 ± 0.04 $\text{mg cm}^{-2} \text{hr}^{-1}$] (Fig. 11A). There were also differences in water loss rates between the two African

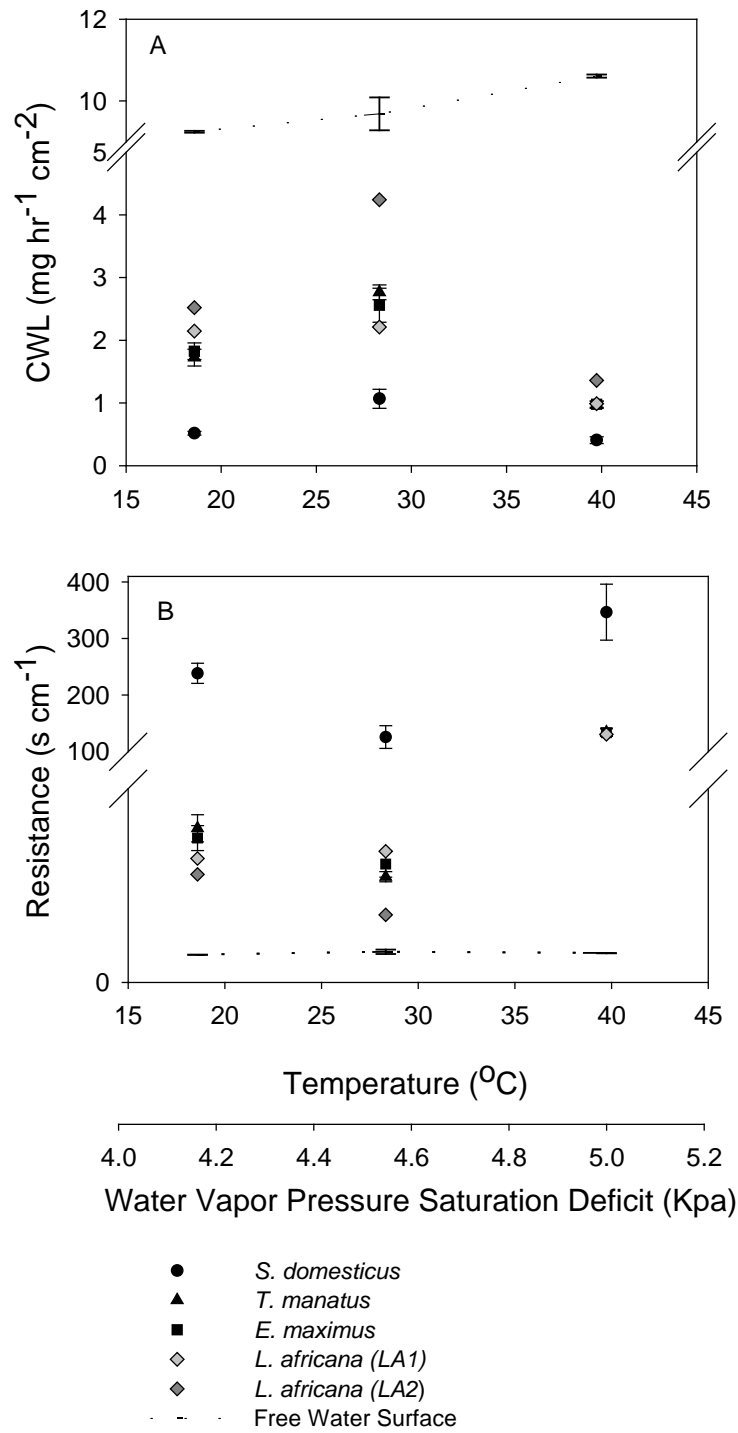


Figure 11: Minimum rate of cutaneous water loss (A) and total resistance to water loss (B) of skin (epidermis) in relation to ambient temperature or water vapor pressure saturation deficit (WVPSD) of pig (*S. domesticus*), manatee (*T. manatus*), Asian (*E. maximus*) and African (*L. africana*) elephant.

Table 2: CWL and resistance of pig, manatee, Asian and African elephant integument measured under three climatic conditions.

Species	Temperature (oC)	WVPSD (Kpa)	n	CWL (mg cm ⁻² hr ⁻¹)	SE	Resistance (s cm ⁻¹)	SE
Pig	18.6	4.1	5	0.5	0.03	238.5	17.88
Pig	28.3	4.7	5	1.1	0.15	125.8	20.22
Pig	39.7	5.1	5	0.4	0.05	346.6	49.42
Tm	18.6	4.1	5	1.7	0.13	63.6	5.57
Tm	28.3	4.7	5	2.8	0.12	43.6	2.10
Tm	39.7	5.1	5	1.0	0.06	134.5	7.12
Em	18.6	4.1	4	1.8	0.13	59.6	5.16
Em	28.3	4.7	4	2.6	0.27	48.8	5.35
Em	39.7	5.1	4	1.0	0.05	133.5	6.72
La1	18.6	4.1	1	2.2	-	51.1	-
La1	28.3	4.7	1	2.2	-	54.1	-
La1	39.7	5.1	1	1.0	-	130.6	-
La2	18.6	4.1	1	2.5	-	44.6	-
La2	28.3	4.7	1	4.2	-	27.9	-
La2	39.7	5.1	1	1.4	-	95.1	-
FWS	18.6	4.1	2	9.3	0.02	11.4	0.03
FWS	28.3	4.7	2	9.7	0.40	12.6	0.93
FWS	39.7	5.1	2	10.6	0.04	12.1	0.04

elephants. LA1 with flatter epidermal pillars had consistently lower rates of water loss relative to the rate from LA2 with more pronounced epidermal pillars. At the moderate temperature trial (28.32°C), the rate of water loss from LA2 was nearly double the rate from LA1 and was the highest of any species at any temperature (Fig 11A). An unexpected pattern was observed in the rate of water loss across temperatures for all species. While the rate of water loss increased with increasing temperature similar to that of the free water surface in the cold to moderate temperature trials, there was a significant reduction in water loss for all species at the highest temperature (39.74°C) (Fig. 11A). This reduction was most pronounced for the manatee and the Asian and African elephant. This pattern is different from that observed for the free water surface which increased at a steady linear rate with temperature (Table 2, Fig. 11A).

We found significant differences in the resistance of the integument to water loss across species at all levels of the water vapor pressure saturation deficit (WVPSD) (overall model $p < 0.0001$, $F = 35.11$, $DF = 4,37$, $R^2 = 0.79$) (Table 2, Fig. 11B). The resistance of manatee and Asian elephant integument was 2.6 to 4 times less than that of the pig across WVPSD's. There were also once again differences between the two African elephant samples. The resistance of the integument of LA2 was always less than that of LA1 and at the moderate WVPSD, was nearly half that of LA1. Similar to the observed pattern for the rate of water loss described above, there was a significant increase in resistance at the highest WVPSD (Fig. 11B). The

slope of the resistance between the low and moderate WVPSD however, was similar to that of the simultaneously measured free water surface (Fig. 11B).

DISCUSSION

Thermal Properties and Composition of Elephant Integument

The integument provides the first defense for controlling heat transfer in animals and as such represents a critical organ for maintaining thermal homeostasis particularly in unstable or extreme environments. Rather than a simple barrier, animal integument is a complex tissue composed of four main materials: fat, protein (collagen and elastin), water, and in furred animals, hair made largely of keratin, and the trapped air between the hairs. Thus, the movement of heat through this tissue is constrained by the thermal properties of several constituent parts each of which can be altered by varying their relative abundance in the integument. Air is an excellent insulator and the dense pelage of arctic and sub-arctic animals have thermal conductivity values as low as 0.03-0.04 W m⁻¹°C⁻¹ (Scholander, Walters, Hock *et al.* 1950). Other constituent materials such as free fatty acids have thermal conductivities between 0.16 W m⁻¹°C⁻¹ (e.g. Stearic Acid) and 0.23 W m⁻¹°C⁻¹ (e.g. Oleic), while water has a thermal conductivity nearly 25 times greater than air (0.61 W m⁻¹°C⁻¹) (Table 3). Thermal conductivity values for specific proteins are less well known and values for muscle, which is largely composed of protein, vary widely, ranging from 0.20 W m⁻¹°C⁻¹ to more than 0.53 W m⁻¹°C⁻¹ largely as a result of

Table 3: Thermal conductivity (k), insulation (R), and thermal conductance (C) values for a variety of terrestrial and marine mammals.

Scientific Name	Common Name	Thermal conductivity (k)(Wm ⁻¹ °C ⁻¹)	Thermal resistance (R) (m ² °C W ⁻¹)	Thermal conductance (C) (Wm ⁻² °C ⁻¹)	Method	Reference	Notes
Temperate Terrestrial							
<i>V. fulva</i>	(New York) Red	0.04	0.50	2.02	G. Hot Plate	(Hammel 1955)	* Average of two
<i>P. lotor</i>	Raccoon	0.05	0.60	1.65	G. Hot Plate	(Hammel 1955)	
<i>O. cuniculus</i>	Domestic rabbit	0.04	0.59	1.70	G. Hot Plate	(Hammel 1955)	
<i>F. catus</i>	House cat	0.04	0.51	1.96	G. Hot Plate	(Hammel 1955)	
<i>O. zibethica</i>	Muskrat	0.04	0.59	1.70	G. Hot Plate	(Hammel 1955)	
<i>D. virginiana</i>	Opossum	0.05	0.68	1.47	G. Hot Plate	(Hammel 1955)	
<i>O. virginianus</i>	Virginia deer	0.04	0.54	1.84	G. Hot Plate	(Hammel 1955)	
<i>O. cuniculus</i>	Rabbit (back)	0.04	0.34	2.93	M. Hot Plate	(Tregear 1965)	
<i>E. ferus caballus</i>	Horse (flank)	0.08	1.49	0.67	M. Hot Plate	(Tregear 1965)	
<i>E. ferus caballus</i>	Horse (belly)	0.06	0.13	7.53	M. Hot Plate	(Tregear 1965)	
<i>S. domesticus</i>	Pig (flank)	0.03	0.11	9.20	M. Hot Plate	(Tregear 1965)	
<i>S. domesticus</i>	Pig (belly)	0.03	0.09	10.88	M. Hot Plate	(Tregear 1965)	
<i>S. domesticus</i>	Pig (flank, shaved)	0.04	0.09	10.88	M. Hot Plate	(Tregear 1965)	
<i>H. sapien</i>	Human (epidermis)	0.21	-	-	Unknown	(Lefever, 1901 in	
<i>H. sapien</i>	Human (dermis)	0.29	-	-	Unknown	(Roeder, 1934 in	
Arctic/Subarctic							
<i>C. familiaris</i>	Husky dog	0.04	0.64	1.57	G. Hot Plate	(Hammel 1955)	
<i>L. americanus</i>	Snowshoe hare*	0.04	0.71	1.40	G. Hot Plate	(Hammel 1955)	* Average of 2 individuals.
<i>L. canadensis</i>	Lynx	0.04	0.81	1.24	G. Hot Plate	(Hammel 1955)	
<i>C. lupis</i>	Gray wolf	0.04	1.02	0.98	G. Hot Plate	(Hammel 1955)	
<i>R. arcticus</i>	Caribou	0.04	0.84	1.19	G. Hot Plate	(Hammel 1955)	
<i>V. Fulva</i>	(Alaska) red fox	0.04	1.05	0.95	G. Hot Plate	(Hammel 1955)	

*G. Hot Plate is guarded hot plate, M. Hot Plate is modified hot plate

Semiaquatic							
<i>O. anatinus</i>	Platypus (in air)	0.33*	0.30	3.33	Heat flux disc	(Grant & Dawson 1978)	*Excluded the skin; dorsal site
<i>O. anatinus</i>	Platypus (in water)	0.11*	0.11	9.09	Heat flux disc	(Grant & Dawson)	*Excluded the
<i>H. chrysogaster</i>	Water Rat (in air)	-	0.34	2.94	Unknown	(Dawson & Fanning)	
<i>H. chrysogaster</i>	Water Rat (in air)	-	0.08	12.50	Unknown	(Dawson & Fanning)	
<i>M. vison</i>	No. Amer. mink (in air)	-	0.30	3.38	Heat flux disc	(Dunkin 2001)	
<i>M. vison</i>	No. Amer. mink (in air)	-	0.13	7.62	Heat flux disc	(Dunkin 2001)	
<i>L. canadensis</i>	River otter (in air)	-	0.27	3.7	Heat flux disc	(Dunkin 2001)	
<i>L. canadensis</i>	River otter (in air)	-	0.11	8.77	Heat flux disc	(Dunkin 2001)	
<i>U. maritimus</i>	Polar bear (in water; summer)	-	0.01	70.29	G. Hot Plate	(Frisch, Øritsland & Krog 1974)	* tanned pelts
<i>U. maritimus</i>	Polar bear (in water; winter pelage)	-	0.02	59.83	G. Hot Plate	(Frisch <i>et al.</i> 1974)	* tanned pelts
<i>U. maritimus</i>	Polar bear (in air)	-	0.60	1.67	Heat flux disc	(Hurst & Øritsland)	
Fully Aquatic							
<i>E. lutris</i>	CA Sea Otter (in air)	-	0.24	4.18	Heat flux disc	(Dunkin 2001)	
<i>E. lutris</i>	CA Sea Otter (in water)	-	0.22	4.5	Heat flux disc	(Dunkin 2001)	
Cetaceans							
<i>B. acutorostrata</i>	Minke Whale	0.20-0.28*	0.13-0.20*	7.69 - 5.0	Standard material	(Kvadsheim, Folkow & Blix 1996)	* Range across the body
<i>B. physalus</i>	Sperm Whale	0.21	0.09	11.66	G. Hot plate	(Parry 1949)	
<i>D. leucas</i> (blubber)	Beluga Whale	0.10	0.46*	2.17*	Heat flux disc	(Doidge 1990)	* Used the mean reported thickness to calculate C and R from k.
<i>D. leucas</i> (epidermis)	Beluga Whale	0.25	0.05	19.64	Heat flux disc	(Doidge 1990)	
<i>P. phocoena</i>	Harbor porpoise	0.06	-	-	Heat flux disc	(Yasui & Gaskin)	
<i>P. phocoena</i>	Harbor porpoise	0.10	0.15	6.67	Heat flux disc	(Worthy & Edwards)	

*G. Hot Plate is guarded hot plate, M. Hot Plate is modified hot plate

<i>S. attenuata</i>	Spotted dolphin	0.20	0.04	25.97	Heat flux disc	(Worthy & Edwards	
<i>T. truncatus</i>	Bottlenose dolphin	0.11-0.18*	0.05-0.18*	25.69-5.74*	Standard material & HF disc	(Dunkin <i>et al.</i> 2005)	* Range for fetus to adult
Pinnipeds							
<i>M. leonina</i>	Southern elephant Seal	0.07	0.31	3.18	Hot plate method (based on Lees, 1898)	(Bryden 1964)	* Used the mean reported thickness to calculate C and R from k.
<i>P. groenlandica</i>	Harp Seal (fat)	0.19	0.35	2.88	Standard material method	(Kvadsheim <i>et al.</i> 1994)	
<i>P. groenlandica</i>	Harp Seal (thin)	0.20	0.18	5.56	Standard material method	(Worthy & Edwards 1990)	
<i>P. hispida</i>	Ringed Seal	0.20	0.29	3.50	Hot plate	(Scholander, Hock, Walters <i>et al.</i> 1950)	
<i>P. vitulina</i>	Harbor Seal	0.18	0.38	2.63	Heat flux disc	(Worthy 1991)	
<i>H. grypus</i>	Gray Seal	0.18	0.38	2.63	Heat flux disc	(Worthy 1991)	
Fatty Acids							
stearic acid (C18:2)	-	0.16	-	-	Unknown		
palmitic acid (C18:3)	-	0.17	-	-	Unknown	(CRC 1967 in Doidge 1990)	
oleic acid (C18:1)	-	0.23	-	-	Unknown		
Miscellaneous							
air	-	0.02	-	-	Unknown	(Schmidt-Nielsen 1997)	
water	-	0.61	-	-	Transient Hot Wire	(Ramires, de Castro, Marks Standard	
white pine wood	-	0.10	-	-	Unknown	(Schmidt-Nielsen 1997)	
iron	-	80.00	-	-	Unknown		

*G. Hot Plate is guarded hot plate, M. Hot Plate is modified hot plate

variation in water content (reviewed in Bowman, Cravalho & Woods 1975). Indeed, it is the percent composition of water that best correlates with the thermal conductivity of a tissue, a pattern that has been observed in marine mammals, the tissues of livestock animals, and in a variety of other materials (Bowman *et al.* 1975; Kvadsheim *et al.* 1996; Dunkin *et al.* 2005). Similarly, we found that the thermal properties of the four species in this study also varied with the water content of the integument (Fig. 9A).

Conductivity values for terrestrial mammals generally range from 0.03-0.04 $\text{W m}^{-1}\text{°C}^{-1}$ in small bodied animals such as the muskrat (*O. zibethics*) to as high as 0.20-0.28 $\text{W m}^{-1}\text{°C}^{-1}$ in several large bodied marine mammals such as the minke (*B. acutorostrata*) and beluga whale (*D. leucas*) (Table 3) (Hammel 1955; Doidge 1990). The thermal conductivity of Asian and African elephant integument lies at the upper end of this range although there was significant inter and intraspecific variation (Table 1, Fig. 12A). This variation was due to differences in morphology and composition. An African elephant with thinner dermis and shorter epidermal pillars (LA1) fell in the moderate range of conductivity values while an African elephant with pronounced epidermal pillars (LA2), had conductivity values among the highest reported in the literature for *in vitro* tissue (0.33 $\text{W m}^{-1}\text{°C}^{-1}$).

There are two main compositional characteristics that have resulted in higher thermal conductivity values as well as the variation in conductivity values across individuals. First, the lack of lipid in both the dermis and epidermis is remarkable. Across both Asian and African individuals, the percent composition of lipid of the

full depth integument was less than 1%. In contrast, the pig had mean lipid composition values of more than 6% (Fig. 6A,B) and the specialized integument of many marine mammals, which rely upon lipid as their primary insulation and for energetic storage, can be composed of more than 60% lipid. Elephant integument is instead, primarily composed of water (Fig. 6C,D) and fibrous protein. Because the thermal conductivity of water is so much greater than that of lipid or air, such high water content values will result in a higher thermal conductivity value. A second unexpected pattern was the positive relationship between thermal conductivity and the thickness of the integument. Such a relationship suggests a fundamental difference in the material properties between thin and thick integument. Further examination of the data demonstrated that indeed, thicker integument samples also had higher water content relative to thinner samples up to a threshold of approximately 65% (Fig 10). Thus, areas of the body with thicker skin or individuals with overall thicker skin will also have higher thermal conductivity values. However, conductivity is ultimately limited by a maximum water content of the tissue which likely represents a mechanical constraint. Support of large bodies requires mechanically tough integument and thus, further increases in water content may not be possible without compromise of the mechanical integrity of the material.

Comparison of the elephant and the pig, both nearly hairless mammals lacking the capacity to sweat, illustrates an additional thermal constraint imposed by large body size. In addition to a lower surface to volume ratio, the integument of large mammals must be sufficiently thick to support a large body mass, thus reducing the

overall thermal conductance of the material. Thermal conductance ($\text{Wm}^{-2}\text{C}^{-1}$) which accounts for both quality and material thickness, was 75% lower in the elephant compared to the pig (Table 1). These results suggest that the movement of heat through the non-living integument of the elephant is significantly lower, despite higher conductivity values relative to the pig.

Interestingly, the results of this study indicate that the thermal conductivity of manatee integument is near the upper end of that measured for a wide variety of marine mammals and the mean conductivity of the manatee was nearly identical to that measured for the Asian elephant (Table 2, Fig.12A). Therefore, despite living in a highly conductive medium (water), manatee integument does not appear specialized for heat conservation as is the case for most other marine mammals. Instead, like the elephant, the dermis of the manatee is almost completely lacking in lipid and is composed of highly-ordered and densely packed collagen fibers (Kipps 2000) and water. In contrast to the elephant, the manatee has a significant amount of epidermal lipid (mean 7.36%), even compared with that of the pig (3.86%). This observation is consistent with that of several other species of marine mammal. Pfeiffer and Jones (1993) observed abundant intracellular lipid droplets in the epidermis of four species of cetaceans and concluded that the most likely hypothesis for their presence was as a metabolic fuel source for the high rate of epidermal growth and maintenance in the aquatic environment. In this study, the observation that manatees, a phylogenetically distinct clade of marine mammals, also have high epidermal lipid content suggests that this trait could be a general adaptation for aquatic living. The integument of the

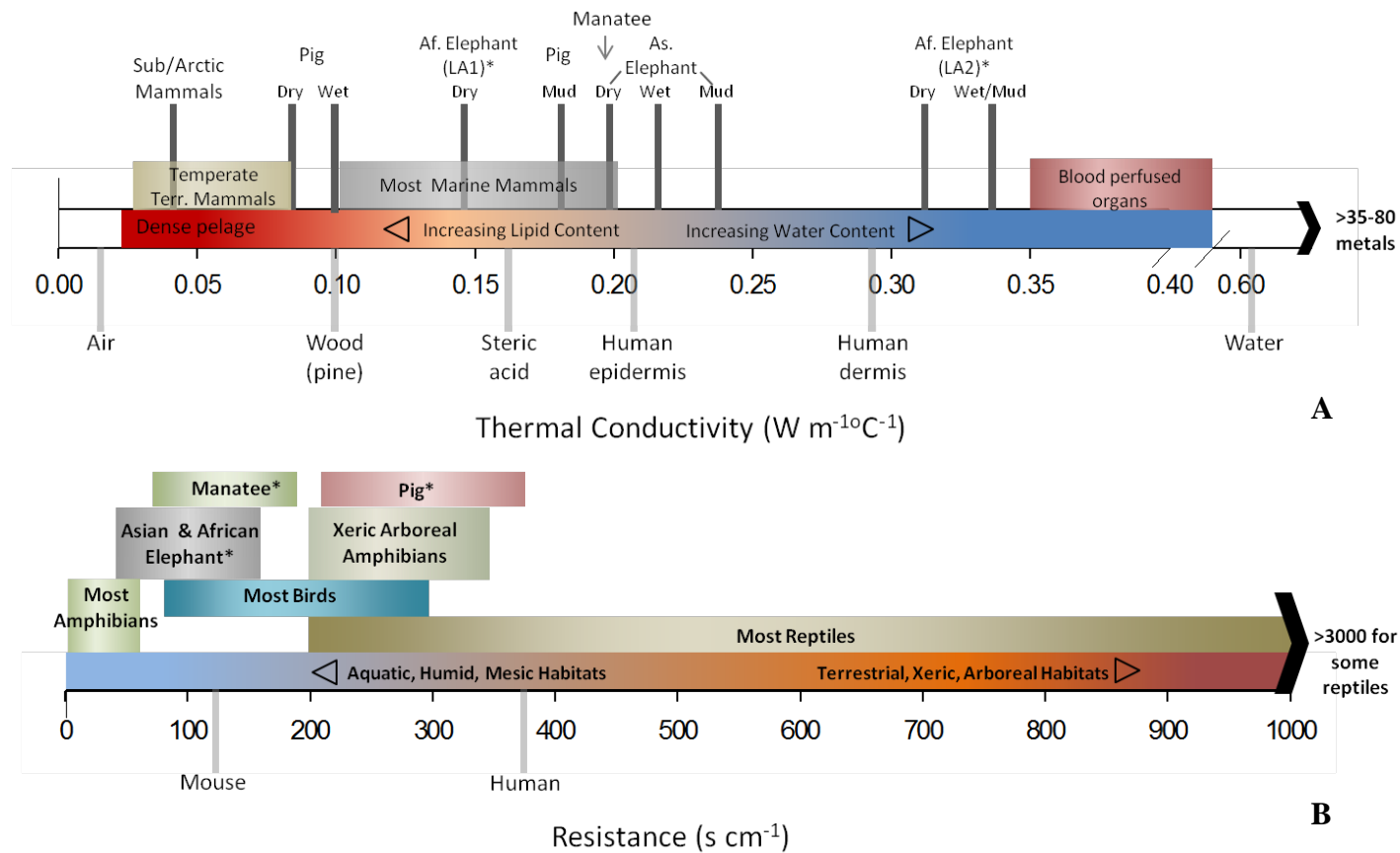


Figure 12: Schematic of the distribution of thermal conductivity values of integument across species in relation to relative composition of the tissue (A). Schematic of the resistance to water loss across groups of species in relation to the relative dryness of the habitat (B). Thermal conductivity values are for the full depth integument with pelage in furred species unless otherwise specified. Resistance includes values of total resistance as well as resistance of skin only and are summarized by Lillywhite, 2006. Sources for the thermal values from the literature are given in Table 2.

manatee was also equally as thick as that of most of the elephants in this study, resulting in a mean thermal conductance of $10.78 \pm 0.67 \text{ Wm}^{-2}\text{C}^{-1}$, a value that is in the middle of the range of thermal conductance values measured for the integument of other marine mammal species. Thus, their integument is not likely to be the primary reason for their known sensitivity to cold stress (Bossart, Meisner, Rommel *et al.* 2003).

We have documented that elephants can have integument that is up to 11 times more thermally conductive relative to that of a sub-arctic or arctic mammal (Table 2). Heat exchange from an animal's body is complex (Gates 1980; Porter & Kearney 2009). However, in the case of simplified conductive heat flow across the skin, this translates into 11 times greater heat loss relative to that through a dense fur pelage. Furthermore, because these measurements are performed on dead tissue in the absence of blood flow, these data represent minimum values. In the living animal, conductance of heat is certainly much greater. Indeed, Williams (1990) calculated whole body conductance for an Asian and African elephant as being 3.0 to 4.8 times greater than predicted from allometric regressions of conductance across mammals. There is also extensive evidence that elephants have fine vascular control of blood flow to the skin not just in the ears but across the entire body surface (Williams 1990; Weissenböck, Weiss, Schwammer *et al.* 2010). Thus, the increased whole body conductance for elephants reported by Williams (1990) is likely a result of a combination of a relatively high thermal conductivity of the integument and extensive control of blood flow to the skin. Phillips and Health (1995) noted that as

body size increases, the dependence on regulation of skin surface temperature to regulate heat loss also increases. Because the increased thickness of the integument is largely a result of a thickening of the vascularized dermis, the results of this study suggest that fine control of skin surface temperature and overall higher whole body thermal conductance is aided by a relatively high thermal conductivity of the integument, facilitating the conduction of heat through elephant's thick skin.

Behavioral Modification of the Thermal Properties of the Integument

Two behaviors commonly employed by both species of elephant and pigs, wallowing and mud bathing, may enhance heat loss by augmenting the effective thermal conductivity of the integument given the high thermal conductivity of water. While the thermal conductivity of wet and muddy integument increased relative to that of dry integument for all three species, the addition of water alone appeared to yield the largest thermal benefit across all three species. The thermal conductivity of the pig integument when covered with water increased by 25% and with the addition of mud, more than doubled. Similarly, the addition of water to the surface of Asian elephant integument resulted in an increase in thermal conductivity of 15.7% and an increase in conductance of 16.1%. While the addition of mud to the surface of both the pig and Asian elephant integument did on average increase the conductivity slightly, the increased thickness made the overall thermal benefit slight. Thus, non-evaporative heat loss is not particularly enhanced by the addition of mud but the addition of water alone appears to be beneficial for non-evaporative heat transfer.

The Water Barrier of Elephant Integument

Wright and Luck (1984) first recognized the importance of evaporative cooling in elephants and identified several features of the integument that likely contribute to higher rates of water loss. These properties include the hydration status of the integument as well as the thick keratinized stratum corneum, both of which increase the rate of water loss from the integument surface (Blank 1952; Vinson, Singer, Koehler *et al.* 1965; Blank, Moloney, Emslie *et al.* 1984; Wright & Luck 1984; Kasting, Barai, Wang *et al.* 2003). However, two important questions remain unanswered. First, do internal water stores significantly contribute to high rates of CWL or does the specialized morphology and thick keratinized stratum corneum primarily function to take up externally derived water for subsequent evaporation? Second, is the resistance of the integument a fixed property or are there climate driven changes in the properties of the stratum corneum that may influence the rate of CWL?

Published rates of CWL for mammals range from $0.15 \text{ mg cm}^{-2} \text{ hr}^{-1}$ in neonatal rats (*Rattus sp.*) and adult guinea pigs (*Cavia porcellus*) to $0.65 \text{ mg cm}^{-2} \text{ hr}^{-1}$ (at 25°C) for dorsal pig skin and as high as $12.5 \text{ mg cm}^{-2} \text{ hr}^{-1}$ in sweating waterbuck (at 45°C) (*Kobus defassa ugandae*) (Vinson *et al.* 1965; Taylor 1969; Ghobrial 1970). In contrast, at about 28°C , slightly below the sweating threshold of 30°C in most mammals, and in the absence of externally derived surface water, the rates of insensible (non-sweating) CWL from non-living elephant tissue ranged from 2.21 to $4.24 \text{ mg cm}^{-2} \text{ hr}^{-1}$, rates that are 3.4 to 6.5 times that measured for *in vivo* human skin

at 25°C (reviewed in Vinson *et al.* 1965). Thus, our results show that there is a significant contribution of internal water to CWL. Furthermore, CWL from dead tissue under steady state conditions as measured in the present study represents a minimum rate of water loss from the integument. It is less clear whether internal water stores are spared when the stratum corneum is fully hydrated such as after a visit to a water hole. Hydration of the stratum corneum increases the diffusivity of water and other polar and some non-polar compounds through the tissue (reviewed in Lillywhite 2006) and therefore could presumably increase the rate of internal water loss through the integument. Yet, the addition of externally derived water to the skin surface will also temporarily reduce the concentration gradient of water between the inside and outside of the animal, and thus, internal water sources may be spared for some period of time after wallowing and mud bathing.

Although there are few measurements of integumental resistance in mammals, the resistance values of both Asian and African elephants fell well below values for the pig at all three climate trials in this study. Elephant integument was also up to 13 times less resistant to water loss relative to humans and significantly lower than that measured for the mouse at all but the highest measured temperature (Fig. 12B).

Although hydration and thickness of the stratum corneum do influence the rate of CWL, differences in integumental resistance between species and across individuals of the same species acclimated to different environments, are primarily a result of changes in the lipid-corneocyte matrix, the structure that forms the primary barrier to water loss in the stratum corneum of mammals and birds (Haugen, Tieleman &

Williams 2003b; Lillywhite 2004; Munoz-Garcia & Williams 2005; Lillywhite 2006).

Organized as a “brick and mortar” type matrix (Elias 1983), the water barrier is composed of keratin filled corneocytes embedded in an extracellular matrix of lipid bilayers. Substantial evidence from humans (Madison, Swartzendruber, Wertz *et al.* 1987; Potts & Francoeur 1991; Lavrijsen, Bouwstra, Gooris *et al.* 1995; López, Cócera, Wertz *et al.* 2007) and birds (Haugen *et al.* 2003b; Munoz-Garcia & Williams 2005; Gu, Munoz-Garcia, Brown *et al.* 2008) has shown that changes in the composition of lipids in the stratum corneum are primarily responsible for changes in rates of CWL. In particular, the proportion of ceramide lipids and free fatty acids seem to be associated with CWL. For example, desert birds having higher amounts of ceramides and lower amounts of free fatty acids and have lower rates of CWL relative to mesic adapted birds (Haugen, Williams, Wertz *et al.* 2003a; Munoz-Garcia & Williams 2005). Similarly, in some human skin diseases, such as psoriasis and atopic dermatitis, increased rates of CWL are associated with decreased amounts of ceramides in the stratum corneum (Jungersted, Hellgren, Jemec *et al.* 2008). Given the low resistance to water loss of elephant integument, it is likely that there has been alteration of the lipid composition of the stratum corneum in these species. In particular, elephants may have reduced amounts of ceramides and greater amounts of free fatty acids relative to other mammals. It is also possible that elephants, like some birds, may undergo facultative changes in the resistance of their integument as a response to seasonal changes in temperature or humidity and that there may be significant differences in integumental resistance across populations. All of the

samples measured in this study were collected from zoo elephants with ready access to water and which were exposed to relatively mild climates. It must be considered that wild elephants living in more arid habitats may have integument with increased resistance to water loss. However, if this were the case it would lend support to the hypothesis that elephants are able to undergo facultative changes in integumental resistance as observed in birds.

The second question we were able to address in this study is whether the resistance of the integument, in the absence of active physiologic changes to the stratum corneum, is a fixed property across different climates? While the resistance of the integument was similar in the two elephant species and in manatees between the 18.6 and 28.3°C trials, we found the surprising result that even in non-living tissue, the resistance of the integument in all species increased significantly at the highest temperature tested (39.7°C). Although the resistance of the pig integument did increase at the highest temperature as well, it was not statistically different from the value at the coolest temperature. Thus, the temperature-dependant change in integumental resistance was most pronounced in the elephants and manatees and in particular the integument of LA2, the African elephant with the tall epidermal pillars, which increased in resistance more than 3 fold. Potential experimental explanations for this pattern include 1) the samples in the cool and moderate trials had not fully reached equilibrium and thus, the rate of loss was artificially high, and resistance artificially low, in these groups or 2) the samples in the high temperature trials became significantly drier and therefore had lower rates of CWL relative to the other

groups. In all trials the samples were allowed to reach a steady state in which the rate of loss was stable, changing less than 5% for several hours before the final measurement was performed and thus, this explanation was ruled out. All samples were also visually inspected after the trial and qualitatively appeared to be equally as dry at the conclusion of each trial, therefore the second explanation is also unlikely. The remaining biological explanation is that as a result of lipids in the stratum corneum changing from a crystalline-gel to a liquid state, the permeability of the membrane was reduced.

As reported by Lillywhite (2004; 2006), the stratum corneum in mammals and birds and the water barriers found in many other biological systems often contain long chain fatty acids. These fatty acids tend to melt at higher temperatures and cause an increase in resistance to water loss (Lillywhite 2004; Lillywhite 2006). Further evidence that this is a plausible explanation for the observed pattern is found in work by Van Duzee (1975) who identified 40°C as one of two reversible transition temperatures attributed to the melting of lipids in the stratum corneum of humans. In the living animal, skin surface temperature is under physiological control, and with alterations in blood flow and through behavioral thermoregulation, skin temperatures may never reach the melting temperature of stratum corneum lipids and the observed increase in resistance may not be biologically relevant. However, of the species considered in this work, Asian and African elephants frequently encounter ambient temperatures well above 40°C and shade is not always readily available. Thus, at very high ambient temperatures and low water availability, it is possible that an

increased resistance to water loss may be important as a water saving mechanism in elephants. Further support for this idea comes from observations that the cuticular permeability ($\text{g m}^{-2} \text{hr}^{-1} \text{kpa}^{-1}$) a measure of water loss in the absence of the effects of climate, of elephant skin *in vivo* decreases at higher ambient temperatures (Dunkin 2012). Whereas this pattern was thought to be mainly associated with changes in blood flow, the results of this study indicate that the properties of the stratum corneum lipids may also play a role. The hydration state and specific lipid composition of the stratum corneum will certainly alter the transition temperature of the stratum corneum lipids, however, a so called “fail safe” water sparing mechanism remains an intriguing and plausible hypothesis for species that rely extensively on insensible water loss for evaporative cooling in extreme and unpredictable habitats.

Given the relatively high rates of CWL from non-living elephant integument under controlled environmental conditions, how do these rates compare with those measured from elephants *in vivo*? At similar temperatures, rates of CWL from live African elephants are between 3.6 and 6 times greater than that measured from non-living elephant tissue (Dunkin 2012) in this study. This difference is in part a result of differences in hydration status of the integument between live and dead tissue (as discussed above) but also demonstrates a significant role for active facilitation of the rate of evaporative water loss in these species. As noted by Munoz-Garcia *et al.* (2005) and Ro *et al.* (2010), the idea that water loss through the stratum corneum is simply a passive process dictated by Fick’s law of diffusion has largely been replaced by the view of the stratum corneum as a metabolically active, highly regulated,

dynamic tissue (Elias 2004). However, in this study we have shown that underlying the role of active facilitation of CWL via blood flow and changes in skin temperature, the water barrier of elephant stratum corneum is fundamentally more permeable to water relative to many other mammals including the pig, a smaller bodied animal that also relies exclusively on insensible water loss.

We have compared the integument of the elephant and pig for their similar reliance on insensible water loss, however comparison with the manatee has also proven interesting. Although manatees and elephants inhabit very different thermal environments, the results of this study have found that the thermal properties of their integuments are quite similar. The same result was true of the water barrier properties of the integument. The resistance of manatee integument was very similar to that of the elephant across all three temperature trials and this low resistance is consistent with the results of several studies of cutaneous water flux in other marine mammals (Hui 1981; Andersen & Nielsen 1983; Elias 1991). Compositional analysis of stratum corneum lipids in a harbor porpoise (*P. phocoena*) found that there was a distinct lack of ceramides as well as a substitution of longer chain fatty acids for shorter chain fatty acids, results that are consistent with high rates of CWL (Menon, Grayson, Brown *et al.* 1986; Elias 1991). Whether manatees have similarly altered lipid composition relative to many terrestrial animals, remains to be seen in future work, however, given the rates of CWL measured in this study this would be a reasonable hypothesis. In terms of function, we have hypothesized that the low resistance to water loss in elephants is a response to the need for heat dissipation

through evaporative cooling. While evaporative cooling is not necessary for an aquatic animal such as the manatee, Menon (1986) suggested that the observed alterations in lipid composition in other marine mammals, which also are associated with high CWL, may serve to maintain the stratum corneum in a fluid state at lower temperatures or may serve a streamlining function. Further work on lipid composition of Asian and African elephants as well as manatees is needed to further clarify the similarities and differences between these groups as well as better discern their function.

Summary

In contrast with many sympatric mammals, the African elephant has been classified as a water dependent species based on its mean distance from water during the dry season (Western & Lindsay 1984). Recent work has shown that both Asian and African elephants are highly dependent on evaporative cooling even at relatively low ambient temperatures (Dunkin 2012). Consistent with these ecological and whole animal observations of elephant water use, we have demonstrated that at the level of the tissue, the problems of heat dissipation associated with large body size and occupation of arid habitat, have resulted in significant adaptations of the integument for non-evaporative and evaporative heat loss. Furthermore the importance of the control of skin surface temperature for the regulation of heat loss by both non-evaporative and evaporative routes is highlighted by comparison of measurements from non-living tissue with *in vivo* data.

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**CHAPTER 2: THE INFLUENCE OF CLIMATE ON THERMAL BALANCE
AND WATER USE IN AFRICAN AND ASIAN ELEPHANTS: A
PHYSIOLOGICAL APPROACH TO UNDERSTANDING DRIVERS OF
ELEPHANT DISTRIBUTION**

ABSTRACT

Elephants are widely classified as a water dependant species and there has been recent interest in using surface water management as a technique for reducing or redistributing elephants within reserves where localized elephant overabundance has decreased biodiversity and increased human elephant conflict. Given that the water dependence of the elephant is likely caused by thermoregulatory mechanisms, we investigated the potential interaction between climate and the use of surface water by elephants. We empirically measured skin surface temperature and cutaneous evaporative water loss from 13 elephants (7 African, $3768 \pm 642\text{kg}$; 6 Asian, $3834 \pm 498\text{kg}$) and determined the contribution of evaporative heat dissipation to the thermal budgets of elephants across a range of ambient temperatures from 8 to 33°C. We also measured respiratory evaporative water loss and resting metabolic heat production using open flow respirometry on a subset of elephants (n=7). To determine the capacity of elephants to control cutaneous evaporative water loss, we calculated cuticular permeability across a range of water vapor pressure saturation deficits and between seasons. We found that across the entire range of temperatures measured in this study both species of elephant relied extensively on evaporative cooling. At 18-20°C, evaporative cooling was used to dissipate more than 50% of resting metabolic heat production and elephants were fully dependant on evaporative cooling at temperatures above 28-30°C. This reliance on evaporative cooling resulted in a significant climate dependant water debt. Simulated thermal and water budgets constructed for elephants using climate data from Port Elizabeth, South Africa and

Okaukuejo, Namibia found that in the mild climate of Port Elizabeth, elephants would incur a water debt of only 22Lday^{-1} from evaporative cooling while animals in the much warmer climate of Okaukuejo could incur a water debt of more than 100Lday^{-1} . We also found evidence that elephants do have some measure of control over evaporative water loss through alteration of skin surface temperature but that this mechanism is only viable at temperatures below body temperature. Elephants may also seasonally alter the cuticular permeability of their integument likely through alteration of integumental lipid composition. The results of this study confirm that elephants are obligate evaporative coolers and that classification of elephants as water dependent requires further characterization based on the climate in which an animal lives. Furthermore, these data highlight the potential use of a physiological based approach to modeling landscape use in elephants and possibly for predicting the utility of surface water management for a particular population.

INTRODUCTION

Recently, there has been significant interest in determining the factors that most strongly influence the use of landscape by elephants (Owen-Smith *et al.* 2006; Chamaille-Jammes & Fritz 2007; Epaphras, Gereta, Lejora *et al.* 2008; Shannon, Matthews, Page *et al.* 2009). This interest stems from the recognition that elephants are water dependent (Western 1975; Western & Lindsay 1984) and that surface water management may be a powerful tool for reducing elephant abundance in areas where surface water provisioning has resulted in high elephant densities (Chamaille-Jammes & Fritz 2007; Chamaille-Jammes, Valeix & Fritz 2007; Smit, Grant & Whyte 2007b). Water provisioning has, in at least some areas, led to use of habitat that was formally inaccessible to elephants with a concomitant loss of biodiversity and increase in human elephant conflict (Owen-Smith 1996; Owen-Smith *et al.* 2006; Chamaille-Jammes & Fritz 2007; Epaphras *et al.* 2008; Shannon *et al.* 2009). The elephant's large body size, low surface to volume ratio, and frequent occupation of arid, hot environments makes heat dissipation a challenge (Benedict 1936; Williams 1990) and reliance on evaporative cooling is hypothesized to be the major contributor to the elephant's dependence on water (Wright & Luck 1984). Thus, the interaction between two abiotic factors, temperature and the distribution of surface water, is likely an important driver of elephant use of landscape. However, despite interest in surface water management, there has been no work to quantify the influence of climate on water use in elephants.

Heat dissipation as a challenge for elephants has long been recognized (Benedict 1936; Wright 1984; Wright & Luck 1984; Lillywhite & Stein 1987; Williams 1990; Phillips & Heath 1992). Elephants overcome this challenge using a variety of strategies including well developed thermal windows in their ears (Buss & Estes 1971; Wright 1984; Phillips & Heath 1992), behavioral strategies such as shade seeking (Sikes 1971; Sukumar 2003), and through evaporative cooling (Wright & Luck 1984; Lillywhite & Stein 1987). Despite lacking sweat glands (Smith 1890; Horstmann 1966; Spearman 1970) elephants have significant rates of insensible water loss across the skin (Wright & Luck 1984), a result of a relatively high integumental permeability relative to other animals (Dunkin 2012). Wallowing and mud-bathing also contribute to the use of evaporative cooling as well (Lillywhite & Stein 1987). While heat transfer across the ears, feet, and body via conduction, convection, and radiation may sufficiently dissipate heat in milder climate conditions, the effectiveness of these strategies diminishes and reverses to heat gain once ambient temperature surpasses skin surface temperature (Gates 1980). At higher ambient temperatures, evaporative cooling or heat storage are the only strategies that a large animal can employ to deal with excess heat. Kinahan *et al.* (2007a) found that even under conditions of mild water stress, elephants do not appear to utilize heat storage to a great extent. Thus, for a large bodied animal in an arid environment, evaporative cooling may in fact be obligatory above a threshold ambient temperature depending upon activity state and climatic conditions. Therefore, the physiological process of

thermoregulation has the potential to play a major role in differential use of landscape across populations inhabiting different climate regions.

Temperature and in particular, surface water distribution have been separately investigated as factors driving landscape use in elephants. Kinahan *et al.* (2007b) found that elephants may preferentially use habitats that cool down faster relative to other areas suggesting that, even within a single population, temperature may influence elephant use of landscapes. There is also significant work on the distribution and abundance of surface water as a driver of landscape use in elephants. The influence of surface water on animal distribution has been recently investigated for elephant and other herbivore populations in several areas across Africa (Redfern, Grant, Biggs *et al.* 2003; Redfern, Grant, Gaylard *et al.* 2005; Chamaille-Jammes & Fritz 2007; Smit, Grant & Devereux 2007a; Shannon *et al.* 2009; Franz, Kramer-Schadt, Kilian *et al.* 2010). In all of these studies, surface water was deemed an important driver of elephant distributions in combination with other factors. Yet, determination of whether a specific elephant population is indeed water limited remains an unanswered, critical question (Chamaillé-Jammes *et al.* 2007; Smit *et al.* 2007b).

As discussed by Smit *et al.* (2007b), surface water management relies upon the assumption that a population is water limited, thus, reasonable prediction of whether this is the case for a particular population and whether the proposed reduction or spatial movement of surface water will bring about the desired changes in elephant density and/or distribution is a critical first step in utilization of this tool.

In most studies, such determinations generally rely upon aerial or ground survey data (Redfern *et al.* 2003; Redfern *et al.* 2005; Chamaille-Jammes & Fritz 2007), telemetry data (Franz *et al.* 2010), or markers of elephant presence such as vegetation trampling or tree damage (Shannon *et al.* 2009) in relation to surface water. These approaches have provided good working hypotheses for several elephant populations but are not generalizable to other populations and are limited by the temporal scope of the collected data. For example, aerial survey data can not be collected at night and may not account for changes in distributions across seasons or during rare extreme events such as droughts.

In contrast with these pattern-driven approaches that rely upon elephant density data in relation to surface water, the tools of comparative physiology can provide insight into, and *importantly*, quantify the mechanistic drivers of elephant distribution. Thus, a physiological based approach to understanding elephant distributions and the use of surface water management offers two specific and related benefits. First, identifying the mechanisms underlying a widespread pattern such as a species' "water dependence" offers an ability to more reliably predict responses for an animal or population in other environments or situations for which there is little or no data. Second, once the mechanism for a pattern has been identified, the relationships between relevant biotic or abiotic variables (e.g. food abundance, ambient temperature, surface water distribution) and the physiological driver of the pattern (e.g. thermal status, water demand) can be quantified. Such a predictive framework can also be used to generate and test new hypotheses for animal

distribution patterns and thus, is highly complementary to the pattern based approaches classically used (for example see Porter, Sabo, Tracy *et al.* 2002; Kearney & Porter 2009).

The main 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 determining the use of landscape by these animals. To meet this objective we developed empirical relationships between ambient temperature, thermal balance and water use for elephants across a range of environmental temperatures and used these relationships to determine the degree to which elephants are obligated to use evaporative cooling in different climates or seasons. We also investigated whether elephants have any capacity to control the rate of evaporative water loss and thus, buffer against extreme temperatures or events such as droughts. We performed these measurements in both African (*Loxodonta africana*, Blumenbach, 1797) and Asian (*Elephas maximus*, Linnaeus, 1758) elephants to test for differences between species given the differences in climate (temperature, humidity) in which each species has evolved. We also examined these relationships separately for the ears and body because the ears are known to be important thermoregulatory sites that may respond differently to changes in ambient temperature relative to the rest of the body. Finally, to determine the importance of wallowing behavior for elephants' thermal and water balance, separate relationships were developed for animals when dry and after simulated wallowing behavior.

METHODS

Approach

To determine the relative contribution of evaporative cooling to the thermal budgets of African and Asian elephants across a range of climates, we measured skin surface temperatures and cutaneous evaporative water loss on dry skin across a nearly 25°C span of ambient temperatures. We also performed these measurements on wet skin after animals had been fully bathed to simulate how wallowing may influence the thermal and water budget of the animals. We then used skin surface temperature measurements and measured surface areas to estimate non-evaporative heat loss via radiation, conduction, and convection across the ambient temperature range. On a subset of animals, we simultaneously measured respiratory evaporative water loss and resting heat production using open flow respirometry to estimate the contribution of respiration to total heat and water loss and to determine heat production for the individuals in this study.

Animals & Facilities

A total of thirteen elephants participated in this study including 7 adult African (6 females, 1 male; mean body mass = 3768 ± 642 kg) and 6 adult Asian (6 females; mean body mass = 3834 ± 498 kg) elephants housed at three U.S. facilities (Wildlife Safari in Winston, OR, Six Flags Discovery Kingdom in Vallejo, CA, and Have Trunk Will Travel in Perris, CA). These facilities were chosen for their access to animals and for the range of climate conditions under which measurements could be

performed across seasons. Though environmental temperature was the main variable across which measurements were performed, we controlled other aspects of climate such as solar radiation and thus, we use the term climate to collectively refer to temperature, humidity, and radiation. Collection of data from animals acclimated to a wide range of climates allowed us to capture a generalized response more broadly applicable for animals across many habitats. Not all measurements were performed on all animals due to training constraints, movement of animals during the course of the study and other factors. 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 access to both indoor and outdoor enclosures throughout the year. During the warmer months, they also often had access to both outdoor and indoor facilities at night. If ambient temperatures were too cold (generally $<4-7^{\circ}\text{C}$), 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 U.C. Santa Cruz Institutional Animal Care and Use Committee (IACUC) and under the approval of each facility's own research approval protocols.

Body Sites, Surface Area, and Body Mass

To examine the range of variation across the surface of the body, measurements were taken at five body sites including 1) the outer margin of the 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 toe nails (Fig. 1A). For consistency, care was taken to avoid sites near large blood vessels when measuring the ears.

The surface area of the body and legs of each elephant (6 *E.m.* and 5 *L.a.*) was estimated by collecting a series of 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 on the ground. These morphometric 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 (Fig. 1B). 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 NIH Image J software (Rasband 1997-2009) (Fig. 1B). The measured surface area of the front side of one ear was multiplied by four to yield total ear surface area.

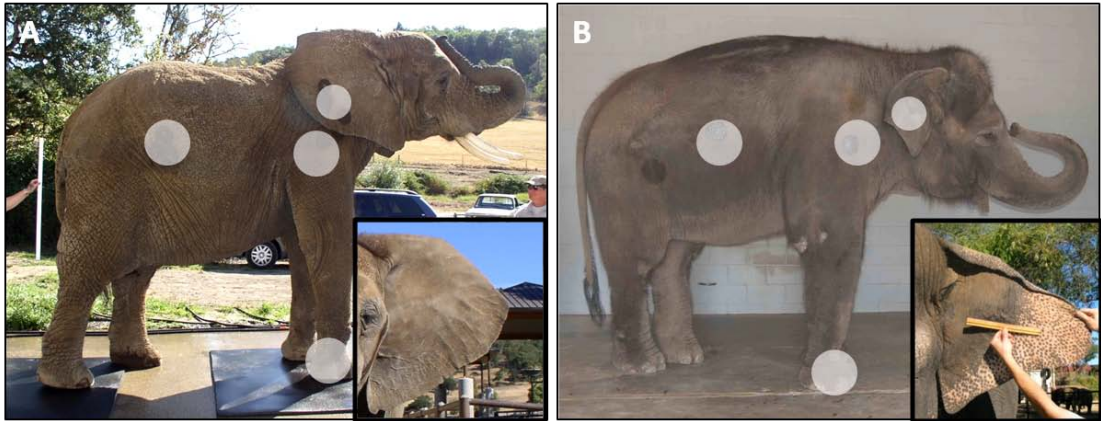


Figure 1: An African (A) and Asian elephant (B) with corresponding ear surfaces and location of measurements on body. Evaporative water loss, skin surface temperature, and heat flux were measured at five body sites including the anterior and posterior outer margin of the ear, the shoulder, the belly and the foot as indicated by the white circles.

Body mass was periodically measured 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 taken within one month of the metabolic measurements. All other mass measurements are presented as the mean of the measurements taken over the course of the study.

Climates

To achieve the widest possible range of ambient temperatures and maximize the number of measurements taken for each individual, measurements were performed across seasons as well as in the morning and afternoon at all three facilities. Ambient temperatures (Perception II, Davis Instruments, Hayward, CA, USA) during data collection days ranged between 8.7 and 32.9°C (overall mean \pm SD: 20.22 \pm 6.12°C) and relative humidity ranged between 21.6 and 91% (overall mean \pm SD: 51.19 \pm 18.28%). To assess differences in the year round climate experienced by individuals at the three facilities, daily maximum, mean, and minimum temperature and relative humidity 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. There were significant differences in climate between facilities (Table 1). As expected, the most southern facility (Perris, CA) experienced significantly warmer temperatures and lower relative humidities relative to that of the other facilities (all $p < 0.0001$) with mean daily maximum temperatures that were 5.2

Table 1: Average minimum, mean, and maximum daily temperature (°C) and relative humidity (%) for each facility during the study and for 1 year prior to the start of measurements.

Facility	T _{min} ± SD	T _{mean} ± SD	T _{max} ± SD	RH _{min} ± SD	RH _{mean} ± SD	RH _{max} ± SD
HTWT (Perris, CA)	A 8.1 ± 6.0	A 16.9 ± 6.5	A 25.8 ± 8.1	A 28.36 ± 18.4	A 59.51 ± 22.4	A 85.2 ± 19.1
SFDK (Vallejo, CA)	B 6.6 ± 4.7	B 13.6 ± 4.9	B 20.6 ± 6.5	B 48.71 ± 17.9	B 73.33 ± 12.3	B 94.17 ± 7.1
WS (Winston, OR)	B 7.0 ± 5.2	C 12.8 ± 6.7	C 18.5 ± 8.8	B 48.79 ± 19.6	B 72.65 ± 14.8	C 91.77 ± 9.5

*Different letters denote facilities that are significantly different from one another.

to 7.4°C greater than that of Vallejo or Winston. The daily minimum and mean relative humidity at the southern facility were also significantly lower than that at the other two facilities. There were significant but much smaller differences in climate between the central (Vallejo, CA) and northern (Winston, OR) facilities (Table 1) but these differences were less than 1.1°C and less than 2.4% relative humidity. To minimize the effects of solar radiation which varies considerably from hour to hour and across days and seasons, all data were collected inside the elephant barns at each facility.

Simulation of Wallowing Behavior

The effects of wallowing on thermal status and evaporative water loss 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 approximately 15 to 20 minutes. Care was taken to ensure that all body surfaces were thoroughly soaked; post-bathing data were collected immediately after completion of the bath (usually within 8-10 min) and the body site order was varied randomly to ensure there were no systematic differences associated with the relative time since the completion of the bath. Thermal and evaporative water loss measurements were collected under four conditions: morning/pre-bathing, morning/post-bathing, afternoon/pre-bathing and afternoon/post-bathing permitting measurement across a wider range of temperatures.

Skin Surface Temperatures & Non-Evaporative Heat Exchange

Skin surface temperatures (T_{ss}) were collected using an infrared thermometer (Raynger PM4L5, Raytec, Inc., Santa Cruz, CA, USA) held 7-10cm from the skin surface. Ambient conditions including air temperature and relative humidity (Perception II, Davis Instruments, Hayward, CA, USA) were recorded simultaneously for each individual measurement of skin surface temperature at each body site. Measurements were performed at least once on all thirteen elephants (total $n = 574$ measurements including all body sites).

Radiant, convective, and conductive heat loss were calculated using methods similar to Williams (1990). Briefly, standard equations for the three non-evaporative routes of heat dissipation have been previously developed and tested in humans (as reviewed in Clark & Edholm 1985) and in various animals and plants (Gates 1980). These equations model heat exchange for various geometric shapes at different orientations and are all dependent upon the gradient in temperature between the skin and ambient environment. The torso and legs of the elephant were modeled as horizontal and vertical cylinders respectively and the ear modeled as a vertical flat plate. The following equations were used to calculate non-evaporative heat exchange:

$$(I) \quad \text{Radiant Heat Exchange} = \sigma \varepsilon (T_{ss}^4 - T_a^4) \times 0.85A$$

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 (Gates 1980; Clark & Edholm 1985), T_{ss} and T_a are the temperature

of the skin and ambient environment respectively ($^{\circ}\text{K}$), and A is surface area (m^2). 0.85 is a correction factor to account for the radiant heat exchange between body surfaces in close contact (Gates 1980; Williams 1990).

$$(II) \quad \textit{Convective Heat Exchange} = h_c A(T_{ss} - T_a)$$

where h_c is a convective coefficient ($\text{W m}^{-2} \text{ }^{\circ}\text{C}$) based on the geometric shape and orientation (vertical and horizontal cylinder and vertical flat plate) of the animal surface (Gates 1980; Clark & Edholm 1985).

$$(III) \quad \textit{Conductive Heat Exchange} = kA(T_{ss} - T_{floor})/b$$

where k is the thermal conductivity of the tissue [0.19 for Asian elephant and 0.23 $\text{W m}^{-1} \text{ }^{\circ}\text{C}$ for African elephants (Dunkin 2012)] and b is the foot thickness across which heat is transferred (0.05 m) (Williams 1990).

Cutaneous Evaporative Water Loss (CEWL) & Evaporative Heat Exchange

Cutaneous evaporative water loss was measured using the ventilated capsule technique adapted from Webster and Bernstein (1987) and Smallwood and Thomas (1985). In this method an ambient air stream was first dried to approximately 25% ($25.0 \pm 0.04\%$) relative humidity by combining an ambient and dry airstream. The stream was then directed to a calibrated ball flow meter (Cole-Palmer EW-03229-17,

Vernon Hills, IL, USA, $\pm 2\%$ accuracy) and the rate of flow adjusted and recorded. The airstream was then passed over the skin of the animal *via* a small PVC capsule fitted with a neoprene gasket. The humidified air was directed from the capsule, through a second calibrated ball flow meter, and then to a water vapor pressure analyzer (RH-100 or RH-300, Sable Systems Inc, Las Vegas, NV, USA) which digitally recorded the data on a laptop computer. The water vapor analyzer was calibrated before each set of measurements according to manufacturer instructions by setting the zero using dry nitrogen gas and the span using a fully saturated airstream with a precisely measured temperature (Bat 5, Physitemp Instruments Inc., Clifton, NJ, USA). Low permeability tubing was used throughout to reduce exchange of water vapor and condensation within the system (Bev-a-Line, Thermoplastic Processes, Georgetown, DE, USA).

To perform 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 relative humidity of the outlet air stream reached an inflection point and began to level or decline (2-5 minutes) (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. Care was taken to avoid sites of previous measurement to ensure skin was free of petroleum jelly.

The ventilated capsule technique relies upon low velocity airflow (mean STDP flow rate \pm SD = 0.79 ± 0.28 L min⁻¹) across the skin, and thus, error resulting from

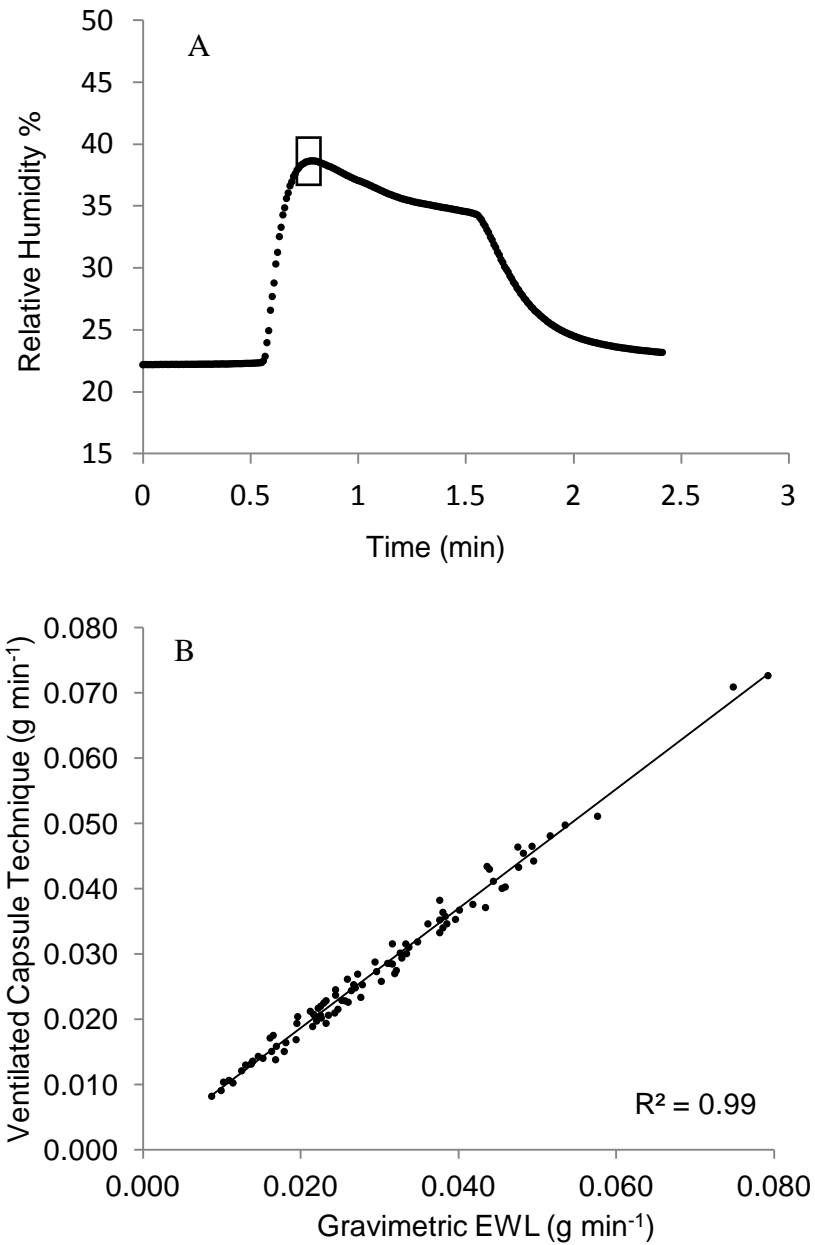


Figure 2: Sample raw data of CEWL stream from an African elephant (A) and the relationship between gravimetric and ventilated capsule measurement techniques across three temperatures and three flow rates (details in text) (B). Box in (A) indicates area where max CEWL value was calculated.

changes in the water vapor pressure directly above the skin and convective effects due to higher velocity air flow across the skin during the experiment are minimized (Smallwood & Thomas 1985). In addition, dehydration effects on the skin that may occur during the course of the measurement which can be problematic in closed capsule measurements, are minimized by taking the maximum rate of water loss initially achieved (Figure 2A) (Smallwood & Thomas 1985).

The amount of water lost through evaporation was then calculated using the following equation (Gates 1980; Webster & Bernstein 1987):

$$(IV) \quad CEWL = \frac{\dot{V} \left(\frac{P_{out} - P_{in}}{T_a \times R} \right)}{A}$$

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

CEWL is governed by properties of the integument as well as the relative saturation of the air above the integument. To understand how the integument and underlying changes in blood flow may alter the rate of CEWL in the absence of the driving climatic force for evaporation, we also computed the cuticular permeability ($\text{g min}^{-1} \text{m}^{-2} \text{kpa}^{-1}$) of the integument for each measurement. Cuticular permeability was

calculated by dividing the rate of cutaneous evaporative water loss by the water vapor pressure saturation deficit (WVPSD) (Kpa). The WVPSD was determined by first calculating the saturated water vapor pressure using the measured T_{ss} . The actual water vapor pressure of the air above the skin 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 determined by subtracting the actual water vapor pressure from the saturated water vapor pressure at skin temperature (Buck 1981).

Calibration of Evaporative Water Loss Device

The evaporative water loss device 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 $13.9 \pm 0.32^{\circ}\text{C}$, $22.8 \pm 0.58^{\circ}\text{C}$, and $27.6 \pm 0.24^{\circ}\text{C}$ respectively. These temperatures represented the lower, middle, and upper end of the ambient conditions under which actual evaporative water loss was measured in this study. Both air temperature and ambient humidity were measured independently for each trial and these temperature values were used in the calculations of error (Perception II, Davis Instruments, Hayward, CA, USA). At each temperature, ten trials were performed at low (mean $0.58 \pm 0.02 \text{ L min}^{-1}$), medium (mean $0.79 \pm 0.01 \text{ L min}^{-1}$) and high (mean $0.96 \pm 0.04 \text{ L min}^{-1}$) 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 precisely weighed to 0.0001g (Model 1712, Sartorius, Goettingen, Germany) and then immediately screwed to the cup of the EWL device. The flow was then directed through the cup and water was allowed to evaporate from the cotton ball for between 2 and 27 minutes. 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 (Las Vegas, NV, USA).

Calibration Results

The mean error and standard deviation for all calibration trials was $-6.7 \pm 5.2\%$ and ranged between -17.5 and 6.7% . 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 not a significant factor in explaining variation in the error rate ($p=0.08$) however, there was a strong positive correlation between ambient temperature and the rate of error ($p<0.0001$) such that higher temperature trials had a higher error rate than low temperature trials. The mean error and standard deviation for the low temperature trials was $-2.46 \pm 4.43\%$, $-7.97 \pm 4.3\%$ for the medium temperature trials, and $-9.76 \pm$

3.73% for the high temperature trials. To remove the systematic error associated with temperature, the raw data were corrected using the equation:

$$(IV) \quad CEWL = [CEWL_R * (-8.5539 + (0.5387 * T_a) + \frac{(4.8819 * F)}{100})] + CEWL_R$$

where CEWL is the temperature and flow corrected rate of evaporative water loss ($\text{g min}^{-1}\text{m}^{-2}$), $CEWL_R$ is the raw rate of evaporative water loss in the same units, T_a is the ambient temperature ($^{\circ}\text{C}$) at which the measurement was performed, and F is the flow rate (L min^{-1}). Flow was included to account for the maximum variation possible in the correction.

After correcting for the systematic temperature effect, the overall error rate of the system was $-0.547 \pm 4.39\%$ and there was no effect of temperature ($p=0.49$, $F=0.71$, $DF=2,88$) on the measurements. The level of error for this system is comparable to that of other systems for measuring evaporative water loss in a field situation (Webster & Bernstein 1987).

Heat Production & Respiratory Evaporative Water Loss

On a subset of animals (*L.a.* = 3 female, 1 male, *E.m.* = 3 female, total n for all trials = 20) resting heat production, measured as the rate of oxygen consumption, and respiratory evaporative water loss (REWL) were measured simultaneously using open flow respirometry. Resting is defined in this study as standing quietly but alert. In addition, to facilitate training and to best approximate a true “resting rate” elephants were not fasted before the measurements. Because elephants eat almost continuously throughout the day, a non-fasted animal better approximated a true

resting rate of heat production relative to a fasted elephant. Elephants were trained 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.* (1995) (Fig. 3) through which a vacuum pump (Flow Kit 500H, Sable Systems, Las Vegas, NV, USA) drew air at a rate of 440 L min⁻¹. A subsample stream of the expired air from the exhaust port was diverted and directed first through a dew point analyzer (RH-100 or RH-300, Sable Systems Inc, Las Vegas, NV, USA), and then scrubbed of water (Drierite) and CO₂ (Sodasorb). The airstream was then directed through an oxygen analyzer (model FC-1B, Sable Systems, Las Vegas, NV, USA). The relative humidity, ambient temperature, and the percentage oxygen in the expired air were continuously monitored and recorded (Expedata, Sable Systems, Las Vegas, NV, USA). The dew point analyzer was calibrated before each set of measurements as described above for the measurement of CEWL. The oxygen analyzer was calibrated before each measurement using dry ambient air (20.95%) and nitrogen gas as described in Fedak *et al.* (1981). Bev-A-Line tubing was used in the connection between the excurrent flow tube and the dew point 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 & Costa 2006). Oxygen consumption was calculated from the output of the oxygen analyzer using equations from Fedak *et al.* (1981) and a respiratory quotient of 0.83 for herbivores (Schmidt-Nielsen 1997).



Figure 3: Flow through respirometry “mask” that was used to measure resting metabolic heat production and respiratory evaporative water loss.

The rate of oxygen consumption was converted to heat production using a conversion factor of $20.1 \text{ KJ L}^{-1} \text{ O}_2$.

Analysis

Separate approaches were used to generate empirical relationships between T_{ss} or CEWL and ambient temperature. Residual maximum likelihood analysis (REML) was used to construct the regressions for log transformed CEWL using ambient temperature and species as main effects as well as the two-way interaction term. In all REML analyses, facility was included as a random effect to account for potential variation between the three facilities. Because we were interested in developing regressions that could later be used in development of a physiological model, we developed separate regressions for the body and ears and for before and after simulated wallowing as these relationships were hypothesized to have different responses to changes in ambient temperature. A subset of the T_{ss} dataset did not meet the linearity assumptions of the REML analysis and could not be transformed and thus, separate linear or non-linear regressions were constructed for each species for the entire T_{ss} dataset. Similar to the CEWL analysis, we constructed separate relationships for the body and ears and before and after simulated wallowing for T_{ss} for each species.

To determine the degree to which elephants are obligated to use evaporative cooling across the range of ambient temperatures we computed heat loss via both non-evaporative and evaporative routes across the range of temperatures. Non-

evaporative heat exchange was computed separately for the body and ears using equations I-III and the T_{ss} 's computed using the regression equations developed as described above. Non-evaporative heat loss was then summed for the whole body and for conduction, convection, and radiation to yield a total non-evaporative rate of heat loss across the measured range of ambient temperatures.

CEWL was computed across the range of ambient temperatures using the regressions constructed through the REML analyses. Respiratory evaporative water loss was measured only across a subset of temperatures. Thus, to validate our measurements and generate a likely relationship between REWL and ambient temperature, we calculated three theoretical rates of REWL corresponding to minimum, moderate, or maximum water saving strategies. The minimum rate of water savings strategy assumed that air left the trunk at the same temperature as core body temperature, the moderate water saving strategy assumed air left the trunk at a similar temperature to that of the skin, and the maximum water saving strategy assumed air left the trunk at ambient temperature. Other large animals including the giraffe have been found to save significant water through cooling of the air before it leaves the body (Langman, Maloiy, Schmidt-Nielsen *et al.* 1979; Schmidt-Nielsen, Schroter & Shkolnik 1981), although the absolute water savings varies across species. We chose the strategy that best fit our measured data and then summed the calculated rate of respiratory water loss with the rate of CEWL to yield a total rate of evaporative water loss across temperatures. The total water evaporated was converted into heat loss using the latent heat of vaporization of water (2257 KJ kg⁻¹).

The total rates of non-evaporative and evaporative heat loss for each species were then plotted against ambient temperature to determine the temperatures at which evaporative heat loss equaled and then exceeded non-evaporative heat loss.

To determine whether elephants have any capacity to control evaporative water loss we also calculated cuticular permeability. We were primarily interested in investigating whether cuticular 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 may be able to acclimate to some extent when temperatures and WVPSD are the highest. All two way interactions and the three way (WVPSD x season x body site) interaction were included in the analysis. Cuticular permeability was log transformed and facility again included as a random factor. We ran separate models for each species and only examined dry skin to avoid the potentially confounding effect of externally derived water on the skin.

All analyses were performed in JMP 9.0 (SAS, Cary, NC, USA). Data are presented as means \pm standard error unless otherwise indicated.

RESULTS

Skin Surface Temperature (T_{ss}) versus Ambient Temperature

T_{ss} increased with ambient temperature in both Asian and African elephants. However, there was a significant interaction effect between species and ambient temperature (all p values less than 0.018) in all four REML models (dry-body, dry-

ears, wet-body, wet-ears). In all cases, the T_{ss} of the Asian elephants rose more rapidly with rising ambient temperature relative to that of African elephants (Fig 4A-D). The two species differed in how the T_{ss} of the dry ears changed with increasing ambient temperature. The T_{ss} of the Asian elephant ears when dry, reached a plateau as T_a approached approximately 26°C (Fig. 4B). Wet skin heightened the effect between species such that the T_{ss} of both the wet body and ears of the Asian elephants rose more steeply relative to that of the African elephant (Fig. 4C,D).

Non-evaporative heat loss is dependent upon the differential between T_{ss} and T_a (Equations I-III). As the $T_{ss} - T_a$ differential approaches 0, heat loss via non-evaporative mechanisms becomes reduced until the animal begins to gain heat as T_a becomes greater than T_{ss} . The T_a 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 deal with metabolic heat production and environmental heat gain. We found that the T_a at which the differential approached 0 differed between body regions (body vs. ears) and species and that water on the skin surface altered this temperature (Fig. 5A-D). For African elephants, the $T_{ss} - T_a$ differential approached 0 at an ambient temperature of approximately 31°C for the dry body and at 29°C for the dry ears. In Asian elephants, the temperature differential of the dry body approached 0 at a similar temperature to that of the African elephants, however, the parabolic pattern observed in T_{ss} for the Asian elephant's ears resulted in the differential approaching 0 at two ambient temperatures, 15 and 32°C.

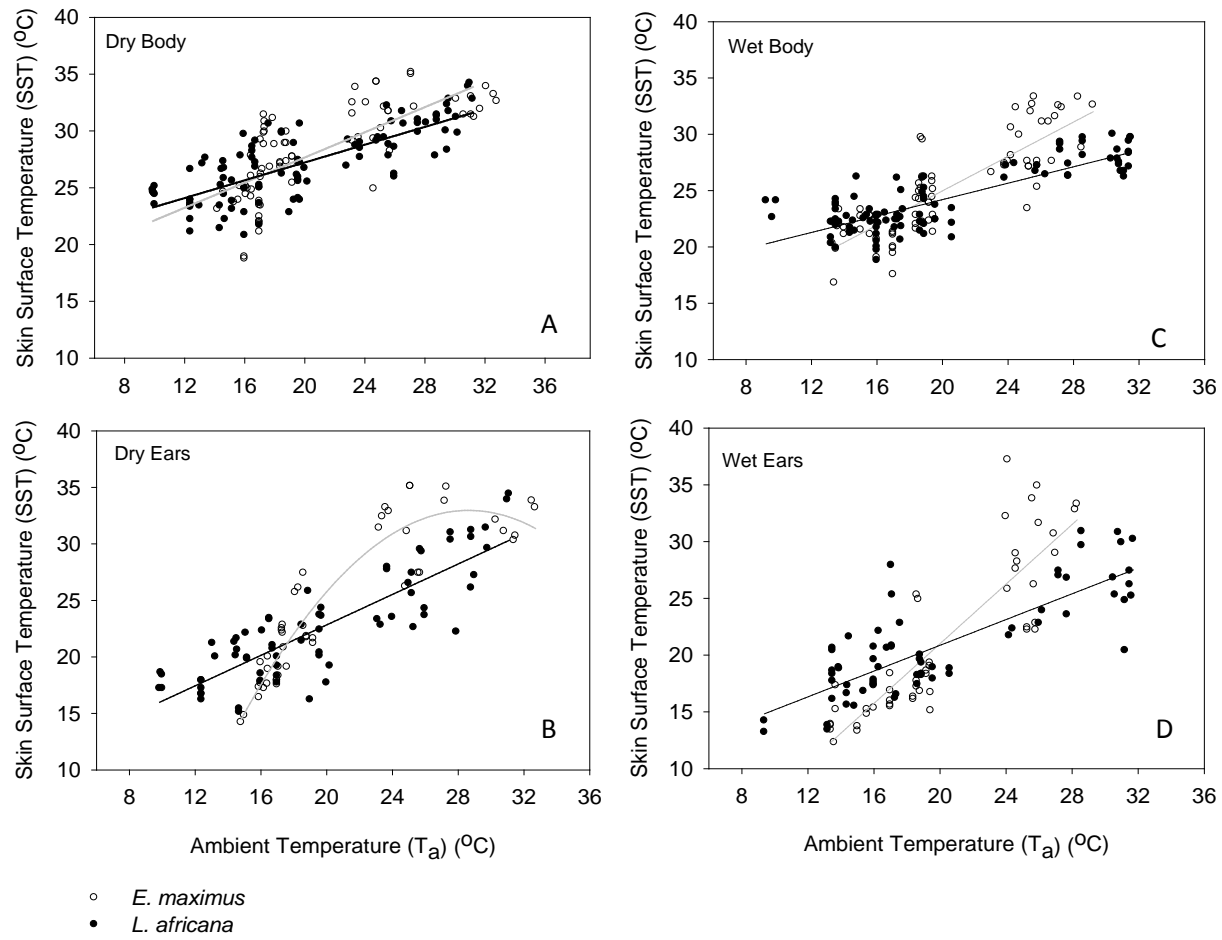


Figure 4: Skin surface temperature (T_{ss}) ($^{\circ}\text{C}$) in relation to ambient temperature T_a ($^{\circ}\text{C}$) of African (black symbols) and Asian (open symbols) elephant skin. Measurements were performed on three sites on the body or two sites on the ears when dry (A,B) or wet (C,D). The lines represent the best fit regression as reported in Table 2.

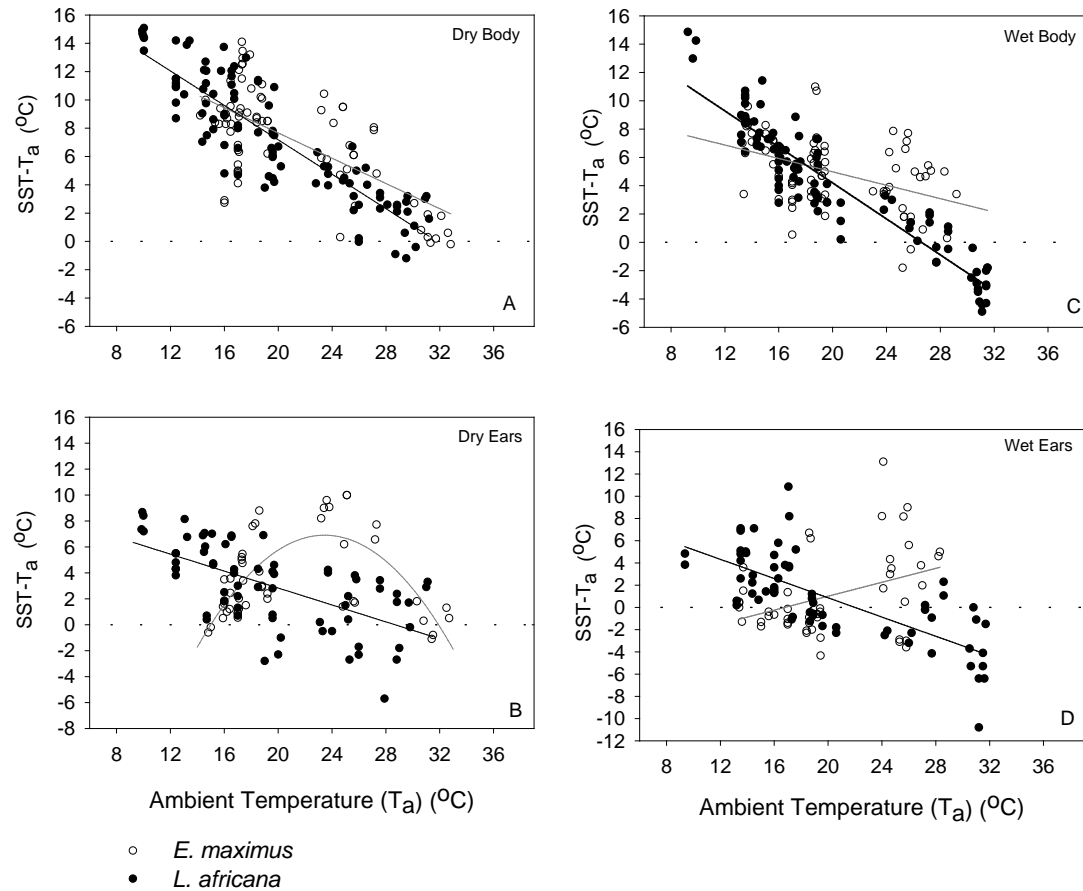


Figure 5: The difference between T_{ss} ($^{\circ}\text{C}$) and T_a ($^{\circ}\text{C}$) in relation to T_a ($^{\circ}\text{C}$) for African (black symbols) or Asian (open symbols) elephants. Measurements were performed on three sites on the body and two sites on the ears when dry (A,B) or wet (C,D). The dotted line represents the point when T_{ss} and T_a are equal and the heat exchange *via* non-evaporative routes falls to 0. Solid black and gray lines represent the best fit equation for the data (see text for details).

After bathing, divergent patterns emerged between the African and Asian elephant T_{ss} differential on the body and ears. The $T_{ss} - T_a$ differential of the wet body of African elephants approached 0 at an ambient temperature of 27°C, a decline from that of the dry body (Fig. 5C). In contrast, the wet body of the Asian elephant actually maintained a larger gradient across the range of measured ambient temperatures, increasing the temperature at which the differential approached 0 to above 33°C. As a result of an overall decrease in ear temperature, the $T_{ss} - T_a$ differential approached 0 near 22°C in African elephants with wet skin, a decrease from that measured for dry skin. The ears of Asian elephants however, responded differently to wetting relative to African elephants. Asian elephants actually increased T_{ss} at higher T_a and thus, the temperature differential was near 0 at approximately 17°C, similar to when the ears were dry, but increased with ambient temperature (Fig. 5D).

Cuticular Evaporative Water Loss (CEWL) & Cuticular Permeability

Cuticular evaporative water loss (CEWL) increased exponentially with increasing ambient temperature across both the body and ears and in wet and dry skin (Fig.6A-D, Table 2). CEWL ranged between 0.31 and 8.9 g min⁻¹m⁻² across the body and ears of dry Asian elephants. These values are slightly greater than those measured from African elephants which ranged between 0.26 and 6.5 g min⁻¹m⁻². REML models were run separately for each species to examine within-species effects of temperature on CEWL between body regions and wet and dry skin. In Asian

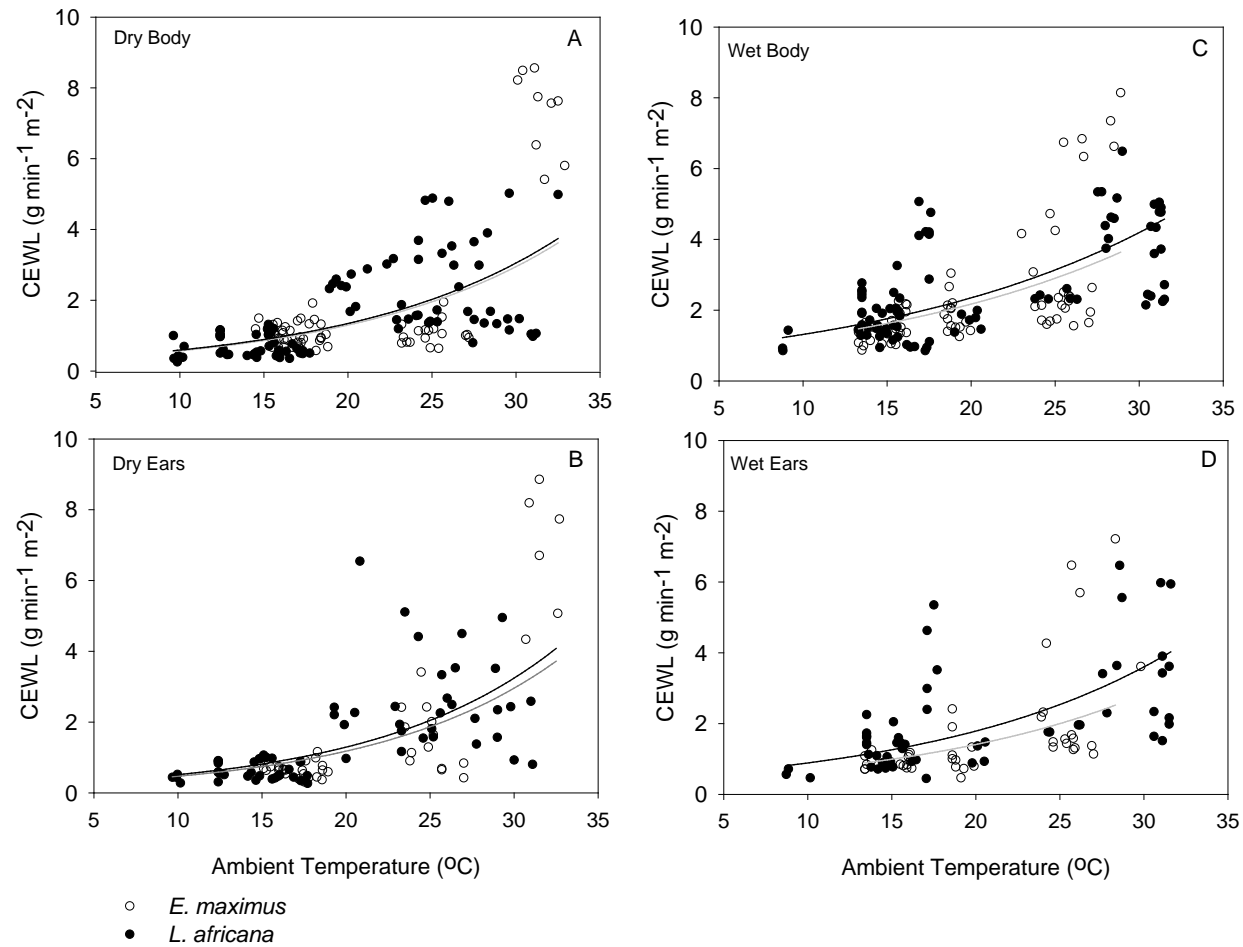


Figure 6: Cuticular evaporative water loss (CEWL) ($\text{g min}^{-1} \text{m}^{-2}$) in relation to T_a for African (black symbols) or Asian (open symbols) elephants. Measurements were performed on three sites on the body and two sites on the ears when dry (A, B) or wet (C, D). Solid black lines represent the best fit regression equation for the data (see text for details).

Table 2: Relationships between skin surface temperature (T_{ss}) or cutaneous evaporative water loss (CEWL) and ambient temperature (T_a) for Asian and African elephants.

Parameter	Body Region	Wet/Dry Skin	<i>E. maximus</i> Regression	<i>L. africana</i> Regression
T_{ss} (°C)	Body	Dry	$16.589 + 0.554T_a$ ($R^2=0.54$)	$19.349 + 0.391 T_a$ ($R^2=0.60$)
	Ears	Dry	$-7.122 + 1.644T_a - 0.097(T_a - 20.120)^2$ ($R^2=0.87$)	$9.356 + 0.674T_a$ ($R^2=0.73$)
	Body	Wet	$9.713 + 0.763T_a$ ($R^2=0.71$)	$16.908 + 0.364T_a$ ($R^2=0.67$)
	Ears	Wet	$-5.257 + 1.313T_a$ ($R^2=0.76$)	$9.514 + 0.567T_a$ ($R^2=0.66$)
CEWL ($gm^{-2}hr^{-1}$)	Body	Dry	$e^{(-1.362 + 0.082 * T_a - 0.017)*}$	$e^{(-1.362 + 0.082 * T_a + 0.017)}$
	Ears	Dry	$e^{(-1.630 + 0.092 * T_a - 0.046)}$	$e^{(-1.630 + 0.092 * T_a + 0.046)}$
	Body	Wet	$e^{(-0.346 + 0.058 * T_a - 0.039)}$	$e^{(-0.346 + 0.058 * T_a + 0.039)}$
	Ears	Wet	$e^{(-0.938 + 0.070 * T_a - 0.119)}$	$e^{(-0.938 + 0.070 * T_a + 0.119)}$

*For all CEWL equations, statistics are given in the results for the REML analyses.

elephants there was a significant interaction between body region (ears/body) and ambient temperature ($p = 0.011$). The rate of CEWL rose more steeply with ambient temperature from the ears relative to the body with the result that the rate of water loss from the ears was below that of the body at low temperature but rose more quickly with increasing ambient temperature and was thus, greater than that from the body at high temperature.

There were significant interactions between dry vs. wet skin and ambient temperature ($p=0.0002$) as well as dry vs. wet skin and body region ($p=0.027$) for African elephants. The rate of CEWL from wet skin was always greater than that from dry skin but the rate of loss from dry skin increased at a faster rate with increasing ambient temperature. Wetting the skin increased the rate of water loss from the body more than wetting the skin of the ears.

Cuticular permeability removes the influence of the climate-imposed potential for evaporation and thus, represents the influence of ambient temperature on the permeability of the skin itself. If the rate of CEWL was due only to the increased WVPSD associated with increasing ambient temperature, cuticular permeability should remain stable across ambient temperatures. We instead found a significant decrease in cuticular permeability with increased WVPSD however, a significant three way interaction between body site, season, and the WVPSD (Asian - $p=0.011$; African - $p = 0.007$) in both species indicated that the magnitude of the pattern was influenced by these factors in a non-uniform way (Fig.7A-D). In summer, the cuticular permeability of the ears is always greater than that of the body but the effect

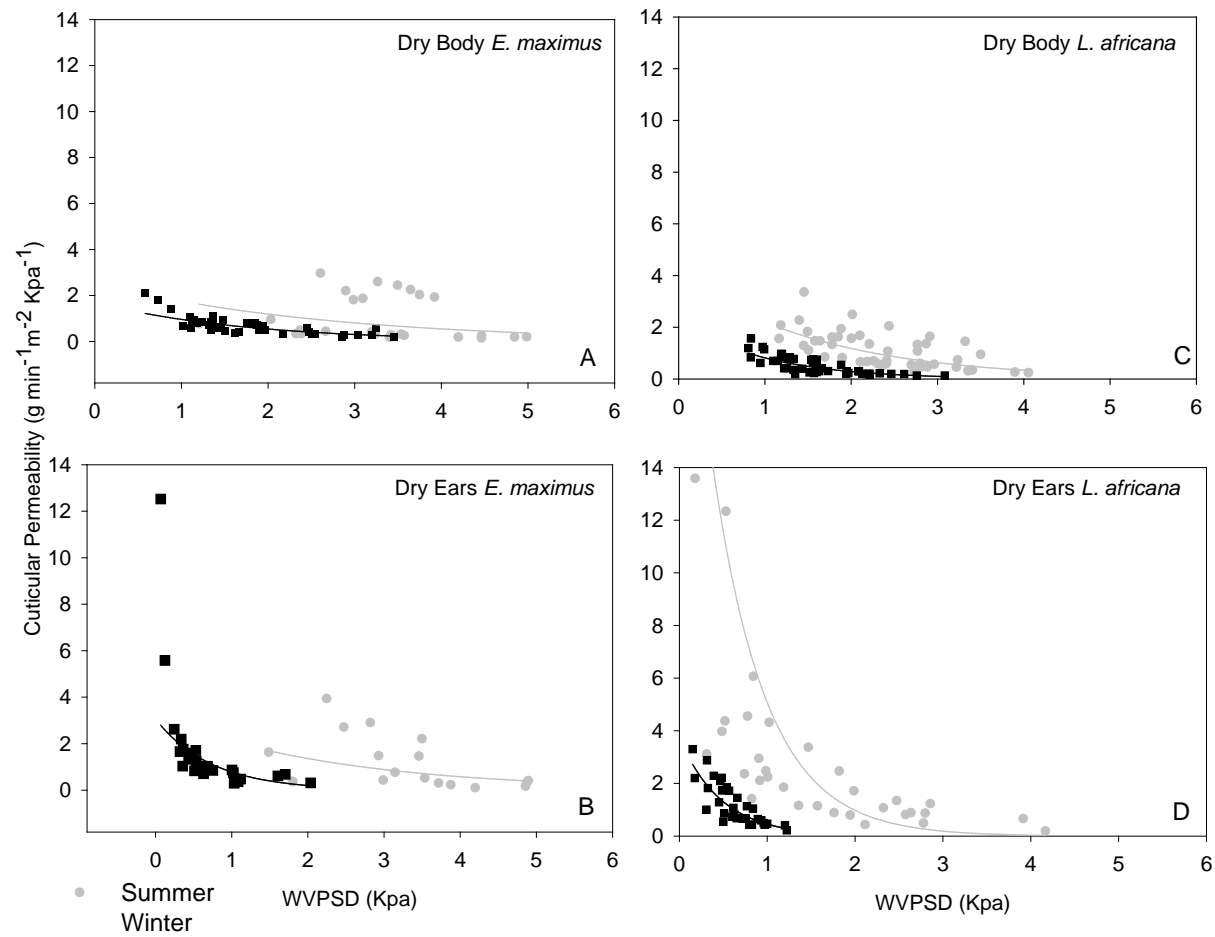


Figure 7: Cuticular permeability in relation to the WVPSD for the body (A,C) and ears (B,D) of Asian and African elephants. Gray symbols indicate summer values while black symbols indicate winter values. The regression lines were generated from a REML analysis which included season, body site, and WVPSD as factors. All values are for dry skin only.

is strongest at lower WVPSD's. The same trend is present in winter but the cuticular permeability of the ears and the body is lower in winter relative to summer. Thus, cuticular permeability does decline with increasing WVPSD and is greater in summer than in winter but these patterns vary in magnitude between body sites.

Metabolic Heat Production & Respiratory Evaporative Water Loss (REWL)

The mean resting metabolic heat production for Asian and African elephants was 0.50 ± 0.02 and 0.58 ± 0.001 W kg⁻¹ respectively (Fig. 8A, total n=20). Metabolic heat production scaled with body mass according to the equation metabolic rate = $16.45 \text{ mass}^{0.59}$ where metabolic rate is in watts and mass is in kilograms ($R^2 = 0.72$).

Of the three water saving strategies that were evaluated against the measured rates of REWL in this study, elephants appear to most closely follow the maximum water saving strategy, even under conditions of no water stress (Fig. 8B). The maximum water saving strategy corresponded to the amount of water that would be lost if the air exiting the trunk under normal breathing conditions approximated ambient air temperature. Under this strategy, a 3800kg elephant would lose 1.64 to 8.9L of water day⁻¹ at temperatures ranging between 10 and 33°C respectively.

DISCUSSION

In this study we investigated how climate influences the thermal and water budgets of African and Asian elephants and posed the question: how important is evaporative cooling to the thermal budget of an elephant? We investigated this

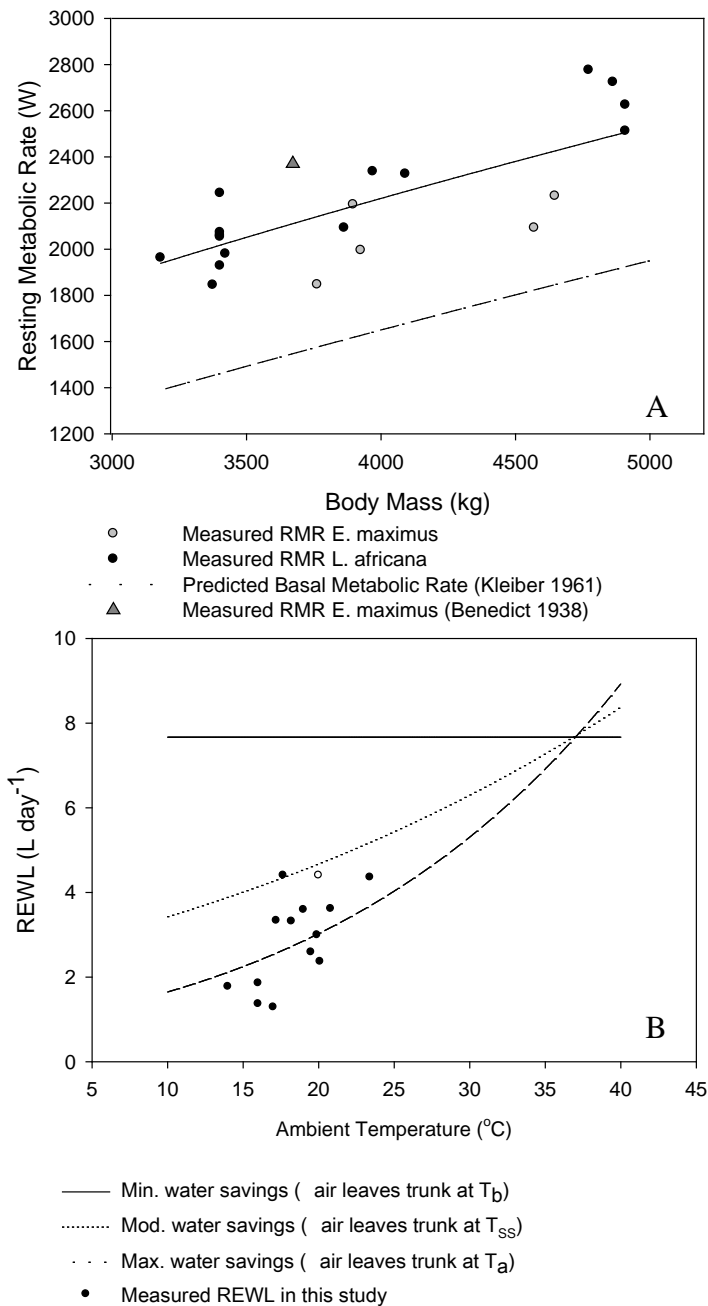


Figure 8: Resting metabolic rate (A) and respiratory evaporative water loss (B) measured for African and Asian elephant. Animals were not fasted prior to measurements to better predict resting heat production for animals in a field environment. Kleiber's 1961 prediction of basal metabolic rate in relation to body mass is shown for reference (dotted line). In B, predicted minimum, moderate, and maximum water saving strategies calculated with three potential air temperatures for air leaving the trunk are shown in relation to measured rates of REWL measured in this study.

question to determine how large body size together with climate may result in a potential constraint on landscape use by elephants by obligating them to use evaporative cooling.

Effects of Climate on Thermal Budgets and Evaporative Water Loss

To determine how the rates of non-evaporative and evaporative heat loss compare to the thermal burden an elephant must dissipate at rest, heat loss was calculated at 12, 30, and 40°C for an African elephant with the mean mass and surface area of the animals in this study (Fig. 9A) and then converted to the percent of the measured resting metabolic heat production. At 12°C, 81% of resting metabolic heat production was dissipated through non-evaporative routes assuming still air and minimal ear flapping. At 30°C, the heat dissipated through non-evaporative routes dropped to 8% and at 40°C, elephants, even standing in the shade, gained the equivalent of 46% of resting metabolic heat production through these routes. Conversely, the amount of heat dissipated through evaporation increased from 28% at 12°C to 1.1 and 2.5 times resting heat production at 30 and 40°C respectively. The corresponding amount of water lost to evaporation at these temperatures was 22 to 200Lday⁻¹ assuming a stable temperature for a 24 hour period (Fig. 9A).

Elephants as Obligate Evaporative Coolers

We have shown that evaporative cooling contributes significantly to balance the thermal budget of both elephant species across all measured temperatures, mainly

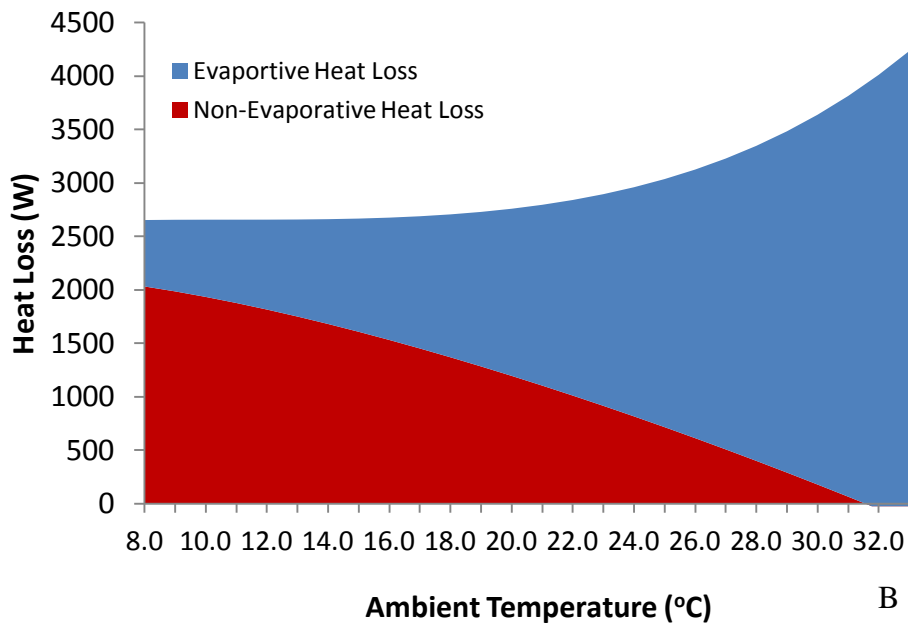
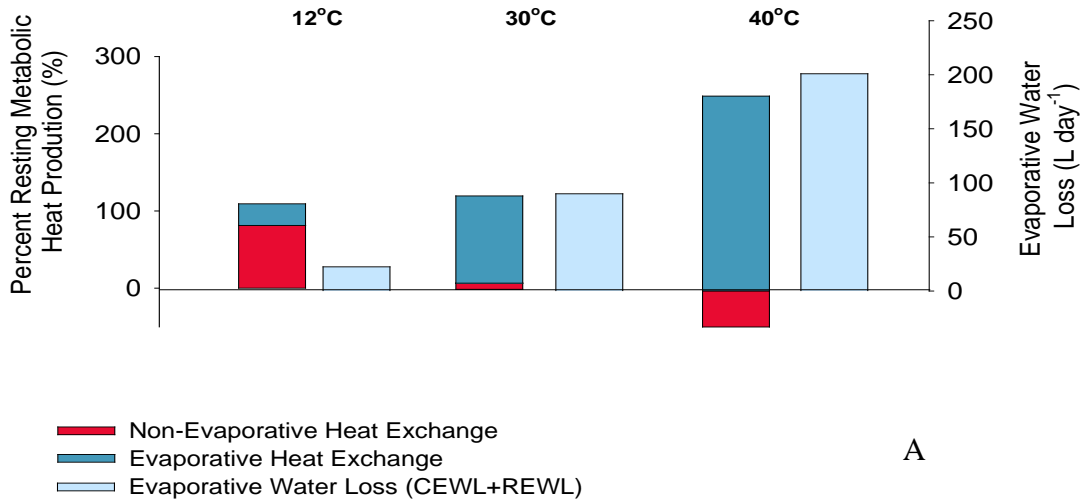


Figure 9: The estimated amount of heat dissipation that occurs through non-evaporative (red) and evaporative (blue) routes as a percent of resting metabolic heat production at three ambient temperatures (A). The corresponding amount of water in liters dissipated through evaporative routes (CEWL and REWL) at each temperature is shown by the light blue bars. The amount of heat dissipated through non-evaporative (red) and evaporative (blue) routes across the temperature range measured in this study (B). Note that the values for 40°C are extrapolated from the measured relationships between 8 and 33°C.

through insensible evaporative water loss across the skin; even under relatively mild ambient temperatures of 18-20°C, more than 50% of the heat generated through resting metabolism is dissipated through evaporative cooling. Interestingly, large body size is often discussed in terms of the opportunities it affords animals such as decreasing the quality of food the animal can consume (Burness, Diamond & Flannery 2001; Clauss, Frey, Kiefer *et al.* 2003a), increasing fasting endurance (Lindstedt & Boyce 1985), or reducing the risk of predation among many others (Schmidt-Nielsen 1984). Here we have demonstrated through empirical measurement that very large body size also imposes a thermoregulatory constraint by limiting an elephant's ability to range from water and that the severity of this constraint is mediated by climate.

Although the data in this study confirm that elephants lose a significant amount of water to cutaneous evaporative cooling, comparison of the rate of cutaneous water loss from elephants with a variety of other arid adapted species yields a surprising result. Table 3 shows the rates of CEWL from a wide variety of African herbivores which have been studied for their relative tolerance of heat and their ability to tolerate heat while dehydrated. These data show that there is a positive correlation between CEWL (per m⁻²) and body mass, a pattern that has been previously described (Crawford & Lasiewski 1968; Peters 1983). However, when the maximum reported rate of CEWL is plotted against the maximum reported body mass for each species (Fig. 10), a distinct breakpoint occurs at approximately 1000kg such

Table 3: Rates of cutaneous evaporative water loss from various arid dwelling herbivores across a range of body sizes.

Common Name	Body Mass (kg)	T _a (°C)	CEWL (g m ⁻² hr ⁻¹)*	Comments	Citation	Classification of water dependence (Western, 1975)
Dik-dik (<i>R. kirkii & guentheri</i>)	2-6	20-45	10-20	low density of sweat glands	Maloiy 1973	Water Independent
Thompson's gazelle (<i>G. thompsonii</i>)	14-15	20-50	50 [†]	sweat glands present	Taylor 1970	Water Dependant
Grant's gazelle (<i>G. granti</i>)	26-34	20-50	75 [†]	sweat glands present	Taylor 1970	Water Independent
Mule deer (<i>O. h. hemionus</i>)	28-78	10-30	0-80	minimal sweating	Parker and Robbins, 1983	NA
Impala (<i>A. melampus</i>)	55-75	22-50	10-65	sweat glands present	Maloiy and Hopcraft, 1971	NA
Oryx (<i>O. beisa</i>)	104-121	20-50	25-130	sweat glands present	Taylor 1970	Water Independent
Hartebeest (<i>A. buscelaphus</i>)	80-130	22-50	5--60	sweat glands present	Maloiy and Hopcraft, 1971	Water Dependant
Elk (<i>C. e. nelson</i>)	76-186	14-30	0-320	sweat glands present	Parker and Robbins, 1983	NA
Waterbuck (<i>K. d.ugandae</i>)	95-105	25-45	50-125	sweat glands present	Taylor <i>et al.</i> 1969	Water Dependant
Wildebeest (<i>C. taurinus</i>)	138-158	20-50	50 [†]	sweat glands present	Taylor 1970	Water Dependant
African buffalo (<i>S. caffer</i>)	202-229	20-50	40-250	sweat glands present	Taylor 1970	Water Dependant
Zebu steers (<i>B.indicus B.indicus</i>)	267-302	20-50	90-210	sweat glands present	Taylor 1970	Water Dependant
Zebra (<i>E. burchelli</i>)	275-420**	29.9	90-291	sweat glands present	Hiley, 1977	Water Dependant
Hippopotamus (<i>H. amphibious</i>)	1500	32-39	86.4-268.8	sweat glands present	Luck and Wright 1963	Water Dependant

Rhinoceros (white & black) (<i>C. bicornis</i> & <i>D. bicornis</i>)	1000-3000**	29.9	210-310	sweat glands present	Hiley, 1977	NA
Asian elephant (<i>E. maximus</i>)	3834 ± 498	8-33	18.6-534	insensible	Present study	Water Dependant
African elephant (<i>L.africana</i>)	3768 ± 642	8-33	15.6-390	insensible	Present study	Water Dependant
African elephant (<i>L.africana</i>)	3000-6000**	25.0	192-493 (means)	insensible, range is for different body sites	Wright and Luck, 1984	Water Dependant
Human (<i>H.sapien</i>)	70-90**	19-28	2.8-37.4 (means)	sweat glands present, across body sites	Reviewed in Pinnigoda <i>et al.</i> 1989	NA

*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 figure 3 for hydrated animals in Taylor 1970. If only one value is given then rates were nearly constant across range of T_a.

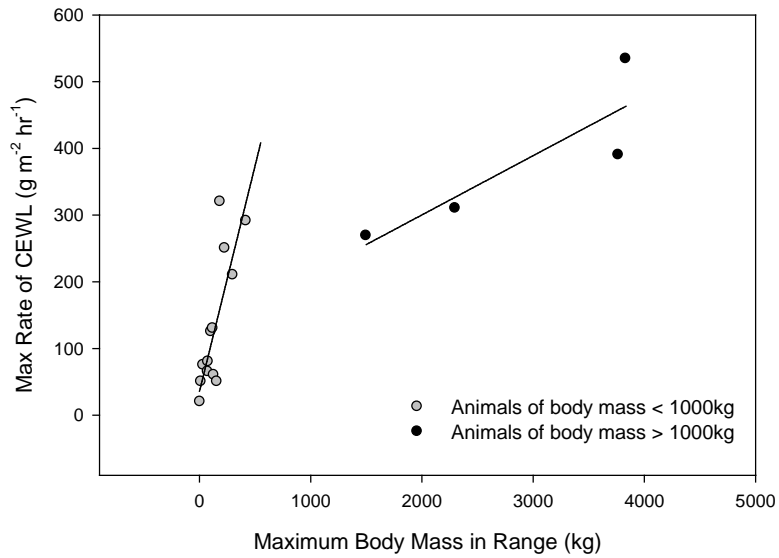


Figure 10: The maximum rate of CEWL reported in the literature for a variety of arid adapted species plotted against the maximum body size reported in each study. The slope of the line for animals of less than 1000kg is significantly different from that for animals of over 1000kg. References and values are given in Table 3.

that animals of less than 1000kg have a much steeper slope ($CEWL = 0.678 \cdot \text{mass} + 35.99$) compared to animals that are over 1000kg ($CEWL = 0.089 \cdot \text{mass} + 122.7$).

Why might very large animals, for whom CEWL is the most critical, have such a decreased per area rate of evaporative water loss compared to smaller bodied animals?

One explanation is that larger bodied animals have thicker skin (Calder 1996) and skin thickness could decrease the skin's permeability. However, the barrier to water loss lies in the outer most layer of the integument, the stratum corneum, and when well supplied with blood, the thickness of the stratum corneum does not necessarily decrease the permeability of the skin. Indeed, a thickened keratinized stratum corneum such as that found in the elephant, can actually increase the permeability of the skin (Vinson *et al.* 1965; Wright & Luck 1984). A second explanation involves the pattern of water content relative to skin thickness. Water content of the skin positively influences skin permeability (Blank 1952; Blank 1953; Blank *et al.* 1984) and Dunkin (2012) found that across four mammalian species varying in skin thickness from less than 0.005 to 0.03m, the water content of the integument increased then reached a plateau at approximately 65% water content. Thus, while large animals may have integument with an overall greater water content relative to smaller animals, the water content does not appear to increase any further in animals greater than about 1000kg likely due to a required minimum density of structural tissue to support a large body mass. This pattern could at least in part account for the overall higher rates of CEWL in large animals as well as the

decreased slope between CEWL and body size in animals over 1000kg relative to smaller bodied animals.

Regardless of the cause of the decreased mass specific rate of CEWL, elephants and other very large mammals maintain a high capacity for evaporative cooling. For each gram of water lost to evaporation at body temperature, approximately 580 calories of heat are lost to the environment. Using the maximum measured rate of CEWL for an African elephant in this study ($6.5 \text{ g min}^{-1} \text{ m}^{-2}$), in one hour at 33°C , an African elephant with a body surface area (ears excluded) of 21.47 m^2 could dissipate approximately 5,648W, or about 2.5 times resting heat production, without even employing convective cooling by ear flapping.

Control of CEWL and Mechanisms of Acclimation

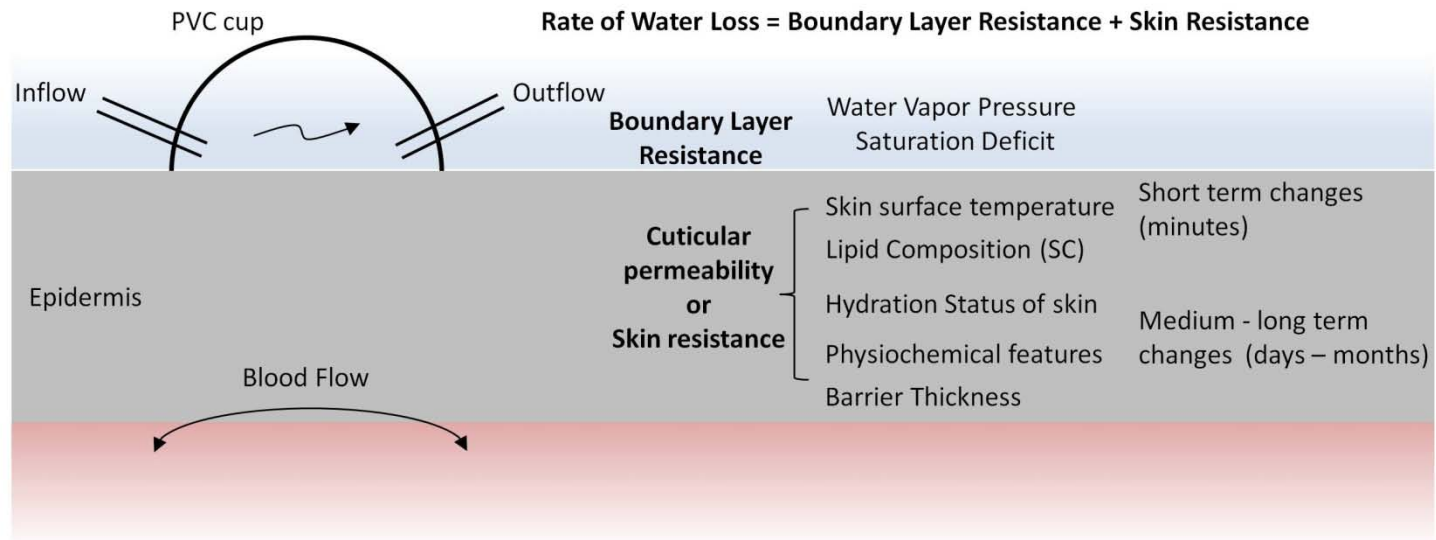
Remarkably, of the megaherbivores only the elephant and hippopotamus do not possess sweat glands (Table 3). Sweat glands circumvent the trade-off between the need to dissipate heat and the need to conserve water because they allow for relatively low rates of insensible water loss when non-evaporative heat dissipation is sufficient but permit increased evaporative cooling when the need arises. Despite lacking sweat glands, both elephants and hippopotamus have relatively high rates of CEWL. Hippopotamus secrete a modified sweat-type substance from subdermal glands which functionally acts as sweat to help the animal thermoregulate but which also provides sun protection and has antibacterial properties (Luck & Wright 1964; Saikawa, Hashimoto, Nakata *et al.* 2004). In contrast, elephants have attained rates of

CEWL that are similar to the other megaherbivores through alteration of their integument which has an increased permeability to water (Dunkin 2012). A critical difference though between elephants and animals which have sweat glands (or functionally similar glands such as the hippopotamus) is the lack of fine neuroendocrine control over the rate of evaporative water loss afforded by sweat glands. In animals with sweat glands, control of sweating is mediated through a variety of sympathetic pathways including through 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 determination of the onset and magnitude of the sweat response. For example, numerous studies have shown that many desert ungulates significantly reduce the rate of both cutaneous and respiratory evaporative water loss when they are dehydrated (Schmidt-Nielsen, Schmidt-Nielsen, Houpt *et al.* 1956a; Maloiy 1973) indicating neuroendocrine integration to balance heat and water loss. The question then remains, for an animal which lacks sweat glands such as the elephant, how much control do they have over the rate of evaporative water loss? This question is important for considering whether elephants have greater or lesser ability conserve water to buffer against extreme or unpredictable events such as drought relative to sweating animals.

Studies of the balance between heat and water loss in desert ungulates have often experimentally deprived animals of water and measured thermal and water budgets using similar methods as those employed in this study (Schmidt-Nielsen *et*

al. 1956a; Maloiy 1973). Such an experimental manipulation was beyond the scope of this work; however, we determined whether CEWL changes as the climate-imposed potential for evaporation (WVPSD) increases. If the rate of evaporative water loss is primarily the result of climate driven processes, indicating little physiological control over CEWL, then the cuticular permeability, which corrects for the effect of climate, should remain unchanged in relation to the WVPSD. We found that elephants are able to modulate water loss when the WVPSD is high (Fig. 7A-D). These data indicate that the rate of water loss from the skin does not increase as fast as would be predicted if climate were the primary driving force for CEWL in these animals. Interestingly though, the rate of water loss (and thus cuticular permeability) is greater in summer relative to winter. Such a pattern suggests that elephants may undergo seasonal acclimation allowing for greater rates of evaporative cooling when the thermal burden is greatest. Further evidence, although not conclusive, for acclimation stems from the higher rates of cuticular permeability in summer, but not winter seen in the Asian elephants at the southern California facility. These animals were exposed to summer temperatures that were on average 7.4°C greater compared to the other two facilities (Table1). Thus, when the WVPSD is high, the rate of water loss from the skin is not as great as would be predicted from the climatic potential for evaporation. Yet between seasons, the permeability of the skin increases in summer, particularly at WVPSD's less than 3Kpa (Fig. 7A-D).

Two main factors that will influence the loss of water from the skin, apart from climate, include the skin surface temperature and the permeability of the



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Figure11: Schematic illustrating the cup used to measured CEWL as well as the various factors that influence CEWL. These factors include the potential for evaporation due to the boundary layer resistance of the air layer above the skin (WVPSD) as well as the properties of the skin that influence water loss over short and longer time scales.

integument (Fig. 11). Skin surface temperature can be altered by regional changes in peripheral blood flow which can occur on short time scales on the order of seconds to minutes. The permeability of the integument will also increase with increasing skin surface temperature (Dunkin 2012) however, longer term changes can also occur in the composition and structure of the epidermis to increase or decrease permeability on the order of days to weeks (Haugen *et al.* 2003b; Lillywhite 2004; Lillywhite 2006) (Fig. 11). Alteration of skin surface temperature is likely the primary mechanism that causes a reduced cuticular permeability at higher WVPSD's within seasons. T_{ss} is positively correlated with the rate of water loss, and in elephants, T_{ss} rises linearly with ambient temperature (Fig. 4A-D) (though the T_{ss} of Asian elephant ear has a parabolic relationship with T_a). In contrast, the saturation water vapor pressure, and thus the WVPSD, rises exponentially (Buck 1981) in relation to temperature. Therefore, it is likely the lower than predicted rate of water loss at high WVPSD's is mediated by a diminishing ability to maintain an increasingly high T_{ss} as ambient temperature approaches body temperature. This study and others (Williams 1990; Weissenböck *et al.* 2010) have shown that elephants maintain their skin surface temperature well below ambient temperature until gradually approaching ambient temperature between 28 and 32°C but that they have fine control over peripheral blood flow (Fig. 5A, B). In some instances, we measured skin surface temperatures on the ears and body that were near 35°C which indicates that elephants may be able to flush their skin with blood that is approximately 1.5-2°C cooler than body temperature. The fine control over peripheral blood flow and skin surface

temperature is supported by observance of heterogeneous thermal windows on the ears and across the body observed in elephants by Weissenböck *et al.* (2010). The elephant's ability to finely control peripheral blood flow suggests a mechanism of control over evaporative heat and water loss similar to animals with sweat glands, however, in contrast with sweating animals, which activate sweat glands to increase evaporative cooling at high temperatures or during exercise, using skin surface temperature as a control for evaporative heat loss is only useful at ambient temperatures below body temperature.

The skin itself can also undergo compositional and structural changes that will alter the permeability of the integument. Studies in humans (Madison *et al.* 1987; Potts & Francoeur 1991; Lavrijsen *et al.* 1995; López *et al.* 2007) and birds (Haugen *et al.* 2003b; Munoz-Garcia & Williams 2005; Gu *et al.* 2008) have shown that changes in the composition of lipids in the stratum corneum, the primary barrier to water loss in these animals, are primarily responsible for changes in the rates of CEWL. These changes include alterations of the lipid composition of the lipid-corneocyte matrix located in the stratum corneum of the integument (Haugen *et al.* 2003b; Lillywhite 2004; Munoz-Garcia & Williams 2005; Lillywhite 2006). In particular, high amounts of ceramide lipids and lower amounts of free fatty acids seem to be associated with decreasing rates of CEWL in birds (Haugen *et al.* 2003a; Munoz-Garcia & Williams 2005). Elephant integument in general has a relatively high permeability to water compared to other mammals such as the pig (Dunkin 2012) suggesting they may have very low amounts of ceramide lipids in their stratum

corneum. Recent work by Meyer *et al.*, (2011) found low levels of glycolipids, the lipid class to which ceramides belong, in elephants relative to 20 other species of mammal. Preliminary work in our lab specifically on the concentration of ceramide lipids, is consistent with the observations of Meyer *et al.*, (2011) as the levels of ceramide lipids that we measured are exceptionally low or absent from the epidermis of elephant integument. Compositional changes in stratum corneum lipids may also be the underlying mechanism leading to higher rates of cuticular permeability in the summer relative to winter and further investigation of the capacity for acclimation in cuticular permeability and possible associated changes in stratum corneum composition is needed (Fig. 11).

The Role of Climate in Water Use

Clearly elephants rely on evaporative cooling across all temperatures measured in this study. However, how does this translate into water dependence in a landscape? To illustrate the disparate impact of climate on the use of water and thermal status of elephants in two different habitats we calculated theoretical thermal status and water lost to evaporative cooling (CEWL and REWL) for a representative African elephant (3800kg) over a 24-hour period (Fig. 12). We used hourly climate data (NOAA, NCDC) from October 2010 from Port Elizabeth, South Africa (-33.983 lat, 25.617 long) and Okaukuejo, Namibia (-19.150 lat, 15.912 long). Both of these regions maintain large African elephant populations that are located within reserves (Addo Elephant Park and Etosha National Park) and each area experiences vastly

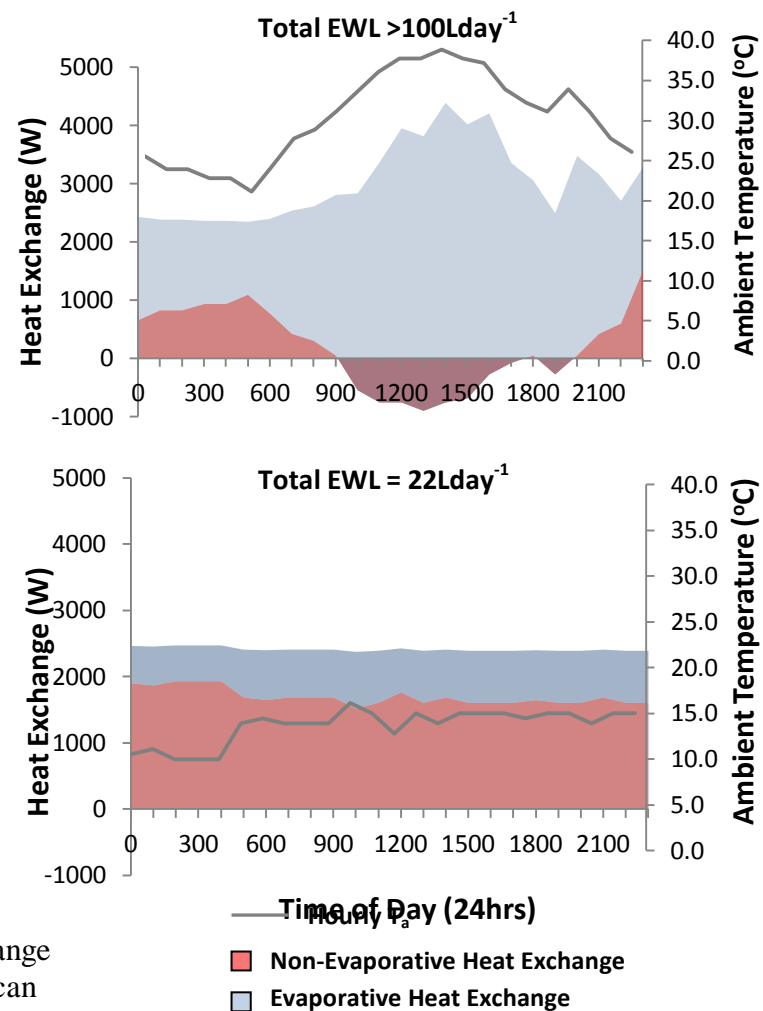
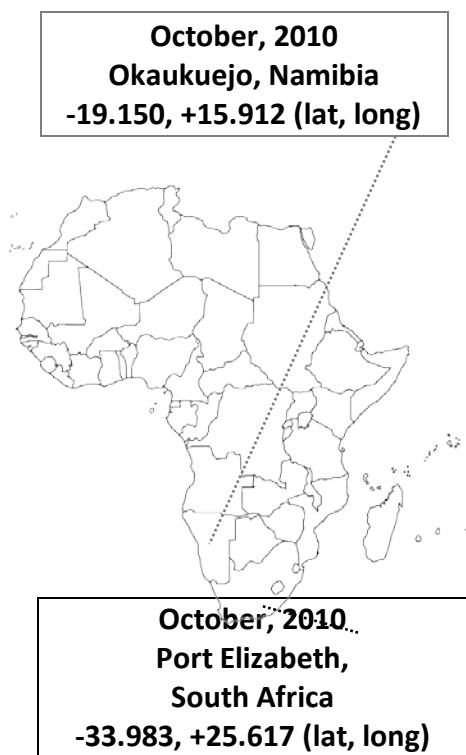


Figure 12: Hourly temperature data from weather stations near Etosha National Park, Namibia (top) and Addo Elephant Park, South Africa (bottom) were used to construct a model of heat exchange and total water lost to evaporative cooling for a representative African elephant in different climate regions. The red area indicates heat exchanged via conduction, convection, and radiation while blue indicates heat exchange via cutaneous and respiratory evaporative cooling.

different climate. We used the measured relationships between skin surface temperature and ambient temperature (Table 2, Fig. 4) to calculate non-evaporative heat loss at each hour over the 24-hour period. For simplicity, we assumed that the elephant was standing still and was not flapping its ears so forced convection was minimal. Cutaneous evaporative water loss was calculated at each hour based on the measured relationships in Table 2 and respiratory evaporative water loss was assumed to follow the maximum water saving strategy in which air is exhaled from the trunk at ambient temperature (Fig. 9). The sum of non-evaporative and evaporative heat loss was then plotted against time along with the corresponding ambient air temperature. The total water lost to evaporation was summed for the 24 hour period in each habitat as well.

The results demonstrate that climate is the single most important factor influencing the need for surface water in elephants. Elephants in the relatively mild climate of Port Elizabeth did rely upon evaporative cooling throughout the day yet these animals are predicted to incur an approximate water debt of only 22L over the 24 hour period. This is in marked contrast with elephants in Okaukuejo, Namibia who are predicted to incur a water debt of over 100L. It is also worth noting that the 24 hour 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 are common in this region. Previous reported values for water requirements for African elephants are between 150 and 200L day⁻¹ (reviewed in Sikes 1971; Fowler & Mikota 2006). Thus, in warm climates, well over

half to three quarters of the water debt per day is incurred through evaporative cooling. Although some of this water debt will be reclaimed through food intake and metabolic water production, the majority will require the animal to visit a water hole, thus limiting the distance the animal can travel from a water source much more severely in hot climates relative to cool climates.

Elephants along with a number of other African ungulates, have been classified as water dependant (Western 1975), a classification based on their mean ranging distance and population density from water during the dry season. Our results demonstrate that a species' relative water dependence is likely to be strongly habitat and climate specific. In addition to surface water, there are a number of factors that influence the home range size of elephants and other large herbivores including most importantly the quality and quantity of food abundance (Redfern *et al.* 2003; Redfern *et al.* 2005) as well as availability of particular nutrients (Rode, Chiyo, Chapman *et al.* 2006), and human presence (Loarie, Aarde & Pimm 2009) among others. 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.

In the past, physiological constraints and the interactions between physiology and the abiotic environment have been thought of as the course filter that most broadly limit an animal's distribution but are not as important as biotic factors such as competition, predation, or social interaction in understanding habitat selection or

animal distribution within landscapes (for example see discussion in Huey 1991). Recently though, the importance of abiotic factors and the interactions between abiotic and biotic factors have been more broadly recognized and incorporated into models of landscape level patterns (Porter, Munger, Stewart *et al.* 1994; Porter *et al.* 2002; Natori & Porter 2007; Kearney & Porter 2009). While many of these models have focused on smaller bodied endothermic or ectothermic species, we believe that a physiological based modeling approach to understanding landscape use in large herbivores may be important for predicting both seasonal and across habitat patterns of landscape use. Furthermore, because a physiological approach is based on understanding the mechanisms underlying resource use (food and water), the results are inherently more generalizable relative to pattern based approaches. Finally, the use of a physiological model of landscape use may be a useful tool for managers charged with determining whether surface water management may be a viable solution for reductions or redistributions of elephants within reserves.

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**CHAPTER 3: A PHYSIOLOGICAL BASED MODEL OF LANDSCAPE USE
FOR ELEPHANTS: INTERACTIONS BETWEEN THERMAL
CONSTRAINTS, WATER USE, AND ENERGY DEMAND**

ABSTRACT

1. Altering the abundance and distribution of surface water to reduce impacts by African elephants, a water dependent species, is a viable alternative to culling and translocation. The complexity of multiple interacting drivers of landscape use in elephants has inhibited the implementation of this strategy where there is debate about potential outcomes and success of such management plans.
2. The elephant's dependence on water is driven by an obligate use of evaporative cooling and daily water use depends on ambient temperature (T_a). Therefore, a mechanistic understanding of the physiological-climate relationships at the individual level may predict population level patterns of landscape use and be used to predict outcomes of water management schemes, climate change, or droughts.
3. We developed a climate-dependent biophysical model of thermal and water balance for African elephants using empirically measured relationships between T_a , skin surface temperature, and cutaneous and respiratory evaporative water loss. The biophysical model was linked to a stochastic dynamic state variable model to investigate the interactions between climate, thermal constraints, water use, and food availability. We simulated landscape use patterns under three climates and two relative productivity treatments. Model outputs included home range size, distance traveled from water,

activity patterns, equilibrium population size, and the spatial patterns of habitat impacts attributable to elephant foraging.

4. We found that a model of dynamic optimization of energy intake coupled with maintenance of thermal and water balance in an uncertain environment was sufficient to generate empirically observed patterns of landscape use in elephants. Model simulations also demonstrated that the primary driver of landscape use is climate dependent. Under cool and moderate climates, primary productivity was the most important determinate of home range size and distance from water; at temperatures above 24-27°C, T_a was limiting as elephants became more tightly tethered to water. T_a has a non-linear influence on landscape use because evaporative cooling increases exponentially with T_a .

5. In view of the complexity of multiple interacting drivers of elephant landscape use, a mechanistic approach permits evaluation of individual drivers in the absence of other confounding factors. This approach offers a predictive framework to evaluate the impacts of surface water management plans, climate change, or drought for specific populations.

INTRODUCTION

Elephants present a complex problem for managers who must balance conservation at the ecosystem level with protection of elephants, a keystone species listed as vulnerable by the IUCN (Blanc 2008). In reserves and other areas where African elephant (*Loxodonta africana*, Blumenbach, 1797) (Fig. 1) movement is restricted by fences or human settlements, high elephant densities can have significant impacts on ecosystems (Guldemon & Van Aarde 2008). These include decreased biodiversity and loss of woodland habitat among many others (Western & Maitumo 2004). Surface water management has emerged as a preferable management strategy to culling or translocation because it relies upon resource limitation, a more sustainable form of population regulation compared to density control (Owen-Smith 1996; Sinclair 2003; Owen-Smith *et al.* 2006; van Aarde & Jackson 2007). The abundance and distribution of surface water has been recognized as an important driver of elephant distribution and landscape use for decades (Western 1975). Yet surface water distribution alone is not sufficient to predict the specific outcomes or ultimate success of a surface water management plan for a particular population. Indeed, even in some of the most well studied reserves it remains unclear whether the population is water limited; multiple interacting factors including spatial and temporal variation in food quality and quantity among other factors have prevented robust prediction of the long term success of water management plans for specific populations (Redfern *et al.* 2003; Grainger, van Aarde & Whyte 2005; Owen-Smith *et al.* 2006; Smit *et al.* 2007b).

One significant source of variation in the observed patterns of landscape use by elephants is climate. Variation in climate influences landscape levels of productivity via temperature and rainfall patterns in turn affecting food quality, quantity, and distribution of elephants. Yet climate also has a direct impact on thermal balance and water use in elephants. Recently we investigated the physiological basis for the elephant's constraint around surface water and through empirical measurements demonstrated that elephants are obligated to use evaporative cooling to maintain thermal balance (Dunkin 2012). Importantly, we also demonstrated that an elephant's water debt is highly coupled to ambient temperature. Thus, climate, and specifically ambient temperature, through its impact on the thermal physiology of the elephant, will also directly impact water demand and therefore shape elephant use of landscape. Previous work has typically relied upon statistical descriptions of correlations between elephant densities and surface water during the dry season to determine whether surface water management would be an effective strategy for a given population. While this approach can be an important tool, it is limited in its ability to forecast the effects of future changes in water availability, primary productivity or temperature change because it does not incorporate the underlying mechanistic drivers of the observed patterns (Stokke & duToit 2002; Redfern *et al.* 2005; Chamaille-Jammes & Fritz 2007; Smit, Grant & Whyte 2007c; de Beer & van Aarde 2008).

Because the water dependence of elephants is coupled with temperature, a biophysical based approach may provide a useful tool to better understand the

underlying drivers of variation in landscape use as well as assist managers in implementation of surface water management, particularly in the context of long term changes in climate. In natural environments, it is challenging to separate the influence of climate driven differences in productivity, from the direct effects of climate on the thermal physiology of the animal, in driving elephant landscape use. It is also impractical to collect sufficiently detailed data or perform the long term experiments required to reliably predict the outcomes of proposed water management plans for every population. Climate change is also disproportionately impacting the African continent where mean ambient temperatures are rising faster than the worldwide rate and the effects of climate change are predicted to be more heterogeneous, with some areas become hotter and drier and others becoming cooler and wetter (Collier, Conway & VENABLES 2008).

In view of these challenges, the main objective of this study was to develop a mechanistic model that can rapidly predict the potential changes in landscape use and changes in elephant induced habitat impacts under various surface water management plans. Such a mechanistic understanding of the fundamental drivers of landscape use at the individual level will also facilitate prediction of likely population level responses to medium and long term changes in climate as well as short term responses to extreme events such as droughts.

To meet this objective we developed a stochastic dynamic state variable (SDSV) model (Clark & Mangel 2000) coupled with a physiologically based biophysical model. An SDSV model is an optimality based framework ideal for

relating physiological status or environmental factors with a metric of fitness. Such a framework permits investigation of how an animal might behave to maximize fitness under various scenarios of temperature and food distribution in relation to available water sources. The biophysical model was developed using empirical measurements of thermal and water demand in relation to ambient temperature and provided the physiological-climate dynamics for the SDSV model. We used this approach to look at four general aspects of landscape use for elephants including the spatial use of habitat in relation to surface water, temporal patterns of activity, relative sustainable population size, and the magnitude and spatial dynamics of elephant impact on vegetation in relation to water. We addressed the following questions: 1) How important is the direct influence of climate on thermal physiology in determining elephant use of landscape? 2) Is the influence of food quality and quantity on elephant landscape use different in cool and warm climates? 3) Are there interactions between climate and food quality/quantity that result in more or less severe impacts on landscape, particularly around waterholes? We do not seek to predict the water dependence of a particular population, rather, we aim to better understand the potential interactions between mechanistic drivers of landscape use, and take a first step at development of a predictive framework that may be applicable to management decisions in the future.

METHODS

Empirical Thermal and Water Measurements

Between 2005 and 2010 measurements of skin surface temperature and cutaneous and respiratory evaporative water loss were collected from seven African elephants (Fig. 1A) (mean body mass = 3768 ± 642 kg) across a 25°C range of ambient temperatures (T_a) (range of $T_a = 8.7\text{-}32.9^{\circ}\text{C}$) and across multiple body sites. Resting metabolic heat production was also measured using open flow respirometry and metabolic water production was estimated from these measurements. These data were then used to determine rates of non-evaporative and evaporative heat and water exchange, as well as construct climate-dependent models of thermal and water balance for African elephants. The methods of these measurements and the results are reported in detail elsewhere (Dunkin 2012).

Stochastic Dynamic State Variable Model

We begin by considering a simplified landscape with a single point source of surface water, from which elephants can travel out into an open savannah ecosystem to forage but to which they must return in order to drink (Fig. 2 A). The quality of vegetation, and thus availability of food resources, is allowed to vary as a function of the distance from the water hole (Fig. 2 B). We seek to model the expected decisions of an elephant over the course of a typical day, given the dynamics of five state variables: core body temperature (H), body water reserves (W), short term energy reserves (E), time of day (T) and distance to water (D) (see Table 1 for a list of all variables for the SDSV and biophysical model). The specific dynamic



Figure 1: Photograph of four African elephants (*Loxodonta africana*) drinking from a waterhole in a South African reserve.

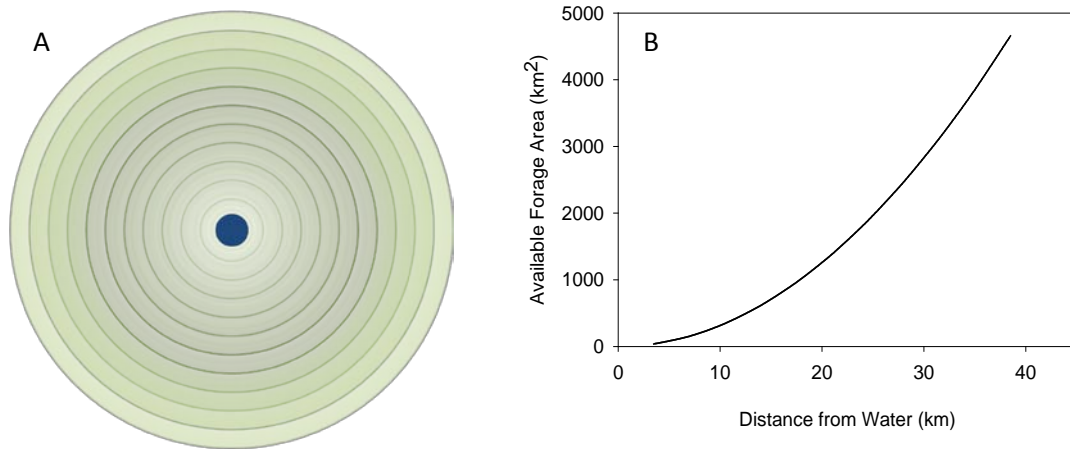


Figure 2: The modeled landscape with waterhole and corresponding available forage area as a function of distance to water. (A) Model elephants could range in a simplified landscape consisting of a single point source of surface water and a series of concentric rings which correspond to the area an elephant could traverse when walking at a moderately quick pace (~ 2 ms⁻¹). (B) The area available for elephants to forage increases exponentially moving out from the waterhole according to equations A-4 and A-5.

Table 1: Parameters, definitions, units, and value ranges for biophysical and SDSV model

Parameter	Definition	Units	Range of Values/Equation	Source
Morphological & Physiological Parameters				
A_{bod}	Surface area of body	m ²	16.5	Measured, mean of n=5
A_{ears}	Surface area of ears	m ²	2.4	Measured, mean of n=5
A_{legs}	Surface area of legs (sum of all four)	m ²	5.0	Measured, mean of n=5
k	Thermal conductivity of skin	Wm ⁻¹ °C ⁻¹	0.23	(Dunkin 2012)
L_{legs}	Length of leg (mean of all four)	m	1.3	Measured, mean of n=5
D_c	Characteristic dimension, diameter for cylinders, width for ear	m	1.5 (body), 0.28 (leg), 0.9 (ear)	Measured n=5
a	Absorbance of skin to radiation (subscripts = direct solar, skylight reflected sunlight, atmospheric, and ground radiation)*	-	0.5	(Gates 1980)
T_s	Skin surface temperature	°C	Equations in Table 3	Measured (Dunkin 2012)
T_b	Starting core body temperature	°C	36.2	(Kinahan <i>et al.</i> 2007a)
x	Ratio of the length of body cylinder to radius of body cylinder	-	3.36	Measured, mean of n=5
ε	Emissivity of skin	-	0.98	Gates (1980)
$MR_{rest, amble, travel}$	Metabolic rate	W	2163, 2375, 3800	Measured, (Langman <i>et al.</i> 1995) see Appendix II

MWP_{rest, amble, travel}

Metabolic water production

Lhr⁻¹

0.218, 0.238, 0.382

(Schmidt-Nielsen 1997; Ostrowski, Williams, Mésochina *et al.* 2006)

Physical/Microclimate Parameters

Cool T_a means = 8-16

T_a Ambient temperature °C Moderate T_a means = 16-24

T_{shade} Ambient temperature in shaded patch °C Warm T_a means = 24-32
On average 5°C cooler than T_a with lower T_{max}

T_{water} Temperature of water in waterhole °C 5°C lower than T_a

T_{ground} Temperature of ground °C Equal to T_a

σ Stephan-Boltzmann constant Wm⁻²K⁻⁴ 5.673 x 10⁻⁸ (Gates 1980)

τⁿ Atmospheric transmittance, sun, shade - 0.6, 0.1 (Gates 1980)

z Zenith angle degrees 0-90, varies with hour, location

S₀ Instantaneous sunlight radiation incident on point just outside of Earth's atmosphere Wm⁻² 1395 ($\frac{\bar{d}}{d}$)² where \bar{d} & d are mean and actual Earth-Sun distance for a given day (Gates 1980)

S Instantaneous sunlight radiation incident on ground attenuated by atmospheric transmittance Wm⁻² S₀* τⁿ (Gates 1980)

SDSV Parameters

H State variable, change in T_b (°C) 36.2 - 46.2 (lethal) see Appendix I for details

W State variable, body water reserves (Liters) 0-20% (lethal)

			loss of body water, see Appendix I for details
E	State variable, short term energy reserves	(kcal)	relative
D	State variable, distance from the water hole	(km)	38.5 (radius of total landscape)
T	State variable, Time	hours	Time step = 1 hr
α	Shape parameter for F(H)	-	3-8 (5) [‡]
β	Shape parameter for F(W)	-	0.4-0.9 (0.6) [‡]
b_i	Behavioral options (activities)		1-7, given in Table 2

*We assumed elephant skin was equally absorbent to long and shortwave radiation and based on absorption values reported in (Gates 1980) we used $a = 0.5$. This value is on the lower end of the range for absorption values and we selected this because of the tendency for elephants to cover themselves with mud which will likely reduce the absorption of radiation by the skin. Values given in ranges are the min and max value used in the sensitivity analysis and the value in parenthesis was the value used in the simulations.

properties of these state variables are discussed in detail in the next section (see *Biophysical Model Dynamics*), but in general they are affected by i) the basic physiological processes that affect body temperature, body water pools and metabolic costs; ii) external drivers such as ambient temperature and solar radiation (which are time-dependent); and iii) previous decisions the elephant has made. In particular, the outcome of feeding activity (in terms of net energy intake) is assumed to be stochastic, representing the effects of habitat heterogeneity and temporal variability in foraging success.

In the interest of model tractability, all state variables, including time and distance to the water hole, are simplified to discrete steps. At each hourly time step, elephants can choose from one of seven behavioral options (b_j) which include staying in the waterhole, traveling outbound from or inbound to the water hole, feeding, amble-feeding outbound or inbound to the water hole, or resting in shade (Table 2). Each of these activities differ with respect to one or more of the following: the rate of heat and water exchange, the rate of energy intake and/or energy utilization (metabolic rate), or the rate at which the elephant moves through the landscape. For example, when the animal is resting in shade, ambient temperature and exposure to solar radiation are reduced relative to the other activities, metabolic rate is at its lowest value (resting), but water intake is limited to that produced by metabolic water production. The general differences in the state dynamics for each activity are given in Table 2 and additional details are provided below and in Appendix II. Our designation of these 7 discrete behavioral categories was based on the most common

Table 2: Possible behavioral decisions in SDSV model with corresponding biophysical features.

Behavioral Decisions	Behavioral options (b_i)	General Features
WATERHOLE	1	Animal is partially submerged in water hole and able to replenish body water at rate of 100 Lhr^{-1} ; there is no feeding. Velocity of water and air past body is low (1 ms^{-1}). Metabolic heat production is equivalent to resting metabolic rate. Overall heat loss is relatively high.
TRAVEL (Inbound or Outbound)	Outbound (2) Inbound (6)	Animal is traveling without feeding. Highest rate of speed (1.94 ms^{-1}). Velocity of air past the body is highest (3 ms^{-1}). Metabolic heat production is highest. Overall heat loss is moderate.
FEED	3	Animal remains at similar distance from waterhole while feeding. Rate of food intake is highest. Velocity of air flowing past the body is low (1 ms^{-1}). Metabolic heat production is equivalent to resting metabolic rate. Overall heat loss is relatively low.
AMBLE FEED (Inbound or Outbound)	Outbound (4) Inbound (5)	Animal is traveling and feeding. Speed is half that of TRAVEL (0.94 ms^{-1}); Feeding intake rate is half that of FEED. Velocity of air past the body is moderate (2 ms^{-1}). Metabolic heat production is moderate. Overall heat loss is moderate.
REST IN SHADE	7	Animal remains at similar distance from water hole without feeding. Velocity of air flow past the body is moderate (2 ms^{-1}) Metabolic heat production is equivalent to resting metabolic rate. Direct solar radiation is reduced to 10% of full sun value. All temperature dependent heat exchange calculated with lower T_a . Overall heat loss is relatively high.

activities that wild African elephants engage in according to observed activity budgets in a variety of habitats (Wyatt & Eltringham 1974; Guy 1976; Shannon, Page, Mackey *et al.* 2008).

The underlying assumption of a stochastic dynamic programming model is that animals will tend to select the decision available to them that is associated with the highest long-term fitness, accounting for the probabilistic outcomes of their current and future decisions (Clark & Mangel 2000). In our model, the fitness at terminal time step T' was calculated as an increasing function of the elephant's thermal, water, and energy status:

$$(I) \quad F(H, W, E, T') = F(H) * F(W) * F(E)$$

where T' ranged from 24 to 36 hours in the future. Note that for the purpose of this model, we make the simplifying assumption that animals with chronically high body temperatures, low body water reserves, and low energy reserves will have lower long term fitness relative to those that do not (Newman, Parsons, Thornley *et al.* 1995). Accordingly, we developed generalized utility functions for relating thermal [F(H)], water [F(W)], and energy status [F(E)] to general “fitness” (Fig. 3A-C). Although there are no data describing the upper lethal temperature or the magnitude of body water loss that can be tolerated for African elephants, we assumed that extreme values of these state variables would result in mortality (and thus have associated fitness of 0), while lower temperatures and ample body water would have no negative

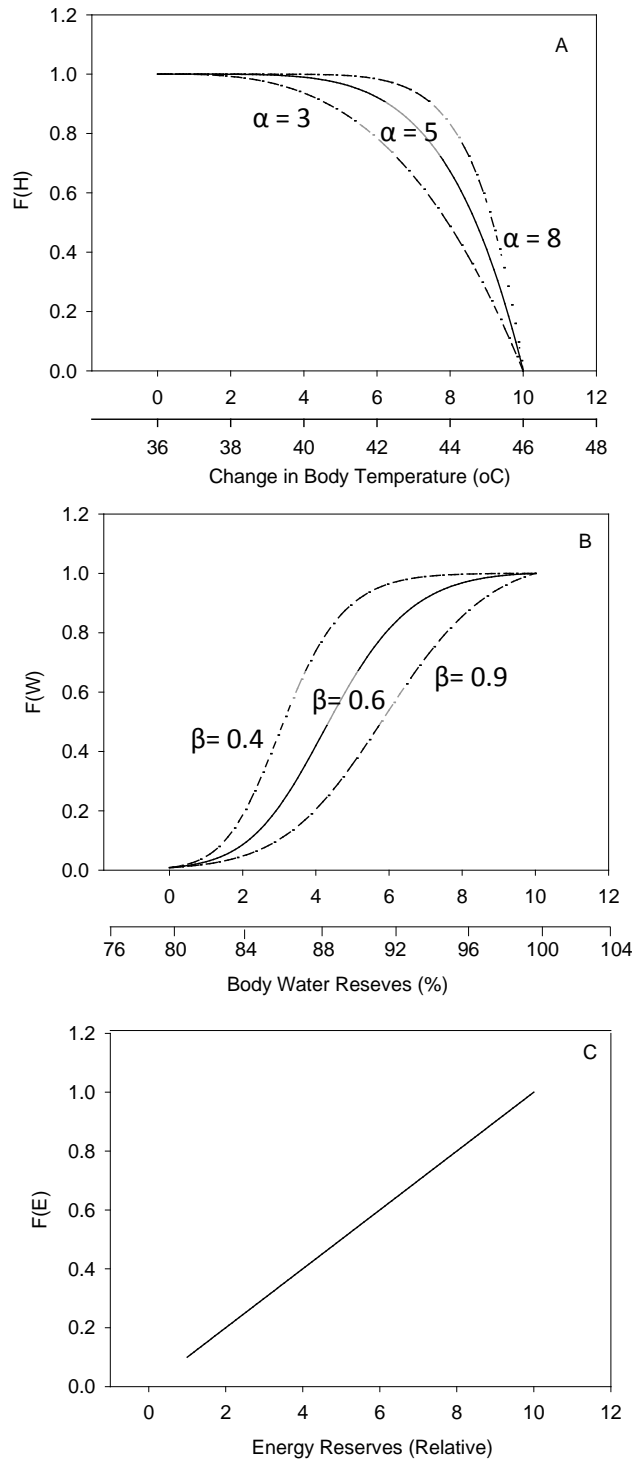


Figure 3: Utility functions relating “fitness” to body temperature (A), body water reserves (B), and energy reserves (C). For A and B, dashed lines represent the values tested in the sensitivity analysis and the solid line represents the value used in the simulations.

consequences (fitness of 1). We further assumed that there would be greater tolerance (over the short term) for variation in energy reserves than for variation in body water or core temperature, and thus $F(E) > 0$ for all values of E . Beyond these basic assumptions we recognized that any shapes of the utility functions were possible, and we evaluated a range of functional forms (Appendix I for details).

For time steps prior to T' , the following stochastic dynamic programming equation was solved to determine the maximum possible fitness given the current status of each of the state variables:

(II)

$$F(h, w, e, d, t) =$$

$$\max \left\{ \begin{array}{l} F_1 \left(h + f_1^h(t), w + f_1^w(t), e - f_1^e(t), d, (t + 1) \right) \\ F_2 \left(h + f_2^h(t), w + f_2^w(t), e - f_2^e(t), (d + 2), (t + 1) \right) \\ \sum_{i=1}^I \lambda_i \times F_3 \left(h + f_3^h(t), w + f_3^w(t, c_{i,d}), e - f_3^e(t) + c_{i,d}, d, (t + 1) \right) \\ \sum_{i=1}^I \lambda_i \times F_4 \left(h + f_4^h(t), w + f_4^w \left(t, \frac{c_{i,d}}{2} \right), e - f_4^e(t) + \frac{c_{i,d}}{2}, (d + 1), (t + 1) \right) \\ \sum_{i=1}^I \lambda_i \times F_5 \left(h + f_5^h(t), w + f_5^w \left(t, \frac{c_{i,d}}{2} \right), e - f_5^e(t) + \frac{c_{i,d}}{2}, (d - 1), (t + 1) \right) \\ F_6 \left(h + f_6^h(t), w + f_6^w(t), e - f_6^e(t), (d - 2), (t + 1) \right) \\ F_7 \left(h + f_7^h(t), w + f_7^w(t), e - f_7^e(t), d, (t + 1) \right) \end{array} \right.$$

where F_b = fitness at time $t + 1$ of an elephant that engages in behavior b at time t

and where f_b^h = behavior-specific function describing the expected change in core temperature (h) given the ambient temperatures and solar radiation experienced at t (these values are specific to the diel temperature cycle being considered; see below)

f_b^w = behavior-specific function describing the expected change in body water reserves (w) given the ambient temperatures and solar radiation experienced at t , and (if appropriate) the amount of food consumed

f_b^e = behavior-specific function describing the expected metabolic costs given the ambient temperatures and solar radiation experienced at t

$c_{i,d}$ = the i^{th} stochastic outcome with respect to energy intake rate for an animal feeding at distance d from the water hole. Each of the i outcomes is drawn from a random normal distribution with mean \bar{c}_d and standard deviation σ_c (Table A-2)

λ_i = the probability of obtaining stochastic foraging outcome $c_{i,d}$, given a random normal distribution with mean \bar{c}_d and standard deviation σ_c (Table A-2).

and where $1 < h < h_{\max}$, $1 < w < w_{\max}$, $1 < e < e_{\max}$, $0 < d < d_{\max}$, $1 < t < T'$. Equation II was iteratively solved, stepping backwards through time from $t = T'-1$ to $t = 1$. For all possible values of the state variables at each time step, the optimal decision, b^* , defined as that which maximized $F(h, w, e, d, t)$, was saved to a decision matrix.

Once the decision matrix was generated for a particular landscape configuration, population simulations were run (Clark & Mangel 2000) to model elephant behavior and spatially explicit landscape impacts (via foraging) under a specified climate and productivity treatment. Simulations were initiated with a population of elephants ($n=25$) having randomly-drawn values for each state variable. For each day of a 100-day season, animals were sequentially stepped through 24

hours in which they were assumed to behave optimally (that is, behave in accordance with the optimal decision matrix calculated by equation II), given the stochastic outcomes of feeding and the resulting variation in each animal's state variables. At the end of the season the fitness of each animal was tallied and survival status was assigned randomly (animals were assumed to survive with probability “ S ”, calculated based on fitness following Equation I), and the population size was adjusted to remove animals that had died. For those animals that survived, the status of their state variables was used as the starting point for the subsequent season. The population was assumed to grow by one animal each season (simulating immigration) so long as the population size was below an arbitrarily set maximum ($P_{\max} = 60$).

These simplified population dynamics were designed to facilitate the achievement of a dynamic equilibrium in population abundance for a given climate/productivity regime. The cumulative impact of elephant feeding over the season was calculated for each value of D (Appendix I), and the renewal rate of the vegetation (e.g. productivity) was applied uniformly across the landscape: the net result of these two opposing forces was a change in the landscape-level pattern of habitat quality, such that food availability (potential energy intake rate) was lower in areas that were more heavily utilized by elephants in the previous season. Equation II was then re-solved to generate a new decision matrix for this updated landscape configuration, and the whole process was repeated over n seasons to allow population size and landscape patterns of habitat impact to reach a dynamic equilibrium. Five of

these n -year simulations were run for each treatment scenario and the mean and standard error of these simulations are reported.

Three climate regimes and two productivity regimes were simulated. To incorporate short term stochasticity in weather, each climate regime was defined by a set of five possible diel temperature cycles, which were drawn from randomly during the population simulations described above. These diel temperature cycles corresponded to daily mean ambient temperatures (T_a) of 8.0, 10.0, 12.0, 14.0, and 16.0 for the cool treatment, 16.0, 18.0, 20.0, 22.0, and 24.0 °C for the moderate treatment, and 24.0, 26.0, 28.0, 30.0, and 32.0 °C for the warm treatment. In this work, we use the term climate to collectively refer to differential long term weather patterns across habitats but in the interest of examining individual drivers of landscape use, we varied only ambient temperature between treatments. Diel variation in solar radiation was also incorporated into the biophysical model (Appendix II) but was held constant across treatments. At the beginning of each season the optimal decision matrix was solved separately (using Equation II) for each of the five possible mean T_a , such that elephants would behave appropriately given the temperature range experienced on any given day. The productivity regimes consisted of a high and low scenario which do not correspond to actual vegetation renewal rates but rather represent arbitrary, relative rates of vegetation renewal. Potential interactions between climate and food availability were investigated by running the following treatments: cool-high productivity, cool-low productivity,

moderate-high productivity, moderate-low productivity, warm-high productivity, and warm-low productivity.

Biophysical Model Dynamics

The biophysical model was developed to characterize the rates of heat and water exchange for each behavioral option for a 3770kg model elephant (based on the mean mass of elephants used in the empirical measurements). For non-evaporative heat exchange including absorbed environmental radiation (H_{AR}), convection (H_{Conv}), and radiation (H_{Rad}), we used the equations derived in Gates (1980). Conduction (H_{Cond}), which occurs between the elephant's feet and the ground, contributes less than 2% to the total thermal budget for an elephant (Williams 1990; Dunkin 2012) and, thus, was omitted from the thermal balance dynamics. We modeled the elephant as a series of geometric shapes (horizontal and vertical cylinders for the body and legs respectively and vertical flat plates for the ears) for which equations for heat exchange via the above routes have been developed (details are given in Appendix II) (Gates 1980; Williams 1990; Phillips & Heath 1992). These non-evaporative forms of heat exchange are largely based on the differential between skin surface temperature (T_s) and ambient temperature (T_a) which were empirically measured across a range of T_a as described above. The main factor that differed between activities for non-evaporative heat exchange was ambient temperature. For example, resting in shade was calculated with a predicted shade temperature that was an average of 5°C cooler and reached a lower T_{max} relative to T_a . The speed of air flow

across the body surface also differed between activities. For example, while traveling, elephants moved at 2 ms^{-1} through the landscape and it was assumed there would be a light wind. Thus, convective heat flow was calculated with a wind speed across the body of 3 ms^{-1} . Details of the calculations and assumptions for each behavioral option for non-evaporative heat exchange are described in Appendix II and Tables A-3 and 4.

Empirically derived equations from Dunkin (2012) were used to calculate evaporative heat and water exchange via both cutaneous and respiratory routes at each T_a (Table 3). Measured values for resting metabolic heat production were used for animals that were in the waterhole, feeding, or resting in shade. Amble-feeding and travel had correspondingly higher rates of metabolic heat production (Table 2, Appendix II). Metabolic water production was estimated by assuming 0.028mL of oxidative water was produced per KJ^{-1} ($0.117\text{mL O}_2 \text{ kcal}^{-1}$) of digested energy (Schmidt-Nielsen 1997; Ostrowski *et al.* 2006). We then assumed the rate of digested energy was equal to the metabolic rate of the animal for each behavioral state and used this to estimate an hourly rate of metabolic water production for each behavioral option (Table 3).

Water intake via food and drink and water loss via urine and feces were estimated based on a review of the literature (Appendix II). Water intake via food was coupled with the rate of energy intake by first estimating the caloric intake per kg wet weight⁻¹ of forage consumed by wild elephants of similar size. Second, the average moisture content of forage (average of 1:1 mixture of grass and browse) over

Table 3: Relationships between skin surface temperature (SST) or cutaneous or respiratory evaporative water loss (CEWL) and ambient temperature (T_a) for African elephants (from Dunkin 2012).

Parameter	Body Region	<i>L. africana</i> Regression
SST ($^{\circ}\text{C}$)	Body	$19.349 + 0.391 T_a$
	Ears	$9.356 + 0.674 T_a$
CEWL ($\text{gm}^{-2}\text{hr}^{-1}$)	Body	$e^{(-1.362 + 0.082 * T_a + 0.017)}$
	Ears	$e^{(-1.630 + 0.092 * T_a + 0.046)}$
REWL ($\text{gm}^{-2}\text{hr}^{-1}$)		$0.0039T_a^2 - 0.029T_a + 1.106.$

a season was estimated and used to determine an average preformed water intake of $5.9 * 10^{-4}$ L H₂O kcal⁻¹ (Appendix II, Tables A-1,2). Reports concerning the amount of water elephants consume in a single drinking bout ranged between 50 to greater than 100L (Sikes 1971; Fowler & Mikota 2006). We considered one drinking bout to last one time step (1 hour), which is a time frame consistent with wild observations of elephants drinking (Sikes 1971). We set the maximum intake rate as 100L hr⁻¹ with no restriction on how many continuous hours elephants could chose to spend in the waterhole nor how many times they could return to the waterhole each day.

Elephants defecate discrete boluses of fairly wet fecal matter. The reported mass of a single bolus ranges between 1-2kg (Sikes 1971; Fowler & Mikota 2006). Defecation rates range between 0.28 and 0.72 times hr⁻¹ (Coe 1972; Wyatt & Eltringham 1974; Ruggiero 1992) with a mean of 10.36 kg per evacuation (Coe 1972). The percent moisture content of elephant fecal matter is estimated at 70-80% (Petrides & Swank 1965 in Coe 1972). Thus, we used a continuous rate of 3.9 Lhr⁻¹ to account for fecal water loss. There are no studies that we are aware of that have measured the capacity of elephants to conserve water by producing drier fecal matter. Thus, we have used a constant value in the model (Appendix II).

Elephants are reported to produce between 25 and 53 L urine day⁻¹ (reviewed in Fowler & Mikota 2006). We assumed that urine is 100% water and used a constant rate of urinary water loss of 1.63 L hr⁻¹. There are no published data to our knowledge of the concentrating ability of elephant kidneys under conditions of water stress, thus, we use a constant value (Appendix II).

Model Outputs & Sensitivity Analysis

We evaluated five specific metrics of landscape use including 1) home range size, 2) maximum ranging distance from water, 3) 24-hr activity budgets, 4) relative population size, and 5) elephant impact on vegetation in relation to point sources of surface water. We also assessed the mean status of the elephant's energy reserves, body temperature, and body water reserves at the end of the simulation to gauge the relative physiological condition of animals under each treatment.

Home range size was defined as the area within which elephants spent 90% of their time. We calculated the home range by determining the best fit regression for area versus the amount of total time spent within each concentric ring (Fig. 2) plus all smaller rings. We solved the resulting equation to determine the area in which elephants spent 90% of their time. The maximum ranging distance from water was defined as the straight line distance from the water hole within which elephants spent 90% of their time and was calculated in the same manner as home range. All regressions used for these calculations had R^2 values greater than 0.95. Analysis of 24-hr activity budgets included both the percentage of the day elephants engaged in each of the behavioral options as well as the temporal use of landscape such as when elephants were most likely to visit the waterhole or feed. Relative population size was defined as the mean number of elephants in the population once the simulation reached equilibrium (resulting from the simplified population dynamics described above) and was scaled such that the treatment with the largest population was set equal to 1. Elephants impact the habitat primarily through eating, debarking, and

trampling vegetation. We constructed an index of elephant impact based on energy intake rates and assumed that this would be a good proxy for total elephant impact. The index was calculated as $\text{elephant impact} = (1/\text{intake rate}) * (1/\text{intake}_{\text{max}})$ where the $\text{intake}_{\text{max}} = 9000 \text{ kcals hr}^{-1}$ (Appendix I). Finally, the physiological condition of the elephants at the end of the final season in each simulation was evaluated by calculating the mean energy, thermal, and water status of the individual's remaining in the population.

To test the sensitivity of the model to a number of key parameters we varied the parameter and evaluated its effect on both home range size and population size at equilibrium using a partial coefficient of determination approach.

Model Validation

To validate the model and ensure that we had successfully captured the main determinants of landscape use for elephants, we evaluated several non-trivial predictions of the model with respect to quantitative and qualitative patterns of behavior and landscape use, to determine their consistency with empirical data sets (Loza, Grant, Stuth *et al.* 1992). The quantitative metrics that we used were 1) the magnitude of predicted home range sizes 2) the magnitude of the distance from water elephants were predicted to travel and 3) the percent of the day devoted to feeding and resting. We also considered how well the model predicted the documented tendency for elephants to rest in the middle of the day when temperatures are at their peak. Observed data for these metrics are given in Tables 4 and 5.

Table 4: Reported home range sizes for African elephants

Source	Study Location	Climate Type*	Home Range Size (mean, range) (km ²)
(Douglas-Hamilton 1973)	Lake Manyara, Tanzania	Semi-arid to mesic	14-52
(Leuthold 1977)	Tsavo-West & Tsavo East, Kenya	Arid, semi-arid	746, 1620 (West, East respectively)
(Merz 1986)	Gola Forest Reserve, Siera Leone	Tropical	210-290
(Dunham 1986)	Zambezi Valley, Zimbabwe	Mesic	94-263
(Viljoen 1989)	Etosha NP, Namibia	Semi-desert to desert	2172.3 (1763-2944)
(Thouless 1996)	Laikipia-Samburu, Kenya	Cool-dry to hot dry	102-5527
(Grainger <i>et al.</i> 2005)	Kruger NP, South Africa	Mesic, varied	988 (72-4451)
(Ntumi, van Aarde, Fairall <i>et al.</i> 2005)	Maputo Elephant Reserve, Mozambique	Tropical	311
(Galanti, Preatoni, Martinoli <i>et al.</i> 2006)	Tarangire NP, Tanzania	Semi-arid	1759 (451-5994)(wet season) 2032 (224-5627)(dry season)
(Shannon, Page, Slotow <i>et al.</i> 2006)	Pongola Game Reserve, South Africa	Hot, arid	17.5-40.0 (summer) 36.7-71.5 (winter)
(Leggett 2010)	Etosha NP, Namibia	Semi-desert to desert	5834.9 (210-14,310)
(Young, Ferreira & Aarde 2009)	Several (Etosha NP to Luangwa NP)	Range from dry/arid to wet savannah	~1700 (dry savannah, wet season) ~500 (wet savannah, wet season) ~700 (dry savannah, dry season) ~250 (wet savannah, dry season)

* When possible the climate type is reported from the cited paper, otherwise, alternative resources were used to give a general classification.

Table 5: Results of observed activity budgets from a variety of elephant populations in disparate climates and habitats.

Source	Study Location	% Time Feeding	% Time Resting	Drinking bouts (% 24 hrs ⁻¹)	Qualitative Comments & Notes
(Wyatt & Eltringham 1974)	Uganda	74.2	~10-20%	~1 (range:0-3)	<i>24-hr observations are reported.</i> 3 feeding peaks – near midnight, early morning, afternoon. Resting peaks between 3am-7am and at midday (11am-2pm) which author attributes to avoiding the hottest part of the day. Increased rates of walking at dusk up to midnight.
(Guy 1975)	Zimbabwe (Rhodesia at publication)	%50-58	NA	NA	NA
(Guy 1976)	Zimbabwe (Rhodesia at publication)	46.9 (cold season) 36.1 (hot season) 56.5 (wet season)	31.4 (cold season) 42.0 (hot season) 21.8 (wet season)	3.0 (cold season) 2.9 (hot season) 5.1 (wet season)	<i>Rates are calculated for daytime hours only.</i> Author notes that there is a strong pattern of resting between 11am and 2pm and this pattern is stronger in the hot season.
(Kalemera 1987)	Tanzania	NA	NA	NA	<i>Rates are calculated for daytime hours only.</i> Increased resting in the middle of the day. Increased feeding in morning and evening.
(Ruggiero 1992)	Central African Republic	70.8	NA	NA	NA
(Shannon <i>et al.</i> 2008)	3 reserves in South Africa	40-70	NA	3 (for 24 hours)	<i>Rates are calculated for daytime periods only.</i> Resting increased at mid-day then tapered off in the evening and this pattern was stronger in summer than winter.
(Loarie <i>et al.</i> 2009)	Many across Southern Africa	NA	NA	NA	<i>Radio and satellite tracking records.</i> Observed peak travel periods at dusk and dawn and rest periods mid-day. This pattern was more pronounced in the dry hot season.
(Leggett 2010)	Namibia	NA	NA	NA	<i>Radio and satellite tracking records.</i> Lowest hourly movement rates are between 11:00am and 1pm in cold dry season and between 12:00pm and 2pm in the hot dry season corresponding with resting periods.

RESULTS

Model Validation

The model predicted home range sizes between 473 and 4050km² which spans the range of most reported home ranges for wild elephants [reported min and max = 14 - 14,310km² (Douglas-Hamilton 1973; Leggett 2010)] (Table 4).

Similarly, the maximum predicted distance from water elephants were predicted to travel in the model was between 12 and 36km which fell within the range of values typically reported for elephants in a wide variety of habitats. For example, Loarie, Van Aarde, and Pimm (2009) examined telemetry data from elephants across a large rainfall gradient spanning seven African countries and found that 93% of their elephant fixes were within 15km of water but elephants in some environments average 25km from water and ranged up to 40km from water (Viljoen 1989).

We also examined how well the model predicted how much time elephants spend feeding and resting, two activities that have been documented from activity budgets of elephants. The model predicted that elephants should feed between 11 and 19 hours day⁻¹ (47-76% of the day). Elephants are reported to feed between 9 and 18 hours day⁻¹ (36-75% of the day) with most reports ranging between 10-17 hours day⁻¹ (Wyatt & Eltringham 1974; Guy 1975; Guy 1976; Ruggiero 1992; Shannon *et al.* 2008) (Table 5). There are fewer reports of the percent of the day spent resting but 24-hr activity budgets of elephants measured by Wyatt and Eltringham (1974) found elephants in Uganda rested between 10 and 20% of the day. These values are

consistent with the model predictions that elephants should rest between 4 and 26% of the day.

In addition to these quantitative metrics, elephants are also reported to have a strong tendency to rest in the middle of the day (Wyatt & Eltringham 1974; Guy 1976; Shannon *et al.* 2008; Leggett 2010). The temporal resting pattern has been hypothesized to be a thermoregulatory behavior in the above studies and the evidence to support this hypothesis includes that 1) resting occurs primarily during the hottest part of the day and 2) the amount of time spent resting increases during summer. The model predicted significantly increased resting rates at midday and this pattern was significantly more pronounced under the warm treatments (Fig. 4A).

Given the model's consistency with observed elephant behavior in both magnitude and temporal patterns we were confident that the model framework captured the most important determinants of landscape use. Furthermore, the predictions of the model appear biologically meaningful and are consistent with reported elephant behavior.

Sensitivity Analysis

We tested how sensitive the model was to changes in the shape parameters of the utility functions (Fig. 3) for body temperature, body water stores, and energy reserves. We specifically assessed the impact that these values had on home range and population size. We found that although the magnitude of the values differed with changes in the shape functions, the overall qualitative patterns were robust.

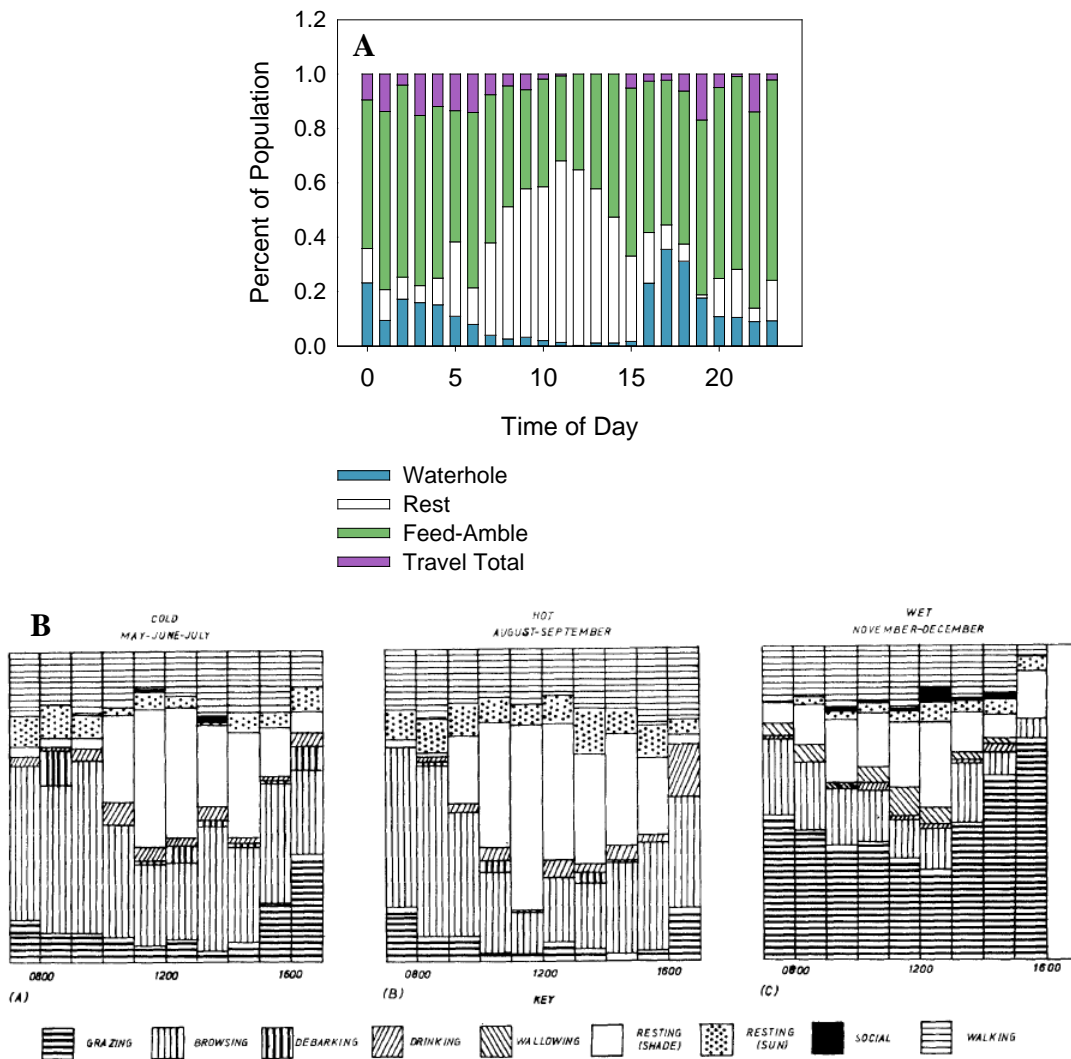


Figure 4: (A) Temporal pattern of resting behavior for elephants over a 24 hour period under a warm climate (similar to summer or hot dry season) as predicted by the SDSV model. (B) Activity budgets across the cold and hot dry season and the wet season for elephants in Zimbabwe as reported by Guy (1976). White bars indicate resting periods over the observation period. Note that (B) is presented for daylight hours only.

Spatial Use of Landscape in Relation to Water

Both productivity and climate significantly influenced how far from water elephants traveled. Across all climate treatments elephants ranged further from water under the low productivity conditions relative to high productivity conditions (Fig. 5). However, there were differences in the magnitude of the effect of productivity across the three temperature treatments. When productivity was high, home range size (km^2) and max ranging distance from water (km) under the cool and moderate climate treatments (mean cool $T_a = 8\text{-}16^\circ\text{C}$, mean moderate $T_a = 16\text{-}24^\circ\text{C}$) were similar but under the warm climate treatment (mean $T_a = 24\text{-}32^\circ\text{C}$) landscape use around the waterhole contracted by nearly 70% (Fig. 5). In contrast, when productivity was low, there was a contraction in elephant use of landscape around water under both the moderate and warm treatment though the magnitude of the contraction was greatest in the warm climate treatment. The home range size of the low productivity-warm treatment was 1.6 times smaller than the home range size under the low productivity-moderate treatment and was only slightly larger than that under the high productivity-warm treatment. Similar patterns were observed for distance to water (Fig. 5B).

The distribution of elephants within the landscape was evenly spaced across all treatments (Fig. 6 A-F) with the exception of the cool-high productivity treatment (Fig. 6 A). In this scenario, animals spent a much greater proportion of time between 20 and 25km from water and there was higher variability across simulations at these distances. In two simulations animals spent most of their time at 20km and in three simulations animals spent most of their time at 25km. There was also a single

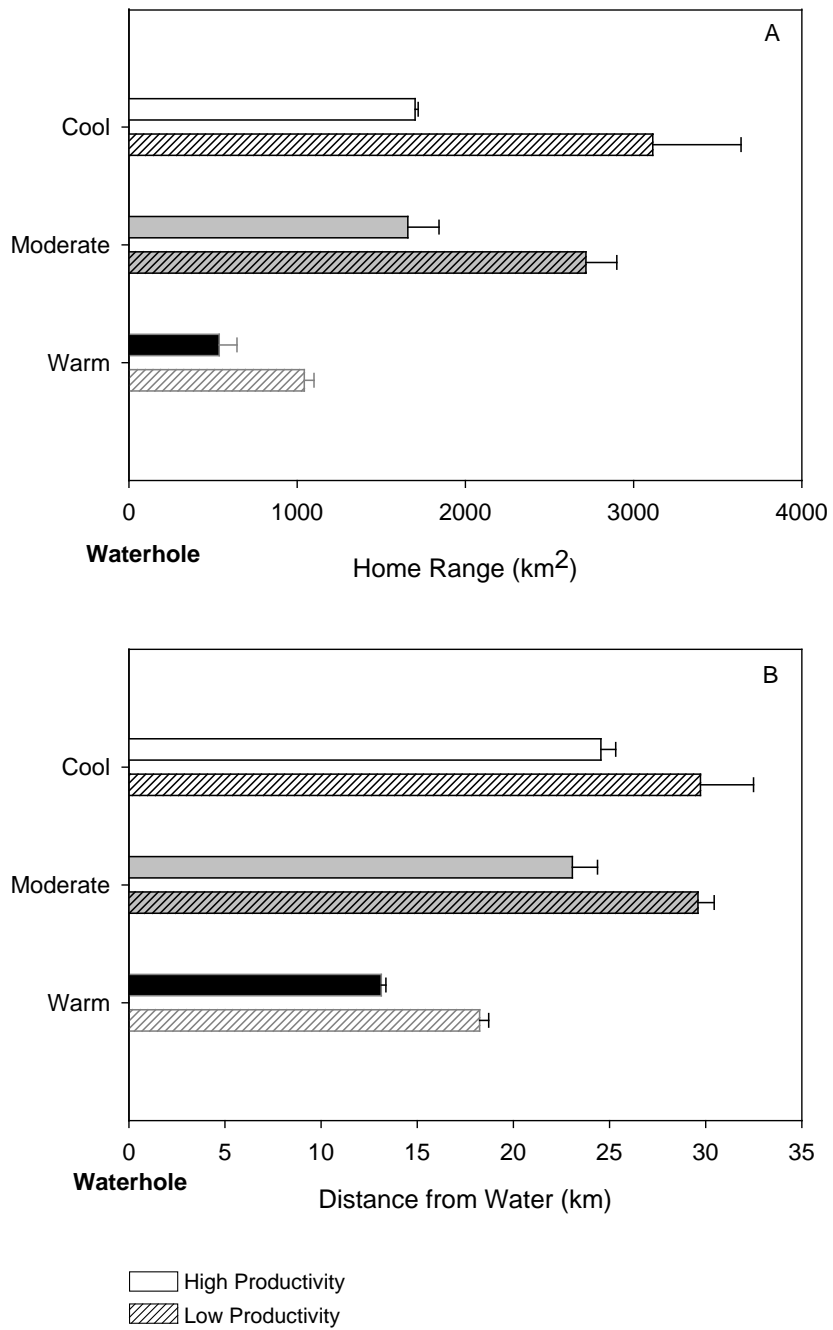


Figure 5: (A) Predicted home range sizes and (B) maximum distance elephants ranged from the water hole under three climates and two productivity treatments. Solid bars indicate high productivity treatments and hatched bars indication low productivity treatments. Data are presented as the mean and standard error.

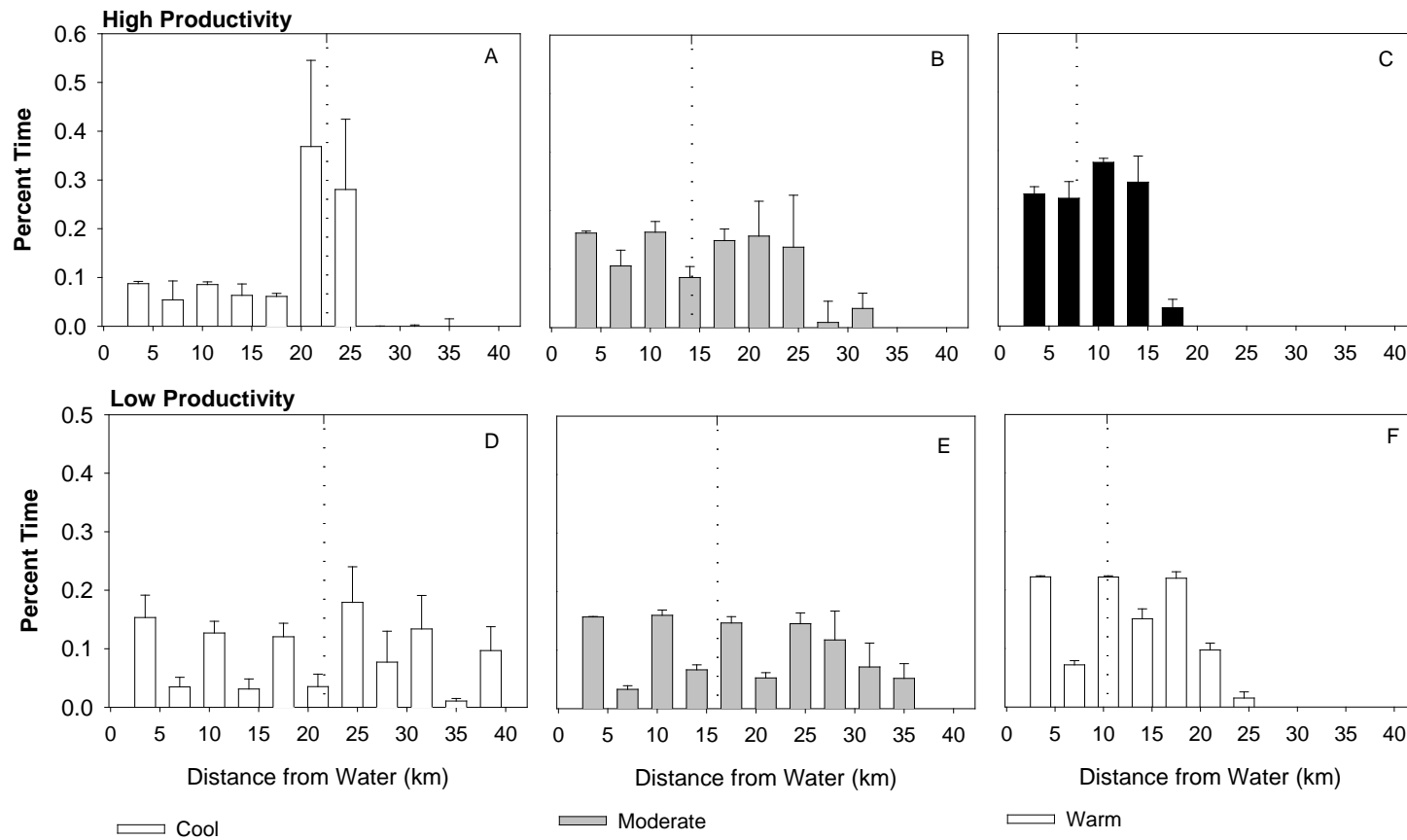


Figure 6: The amount of time elephants spent at discrete distances from water in high productivity (A-C) and low productivity (D-F) landscapes across the three climate treatments. The dotted line in each panel indicates the distance within which elephants spent 50% of their time.

simulation under this treatment in which elephants traveled out significantly further to 35km.

Activity Patterns

Two main patterns emerged in terms of how elephants allocated their time across treatments. First, in low productivity landscapes, elephants spent a much greater proportion of their time traveling in order to reach areas where vegetation was more abundant (Fig. 7 A, B). On average, elephants spent 9-13% (2-3 hours day⁻¹) longer traveling between the waterhole and feeding areas in the low productivity landscapes relative to high productivity landscapes. The second pattern that emerged, as mentioned above, was that a greater proportion of the day in both high and low productivity landscapes was allocated to resting under the warm climate treatments. Under the cool treatment elephants never rested in shade, but resting increased under the moderate and warm climate treatments such that elephants spent up to 26% (~6 hours day⁻¹) of the day resting in shade (Fig. 7 A, B). The time spent in the waterhole under all treatments remained fairly stable. However, as a result of the greater amount of time allocated to either travel (in low productivity landscapes) or to resting (in warm landscapes) the amount of time elephants were able to feed was reduced. This effect was most pronounced in the combined low productivity-warm climate treatment where elephants had to both travel and rest. Consequently, elephants in this treatment fed an average of 6.7 fewer hours per day relative to the high productivity-cool treatment.

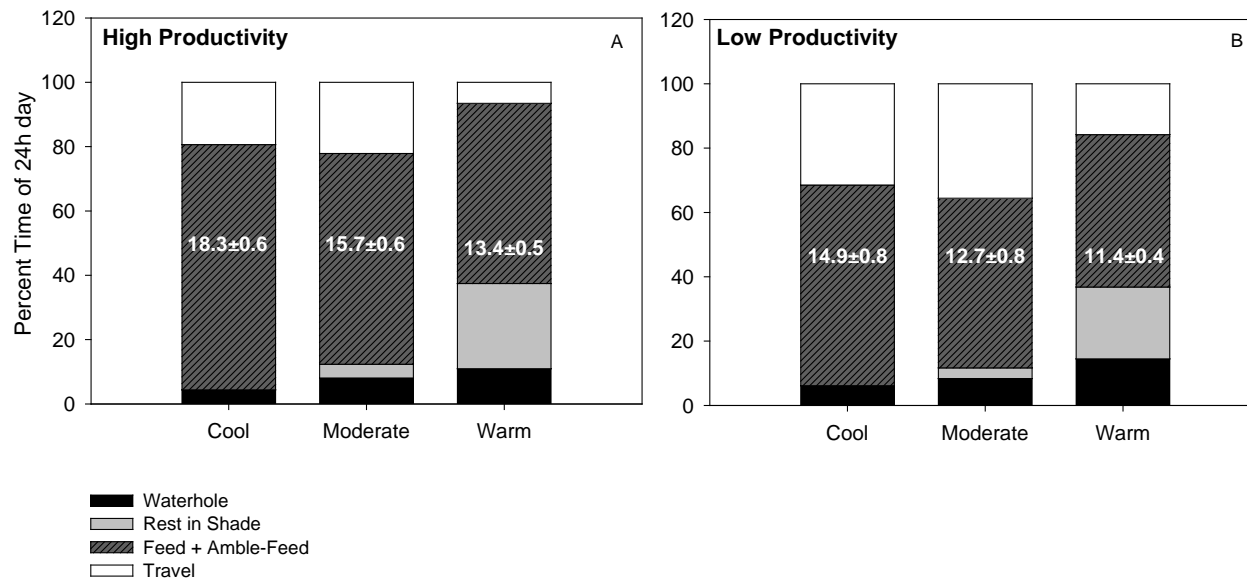


Figure 7: Predicted 24-hr activity budgets presented as the percent time of day engaged in each behavioral option for elephants in a high (A) and low (B) productivity landscape and across three climate treatments. Values written in white are the total number of hours elephants spent feeding across the treatments.

There were also several temporal activity patterns that emerged across climate treatments. As previously mentioned, most elephants rested primarily during midday when ambient temperatures were the warmest, a pattern that significantly increased in the warmest climate treatment (Fig. 8 A-F). Under the moderate climate treatment in both the high and low productivity landscapes there was a peak in travel to the water hole in the early evening and a second smaller peak in travel to the waterhole in the early morning indicating that elephants were more active near dusk and dawn, a pattern also observed in wild populations by Loarie, Van Aarde, and Pimm (Loarie *et al.* 2009). Peak feeding times occurred in the midmorning and increased toward midnight. Under the warmest climate treatment and in both productivity landscapes, elephants also rested for one to four hours in the late evening (Fig. 8 C,F).

Elephant Impacts on Landscape

The time elephants spend in a given area of the landscape as well as the number of elephants in the landscape will influence the ultimate impact elephants have on the habitat. We constructed an index of elephant impact in relation to water which was dependent on the relative intake rates of energy that elephants consumed in a given area. We found that the highest elephant impacts occurred within 10km of water under both productivity treatments but that elephant impact extended up to 20km from the waterhole under the low productivity scenario (Fig. 9 A,B). There were only slight differences between climate treatments in the extension of the impact from water and this was primarily due to the significant differences in equilibrium

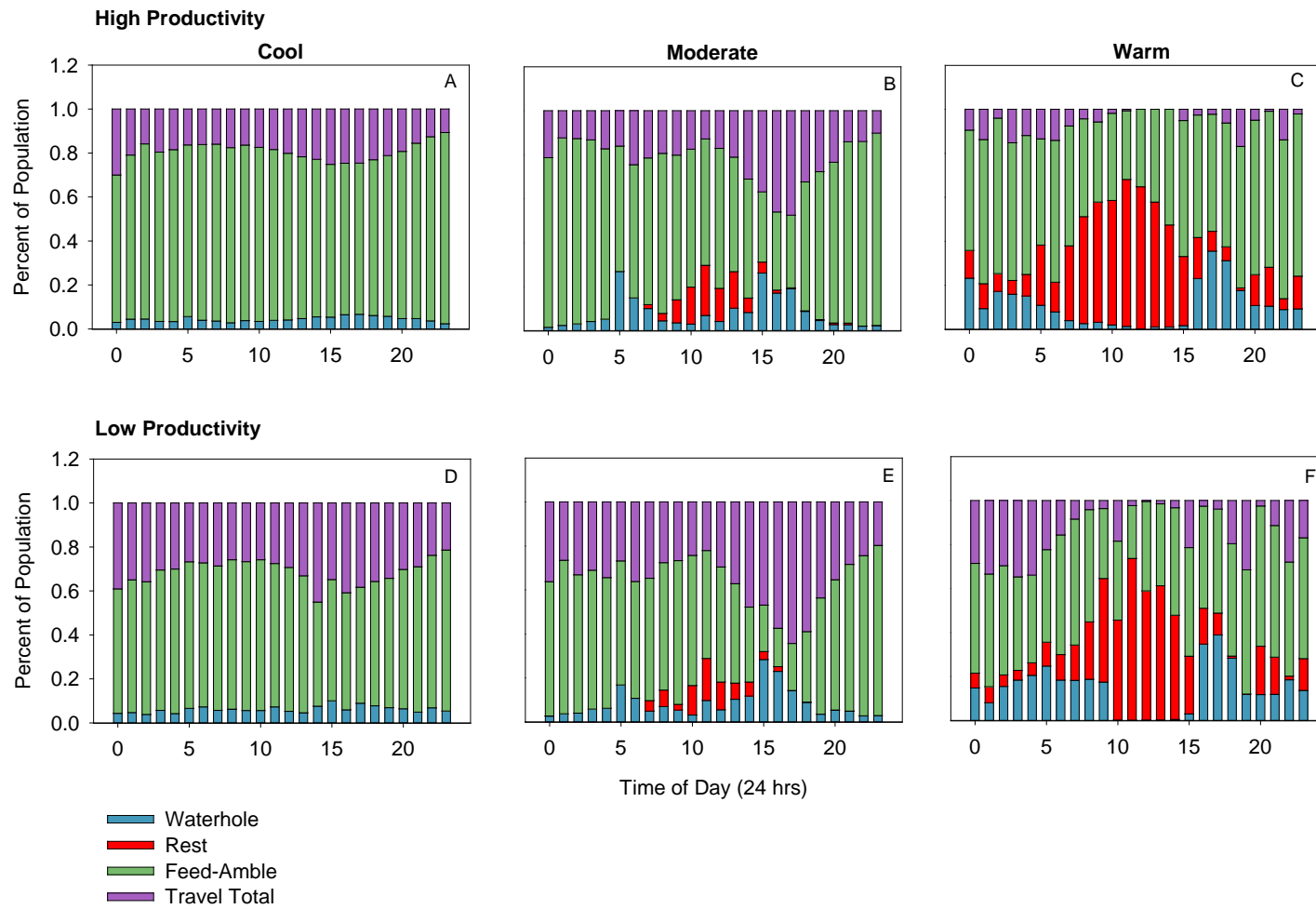


Figure 8: Predicted temporal patterns of activity for elephants in high (A-C) and low (D-F) productivity landscapes for each climate treatment.

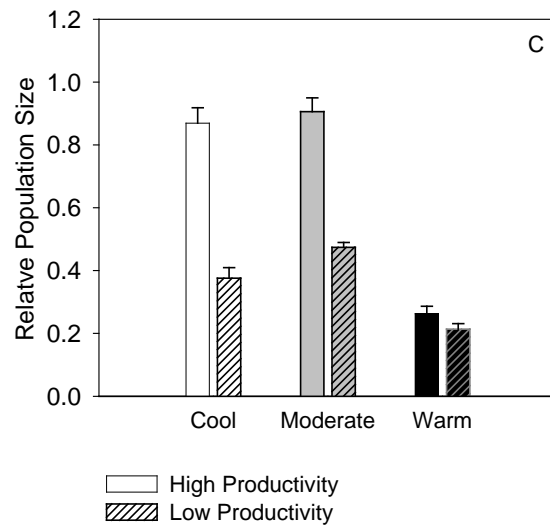
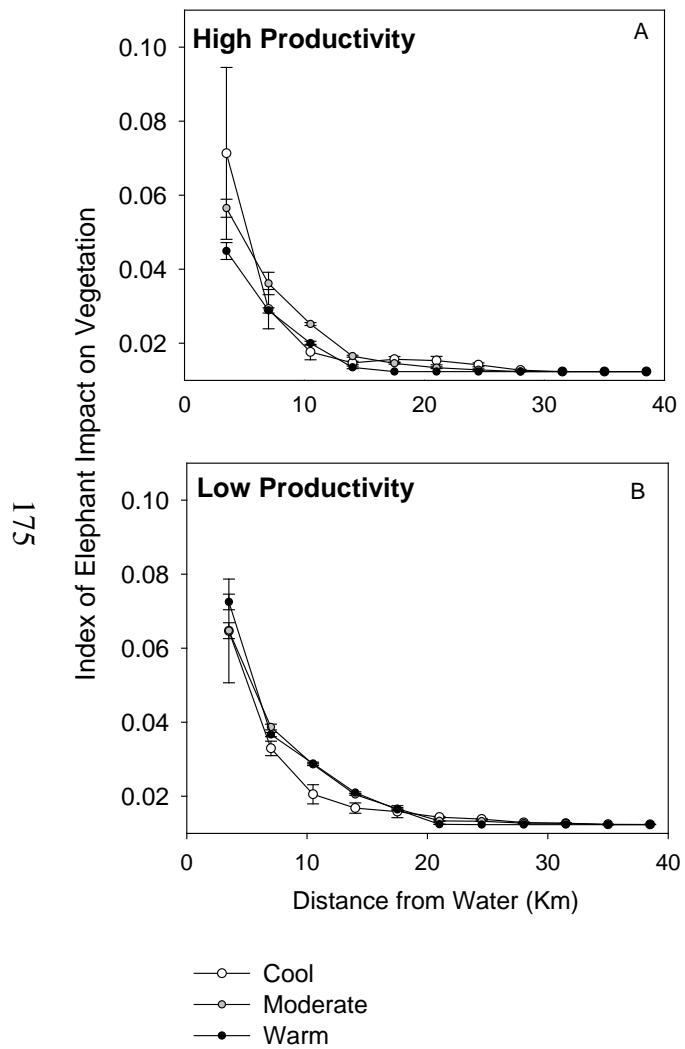


Figure. 9: An index of elephant impact based upon relative caloric consumption at varying distances from water under high (A) and low (B) productivity landscapes and for three climate treatments. (C) The relative equilibrium population size supported under each treatment

population size under the three climate treatments (Fig. 9C). In the high productivity landscapes, elephant populations were similar under the cool and moderate climate treatments. In the high productivity-warm climate treatment however, the relative population size was reduced by nearly 75%. In contrast, in the low productivity treatments, the population size in all climates was significantly reduced; relative population sizes in the cool and moderate climates were between 40 and 55% of their respective sizes in the high productivity landscape. The population size under the low productivity-warm climate treatment was the smallest of all treatments and was reduced by approximately 20% compared to the low productivity-moderate climate (Fig. 9C).

Physiological Condition

The status of the elephant's energy reserves, their mean body temperature, as well as their body water status at the end of the simulation indicated the relative physiological condition of the elephants under each treatment (Fig. 10A-C). The model predicted animals are able to maintain both body temperature and body water reserves near the physiological set point under the cool and moderate climate treatments. Similarly, energy reserves under the cool and moderate treatments were consistently high. In contrast, under the warm climate treatments, body temperature rose by up to 2.5 °C in the high productivity-warm landscape and up to 2°C in the low productivity-warm landscape. Elephants were also not able to achieve the same level

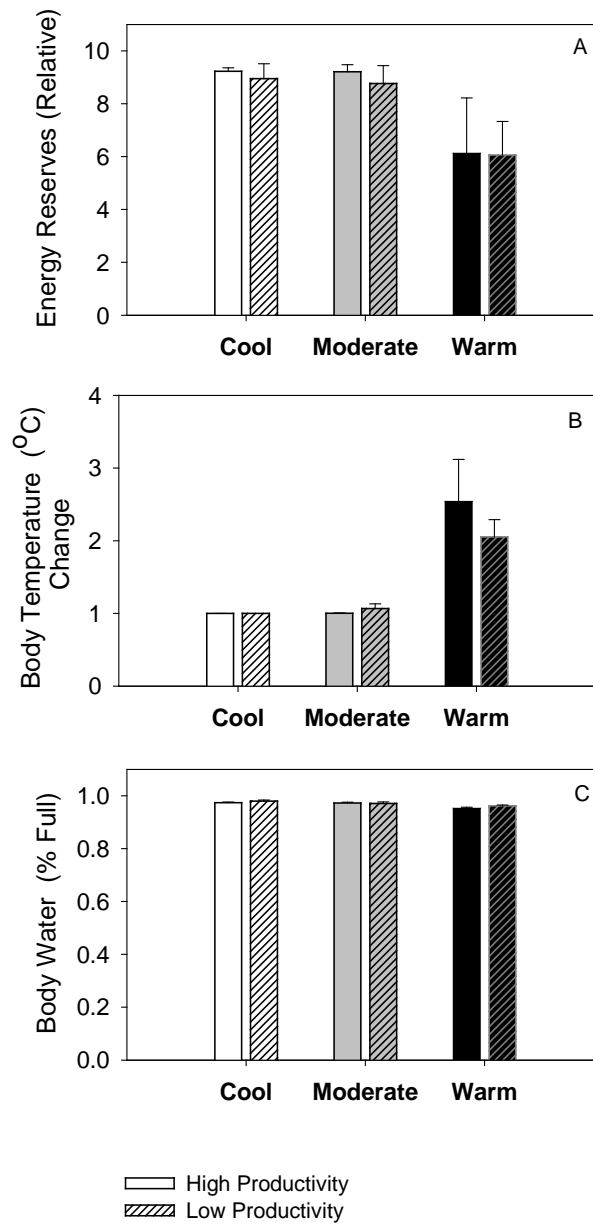


Figure 10: The status of the state variables at the end of the simulation under each treatment including relative energy reserves (A), the change in body temperature from the starting T_b of 36.2°C (B), and the relative status of the body water reserves (C)

of energetic reserves achieved under the cool and moderate treatments. Body water reserves remained high under all treatments.

DISCUSSION

The spatial distribution of elephant landscape impacts is not random. Rather, because elephants are a water dependent species, they must shuttle between water, usually a point source, and food. Because food resources close to water are the first to be depleted, over time it is inevitable that food quality and quantity becomes an increasing function of distance from water due to impacts from elephants and other herbivores. This pattern has been termed a piosphere (Lange 1969). There is an extensive literature on piosphere dynamics (reviewed in Thrash & Derry 1999) and the ecological gradients that exist as a function of distance from water. However, the factors that determine the severity of elephant impacts on landscapes in general and in the context of piospheres in particular, are poorly understood. The mechanistic model developed here, separately quantifies the influence of several interacting drivers of landscape use to better understand and predict how climate and food availability may alter elephant use of landscape.

The direct influence of climate on thermal physiology in determining elephant use of landscape

Climate, and in particular ambient temperature, is a primary determinate of several aspects of landscape use for elephants. The model allowed us to examine the separate influences of climate and food availability apart from the confounding

influence of climate on productivity. We found that the influence of increasing mean ambient temperature alone (holding daily solar radiation exposure constant), in both a high and low productivity environment, caused contraction of elephant use of landscape around water. Under the warmest climate treatments, elephants used only about 30% of the landscape that they used under the cool climate treatment. Under the high productivity-warm climate treatment elephants spent 50% of their time within 7.7km of water compared to 23km in the high productivity-cool climate treatment. The magnitude of these range contractions fall within reported changes in home range size between wet and dry (also reported as cool/hot and winter/summer) seasons for several elephant populations. For example, Galanti, Preatoni, Martinoli *et al.*, (2006) reported that dry season home ranges for elephants in the Tarangire-Manyara ecosystem in Tanzania were 23 to 56% the size of the wet season home range for most individuals and De Villiers and Kok (1997) report that dry season ranges for elephants in several private reserves near Kruger National Park, South Africa were 50 to 55% smaller than the wet season ranges.

The results of this model reveal that even in the absence of changes in food abundance between seasons, increased ambient temperature is sufficient to cause significant range contraction even in low productivity landscapes where food is less abundant and elephants have to move out further in the landscape to acquire adequate energy. The model results demonstrate that home range size does not decrease as a linear function of temperature, but rather the most severe range contraction associated with thermoregulatory constraints likely occurs once mean ambient temperature

reaches a threshold value above approximately 24-27°C. This threshold is associated with the range of ambient temperatures in which evaporative cooling begins to rapidly increase and elephants become fully dependent on evaporative cooling to dissipate excess heat (Fig. 11).

Climate also impacted the temporal dynamics of how elephants used the landscape. The most pronounced pattern was an increase in time that elephants would need to devote to resting in shade as mean ambient temperature increases. This has marked effects on the ability of the animal to maintain body condition. The model predicted that elephants may rest for up to 6.7 hours day⁻¹ under the warm climate scenario (Fig. 8 C,F). If presumed to eat at the highest potential intake rate for those 6.7 hours, this translates into an opportunity cost of up to 60,300kcal day⁻¹. It is worth noting that the warm climate treatment was, in the context of many African habitats, a relatively mild climate. Thus, we would expect that the hours devoted to resting or alternatively, the amount of time the elephant spends traveling to and from the waterhole, would also increase under even warmer conditions, thereby reducing further the amount of time elephants can feed. Based on these results, we would also predict that male elephants may have to spend more time resting under hot climate conditions than females. We base this prediction on the fact that adult male body size is significantly larger and males have a lower surface to volume ratio to dissipate heat than younger animals or females.

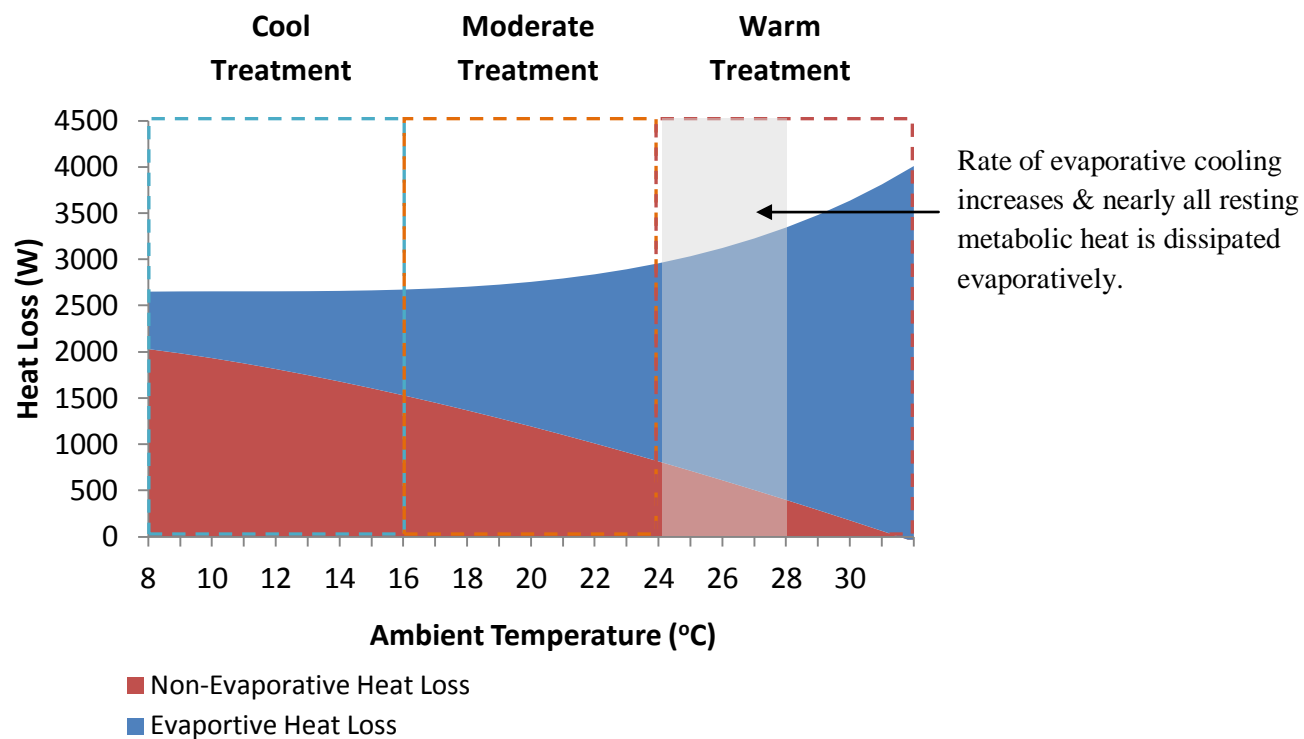


Figure 11: The non-linear relationship between evaporative water loss and ambient temperature from Dunkin (2012). The mean ambient temperature range for each of the climate treatments in the model is overlaid. The grey box indicates the region of ambient temperatures where the rate of evaporative cooling begins to rapidly increase and nearly all metabolic heat must be dissipated through evaporative routes.

The influence of food abundance on elephant landscape use in cool and warm climates

Primary productivity is a main driver of abundance and landscape use patterns of elephants (Phillipson 1975; Coe, Cumming & Phillipson 1976). Yet primary productivity varies not only across habitats but also temporally on both seasonal and long term time scales. Elephants must therefore balance energy and thermoregulatory constraints under both high and low food abundance. The results of the model suggest that on long term time scales, assuming an elephant population has reached an equilibrium state, primary productivity is the limiting factor for population size in habitats with mean ambient temperatures below the thermoregulatory threshold described above (cool and moderate treatments) (Fig. 9C). Above this threshold (warm climate treatments) ambient temperature likely becomes the primary constraint, indirectly limiting food intake and ultimately population growth by tethering elephants within a smaller area around water.

This conclusion is supported by the model results of population size under the different treatments. If productivity were the primary limiting factor across all climates then we would expect uniformly lower population size at equilibrium across the three climate treatments. Conversely, if climate were the primary limiting factor, we would expect a steady decrease in population size with increasing ambient temperature. We found that under the cool and moderate climate treatments, population size was lower in the low productivity versus high productivity landscapes and similar between the low and moderate climate treatments, consistent with

productivity being the limiting factor (Fig. 9C). However, under the warm climate treatment, population size was smaller compared to the cooler climate treatments and was similar between the low and high productivity treatments. These results indicate that climate became the primary limiting factor under these warm conditions.

Interactions between food abundance and climate are also likely to be important during drought conditions. Droughts are typically characterized by lower than normal precipitation which reduces the abundance and distribution of surface water as well as the availability and water content of food. Droughts can also co-occur with intense hot spells with higher than average ambient temperatures (Mishra & Singh 2010). Thus, drought-induced mortality of elephant and other species will occur because of prolonged starvation, acute dehydration, or an interaction between these stressors. A complex set of factors will influence how elephants are affected by drought (e.g. body size, energetic requirements, food water content, walking speed) and therefore prediction of drought-induced mortality for a whole population as well as differential mortality across age and reproductive classes is challenging. Indeed, drought mortality varies greatly ranging from minimal (Walker, Emslie, Owen-Smith *et al.* 1987) to severe (Corfield 1973). There is also evidence that the spatial arrangement of surface water availability can play a major role in driving such variation. Walker, Emslie, Owen-Smith *et al.*, (1987) report that the spatial distribution of food specifically resulting from the relative spacing of water holes within the landscape played a role in the differential mortality of elephants and other

species between four reserve areas during the drought that affected South Africa in the early 1980's.

There is also documented differential mortality associated with age and reproductive classes during droughts. For example, Conybeare & Haynes (1984) report high juvenile mortality (animals aged 2-8yrs) resulting primarily from dehydration during a drought in Hwange National Park, Zimbabwe. Unlike adults, the trunks of juveniles were too short to reach down into the deep holes dug by elephants in dry river beds under conditions of scarce surface water availability. However, mortality due to starvation also differentially impacted both juveniles and adult females resulting in greater than 5000 elephant deaths in the drought that occurred between 1970 and 1971 in Tsavo National Park, Kenya (Corfield 1973; Phillipson 1975).

Drought is a natural component of African savannah ecosystems and plays an important role in population regulation (Walker *et al.* 1987). However, climate change appears to be increasing the frequency and severity of droughts in this region (Mishra & Singh 2010). Furthermore, there is concern that water provisioning has artificially increased the carrying capacity in many reserves and that these populations are now at risk for greater mortality under drought conditions (Corfield 1973; Phillipson 1975; Walker *et al.* 1987). The above examples demonstrate the complex interactions that can influence the population level effects of drought. The mechanistic model presented in this work is an ideal tool with which to better

understand how these interactions lead to such wide variation in mortality across and within populations.

Interactions between climate and food quality/quantity

Under equilibrium conditions, the model predicted that elephant impacts within 10km of water would be similar between climate treatments in both the high and low productivity landscape (Fig. 9 A,B). There was a difference however in how far out the elephant impact extended in the low versus high productivity environment. Our model predicts an expansion of the biosphere when productivity is low (such as during low rainfall years) rather than a major decrease in overall biomass close to water. These results agree with the conclusion of Franz, Kramer-Schadt, Kilian *et al.*, (2010) who investigated the influence of changes in rainfall on elephant-vegetation dynamics in Etosha National Park, Namibia. In response to increased elephant densities and decreased rainfall during a drought, their simulations resulted in an extension of the vegetation impacts away from water. This supports observed patterns from empirical data in this area. As these authors suggest however, empirical studies of the extent of elephant impact as a function of distance from water have also shown the opposite trend, that overall biomass was reduced close to water, (Thrash 2000) though these differences may be attributed to variation in temporal scale. Our model predicts patterns over many seasons and assumes a population at equilibrium whereas empirical studies may not be able to detect long term changes in utilization gradients around water.

In wild populations, high elephant densities are obviously associated with much more severe impacts on the landscape (Owen-Smith *et al.* 2006; Guldmond & Van Aarde 2008). We did not detect large differences between treatments in elephant impact in the model likely because we modeled landscape use and impacts once a population has reached carrying capacity. Thus in our model, population size is able to adjust to the equilibrium density that is sustainable by the local resources, and does not have the opportunity to be subsidized by outside resources, as might happen in empirical studies. Because of this we found similar net impacts in the high and low productivity treatments. To better understand the impacts of non-equilibrium populations, or open populations where there are spatial subsidies and source-sink dynamics are possible, future versions of this model could be embedded in more realistic landscapes with multiple water sources and spatially heterogeneous food resources. This would be particularly relevant in the context of the suggested metapopulation management that is being pursued for much of Southern Africa (van Aarde & Jackson 2007).

Model Improvements & Limitations

The basic framework we present here appears to predict well many spatial and temporal patterns previously observed for elephant populations. There were areas where the model could be improved to extend its utility and provide more quantitative results. For example, in its current form the model uses a relative scale for productivity. Linking the productivity of the modeled landscape to an actual metric

of productivity for the starting conditions would improve the ability to make predictions for specific populations. Furthermore, productivity is primarily determined by rainfall (Phillipson 1975; Coe *et al.* 1976; Chamaillé-Jammes, Fritz, Valeix *et al.* 2008) and fluctuates stochastically within a given environment. Stochastically drawing a level of primary production from a realistic distribution at the beginning of each season would likely yield better estimates of long term impacts of elephants on a landscape by allowing more realistic population densities within the modeled landscape. Such a modification would also permit better site specific investigations of landscape impacts as seasonal changes in primary productivity will vary considerably between environments.

There are also several areas of the biophysical model that could be improved with additional physiological measurements. For example, we have not linked fecal and urinary water output to food and water intake in the current version of the model but rather used estimated mean values based on reports from the literature. Linking these water outputs with water and food inputs would be needed in order to look at more refined predictions such as interactions between climate, productivity, and food water content at the beginning and end of the dry season for example (see below). The ratio of food water content to kilocalories that is currently used in the model is likely to change across a season, thus measurements of wet to dry mass ratios for a variety of both woody and grass species at the beginning, middle and end of the dry season would be useful.

Perhaps the most important improvement that would extend the utility of this model is collection of empirical thermal and water budget parameters at higher ambient temperatures and from animals under a variety of climates in Africa. The use of zoological animals permitted collection of physiological measurements across a wide range of ambient temperatures similar to many climate regions in Africa. However, we were unable to perform measurements at some of the extreme temperatures elephants are exposed to in the wild. It is very likely that the rate of cutaneous and respiratory evaporative water loss at temperatures above 33°C will increase exponentially with increased temperature following the exponential increase in the capacity of the air to hold water at higher temperatures (Anderson 1936). However, the relationship between temperature and the rate of cutaneous water loss in particular is unknown at these higher temperatures. If the rate of cutaneous water loss rises exponentially, home range may contract more severely as the mean temperature increases. Furthermore, the influence of solar radiation has been held constant across climate treatments in this investigation but solar radiation exposure can significantly contribute to the thermal burden of an elephant and will vary seasonally and with latitude. Thus, further work to validate the influence of solar radiation on elephant thermal balance, specifically through collection of skin surface temperatures under a variety of solar radiation conditions, would improve the model.

Future Work

We have demonstrated that the interactions between climate, thermal physiology and energetic demand are important in establishing the fundamental spatial and temporal patterns that have been previously observed for wild elephant populations and we have developed a quantitative framework for investigating these interactions. Expansion of this basic framework can now be used to investigate new processes and sources of variability. Below are some of the scenarios that we believe would be most useful:

Spatial

- 1) *How does the spacing and distribution of water holes alter elephant use of landscape under different climate and productivity regimes?*

Modification of the model to include multiple point sources of water would allow for manipulation of the spacing between water holes as well as the distribution of water holes to be examined. Owen-Smith (1996) recommended that waterholes be placed at least 15km apart however, there are likely to be habitat specific differences in not only how far apart waterholes should be spaced but also how they are distributed. For example, placement of artificial waterholes closer to natural water sources may minimize impacts at further distances in the landscapes.

- 2) *How does the temporal and spatial distribution of perennial and ephemeral water sources influence elephant use of landscape under different climate and productivity regimes?*

Redfern *et al.*, (2005) stressed the importance of temporal fluctuations in surface water and the disappearance of ephemeral water sources as the dry season progresses. These authors suggest that habitats exist along a continuum characterized primarily by ephemeral water sources on one end or perennial water sources on the other. These differences will have direct impacts on how surface water management may be implemented or not within a landscape. Model simulations in which various ratios of perennial to ephemeral water sources exist within the landscape as well as the relative rate of disappearance of ephemeral water sources with progression of the dry season may prove useful in understanding how such a continuum of surface water may result in differences in landscape use across habitats.

- 3) *Does the impact of movement barriers (fences, large rivers, large population centers) vary with differences in climate or productivity?*

Loarie *et al.*, (2009) found that fences cause elephants to “bunch up” within the landscape potentially increasing vegetation impacts in the vicinity of fences or other barriers. Spatially explicit model simulations in which a barrier is included at various distances from water under different climate and

productivity treatments would allow prediction of the severity and spatial distribution of elephant landscape use in relation to movement barriers.

Physiological

1) *How do elephant patterns of landscape use vary under more extreme climates?*

As mentioned above, collection of empirical physiological data is needed to parameterize the model at more extreme temperatures. We predict that home range size at temperatures greater than 33°C decreases exponentially as a result of a rapid increase in evaporative cooling. However, elephants may be able to modulate cutaneous evaporative water loss under extreme temperatures and rely more on heat storage. Differences in how elephants handle heat stress at these higher temperatures could have important impacts on landscape use.

2) *How does the contribution of preformed water in food alter landscape use patterns under different climates and productivity scenarios?*

At cool and moderate temperatures, preformed water ingested with food can make up a significant portion of the water intake for an elephant because their consumption of food is so high. However, several processes reduce the contribution of water from food to the overall water budget of elephants as the dry season progresses. First, the moisture content of food will decline as the

dry season progresses in some cases reaching 10% or less (see Table A-1). Second, food intake declines as the dry season progresses because elephants are forced to spend more time resting in shade as the mean ambient temperature increases and because the abundance of food declines. Thus, the contribution of water from food to overall water balance is predicted to decline as the dry season progresses however, the rate and magnitude to which it declines will be climate and habitat specific. Simulations in which the moisture content of the food declines from the start to the end of the dry season under various climate and productivity treatments would permit investigation of the likely interactions between moisture content of food, energy intake, and the effects of climate on evaporative water loss.

3) *How does body size and reproductive status influence landscape use patterns under various climate and productivity scenarios?*

Female elephants are significantly smaller than males and males and females are known to use landscape differently, though the cause of these patterns is unknown (Shannon *et al.* 2008). Females with juveniles are also known to stay closer to water than males presumably because the young animals can not walk as far as adults (Sikes 1971). Collection of physiological data from young animals as well as much larger male elephants would permit a quantitative assessment of the influence of climate and productivity on landscape use as a function of body size. With body size, thermoregulatory

constraints will not be as severe because smaller animals have a larger surface to volume ratios. However, smaller animals will also not be able to walk as far in a single day and may also have increased rates of mass specific cutaneous water loss. How the interaction of these factors influences home range size or maximum distance from water is unclear. Incorporation of water loss due to lactation would also further extend our ability to investigate differential landscape use between reproductive classes.

Conclusions

From an ecological perspective, a better understanding of the fundamental mechanisms that drive spatial patterns of landscape use and variability in the severity of landscape impacts by animals is a basic goal of landscape ecology (Turner 1989; Bailey, Gross, Laca *et al.* 1996). From a management perspective, the use of surface water manipulation is a promising tool but remains challenged by disagreement over the ultimate effect specific water management plans will have for particular populations (Owen-Smith *et al.* 2006; Chamaillé-Jammes *et al.* 2007; Smit *et al.* 2007b). We have demonstrated that the influence of climate alone is sufficient to produce many of the empirically observed patterns of landscape use for wild elephant populations. Importantly, we have also shown that because the physiological response to ambient temperature is non-linear (e.g. exponential increases in evaporative water loss) landscape use patterns are also likely non-linear, a result that has not been previously reported for large mammals. This work also demonstrates the power of using physiological measurements to understand population level

patterns. Such a framework can play an important role in management and conservation of elephants and other species by identifying and quantifying the underlying mechanisms of population level patterns, therefore increasing our ability to predict how these patterns may be altered by management schemes, climate change, land use practices, or droughts.

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APPENDIX I

Utility Function and Starting Parameters for F(H)

African elephant core body temperature (T_b) has been reported to be between 36.1 and 36.8 in non-immobilized elephants (Buss & Wallner 1965; Kinahan *et al.* 2007a). We chose a starting $T_b = 36.2^\circ\text{C}$ which was the mean T_b measured for semi-free ranging African savannah elephants by Kinahan *et al.* (2007a). To determine the most appropriate shape for $F(H)$, we reviewed the literature on upper lethal temperatures and heat storage in mammals. There has been debate about whether elephants, particularly because of their large body size, can undergo significant heat storage similar or even greater than that documented in camels and oryx (Schmidt-Nielsen *et al.* 1956a; Elder & Rodgers 1975; Ostrowski, Williams & Ismael 2003; Weissenböck, Arnold & Ruf 2011). While it was hypothesized that large body size would make heat storage a useful water saving mechanism for elephants, there is mixed evidence that this occurs to a significant degree in free ranging African elephants. Kinahan *et al.* (2007a) found that body temperature did undergo predictable daily rhythms in which T_b was highest at night and fell by morning, presumably decreasing when T_a was most favorable for non-evaporative heat loss. However, the magnitude of this variation was small, $36.2 \pm 0.49^\circ\text{C}$. More recently, Weissenböck *et al.* (2011) found evidence for moderate heat storage in Asian elephants housed in warmer climate conditions where $T_a \sim 30^\circ\text{C}$ and $T_b = 36.17 \pm 1.15^\circ\text{C}$. These changes in T_b were also associated with daily fluctuations in T_a . Based on this information we let:

$$(A-1) \quad F(H) = \left(1 - \left(\frac{H}{H_{\max}}\right)^\alpha\right)$$

where H is heat storage in units of body temperature ($^{\circ}\text{C}$) at time t , $H_{\max} = 10$ corresponding to an upper lethal temperature of 46.2°C , and α is a shape parameter that adjusts the steepness with which fitness decreases as H approaches H_{\max} (Fig. 3A). We chose to parameterize $F(H)$ to allow a fairly wide range of change in T_b before fitness was significantly reduced. This represents a conservative physiological viewpoint because of the uncertainty about whether elephants, under extreme water stress, are able to undergo significant thermal storage. Camels for example, show more extreme heat storage when dehydrated, allowing T_b to increase up to 6°C above the normal mean and several species of African antelopes can tolerate body temperatures in excess of 46.5°C for a number of hours (Schmidt-Nielsen, Schmidt-Nielsen, Jarnum *et al.* 1956b; Taylor 1970). We set $\alpha = 5$ such that when body temperature exceeds approximately 40.2°C , a 4°C increase in core body temperature, fitness will begin to decline sharply (Fig. A1) reaching 0 at $H = 46.2^{\circ}\text{C}$.

Utility Function and Starting Parameters for $F(W)$

The amount of body water loss that an animal can endure before dehydration becomes lethal varies across species from less than 12% up to 30% of body mass in some desert adapted species such as the camel (Adolph 1947; Schmidt-Nielsen *et al.* 1956a). We set $F(W) = 0$ to correspond to a loss of 20% of total body mass, or 754L for the 3770kg elephant in our model. This is a moderate value and assumes that elephants have some level of adaptation to withstand moderate to severe dehydration

under extreme circumstances. $F(W)$ represented the decline in fitness associated with a loss of body water according to:

$$(A-2) \quad F(W) = \left(\frac{1}{1+(W_{max}-W)*e^{(-\beta*W)}} \right)^2$$

where W represents the relative amount of onboard water in arbitrary units at time t but which can be converted to liters with the conversion factor of 75.41 (1/0.01326), W_{max} is the body water reserve when full ($W_{max} = 10$), and β is a shape parameter that adjusts the slope of the curve as $F(W)$ falls to 0 with declining body water. We set $\beta = 0.6$ such that after about 5-6% loss of body water was reached, fitness began to precipitously decrease (Fig. 3B).

Utility Function for F(E)

More energy intake is generally associated with better fitness because the organism is able to meet its maintenance costs and then use surplus energy to reproduce. Thus, we set the relationship between fitness and energy in the model to correspond linearly according to:

$$(A-3) \quad F(E) = \frac{E}{E_{max}}$$

where E is the net energy intake of the elephant at time t in arbitrary units but can be converted to kcals by the conversion factor $E/0.0005\text{kcals}$. We also used energy intake as a metric of elephant impact on the landscape. The number of elephants and the amount of vegetation (e.g. energy intake in the model) they consume in a season can be used as metrics of landscape impact because elephants eat copious amounts of low quality vegetation and, due to their large body size, they also have significant

trampling effects on the landscape which may prevent the recruitment of many plant species (Du Toit, Rogers & Biggs 2003).

Vegetation Availability and Energy and Water Intake Rates

We began by reviewing intake rates recorded for wild elephants as well as the moisture and energy contents of various grass and browse species (Table A-1). We compiled fresh weight food intake rates (kg day^{-1}) from a number of studies (reviewed in Guy 1975) and generated a likely mean intake rate and standard deviation for an average adult elephant (Table A-2). We then chose a moderate value for water content (50%) and for metabolisable energy (ME, $7.1 \text{ MJ kg}^{-1} \text{ DM}$) of various grass and browse species and used these values to estimate the mean and standard deviation for total daily caloric intake ($151,695 \pm 63,744 \text{ kcals day}^{-1}$) (Table A-2). We divided this daily caloric intake rate by the mean time elephants are reported to feed per day ($18.5 \text{ hrs day}^{-1}$) (Wyatt & Eltringham 1974; Guy 1976; Vinod & Cheeran 1997) to get a plausible hourly intake rate for energy for an adult elephant (Table A-2). We linked water intake to food intake by calculating the amount of water consumed per kcal (Table A-2) and used this to determine preformed water intake via food.

Table A-1: Moisture and energy content of grass and browse from various sources.

Vegetation Type	Moisture Content %	Metabolisable Energy (ME) Content MJ kg ⁻¹ DM	Season?	Source
Grass	40		Late wet season	(in Coe 1972 Osborn 2004)
	50			(Clauss, Loehlein, Kienzle <i>et al.</i> 2003b)
	72.3			(Ruggiero 1992)
	38.7-82.4		Late/early in season respectively	(Georgiadis & McNaughton 1990)
		6.90 mean 4.85-9.23 range		(Mlay, Pereka, Phiri <i>et al.</i> 2006)
Browse	25-29		Late wet season	(Osborn 2004)
	50-60			(Taylor 1968; Taylor 1972)
	"twig" 25			(Clauss <i>et al.</i> 2003b)
	52.4			(Ruggiero 1992)
		7.31 mean 3.57-9.46 range		(Mlay <i>et al.</i> 2006)

Table A-2: Values and calculations for parameterization of F(E).

Calculation of Energy Intake Ranges	Source	
Daily rates of consumption kg wet weight day ⁻¹ Used the range of values from all studies for free ranging animals in Table 2 of Guy, 1975	178.94 ± 75.19	Reviewed in (Guy 1975)
Mean water content of food %	50%	See Table A-1
Metabolisable energy content of food MJ kg ⁻¹ DM Mean value for browse + grass eaten in a 1:1 ratio	7.1	See Table A-1
Conversion from MJ to kcals	238.8	
Daily energetic intake kcals day ⁻¹	151,695 ± 63,744	
Average time spent feeding hr day ⁻¹	16-21	(Ruggiero 1992; Vinod & Cheeran 1997)
Energy intake kcals hr ⁻¹ Assuming 18.5 hours feeding day ⁻¹ to get a mean hourly intake rate	8,199 ± 3445	
Water intake from food L kcal ⁻¹	5.9 x 10 ⁻⁴	

APPENDIX II

The biophysical model was composed of a thermal balance and water balance model which are primarily linked by cutaneous and respiratory evaporative cooling. We largely followed the equations summarized in Gates (1980) and Denny (1993). Table A-3 outlines several simplifying assumptions which we made because of either a lack of empirical data or to reduce the number of varying parameters in the model. The specific parameters and range of values for each behavioral type are described in Tables 1 and 3.

We begin with the summary equations for thermal balance:

$$(A-6) \quad H_m + H_{AR} = H_{Con} + H_{Conv} + H_{Rad} + H_{CEWL} + H_{REWL} + H_{Store}$$

and water balance:

$$(A-7) \quad W_m + W_{Food} + W_{Drink} = W_{CEWL} + W_{REWL} + W_{Urine} + W_{Feces} + W_{Lactation}$$

where H_m is metabolic heat production, H_{AR} is absorbed radiation from the environment, H_{Con} is conductive heat exchange, H_{Conv} is convective heat exchange, H_{Rad} is radiant heat exchange, H_{CEHL} and H_{REHL} represent heat loss through evaporative routes (cutaneous and respiratory respectively), and H_{Store} is heat storage. Conduction makes up a very small percentage (<2%) of the thermal balance equation for an elephant (this study and Williams 1990) and was thus excluded from

the thermal balance model. For the water balance model, W_m is metabolic water production, W_{Food} and W_{Drink} are water intake via food and drinking, W_{CEWL} and W_{REWL} are evaporative water losses from the skin and respiration, W_{Urine} and W_{Feces} are water losses through waste products, and $W_{Lactation}$ is for water loss through lactation for females. Lactation was excluded from our model as we assumed an adult, non-lactating female elephant.

Metabolic Heat and Water Production (H_m and W_m)

In an earlier paper, we empirically measured resting metabolic heat production using open flow respirometry with the detailed methods described in Dunkin (2012). To determine appropriate metabolic rates for the two speeds that elephants were simulated to walk in the model, we used the cost of transport results of Langman *et al.* (1995) to scale up our resting values to estimate walking metabolic rates at 1 and 2ms⁻¹. We chose these speeds based on the minimum cost of transport speed for the “ambling” elephant and a slightly faster speed for the “traveling” elephant. We did not directly use the values given by Langman *et al.* (1995) because their reported resting values were considerably higher than our values likely as a result of the much smaller body size (1542kg versus 3768kg in this study) and younger age of the animals relative to the animals in our measurements. Thus, we assumed that the relative magnitude in the cost of transport between rest and walking remained similar between smaller, younger animals and larger adult animals. The

rate of oxygen consumption was converted to heat production using a conversion factor of 20.1KJ L⁻¹O₂ and the final values are given in Table 3.

Metabolic water production was estimated by assuming 0.028mL of oxidative water was produced per KJ⁻¹ (0.117mL O₂ kcal⁻¹) of digested energy (Schmidt-Nielsen 1997; Ostrowski *et al.* 2006). We then assumed the rate of digested energy was equal to the metabolic rate of the animal for each behavioral state and used this to determine an hourly rate of metabolic water production (Table 3).

Radiant Heat Exchange with the Environment (H_{AR})

Animals absorb radiation from the sun as well as from diffuse sources including the sky, atmosphere, reflected sunlight from objects in the environment, and the ground. The amount of radiation that actually is absorbed as heat into the body depends upon the surface area exposed to the radiation and the ability of the skin to absorb radiation of different wavelengths (Porter & Gates 1969; Gates 1980; Walsberg 1992). Absorption of radiation from the environment can be the largest source of heat exchange in an animal's thermal budget during parts of the day but quantification of radiant heat gain is extremely complex. We rely upon the work of Gates (1980) to estimate absorbed radiation by an elephant. We make several assumptions which are pointed out below.

The sources of radiation that contribute to heat gain include:

$$(A-8) \quad H_{AR} = H_{Solar} + H_{Sky} + H_{Ref} + H_{Atm} + H_{Grd}$$

direct solar radiation (H_{Solar}), diffuse skylight radiation (H_{Sky}), reflected skylight radiation (H_{Ref}), atmospheric radiation (H_{Atm}) and ground radiation (H_{Grd}). To estimate the relative contribution of each of these sources to heat gain by the elephant, we modeled the elephant as a series of geometric shapes. We considered the body to be a horizontal cylinder, the legs to be vertical cylinders, and the ears to be vertical flat plates. The head and trunk were excluded. The dimensions required for these equations were empirically measured on African elephants (n=5) and the mean value used for our model elephant.

For a horizontal or vertical cylinder of any orientation:

$$(A-9) \quad H_{AR} = \frac{1}{2} \left\{ \begin{array}{l} a_{Solar} \left[\frac{2x \sin \theta + \pi \cos \theta}{\pi(x+1)} \right] S + \\ a_{Sky} [(S_o(0.271 - 0.294\tau^m) \cos z)] + \\ a_{Ref} [r(S_o\tau^m \cos z + S_o(0.271 - 0.294\tau^m) \cos z)] + \\ a_{Atm} [1.22\sigma(T_a + 273)^4 - 171] + \\ a_{Grd} [5.05T_{bb} + 307] \end{array} \right\}$$

where a is the wavelength-specific absorbance of the skin of an organism, θ is the angle between the axis of the cylinder and the direction of the sun's rays, x is the ratio of the cylinder's length to its radius, S_o is the instantaneous radiation incident just outside the earth's atmosphere, S is the instantaneous radiation on the ground accounting for, τ^m , the atmospheric transmittance, z is the zenith angle of the sun, r is

the reflectance of the ground surface, and T_{bb} is the black body temperature of the ground.

According to Gates, the orientation of a horizontal cylinder to the sun does not greatly influence the total irradiance of the body because so much of the radiation is diffuse rather than from a point source (the sun). We therefore made the simplifying assumption that the animal was always perpendicular to the sun's axis and thus, radiation absorbed by the body from direct solar radiation was:

$$(A-10) \quad H_{Absorbed\ Solar} = a_1 \left[\frac{2x \sin \theta + \pi \cos \theta}{2\pi(x+1)} \right] S = a_1 \left[\frac{2\rho h S}{2\pi(\rho h + \rho^2)} \right]$$

where ρ is the radius of the cylinder and h is the length of the cylinder (Gates 1980). Furthermore, there is significantly less radiation incident upon a vertical cylinder, such as the legs of the elephant, relative to a horizontal cylinder (Gates 1980) and the legs will largely be shaded from direct solar radiation by the body of the animal, therefore, we excluded direct solar radiation in calculation of the irradiation of the legs.

We excluded heat gain from environmental radiation incident upon the ears from the model for several reasons. First, the ears are specialized for heat dissipation and have fine vascular control in these structures which permits elephants to turn blood flow “on” and “off” depending on the thermal status of the animals (Wright 1984; Williams 1990; Phillips & Heath 1992). Thus, the amount of heat absorbed by radiant heat gain that is actually transferred via blood flow to the body core is likely

to be highly dynamic. Second, we have modeled the elephant as always being perpendicular to the sun, thus, one ear will be shaded from direct sunlight at all times and when the sun is at the zenith, direct sunlight on the vertically oriented ears will be minimal. Third, when temperatures are cooler elephants often times will maintain the ears flush against the body, effectively covering the cylinder of the body and reducing the total surface area available for heat loss. In this case, the ears essentially are acting as part of the body wall and heat loss can be assumed to be equivalent to the cylinder model described above for the body. Finally, more detailed skin surface temperature and blood flow measurements are needed under various wind and radiant conditions to effectively estimate how the ears might function under natural conditions.

Convection (H_{Cov})

Natural and forced convection can both be calculated with the same equation:

$$(A-11) \quad \textit{Convective Heat Exchange} = H_{Conv} = h_c A(T_s - T_a)$$

where h_c is the convection coefficient, A is the surface area, and T_s and T_a are the skin and ambient temperature (Gates 1980). The convection coefficient, h_c , differs between the two forms of convective heat transfer reflecting the relative importance of buoyancy forces versus inertial forces which govern natural and forced convective flow respectively. Following the rule of thumb given by Gates (1980) for the relative

importance of free or forced convection and through calculation of the Richardson number, we determined that both forms of convection were likely important for an animal the size of an elephant under the wind velocities (1-3 m s⁻¹) and temperatures that we modeled. The convection coefficient (h_c) is further defined as:

$$(A-12) \quad h_c = \frac{Nu * k}{D_c}$$

where k is the thermal conductivity of the fluid (air or water), and Nu is the Nusselt number, a dimensionless parameter that reflects the ratio of the characteristic dimension, D_c , of the object to the boundary layer thickness surrounding the object. For the characteristic dimensions, we took the diameter of the cylinders for the body or legs and the width of the ear from the cranial to caudal margin. Because h_c will vary with the characteristic dimension of the object and the fluid in which the object is immersed, it was necessary to calculate the coefficient separately for the body, legs, and ears and for when the animal was in air or in water.

For free convection from a horizontal cylinder, a vertical cylinder, and a vertical flat plate the Nusselt number is defined as:

$$(A-13) \quad Nu_{Body} = 0.530(Gr * Pr)^{0.25}$$

$$(A-14) \quad Nu_{Legs} = 0.726(Gr * Pr)^{0.25}$$

$$(A-15) \quad Nu_{Ears} = 0.130(Gr * Pr)^{0.333}$$

where Gr is the Grashof number which is a dimensionless group that reflects the properties that govern the relative buoyancy of a fluid surrounding an object and Pr is the Prandtl number which reflects the static properties of a fluid (Gates 1980; Denny 1993). While the Prandtl number is relatively constant at biologically relevant temperatures for air and water, the Grashof number will vary with the temperature differential between the object and the fluid medium, the coefficient of volumetric expansion with changes in temperature, the kinematic viscosity of the fluid, and the characteristic dimension of the object. Combining the constants for each fluid, the Grashof number in air is defined as:

$$(A-16) \quad Gr_{air} = (1.425 \times 10^8)(D_c^3)(T_s - T_a)$$

and in water is defined as:

$$(A-17) \quad Gr_{water} = (2.015 \times 10^9)(D_c^3)(T_s - T_a)$$

(Gates 1980).

For forced convection the Nusselt number is defined as:

$$(A-18) \quad Nu = cRe^n$$

where c and n are constants which are determined by the magnitude of the Reynolds number (Re). The Reynolds number is a dimensionless group defined as:

$$(A-19) \quad Re = \frac{VD_c}{\nu}$$

where V is the velocity of the fluid moving over the object and ν is the kinematic viscosity of the fluid. For the body, legs, and ears in water and for the body and ears in air the Reynolds number was in the range between 40,000-400,000 and Nu was defined as:

$$(A-20) \quad Nu = 0.024Re^{0.805}.$$

For the legs in air however, the Reynolds number was in the range between 4,000 and 40,000 and thus Nu was defined as:

$$(A-21) \quad Nu = 0.174Re^{0.618}.$$

Emitted Radiation (H_{Rad})

All bodies emit heat according to:

$$(A-22) \quad H_{Rad} = \sigma\varepsilon(T_s^4 - T_a^4) \times 0.85A$$

where σ is the Stephan-Boltzmann constant, ϵ is the emissivity of the skin, and T_s and T_a are in units of absolute temperature (Kelvin). 0.85 is a correction factor to account for the radiant heat exchange between body surfaces in close contact (Gates 1980; Williams 1990). Skin surface temperature was determined from paired empirical measurements of skin surface temperature and ambient temperature across a range of 25°C and at multiple body sites (n=7) (Table 3).

Cutaneous Evaporative Heat and Water Loss (H_{CEHL} and W_{CEWL})

Relationships between cutaneous evaporative water loss and ambient temperature were empirically measured from 7 adult African elephants across a range of 25°C and for the ears and the body separately. These regressions are shown in Table 3. Evaporative water loss was converted to units of heat loss by multiplying by the latent heat of vaporization of water (Table 1). Detailed methods for measurement of evaporative water loss are given in Dunkin (2012).

Respiratory Evaporative Heat and Water Loss (H_{REHL} and W_{REWL})

Respiratory evaporative heat and water loss were simultaneously measured with metabolic heat and water production using open flow respirometry with detailed methods described in Dunkin (2012). Respiratory evaporative water loss was measured only across a subset of ambient temperatures, thus, we tested our empirical results against theoretical water loss rates assuming the air leaving the elephant's trunk was at body temperature, mean skin surface temperature, or ambient

temperature corresponding to minimum, moderate, and maximum water saving strategies respectively. We determined that our empirical results most closely suggested that elephants use a maximum water saving strategy and thus, REWL was calculated according to:

$$(A-23) \quad REWL = 0.0039T_a^2 - 0.029T_a + 1.106.$$

Heat Storage (H_{Store})

Heat storage is negative when body temperature drops below the mean body temperature set point and positive when body temperature rises. In the model, elephants were permitted to undergo heat storage but the magnitude of heat storage was linked to fitness as outlined in Appendix I. Empirical measurements of elephant body temperatures that have recently been reported have shown that elephants do not appear to undergo the large fluctuations in body temperature that have been reported for several arid adapted desert ungulates. However, because detailed measurements of elephants under conditions of water and heat stress have not been performed, we assumed that elephant do have some capacity to tolerate high body temperatures but that there will be a decrement to fitness if body temperature chronically exceeds 42.6°C (see Appendix I for detailed explanation).

Water Intake via Food and Drinking

Preformed water intake with food was linked to ingested caloric intake as described in Appendix I. One of the behavioral choices that simulated elephants could make was to return to the waterhole and drink. Reports for how much water elephants can consume in a single drinking bout range between 50 to greater than 100L (Sikes 1971; Fowler & Mikota 2006). In the model, we considered one bout to last one time step = 1 hour, which is a time frame consistent with wild observations of elephants drinking. We set the maximum intake rate as 100L hr^{-1} with no restriction on how many continuous hours elephants could chose to spend in the waterhole nor how many times they could return to the waterhole per day.

Water Loss via Feces and Urine

Elephants defecate discrete boluses of fairly wet fecal matter. The reported mass of a single bolus ranges between 1-2kg (Sikes 1971; Fowler & Mikota 2006). Defecation rates range between 0.28 and 0.72 times hr^{-1} (Coe 1972; Wyatt & Eltringham 1974; Ruggiero 1992) with a mean of 10.36 kg per evacuation (Coe 1972). The percent water of elephant fecal matter is estimated at 70-80% (Petrides & Swank 1965 in Coe 1972). Thus, we used a continuous rate of 3.9Lhr^{-1} to account for fecal water loss. There are no studies that we are aware of that have measured capacity of elephants to conserve water by producing drier fecal matter, thus, we have used a constant value in the model.

Elephants are reported to produce between 25 and 53 L urine day⁻¹ (reviewed in Fowler & Mikota 2006). We assumed that urine is 100% water and used a constant rate of water loss via urine of 1.63 L hr⁻¹. There are no published data to our knowledge that have tested the elephant's ability to concentrate urine under conditions of water stress.

Table A-3: Simplifying assumptions for thermal and water biophysical models

- 1) The body of the animal is modeled as a horizontal cylinder, the legs as vertical cylinders, and the ears as vertical flat plates (Gates 1980)
 - 2) No heat is lost through urine and fecal output
 - 3) Energy lost to work is ignored.
 - 4) In calculations of radiant heat exchange with the environment the animal remains perpendicular to the sun along the long axis of its body.
 - 5) In calculations of convective heat loss, both natural and forced convection were important based on calculation of the Richardson number and are included in the model.
 - 6) The contribution of pure conductive heat loss through the feet was small and was excluded from the model (this study and Williams 1990).
 - 7) The amount of water taken in through food is a constant based on the number of calories consumed.
 - 8) Fecal and urinary water content are constant and are uncoupled from food and water intake.
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CONCLUSION

The work in the preceding chapters began from questions rooted in physiological concepts including the influence of large body size on thermal and water balance. However, the most important and unique contribution of this work is the integration of these physiological concepts into the larger understanding of elephant ecology and management. In the context of a changing climate, increasing habitat destruction, pollution, and a host of other anthropogenic influences, Carey (2005) argues that physiology can and should make more of a contribution to conservation biology. Cooke and O’Conner (2010) take this argument a step further by discussing some of the specific barriers that have thus far prevented widespread use of physiological approaches to conservation and management problems. Among these barriers, these authors suggest that physiological research, which is typically performed at the whole organism level, must be linked to population level processes through the use of relevant biomarkers (Cooke & O’Connor 2010). Both Carey (2005) and Cooke and O’Connor (2010) note that the established methodologies and track record of physiological research in establishing cause and effect relationships is particularly useful in the context of conservation and management.

The work presented here demonstrates how the whole organism to population level link can be made for a large mammal such as an elephant. In chapters 1 and 2, the mechanism underlying the elephant’s dependence on water is clearly established at both the tissue and whole organism level. Furthermore, the nature of the relationship between water use and ambient temperature was identified as non-linear.

The quantification of this basic biophysical relationship permitted the development of a modeling framework in chapter 3 that successfully predicted non-trivial patterns of spatial and temporal landscape use by elephants. The resulting modeling tool, built upon an understanding of the mechanistic drivers of the elephant's dependence on water, is generalizable and can be easily adapted for direct use by managers. Cooke and O'Connor (2010) stress that this last step, the transformation of physiological information into usable management tools, is a critical but often overlooked step which prevents the widespread incorporation of physiological data into conservation science.

The call for physiological approaches to conservation challenges has grown stronger over the past decade as it becomes clear that a better understanding of how organisms are likely to respond to change, from many fronts, is needed to inform policy and develop evidence based conservation plans. The work presented here was developed in the context of this call and will hopefully be one of an increasing number of studies that undertakes a physiological ecology approach to conservation and management challenges.

Carey, C. (2005) How physiological methods and concepts can be useful in conservation biology. *Integrative and Comparative Biology*, **45**, 4-11.

Cooke, S.J. & O'Connor, C.M. (2010) Making conservation physiology relevant to policy makers and conservation practitioners. *Conservation Letters*, **3**, 159-166.