SEASONAL BIOPHYSICAL VARIATIONS IN RESTING AND EXERCISING
ELEPHANTS: ENERGETIC, THERMOREGULATORY, AND
BEHAVIORAL ADAPTATIONS

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PREFACE

Elephants have always fascinated me. African and Asian elephants are the two largest living terrestrial mammal species. My passion for elephants grew as an undergraduate research assistant and later as a master’s student at Louisiana State University working under the mentorship of Vaughan Langman, PhD. During this time, I was able travel to Kenya and observe elephants in the wild. While in Kenya, I met and collaborated with Professor Geoffrey Maloiy, PhD. who has also had a great influence on my understanding the unique physiological characteristics of large mammals. After losing three years of work as a Ph.D. student in the lab of Patrice Boily, PhD. at the University of New Orleans, to Hurricane Katrina in 2005, I had little to show for my time there except an appreciation for intraspecific variation within species, which had a great influence on forming the questions addressed in this dissertation. Following Hurricane Katrina, I was fortunate to be accepted into George S. Bakken’s PhD. lab at Indiana State University, where my knowledge of biophysical ecology has grown immensely. I am forever indebted to Dr. Bakken for giving a very nontraditional student the opportunity to salvage his academic career. The purpose of this dissertation is to provide a greater understanding of the energetic, thermoregulatory and behavioral responses of elephants to activity and changing environmental conditions. In light of the gigantic size of elephants, the loss of suitable elephant habitat, and the decline in both wild and captive population, the results from this research should be of great interest to physiologists, conservationists, ecologists, and managers of elephants. From September 2008 through December 2009, I traveled almost
continuously between Audubon Zoo in New Orleans, LA, Indianapolis Zoo, Indianapolis, IN, and Pittsburgh Zoo, Pittsburgh, PA, collecting data for this dissertation. I have had the opportunity to work with magnificent elephants and some of the finest free-contact elephant managers and their keeper staffs, in the United States, if not the world. This study would not have been possible without their cooperation and assistance.

“In the end we will conserve only what we love. We will love only what we understand. We will understand only what we are taught.”

Baba Dioum (Senegalese environmentalist, 1968)
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This research would not have been possible without the support and understanding of my family, particularly my daughters Emily and Lily. I am forever indebted to George S. Bakken, PhD. for giving me the opportunity to join his lab in the aftermath of Hurricane Katrina. This research would not have been possible without the very cooperative elephants and their managers and keepers at the Audubon Zoo in New Orleans, LA., Indianapolis Zoo in Indianapolis, IN. and Pittsburgh Zoo in Pittsburgh, PA. In addition, I would like to thank my committee members, including: Michael Angilletta, Ph.D., Diana Hews, PhD., Vaughan Langman, PhD. and Steve Lima, PhD. for their valuable comments and criticisms of this dissertation. Specific contributions are acknowledged in each chapter.
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CHAPTER 1

GENERAL INTRODUCTION

Family Elephantidae

Mammoths (*Mammuths*), and Asian (*Elephas*) and African elephants (*Loxodonta*) comprise the one extinct and two extant Genera of the family Elephantidae. Elephantidae appeared in sub-Saharan Africa between 3 and 6 million years ago (Haynes, 1991; Springer et al., 1997; Krause et al., 2006). Divergence occurred over a relatively short time period, approximately 7% of the total length of the phylogenetic tree for the three lineages (Krause et al., 2006). *Mammuths* went extinct in Africa by the early Pleistocene; however, over time *Mammuths* dispersed throughout the Eurasia steppe and North America temperate grasslands. *Elephas* disappeared from the fossil record in Africa ca. 400,000 years ago; however, it dispersed throughout tropical forests in southern Asia where its home range has been fragmented into relatively small patches of suitable habitat. *Loxodonta* has never left Africa; it inhabits a variety of habitats ranging from tropical forest to semi-arid savanna, and like *Elephas* its former home range has been highly fragmented.

*Mammuths* have been divided into three chronospecies: *M. meridionalis* of the Early Pleistocene [ca. 2.6 to 0.7 million years ago (Ma)], *M. trogontherii* of the Middle Pleistocene [0.7 to 0.5 Ma], and the wooly mammoth *M. primigenius* of the Late Middle and Late Pleistocene [0.35 to 0.01 Ma] (Lister and Sher, 2001; Ukkonen et al., 2007). Over time, *Mammuths* became progressively cold-adapted and underwent a rapid evolution in dental structure in response to a shift from browsing to grazing in open grassland habitats (Lister and

**Mammoth Extinction and the Fate of Modern Elephants**

Although the exact cause remains elusive, a combination of climate change, geographic range contraction and anthropogenic pressure (e.g. hunting) resulted in the extinction of *M. primigenius* approximately 3.6 thousand years ago (Stanley, 1980; Nogués-Bravo et al., 2008; Lorenzen et al., 2011). The prospects for long-term survival of Asian and African elephants are dim. The International Union for the Conservation of Nature (IUCN) classifies Asian and African elephants as threatened and vulnerable species, respectively. Indeed, modern elephants, in the wild, experience similar ecological challenges and anthropogenic pressures that led to the extinction of *Mammuths* (Davidson et al., 2009). The destruction and fragmentation of elephant habitat and poaching of elephants for ivory is having a devastating effect on wild elephant populations (Leimgruber et al., 2003; Fernando et al., 2005; Joshi and Singh, 2008). In addition, the long-term sustainability of captive elephant populations is also uncertain. Sustaining captive elephant populations in North America and Europe, without the importation of wild caught elephants, will be challenging (Olson and Wiese, 2000; Wiese, 2000; Wiese and Willis, 2004 and 2006; Faust et al., 2006). Several factors must be addressed to reverse or reduce the rate of decline in the captive elephant population, including; increasing reproduction rates, lowering rates of infant mortality and increasing variance in the captive gene pool of breeding bulls. Therefore, to increase the chances of survival of both wild and captive elephant populations a
greater understanding of elephant physiology and ecology, and the implementation of science-based management of elephants is imperative at this time.

Physiological Consequences of Gigantic Body Size and Research Objectives

The enormous body size of adult elephants has a dynamic effect on both the energy demands for locomotion and the exchange of thermal energy with the environment (Schmidt-Nielsen 1991; Calder, 1996; Gates, 1980). Per kilogram body mass, elephants have very low energy requirements, and thus heat production (Langman et al., 1995; Langman et al., 2012). However, metabolic heat production (internal heat load) is proportional to volume, while the area through which heat may be exchanged with the environment (external heat transfer) is proportional to surface area. Because metabolic heat production can increase 5-fold in walking elephants, locomotion and thermoregulation may be closely linked. Similarly, heat loss from the skin surface is influenced by the level of radiant environmental heat; therefore, thermoregulation in active elephants may be affected by radiant environmental heat and behavioral choices may be necessary to increase heat loss.

My objective in performing this study was to gain a better understand of the energetic and thermoregulatory consequences of gigantic body size in elephants. By performing this study, I hope to provide a quantitative description of the relationships between the energetic, thermoregulatory and behavioral responses in elephants. I sought to answer four questions. First, do sub-adult and adult elephants exhibit similarity in the mass-specific minimum cost of locomotion? Second, can exercising elephants be used to model the thermoregulatory constraints in endothermic gigantotherms generally? Third, do the pinnae of elephants play a functionally significant role dissipating active metabolic heat production? Fourth, does pinna
flapping increase heat transfer from the pinnae sufficiently to dissipate a large fraction of resting metabolic heat production in elephants?

Intra- and Interspecific Cost of Locomotion

In chapter two, I will address the first question: do sub-adult and adult elephants exhibit similarity in the mass-specific minimum cost of locomotion (COT_{min})? In animals ranging in size from 0.8 g roach to 260 kg zebu steer, the COT_{min} decreases with increasing body size roughly as $COT_{min} \propto \text{body mass}^{-0.316}$ (Taylor et al., 1982; Full and Tu, 1991). Typically, the variation of COT_{min} with body mass is weaker at the intraspecific level as a result of physiological and geometric similarity within closely related species (Griffin et al., 2004). In chapter two, I will describe the quasi-intraspecific relationship between the COT_{min} in sub-adult African and adult Asian elephants and discuss the effect the quasi-intraspecific relationship between COT_{min} and body mass in elephants has on the allometric relationship describing the interspecific decrease in COT_{min} with increasing body mass in animals.

Endothermic Gigantothermy

In chapter three, I will address the second question: can exercising elephants be used to model the proposed thermoregulatory constrains on locomotion in endothermic gigantotherms? Gigantothermy (Paladino et al., 1990) is a combination of ectothermic homiothermy, the maintenance of a relatively high body temperature by vascular adjustments in tissue insulation (Spotila et al., 1973), with inertial homiothermy resulting from large body mass (McNab and Affenberg, 1976). In tropical environments, it has been suggested in both elephants and endothermic dinosaurs that substantial amounts of heat storage in tissues might result in a potentially lethal rise in core body temperature (Spotila et al., 1991; O’Connor and Dodson, 1999). In chapter three I will test the hypothesis that there is a functionally significant
relationship between heat storage and locomotion in adult Asian elephants (*Elephas maximus*), and I will test the proposed thermoregulatory constraints on locomotion in elephants and a similarly sized migratory dinosaur, *Edmontosaurus*. In addition, I will describe how the potentially lethal heat storage in active gigantotherms might be behaviorally regulated by nocturnal activity (Guy, 1976; Douglas-Hamilton et al., 2005; Kinahan et al., 2006; Graham et al., 2009; Joshi, 2009).

Large Pinnae and Activity

In chapter four, I will address the third question: do the large pinnae of elephants play a functionally significant role dissipating metabolic heat production during activity? The only published data describing heat transfer in the pinnae of active elephants is a theoretical model of heat transfer in the pinnae of the fictional flying elephant, *Dumbo* (Phillips and Heath, 2001). Vascular responses in the pinnae of elephants’ suggest that they are “thermal windows” that can be "opened" or "closed" to vary heat loss (Wright, 1984; Williams, 1990; Weissenböck et al. 2010). However, during daylight hours in hot weather, environmental radiation can heat the pinnae surfaces so that heat would be gained rather than lost. In chapter four, I will describe how vasodilatation in combination with behavioral choices affect the portion of active metabolic heat production that can be dissipated via the large pinnae of elephants, and I will discuss the possibility that the pinnae play a more localized thermoregulatory function in regulating brain temperature.

Pinna Flapping

In chapter five, I will address the fourth question: does pinna flapping increase heat transfer from the pinnae sufficiently to dissipate a large fraction of resting metabolic heat production in elephants? Heat transfer resulting from pinna flapping has been estimated to dissipate from 33%
to 100% of resting metabolic heat production and in Asian elephants (Narasimhan, 2008) and African elephants (Phillips and Heath, 1992), respectively. However, these estimates are based on unrealistically large temperature differential between pinna skin and ambient air temperature and equally unrealistic pinna flapping speeds. In the chapter five, I will quantify radiant and convective heat transfer mechanisms in the pinnae of resting Asian and African elephants that are subjected to a wide range of radiant environmental heat loads and free to make behavioral choices that influence heat transfer, such as microclimate selection, pinna position, and pinna flapping rate. In addition, I will discuss further evidence that the pinnae play a more localized thermoregulatory function in regulating brain temperature.
REFERENCES


CHAPTER 2

MINIMUM COST OF TRANSPORT IN ASIAN ELEPHANTS: DO WE REALLY NEED A BIGGER ELEPHANT?

V. A. Langman, M. F. Rowe, T. J. Roberts, N.V. Langman, and C. R. Taylor

ABSTRACT

Body mass is the primary determinant of an animal’s energy requirements. At their optimum walking speed, large animals have lower mass-specific energy requirements for locomotion than small ones. In animals ranging in size from 0.8 g (roach) to 260 kg (zebu steer), the minimum cost of transport ($COT_{\text{min}}$) decreases with increasing body size roughly as $COT_{\text{min}} \propto \text{body mass} \left(M_b\right)^{-0.316 \pm 0.023}$ (95% CI). Typically, the variation of $COT_{\text{min}}$ with body mass is weaker at the intraspecific level as a result of physiological and geometric similarity within closely related species. The interspecific relationship estimates that an adult elephant, with twice the body mass of a mid-sized elephant, should be able to move its body approximately 23% cheaper than the smaller elephant. We sought to determine whether adult Asian and sub-adult African elephants follow a single quasi-intraspecific relationship, and extend the interspecific relationship between $COT_{\text{min}}$ and body mass to 12-fold larger animals. Physiological and possibly geometric similarity between adult Asian elephants and sub-adult African elephants caused body mass to have no effect on $COT_{\text{min}}$, $(COT_{\text{min}} \propto M_b^{0.007 \pm 0.455})$. The $COT_{\text{min}}$ in elephants occurred at a walking speeds between 1.3 and ~1.5 m.s$^{-1}$, and Froude numbers between 0.10 and 0.24. The addition of adult Asian elephants to the interspecific relationship resulted in $COT_{\text{min}} \propto M_b^{-0.277 \pm 0.046}$. The quasi-intraspecific relationship between body mass and $COT_{\text{min}}$ among elephants caused the interspecific relationship to underestimate $COT_{\text{min}}$ in larger elephants.
INTRODUCTION

Body mass is the primary determining factor of an animal’s total energy requirements (Calder, 1984; Schmidt-Nielsen, 1984; West & Brown, 2005; McNab, 2008). Large animals use less energy per kg body mass for locomotion than small animals. African (*Loxodonta africana*) and Asian elephants (*Elephas maximus*) represent the upper limit of body mass in extant terrestrial mammals, and large bulls can weigh up to 7500 kg (Nowak, 1999). Although physiological measurements on elephants are technically challenging, experiments using well-trained captive elephants allow modeling of the biomechanical and energetic characteristics of locomotion in the largest terrestrial mammals (Alexander et al., 1979; Langman et al., 1995; Hutchinson et al., 2003 & 2006; Ren & Hutchinson, 2008 & Ren et al., 2010; Genin et al., 2010).

The mass-specific total cost of transport ($COT_{tot}$) reports the amount of energy required to move a kg of body mass over 1 meter. Animals, including elephants, prefer to walk at a speed near the mid-range within a walking gait, where the $COT_{tot}$ is minimized (Pennycuik, 1975; Hoyt & Taylor, 1981; Taylor et al., 1982; Alexander, 1989; Full & Tu, 1991; Griffin et al., 2004; Rubenson et al., 2007; Maloiy et al., 2009). Because the minimum total cost of transport ($COT_{min}$) provides a biologically meaningful parameter for comparison, Taylor et al. (1982) used data from approximately 90 species of mammals ranging in size from 7g (pygmy mouse) to 260 kg (zebu steer) to develop an interspecific allometric equation that describes the decrease in $COT_{min}$ with increased body mass,

$$COT_{min} = 10.7 \pm 0.663 \ M_b^{-0.316 \pm 0.023},$$  

(1)
where $M_b$ is body mass (kg) [values shown are presented ±95% confidence intervals (CIs)]. To extend the range of data towards the lower limits of body mass, Full & Tu (1991) added reptiles, crustaceans, myriapods and insects with body mass as low as 0.8 g and obtained approximately the same equation as that reported by Taylor et al. (1982), $COT_{\text{min}} = 10.8 M_b^{-0.32}$. To extend the range of data towards the upper limits of body mass, Langman et al. (1995) added sub-adult African elephants, with an average body mass 6 times that of the largest animal used in Taylor et al. (1982). The $COT_{\text{min}}$ of young African elephants were within the 95% CI of equation 1. The application of equation 1 to adult Asian elephants, twice the size of the elephants reported by Langman et al. (1995), estimates that $COT_{\text{min}}$ in larger elephants should be reduced by approximately 23% when compared with $COT_{\text{min}}$ in sub-adult African elephants.

An analysis of intraspecific variability is complementary to interspecific analyses (Bennett, 1987). Because of geometric and physiological similarity, body mass does not have the same effect on $COT_{\text{min}}$ at the intraspecific level, or between closely related species, as it does at the interspecific level. In geometrically similar species, juveniles have the same relative dimensions as adults, just on a smaller scale. As a result, muscle and skeletal morphology of small and large individuals are similar. Both equines and camels show intraspecific geometric similarity. The slope of the intraspecific relationship between $COT_{\text{min}}$ and body mass is nearly flat ($\approx M_b^{0.0}$) in both horses from 90 to 720 kg (Griffin et al., 2004), and in camels from 240 to 580 kg (Yousef et al., 1989; Maloiy et al., 2009), compared with the interspecies relationship, $M_b^{-0.316}$ (Eqn 1). African and Asian elephants, along with extinct mammoths ($Mammuthus$), comprise the family Elephantidae and share common ancestry (Haynes, 1991; Krause et al., 2006). All elephants are graviportal species, i.e. species with column-like limbs and a bone structure that distributes their enormous body mass across a sizeable foot surface (Gray, 1968;
Coombs, 1978; Yates & Kitching, 2003). However, subtle differences in limb geometry exist between African and Asian elephants (Kokshenev & Christiansen, 2010). Sub-adult African and adult Asian elephants might be geometrically similar enough that they follow a quasi-intraspecific relationship, where the decrease in $COT_{\text{min}}$ with increasing body mass is less than $M_b^{-0.316}$.

In this study, we first test the hypothesis that adult Asian elephants and sub-adult African elephants are physiologically similar and geometrically similar enough, as reported in horses and camels, that larger body mass will not bring about a reduction in $COT_{\text{min}}$. If elephants within a 2.5-fold range of body mass are physiologically and geometrically similar, then the slope of $COT_{\text{min}}$ versus body mass will approach $M_b^{0.0}$. Second, we discuss the effect that the addition of elephants, with 12 times the body mass of the largest animal used by Taylor et al. (1982), has on the interspecific relationship between $COT_{\text{min}}$ and body mass. If the intraspecific relationship applies to elephants, then $COT_{\text{min}}$ measured in increasingly larger elephants will show sequentially greater deviation away from $COT_{\text{min}}$ estimated using the interspecific relationship of $M_b^{-0.316}$. Therefore, we have measured the $COT_{\text{min}}$ in adult Asian elephants and combine these results with those for smaller African elephants reported by Langman et al. (1995).

**METHODS AND MATERIALS**

Elephants

Two adult female Asian elephants (Panya and Jean, Table 1) housed at the Audubon Zoo in New Orleans, LA, USA, were used for all of the metabolic measurements. Both elephants were very tractable and well trained by their keepers. Their feeding schedule was unaltered and water was available *ad libitum* except during the exercise trials. All methods were approved by the Audubon Zoo institutional animal care and use committee.
Experimental Procedure

Oxygen consumption was measured using the techniques reported by Langman et al. (1995) to quantify metabolic rates at rest and during exercise from African elephants. The elephants were trained, for one week prior to measurements, to wear a loose fitting mask that enclosed both the trunk and mouth for open-system oxygen consumption measurements. The elephants were fitted with the mask, and metabolic measurements then made while the elephants stood quietly or walked up to three laps around the level 0.5 km oval track in the interior of the zoo (Fig. 1). The mask was connected to a one horse power industrial blower (Dayton, Niles, IL, USA) mounted on a motorized golf cart that was fitted with a bicycle wheel equipped with a calibrated electronic speedometer to record speed. The blower was previously calibrated in laboratory conditions to meter air flow through the mask at a rate of 108 l s$^{-1}$, a flow rate that ensured the elephants’ exhaled air was drawn through the mask. The elephants walked the first lap at a slow pace and sequentially increased speed on the following laps. A small sample of the air flow exiting the mask was collected in a 200 l Douglas bag (Harvard Apparatus, Holliston, MA, USA) over a 5-minute period in the later stages of walks. The sample was analyzed for oxygen concentration with a paramagnetic oxygen analyzer (Taylor Servomex OA272, Woburn, MA, USA). The entire system was calibrated by metering nitrogen into the mask (Fedak et al., 1981) and the accuracy was better than ± 2%.

Data Analyses

Mass-specific total energy expenditure ($EE_{tot}, \text{W} \cdot \text{kg}^{-1}$) is the amount of energy expended per kg body mass, for both the postural cost of standing, i.e. standing metabolic rate, and the energy expended to move the body’s center of mass both horizontally and vertically during locomotion (Schmidt-Nielsen, 1972). The $EE_{tot}$ in the elephants was calculated from the rate of
oxygen consumption recorded during exercise and applying an energetic equivalent of 20.1 J to 1 ml O₂ consumed.

Mass-specific net energy expenditure ($EE_{\text{net}}$) is the amount of energy required for locomotion above that required for the postural cost of standing (Schmidt-Nielsen, 1972). The $EE_{\text{net}}$ was calculated by subtracting resting energy expenditure (Table 1) from $EE_{\text{tot}}$ recorded during exercise. It was not always possible to make resting measurements prior to each exercise trial or make an equal number of trials at each walking speed. Therefore, the mean resting energy expenditure recorded for individual elephants was used to calculate $EE_{\text{net}}$.

Mass-specific $COT_{\text{tot}}$ was calculated by dividing the $EE_{\text{tot}}$ measured during exercise by the speed of locomotion ($ms^{-1}$). The net cost of transport ($COT_{\text{net}}$) estimates the amount of energy required to move a kg of body mass over one meter during locomotion, above that required for standing quietly (Schmidt-Nielsen, 1972). $COT_{\text{net}}$ was calculated by subtracting the average resting energy expenditure of individual elephants from $EE_{\text{tot}}$ prior to dividing by the speed of locomotion.

Energetic similarity between adult Asian and sub-adult African elephants was determined by plotting $COT_{\text{tot}}$ versus Froude number,

$$Fr = v_f^2 / (g * h_{\text{hip}}),$$

(2) a dimensionless measure of speed calculated by dividing the squared forward velocity of locomotion ($v_f^2; ms^{-1}$), by gravitational acceleration ($g, 9.8 ms^{-2}$) and hip height ($h_{\text{hip}}; m$) (Alexander & Jayes, 1983). The $COT_{\text{min}}$ for individual elephants was estimated from second-order polynomial equations that describe the relationship between $COT_{\text{tot}}$, and Froude number. The estimated $COT_{\text{min}}$ was compared with minimum recorded $COT_{\text{min}}$ (Table 2). However, because there was no clearly distinguishable $COT_{\text{min}}$ in adult Asian elephant, we calculated the
mean (± s.d.) $COT_{min}$ by averaging the $COT_{tot}$ measured over the range of Froude numbers that minimized cost in individual elephants (Table 3). The calculated mean $COT_{min}$ was used to develop intraspecific and interspecific allometric relationships between $COT_{min}$ and body mass.

Studies of animal energetics are usually conducted by subjecting animals to evenly spaced increases in treadmill speed (Hoyt & Taylor, 1981; Taylor et al., 1982; Full & Tu, 1991; Griffin et al., 2004; Rubenson et al., 2007; Maloiy et al., 2009). These conditions allow for equal sample sizes of repeated trials at each tread speed. i.e. treatment groups. However, treadmills suitable for elephants are rare, and so our data and those reported by Langman et al. (1995) were obtained by walking zoo elephants on an outdoor track. The resulting small sample size and unpaired continuous data reduced the power of our statistical analyses (Sokal and Rohlf, 1995). KaleidaGraph 4.03 (Synergy Software, Reading, PA, USA) was used for graphing and statistical analyses.

RESULTS

Energy Expenditure

The results of our measurements of resting energy expenditure in Asian elephants (Table 1) were similar to those reported by Benedict (1936). During locomotion at speeds ranging from 0.13 to 2.2 ms$^{-1}$, the $EE_{tot}$ for the larger Asian elephant, Panya, generally was less than that measured for the smaller elephant, Jean (Fig. 2). At the fastest walking speed, $EE_{tot}$ increased approximately 4.5-fold over resting measurements. Over approximately the same range of walking speeds, from 0.4 to 2.5 ms$^{-1}$ the $EE_{tot}$ in sub-adult African elephants reported by Langman et al. (1995) was comparable to $EE_{tot}$ measured in Asian elephant (Fig. 2). Similarly, $EE_{net}$ (Fig. 2) tended to be lower in Panya, the larger elephant. At the fastest walking speed of 2.2 ms$^{-1}$ $EE_{net}$ increased about 11-fold over the slowest walking speed of 0.13 ms$^{-1}$. The $EE_{net}$ in
Asian elephants was comparable to $EE_{\text{net}}$ in sub-adult African elephants reported by Langman et al. (1995).

**Cost of Transport**

Over the range of walking speeds tested, the $COT_{\text{tot}}$ was generally lower in the larger Asian elephant, Panya (Fig. 3). The $COT_{\text{min}}$ values, calculated from the polynomial equation describing the relationship between $COT_{\text{tot}}$ and walking speed, in adult Asian elephants (Fig. 3) were less than recorded $COT_{\text{min}}$. Similarly, the larger elephant, Panya, recorded lower $COT_{\text{net}}$.

The $COT_{\text{net}}$ recorded in Asian elephants in the present study was comparable to $COT_{\text{net}}$ in African elephants reported by Langman et al. (1995). The $COT_{\text{min}}$ calculated from the polynomial equation describing the relationship between $COT_{\text{net}}$ and walking speed, of $0.80 \text{ J.kg}^{-1}\text{m}^{-1}$ recorded in Asian elephants (Fig. 3) was similar to the $COT_{\text{min}}$ of $0.78 \text{ J.kg}^{-1}\text{m}^{-1}$ reported in African elephants (Langman et al., 1995).

**DISCUSSION**

**Optimum Walking Speed in Asian Elephants**

Elephants in nature generally choose to walk at a slow pace and only use fast locomotion when disturbed (Moss, 1988; Douglas-Hamilton et al., 2005; Joshi, 2009). At slow walking speeds kinematic and kinetic variables that define the walking gait in African and Asian elephants are quite similar (Hutchinson et al., 2006; Ren and Hutchinson, 2008; Genin et al. 2010). Analyses of $COT_{\text{tot}}$ and $COT_{\text{net}}$ using polynomial equations (Fig. 3) could not characterize optimum walking speed in Asian elephants because of the similarity in $COT_{\text{min}}$ measurements recorded at speeds between 0.5 and 2.2 $\text{m.s}^{-1}$. However, recorded and estimated $COT_{\text{min}}$ (Table 2 and Fig. 4) occurred at speeds and Froude numbers similar to the biomechanical optimum.
walking speed of approximately 1.3 ms\(^{-1}\), and Froude number of 0.09 reported by Ren and Hutchinson (2008) and Genin et al. (2010).

The minimum walking speed reported here of 0.13 ms\(^{-1}\) was the result of the Asian elephants' willingness to walk at an extremely slow pace, in comparison to the reluctance of young African elephants to walk slower than 0.44 ms\(^{-1}\) (Langman et al., 1995). Therefore, the large difference in COT\(_{\text{tot}}\) between slow walking Asian and African elephants (Fig. 3) is the result of different sampling intervals and not physiological differences between species. The maximum walking speed of Asian and African elephants, 2.2 ms\(^{-1}\) and 2.5 ms\(^{-1}\), respectively, was limited by the maximum speed of the golf cart when heavily loaded with respirometry equipment (Fig. 1), not by the ability of the elephants to walk faster.

Indeed, elephants are capable of fast locomotion; they have a maximum recorded walking speed of 6.8 ms\(^{-1}\) (Hutchinson et al., 2003). However, fast locomotion comes with a high energetic cost (Fig. 2). At fast speeds of locomotion, nearly all animals switch from the pendulum-like mechanism characteristic of the walking gait to a more elastic mechanism characteristic of a running gait (Alexander, 1991). Elephants differ somewhat from this pattern. Elephants exhibit substantial limb compliance during the walking gait (Ren et al., 2010), which defies the characterization of elephants as stiff legged graviportal species (Gray, 1968; Coombs, 1978; Yates & Kitching, 2003). In elephants, limb compliance increases with locomotion speed, which results in increased joint flexion and dampening of ground forces on the limbs (Ren et al., 2010). However, as joint flexion increases a greater muscle volume is required to support the great body mass of elephants (Ren et al., 2010). In response, elephants may experience a linear increase in energy expenditure at walking speeds greater than the maximum we report in the present study. Although we acknowledge the dangers of extrapolation, using the second-order
polynomial equation relating $EE_{\text{tot}}$ to walking speed (Fig. 2, $R^2=0.88$), we estimate that it would require a 26-fold increase $EE_{\text{tot}}$ above rest (Table 1) for the Asian elephants reported here to walk at 6.8 ms$^{-1}$. The estimated increase in $EE_{\text{tot}}$ in fast-walking elephants is comparable to near maximum increases in energy expenditure recorded in donkeys and camels of 22- and 32-fold, respectively (Evans, et al., 1994; Mueller et al., 1994).

Physiological Similarity Between Adult Asian and Sub-Adult African Elephants

African and Asian elephants ranging in body mass from 1435 to 3545 kg are physiologically similar, and geometrically similar enough, that mass-specific $COT_{\text{min}}$ among individual elephants is similar (Table 3 and Fig. 4). However, it should be noted that the whole-animal minimum energetic cost of transport $COT_{\text{min}}$ (Jm$^{-1}$), the ecologically relevant level of analyses, indicates that the two larger Asian elephants would require 1.6- to 2.4-fold more energy for locomotion than the three smaller African elephants (Table 3). Some populations of both African and Asian elephants engage in seasonal migrations (Guy, 1976; Sukumar, 1989; Tchamba, 1993; Thouless, 1995; Joshi, 2009). As a result of variations in whole animal $COT_{\text{tot}}$ between adult and sub-adult elephants, migration, might result in differential intraspecific energetic challenges, a topic worthy of further investigation.

The recorded mean (±s.d.) $COT_{\text{min}}$ in all elephants occurred over a narrow range of Froude numbers (Table 3 and Fig. 4). The equation describing the quasi-intraspecific relationship between $COT_{\text{min}}$ and body mass within elephants is, $COT_{\text{min}} = 1.44±0.07 M_b^{0.007±0.455}$, $R^2 = 0.01$ (Fig. 5). Within elephants, the $COT_{\text{min}}$ is not a function of $M_b^{-0.316}$, as is characteristic of the interspecific relationship Eqn 1 reported by Taylor et al. (1982), but is a function of $M_b^{0.0}$ characteristic of the intraspecific relationship reported in horses and camels (Yousef et al., 1989; Griffin et al., 2004; Maloiy et al., 2009).
Do We Really Need a Bigger Elephant?

Adult Asian and sub-adult African elephants are physiologically similar, and geometrically similar enough, to influence the interspecific relationship between $COT_{\text{min}}$ and body mass. The addition of Asian elephants, with a 12-fold increase in body mass over the largest animal used by Taylor et al. (1982), produced an allometric relationship for mammals ranging in size from 7 g to 3545 kg ($COT_{\text{min}} = 11.9 \pm 3.30 M_b^{-0.277\pm0.046}$; Fig. 5).

The mean $COT_{\text{min}}$ in two adult Asian elephants (Table 3) was approximately the same as the mean $COT_{\text{min}}$ in three sub-adult African elephants reported by Langman et al. (1995), not 23% lower as estimated by Eqn 1. The difference between of $COT_{\text{min}}$ measured in elephants and $COT_{\text{min}}$ predicted by equation 1 was due to the influence of physiological similarity within elephants. The mean $COT_{\text{min}}$ in individual elephants (Table 3) ranged from 27 to 88% above $COT_{\text{min}}$ predicted by Eqn 1. If the intraspecific relationship is extrapolated to even larger elephants, physiological similarity will cause greater divergence from the Taylor et al. equation. It is unlikely that the $COT_{\text{min}}$ in a larger elephant (with a body mass of 7500 kg) would be significantly lower than the values we report here. Based on the slopes of the relationship between $COT_{\text{min}}$ and body mass within elephants, i.e. $M_b^{0.007}$, and that of the interspecific relationship, i.e. $M_b^{-0.316}$, the $COT_{\text{min}}$ of a large bull elephants will be approximately 138% above that predicted by Eqn 1.

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Mechanical stress in fast locomotion of buffalo (Syncerus caffer) and elephant (Loxodonta africana). J. Zool. Lond. 189, 135 - 144.


Fig. 1. Open-system measurement of resting oxygen consumption in a female Asian elephant prior to exercise at Audubon Zoo, New Orleans, LA, USA.

Table 1. Characteristics and mean (±s.d.) resting mass-specific energy expenditure in two Asian elephants.

<table>
<thead>
<tr>
<th>Elephant</th>
<th>Age (years)</th>
<th>Mass (kg)</th>
<th>Energy Expenditure (Wkg^{-1})</th>
<th>Trials (n)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Panya</td>
<td>31</td>
<td>3545</td>
<td>0.74±0.11</td>
<td>10</td>
</tr>
<tr>
<td>Jean</td>
<td>23</td>
<td>2682</td>
<td>0.77±0.11</td>
<td>10</td>
</tr>
</tbody>
</table>

Note: these measurements were similar to a resting energy expenditure of 0.60 W.kg^{-1} in a female Asian elephant (3672 kg) reported by Benedict (1936).
Fig. 2. Mass-specific total and net energy expenditure ($EE_{\text{tot}}$ and $EE_{\text{net}}$, W.kg$^{-1}$) in two adult Asian elephants (Panya, red circles; Jean, blue squares) at walking speeds ranging from 0.13 to 2.2 ms$^{-1}$. The equation describing the curvilinear increase in $EE_{\text{tot}}$ with walking speed is, $EE_{\text{tot}} = 0.35 v_f^2 + 0.42 v_f + 0.75$, $R^2=0.88$, where $v_f$ is walking speed in ms$^{-1}$. The equation describing the curvilinear increase in $EE_{\text{net}}$ with walking speed is, $EE_{\text{net}} = 0.38 v_f^2 + 0.32 v_f + 0.08$, $R^2=0.75$. The mean $EE_{\text{tot}}$ and $EE_{\text{net}}$ in three sub-adult African elephants (dashed lines) walking at speeds ranging from 0.44 to 2.5 ms$^{-1}$ reported by Langman et al. (1995) are presented for comparison.
Fig. 3. Mass-specific total and net cost of transport \((COT_{tot} \text{ and } COT_{net}, \text{J.kg}^{-1}\text{m}^{-1})\) in two Asian elephants (Panya, red circles; Jean, blue squares) at walking speeds from 0.13 to 2.2 m.s\(^{-1}\). The equation describing the curvilinear relationship between \(COT_{tot}\) and walking speed is \(COT_{tot} = 2.8 v_f^2 - 8.7 v_f + 7.8, R^2=0.85\), where \(v_f\) is walking speed in m.s\(^{-1}\). Note that the curve for Asian elephants is strongly affected by the high leverage of the data points at the exceptionally slow walking speed of 0.13 m.s\(^{-1}\), and thus the walking speed for minimum \(COT\) \((COT_{min})\) is not clearly defined. The equation describing the curvilinear relationship between \(COT_{net}\) and body mass is \(COT_{net} = 0.64 v_f^2 - 1.6 v_f + 1.8, R^2=0.40\). The mean \(COT_{tot}\) and \(COT_{net}\) in three sub-adult African elephants (dashed lines) walking at speeds ranging from 0.44 to 2.5 m.s\(^{-1}\) reported by Langman et al. (1995) is presented for comparison.
Table 2. Minimum mass-specific total cost of transport ($COT_{\text{min}}$) recorded in elephants, the Froude number ($Fr$) at which $COT_{\text{min}}$ occurred, second-order polynomial equations and estimated $COT_{\text{min}}$ in three African and two Asian elephants.

<table>
<thead>
<tr>
<th>Genus</th>
<th>Elephant</th>
<th>Mass (kg)</th>
<th>Hip Height (m)</th>
<th>$COT_{\text{min}}$ Recorded (Jkg$^{-1}$m$^{-1}$)</th>
<th>Fr</th>
<th>Polynomial Equation</th>
<th>$COT_{\text{min}}$ Estimated (Jkg$^{-1}$m$^{-1}$)</th>
<th>$R^2$</th>
<th>Trials (n =)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Loxodonta</td>
<td>Kelly</td>
<td>1435</td>
<td>1.52</td>
<td>*1.35</td>
<td>0.11</td>
<td>$16.7Fr^2 - 6.96Fr + 2.27$</td>
<td>1.54</td>
<td>0.56</td>
<td>12</td>
</tr>
<tr>
<td></td>
<td>Tara</td>
<td>1525</td>
<td>1.55</td>
<td>*1.19</td>
<td>0.12</td>
<td>$84.7Fr^2 - 25.8Fr + 3.18$</td>
<td>1.21</td>
<td>0.98</td>
<td>5</td>
</tr>
<tr>
<td></td>
<td>Dottie</td>
<td>1667</td>
<td>1.53</td>
<td>1.62</td>
<td>0.14</td>
<td>$86.0Fr^2 - 17.5Fr + 2.51$</td>
<td>1.62</td>
<td>1.21</td>
<td>3</td>
</tr>
<tr>
<td>Elephas</td>
<td>Jean</td>
<td>2682</td>
<td>1.68</td>
<td>1.34</td>
<td>0.09</td>
<td>$181.6Fr^2 - 56.1Fr + 5.36$</td>
<td>1.03</td>
<td>0.58</td>
<td>15</td>
</tr>
<tr>
<td></td>
<td>Panya</td>
<td>3545</td>
<td>1.83</td>
<td>1.11</td>
<td>0.08</td>
<td>$112.5Fr^2 - 37.1Fr + 3.94$</td>
<td>0.88</td>
<td>0.60</td>
<td>24</td>
</tr>
</tbody>
</table>

Table 3. Range of Froude numbers ($Fr$), and mean (± s.d.) walking speed, mass-specific minimum cost of transport ($COT_{\text{min}}$), and whole animal $COT_{\text{min}}$ recorded in three African and two Asian elephants.

<table>
<thead>
<tr>
<th>Genus</th>
<th>Elephant</th>
<th>Mass (kg)</th>
<th>Froude Range</th>
<th>Speed (m$^{-1}$)</th>
<th>$COT_{\text{min}}$ (Jkg$^{-1}$m$^{-1}$)</th>
<th>$COT_{\text{min}}$/elephant (Jm$^{-1}$)</th>
<th>Trials (n =)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Loxodonta</td>
<td>Kelly</td>
<td>1435</td>
<td>0.11 – 0.24</td>
<td>1.5 ± 0.2</td>
<td>1.54 ± 0.13</td>
<td>2210 ± 187</td>
<td>5</td>
</tr>
<tr>
<td></td>
<td>Tara</td>
<td>1525</td>
<td>0.12 – 0.19</td>
<td>1.5 ± 0.2</td>
<td>1.33 ± 0.17</td>
<td>2029 ± 260</td>
<td>3</td>
</tr>
<tr>
<td></td>
<td>Dottie</td>
<td>1667</td>
<td>0.10 – 0.14</td>
<td>1.4 ± 0.1</td>
<td>1.69 ± 0.09</td>
<td>2817 ± 150</td>
<td>2</td>
</tr>
<tr>
<td>Elephas</td>
<td>Jean</td>
<td>2682</td>
<td>0.10 – 0.17</td>
<td>1.5 ± 0.2</td>
<td>1.66 ± 0.22</td>
<td>4452 ± 590</td>
<td>7</td>
</tr>
<tr>
<td></td>
<td>Panya</td>
<td>3545</td>
<td>0.10 – 0.17</td>
<td>1.5 ± 0.2</td>
<td>1.42 ± 0.15</td>
<td>5034 ± 532</td>
<td>9</td>
</tr>
</tbody>
</table>
Fig. 4. Second-order polynomial equations (Table 2) describing the quasi-intraspecific relationships between total cost of transport ($COT_{\text{tot}}$) and Froude number in two adult Asian elephants (Panya, red solid line and Jean, blue solid line) and three sub-adult African elephants (Kelly, dotted line; Tara, short dashed line; Dottie, long dashed line). The recorded and estimated minimum cost of transport ($COT_{\text{min}}$) occurred over a narrow range of Froude numbers.
Fig. 5. Interspecific relationship between minimum cost of transport ($COT_{\text{min}}; \text{J.kg}^{-1}\text{m}^{-1}$) and body mass ($M_b; \text{kg}$) in terrestrial animals ranging in size from 0.8 g to 3545 kg. The relationship between $COT_{\text{min}}$ and body mass in reptiles, amphibians, crustaceans, myriapods and insects ranging in size from 0.8 g to approximately 1 kg is represented by the allometric equation, $COT_{\text{min}} = 10.8 M_b^{-0.32}$ (dotted line), reported by Full and Tu (1991). The relationship between $COT_{\text{min}}$ and body mass in mammals ranging in size from 7 g to 260 kg is represented by the allometric equation, $COT_{\text{min}} = 10.7 \pm 0.663 M_b^{-0.316 \pm 0.023}$ (95% CI) (solid line), reported by Taylor et al. (1982). The addition of adult Asian elephants and sub-adult African elephants (blue circles) to data from Taylor et al. (1982) data produced the equation, $COT_{\text{min}} = 11.9 \pm 3.30 M_b^{-0.277 \pm 0.046}$ (95% CI) (long dashed line). The quasi-intraspecific relationship within elephants is described by the allometric equation $COT_{\text{min}} = 1.43 \pm 0.07 M_b^{0.007 \pm 0.455}$ (95% CI) (solid line). We estimate the $COT_{\text{min}}$ in a large (7500 kg) elephant (red diamond) to be approximately 1.52 J.kg$^{-1}$m$^{-1}$. 
CHAPTER 3

HEAT STORAGE IN ASIAN ELEPHANTS DURING SUBMAXIMAL EXERCISE:
BEHAVIORAL REGULATION OF THERMOREGULATORY CONSTRAINTS ON
ACTIVITY IN ENDOThERMIC GIGANTOTHERMS

M.F. Rowe, G.S. Bakken, J.J. Ratliff, and V.A. Langman

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ABSTRACT

Gigantic size presents both opportunities and challenges in thermoregulation. Allometric scaling relationships suggest that gigantic animals have difficulty dissipating metabolic heat. Large body size permits the maintenance of fairly constant core body temperatures in ectothermic animals by means of gigantothermy. Conversely, gigantothermy combined with endothermic metabolic rate and activity likely results in heat production rates that exceed heat loss rates. In tropical environments, it has been suggested that substantial amounts of heat storage in tissues might result in a potentially lethal rise in body temperature in both elephants and endothermic dinosaurs. However, the behavioral choice of nocturnal activity might reduce heat storage. We sought to test the hypothesis that there is a functionally significant relationship between heat storage and locomotion in Asian elephants (*Elephas maximus*), and model the thermoregulatory constraints on a similarly sized migratory dinosaur, *Edmontosaurus*. Pre- and post-exercise (n = 37 trials) measurements of core body temperature and skin temperature, using thermography were made in two adult female Asian elephants, at the Audubon Zoo in New Orleans, Louisiana, USA. Measurements were made over three seasons at ambient air temperatures ranging from 8 to 34.5°C. When elephants exercised in full sun between 56% and 100% of active metabolic heat production was stored in tissues. We estimate that during nocturnal activity, in the absence of solar radiation, between 5% and 64% of metabolic heat production would be stored in tissues. Potentially lethal heat storage in active elephants and *Edmontosaurus* could be behaviorally regulated by nocturnal activity.
INTRODUCTION

Scaling relationships suggest that gigantic animals have difficulty dissipating metabolic heat. Resting metabolic heat production, $M$, is proportional to body mass, $m_b$, for mammals $M \propto m_b^{0.75}$ and $M \propto m_b^{0.83}$ in reptiles, while the total skin surface area, $A$, is proportional to $m_b^{0.67}$ (Benedict, 1932; Benedict, 1936; Calder, 1984; Schmidt-Nielsen, 1984). Therefore, as $m_b$ increases, $M$ increases at a faster rate than $A$ ($M/A \propto m_b^{0.08-0.16}$). Further, the distance, $x$, that heat must be transferred from metabolically active organs in the body core to the skin surface increases with body size ($x \propto m_b^{0.33}$). Gigantic animals are thus predisposed to storage of metabolic heat in core tissues.

Gigantic size presents both opportunities and challenges in thermoregulation. On one hand, large body size permits the maintenance of fairly constant core body temperatures in animals with low reptile-like metabolic rates by means of gigantothermy (Paladino et al., 1990). Gigantothermy is a combination of ectothermic homiothermy (Spotila et al., 1973), the maintenance of a relatively high body temperature by vascular adjustments in tissue insulation (Fig. 1), with inertial homiothermy resulting from large body mass (McNab and Affenberg, 1976). Gigantothermy has been demonstrated in leatherback turtles (Dermochelys coriacea) with adult body mass up to 900 kg and hypothesized for an approximately 3700 kg migratory dinosaur, Edmontosaurs, assumed to have a low reptile-like metabolism (Paladino et al., 1990; Spotila et al., 1991).

However, gigantothermy combined with a high mammal-like metabolic rate and activity likely results in heat production rates exceeding heat loss rates (Spotila et al., 1991; O’Connor
and Dodson, 1999). In tropical environments, it has been sugested in both elephants and endothermic dinosaurs that substantial amounts of heat storage in tissues might result in a potentially lethal rise in core body temperature (Spotila et al., 1991; O’Connor and Dodson, 1999). Indeed, studies of both wild and domesticated elephants have found that activity can result in a rapid increase in core temperature, ranging from 0.5 to 6.0 °C (Baldwin, 1974; Toscano et al., 2001). However, by concentrating activity at night, when radiant environmental heat is at a minimum (Elder and Rogers, 1975; Guy, 1976; Douglas-Hamilton et al., 2005; Kinahan et al., 2006; Graham et al., 2009; Joshi, 2009), elephants may behaviorally reduce the amount of metabolic and environmental heat stored in tissues and facilitate activity without risk of a lethal increase in core body temperature.

Mathematical heat transfer models have provided valuable estimates of thermoregulatory constraints on gigantotherms with low reptile- or high mammal-like metabolism (Spotila et al., 1991; O’Connor and Dodson, 1999). Few living animal models are available for validating computer models of gigantothermy. However, well trained captive elephants are large, tractable, and utilize vascular adjustments to regulate heat transfer from the body core to the skin surface (Phillips and Heath, 1995). Therefore, captive elephants are an excellent model for thermoregulatory constraints on activity in endothermic gigantotherms. In the present study, we use active Asian elephants (*Elephas maximus*) as a model animal for endothermic gigantothermy, much as leatherback turtles have been used as models for ectothermic gigantothermy (Paladino et al., 1990).

Specifically, we test the hypothesis that there is a functionally significant relationship between heat storage and locomotion in elephants, and that this relationship is sensitive to the level of radiant environmental heat (Fig. 2). Several studies have reported on the energy budgets
of resting elephants in both outdoor (Hiley, 1975; Rowe, 1999) and indoor conditions (Williams, 1990). However, no published studies have examined thermoregulation of active elephants in quasi-natural context where they are subjected to a wide range of environmental heat loads. Specifically, we expect to shed light on the thermoregulatory constraints on endothermic gigantotherms, and use these results to model and discuss behavioral regulation of heat storage resulting from activity in elephants and a similarly sized dinosaur, *Edmontosaurus*.

**METHODS AND MATERIALS**

**Elephants**

Two adult female Asian elephants *Elephas maximus* Linnaeus 1758 (Panya and Jean; Table 1), at the Audubon Zoo in New Orleans, LA, USA were used for all of the measurements. Both elephants were managed in free-contact with keepers, and were very tractable and well trained. Their feeding schedule was unaltered and water was available *ad libitum* except during the exercise trials. All methods were approved by the Indiana State University and the Audubon Zoo Institutional Animal Care and Use Committees. As is commonly the case when working with large, rare animals, sample size was limited by availability. Thus, our results are strictly valid only for these two elephants, but we have no reason to believe they are not typical.

**Experimental Procedures**

All of the exercise trials during the June 2009 study period were started before 1000 h (1500 UTC) or after 1720 h CDT (2220 UTC). During the February and November 2009 study periods, all trials were started in before 1000 h CST (1600 UTC). At the start of each exercise trial the elephant(s) were led by their keepers from the exhibit area into the barn or to a shaded area outside of the elephant exhibit, where thermograms and rectal temperatures were recorded. Thermograms of the elephants and track were recorded using a FLIR ThermaCAM™ PM575 (FLIR inc., Portland, OR) radiometric thermal imaging camera (sensitivity of ca. ±0.1°C) fitted
with a 45° lens. Images were taken from a distance of approximately 5 m from the elephant. The mean (±s.d.) temperature (°C) of the elephants’ skin, $T_r$ (Fig.3), and the track surface temperatures, $T_g$ (°C), were measured using ThermaCAM™ Researcher Professional version 2.7 software (FLIR inc., Portland, OR). Thermal radiation was converted to surface temperatures using concurrently recorded ambient air temperature and relative humidity and assuming radiating surface emissivities were 0.96 for elephant skin and 0.93 for asphalt (Gates, 1980).

As a measure of core body temperature (°C), rectal temperature, $T_b$ (Fig. 3), was measured for 5 to 7 minutes prior to the start of each exercise trial using a 35 cm thermocouple probe attached to a COMARK N9002 (COMARK, Ltd., Hitchin, United Kingdom) thermocouple thermometer (accuracy ±0.1°C). We attached an accelerometer (SENSR, GP1 programmable accelerometer, Elkader, IA) on the right rear leg of the elephants to provide a time stamp for determining walking speed. The elephants either walked one lap (945 m) or two laps (1614 m) around a closed circuit at speeds ranging from 0.56 to 1.25 ms$^{-1}$ (Table 2). The length of the track was measured using a Bushnell (Yardage Pro Compact 800, Bushnell Corp. Overland Park, KS) range finder, and average speed computed by dividing track length by time needed to complete the circuit. At the end of each trial thermograms and rectal temperatures were again recorded.

Environmental conditions needed for heat transfer calculations (Table 3) were recorded during exercise trials. Parameters were measured every five-minutes, and averaged and recorded every thirty-minutes using a HOBO® Micro-Station (Onset Computer Corp. Bourne, MA). The station was located in an exposed position on the periphery of the exercise track. A shielded thermistor measured ambient air temperature, $T_a$ (±0.2 °C), a capacitive humidity sensor measured relative humidity, RH% (±2.5%; used to correct thermograms) and a cup anemometer measured sustained wind speed ($u$, ±1.1ms$^{-1}$). A silicon pyranometer measured (±10 Wm$^{-2}$)
global solar radiation, and a second silicon pyranometer shielded from direct sunlight by a shade ring measured diffuse solar radiation. Direct solar radiation was determined by subtracting diffuse from global and dividing by the cosine of the zenith angle of the sun. Zenith angle at the time of each exercise trial was determined using the online solar position calculator available at the U.S. Department of Commerce, www.esrl.noaa.gov/gmd/grad/solcalc. The sensors were set at elephant head height (i.e., 2 to 2.75 m above ground).

Data Analysis

Thermal Energy Budget

We computed seasonal thermal energy budgets of exercising elephants using a modified version of the non-steady-state thermal energy budget developed by Porter and Gates (1969),

\[ M_{ex} - E_b = \pm Q_n + C_{ex} + K \pm X, \]  

(1)

Here, \( M_{ex} \) (W) is active metabolic heat production, \( E_b \) (W) is respiratory evaporative heat loss, \( Q_n \) (W) is net radiation heat transfer, \( C_{ex} \) is convective heat exchange with air, \( K \) (W) is conductive heat exchange with the ground, and \( X \) (W) is heat stored or released by a change in core body temperature.

Active Metabolic Heat Production

The metabolic heat production during exercise, \( M_{ex} \) was estimated from an earlier study of the same Asian elephants (Langman et al., 2012). They described metabolic heat production during exercise with the polynomial regression,

\[ M_{ex} = 0.35 v_f^2 + 0.42 v_f + 0.75, \]  

(2)

Here, mass-specific metabolic heat production is \( M_{ex} = M/m_b \) (W kg\(^{-1}\)), and walking speed is \( v_f \) (m s\(^{-1}\); Table 2). Mass-specific metabolic heat production for each exercise trial was converted to whole-animal heat production \( M_{ex} \) (W) in this study by multiplying the estimated mass-specific
measurements by the current body mass of each elephant (Table 1). Seasonal mean (±s.d.) $M_{ex}$ (Table 2) was estimated by pooling whole-animal $M_{ex}$ estimates for individual elephant trails ($n = 37$) and dividing by the number of exercise trials conducted during a season (Table 2).

**Evaporative Heat Loss**

Evaporative heat loss, $E$, has both skin, $E_r$, and respiratory, $E_b$, components. Asian elephants may increase skin evaporative heat loss by wallowing and bathing (Lillywhite & Stein, 1987), but not by sweating, as the only sweat gland identified in Asian elephants are located interdigitally (Lamps et al., 2001). Therefore, $E_r$ is assumed negligible as the elephants were dry at the start of the trials. We estimated $E_b$ ($W$; Table 2) using Langman's equation (1985) where,

$$E_b = V*2*[c_p * (T_E - T_I) * \rho_E + (W_E - W_I) * \lambda].$$

Here, $V$ is the estimated respiratory minute volume (ca. 5.2±1.1 l s$^{-1}$, Benedict, 1936), multiplied by two to account for the approximate two-fold increase in $M_{ex}$ resulting from exercise. The heat capacity of air is $c_p$ (1003.5 J°C$^{-1}$kg$^{-1}$), $T_E - T_I$ is the temperature of exhaled minus inspired air (°C), $\rho_E$ is the density of air (0.0011 to 0.0012 kg l$^{-1}$ air), $W_E - W_I$ is the water content of exhaled air minus inspired air (mg H$_2$O l$^{-1}$ air), and $\lambda$ is the latent heat of vaporization ($\approx$ 2.43 Jmg$^{-1}$ H$_2$O). Exhaled air temperature $T_E$ was estimated to be approximately 31.3±0.95 °C based on the mean of the maximum $T_E$ recorded in elephants ($n = 3$) exposed to $T_a$'s of 12.5° to 25.3 °C (Benedict, 1936).

**Effective Tissue Insulation**

We estimated effective tissue insulation, $I$ (m$^2$ s °C J$^{-1}$), using data from individual elephants where,

$$I = (T_b - T_i) / (M_{ex} - E_b).$$
Here, \( T_b \) minus \( T_r \) is the temperature gradient (°C) between body core and skin and \( M_{ex} \) minus \( E_b \) is dry active metabolic heat production (Wm\(^{-2}\)) (Gates, 1980). The means of pre- and post-exercise \( T_b \) and \( T_r \) (Fig. 3) were used to calculate \( I \) during exercise (Fig. 4).

**Radiant Heat Transfer**

Radiant heat transfer was averaged over 1 or 2 complete circuits of the track during which the elephants rotated 360° relative to directional radiation sources. Thus, we approximated the elephants by a sphere (O’Connor and Spotila, 1992) for radiation calculations (Table 1). The whole-animal net radiant heat exchange, \( Q_n \) (W), during each exercise event was calculated by subtracting radiant environmental heat absorbed, \( Q_a \) (W), from thermal radiation emitted from the skin surface, \( R_s \) (W), so that net heat loss is defined as positive and net heat gain is defined as negative,

\[
Q_n = R_s - Q_a. \tag{5}
\]

The whole-animal \( R_s \), during each exercise trial was calculated from the mean of pre- and post-exercise \( T_r \) (°C) measured by radiometric thermal images (Fig. 3),

\[
R_s = \sigma \varepsilon A(T_r + 273)^4. \tag{6}
\]

Here, \( \sigma \) is the Stefan-Boltzmann constant \( 5.67 \times 10^{-8} \text{ Wm}^{-2}\text{K}^{-4} \), \( \varepsilon \) is skin emissivity of 0.96 (Gates, 1980), and \( A \) is the total skin surface area in m\(^2\) (Table 1).

The whole-animal rate of heat gain from environmental radiation \( Q_a \) (W), is the sum of radiation absorbed from short wave solar plus long wave thermal radiation from the atmosphere and ground:

\[
Q_a = \alpha_1 A_1 S_n + \left[ \alpha_1 A_2 s + \alpha_1 A_2 r s (S_h + s) + \alpha_2 A_2 (R_a + R_g) \right]. \tag{7}
\]

The absorptance of elephant skin for short wave solar radiation is \( \alpha_1 \) (Table 1), \( S_n \) (Wm\(^{-2}\); Table 3) is the solar radiation falling on a plane perpendicular to the sun’s rays, \( S_h \) (Wm\(^{-2}\); Table 3) is
the solar radiation falling on a horizontal surface, \( s \) (Wm\(^{-2}\); Table 3) is diffuse solar radiation, \( S_{h} + s \) is the total shortwave radiation falling on the horizontal surface, and \( r \) is the reflectance (0.15) of the asphalt track surface. The cross-sectional area of the spherical elephant is \( A_{1} \) (m\(^{2}\); Table 1), \( A_{2} \) is 50\% of the total surface area of the spherical elephant (Table 1). For long wave thermal radiation, the absorptance and emittance of elephant skin are equal, \( \varepsilon = \alpha_{2} \approx 0.96 \) (Gates, 1980).

Atmospheric thermal radiation, \( R_{a} \) (Wm\(^{-2}\); Table 3), was estimated by using the modified Swinbank (1963) relation,

\[
R_{a} = 1.22 \sigma (T_{a} + 273)^{4} - 171,
\]

where \( T_{a} \) (°C; Table 3) is the mean of pre- and post-exercise values recorded at the environmental station. Thermal radiation emitted by the ground (track), \( R_{g} \) (Wm\(^{-2}\); Table 3),

\[
R_{g} = \sigma \varepsilon (T_{g} + 273)^{4},
\]

where \( T_{g} \), (°C) is mean of pre- and post-exercise radiant temperature of the track as recorded in the thermograms.

Seasonal mean (±s.d.) \( Q_{n} \) (Table 4) were then estimated from means of \( R_{s} \) and \( Q_{a} \) from individual elephant by pooling estimates for each trail and dividing by the number of exercise trials conducted during a season.

**Convective Heat Transfer**

Heat loss by convection during exercise, \( C_{cx} \) (W), was calculated using the empirical relation,

\[
C = h_{c} A (T_{r} - T_{a}).
\]

The convection coefficient, \( h_{c} \) (Wm\(^{-2}\)°C\(^{-1}\)), was estimated using the approximation developed by Mitchell (1976) to describe convection from a variety of species, \( A \) is the total surface area (m\(^{2}\)).
of the elephant (Table 1) and $T_r$ minus $T_a$ is the temperature gradient (°C) between elephant and surrounding air. When the elephants were walking, both environmental wind, $u$ (ms$^{-1}$), and wind created by walking speed, $v_f$ (ms$^{-1}$), contributed to exercise convection $C_{ex}$ (W). We were unable to determine the direction of $u$ in relationship to the elephants when they were walking on an oval track. Therefore, we chose to use the higher of the two wind speed values and a turbulent enhancement of 1.3 (Mitchell, 1976) to estimate the $h_c$. Seasonal mean (±s.d.) $C_{ex}$ (Table 4) were then estimated from $C_{ex}$ from individual elephants by pooling estimates for each trail and dividing by the number of exercise trials conducted during a season.

**Conductive Heat Transfer**

Conductive heat loss, $K$ (W), refers to heat exchanged through the area of contact between the plantar surface of elephant’s feet and the supporting ground surface. During locomotion the bottom of the elephants’ feet is only in contact with the ground a small portion (i.e., the stance phase) of a stride. No skin temperatures of the bottom of the elephant’s feet were recorded. Published estimates indicate that $K$ through the plantar skin surface accounts for $< 2\%$ of the total heat loss in a standing elephants (Hiley, 1975; Williams, 1990; Rowe, 1999). In addition, during the June trials track temperature was hotter than core body temperature, which would cause a conductive heat gain. Therefore, we omitted conductive heat transfer $K$ due to its minor contribution to overall thermal balance.

**Heat Storage**

Heat storage, $X$ (W), occurs when core body temperature changes. The basic heat storage relation (Bakken and Gates, 1975) is,

$$X = 3430 \times (\Delta T_b / \Delta t) \times m_b.$$  

(11)
Here $3430 \text{Jkg}^{-1}\text{°C}^{-1}$ is the specific heat of tissue (Gates, 1980), $\Delta T_b \text{ (°C)}$ is the difference between pre- and post-exercise core body temperature, and $\Delta t \text{ (s)}$ is the duration of the exercise event and $m_b$ is the total body mass (kg). Seasonal mean (±s.d.) $X$ (Table 4) were then estimated from $X$ from individual elephants by pooling estimates for each trail and dividing by the number of exercise trials conducted during a season. Because of their gigantic body size, internal thermal gradients may exist in the core tissues of elephants. Therefore, it is difficult to determine whether core temperatures (i.e., rectal temperatures) represent the temperature of the entire internal tissue mass of the elephants. Thus, we estimated the effect of effective body core size on heat storage by varying $m_b$ from 50% to 100% of total body mass (Fig. 5).

*Behavioral Regulation of Heat Transfer and Heat Storage*

We modeled behavioral regulation of heat transfer in elephants by modeling thermal energy budgets based on exercise in full sun, $Q_{a\text{sun}}$ (Eqn 6), and nocturnal exercise, $Q_{a\text{night}}$, by excluding direct, diffuse and reflected solar radiation ($\alpha_1*A_1*S_n + [\alpha_1*A_2*s + \alpha_1*A_2*r*(S_n + s)]$) from the environmental radiation computation (Eqn 6). We modeled seasonal changes and behavioral regulation of heat storage by adjusting heat storage, $X_{adj} \text{ (W)}$, to balance heat gains and losses (Fig. 6A and B). To make estimates of the effective core size required for $X_{adj}$ to balance heat gains and losses, we used the seasonal linear regressions describing the relationship between $X_{adj}$ and effective core size (Fig. 5). Our model of $X_{adj}$ bases heat storage on seasonal mean (±s.d.) post-exercise increases in core body temperature (Fig. 5), in a core of variable size. Alternatively, one could model heat storage based on a smaller increase in core body temperature in 100% of core tissues. However, we though our approach was acceptable given the large size of elephants and evidence supporting changes in tissue insulation (Fig.4 and 5) and, thus, a core of variable size.
Thermoregulatory Constraints on Activity in Gigantotherms

We modeled (Fig. 8) and discuss the thermoregulatory constraints on activity proposed in elephants, and endothermic and ectothermic dinosaurs (Spotila et al., 1991; O’Connor and Dodson, 1999). Our model makes the following 6 assumptions: (1) a 3655kg *Edmontosaurus* (Spotila et al., 1991), (2) a spherical model (O’Connor and Spotila, 1992), which assumes that the rates of heat transfer and heat storage were not affected by differences in body shape between elephants and *Edmontosaurus*, (3) metabolic costs of locomotion in endothermic and ectothermic *Edmontosaurus* that were about 4% and 30% less than values recorded in elephants, respectively (Spotila et al., 1991; Langman et al., 1995; Langman et al., 2012), (4) a starting core body temperature of 35.3±0.44 °C, the mean (±s.d.) pre-exercise $T_b$ recorded during the June trials, (5) solar absorptance of *Edmontosaurus* skin was similar to elephants’ (Table 1), and (6) the mean environmental conditions recorded during the June trials (Table 3).

Statistical Analysis

Graphing and statistical analyses were performed using KaleidaGraph 4.03 (Synergy Software, Reading, PA, USA). Data are presented as mean ±1 standard deviation (±s.d.).

RESULTS

Metabolic Heat Production and Respiratory Evaporation

During slow walks the two Asian elephants in the present study had an estimated 2 to 2.5-fold increases in metabolic heat production above resting values (Langman et al., 2012). Active dry metabolic heat production (Eqn 2 and 3) was similar between seasons (Table 2). Estimates of respiratory evaporative heat loss were 4.7%, 12.4% and 12.8% of active metabolic heat production during June, February and November trials, respectively (Table 2). Our estimates of respiratory evaporative heat loss were similar to previous estimates of 10% to 12%
of resting metabolic heat production in elephants exposed to ambient air temperatures that ranged from approximately 12.5 °C to 25°C (Benedict, 1936; Williams, 1990). Our lowest estimate of respiratory heat loss, recorded during the June trials was the result of hotter ambient air temperatures that averaged 31.4±1.7°C (Table 3) and high absolute humidity.

Post-Exercise Increases in Core Body and Skin Temperature

Core body temperature in two Asian elephants increased following all exercise trials (Fig. 3). The seasonal post-exercise increases in core body temperature recorded in elephants were 0.38±0.19 °C (mean trial time of 23.9±2.9 min), 0.48±0.21°C (mean trial time of 18.9±4.5 min) and 0.70±0.39 °C (mean trial time of 21.7±5.5 min), in February, November and June trials, respectively. Seasonal mean walking speeds (Table 2) were similar to the range of walking speeds (from approximately 1.0 to 1.3 ms⁻¹) that minimize the energetic and biomechanical costs of locomotion in elephants (Langman et al., 1995 and 2012; Hutchinson et al., 2003 and 2008; Ren and Hutchinson, 2008; Genin et al., 2010). The maximum recorded increase in core body temperature of 1.4°C occurred following 26 minutes of locomotion at an average speed of 1.0 ms⁻¹ and ambient air temperature of 32.7°C.

Skin temperature in elephants increased with increasing ambient air temperature (Fig. 3). Skin temperature increased, by 0.6±2.1°C, 1.4±1.7°C and 1.7±1.3°C following exercise in the November, February and June trials, respectively. During the hot weather, June trials, pre-exercise skin temperature of 35.5±1.2°C was approximately equal to core body temperature, 35.3±0.4°C, indicating vasodilatation and full perfusion of peripheral tissues (Fig. 1 and Fig. 3). Following exercise in full sun, skin and core body temperatures increase to 37.3±1.1 °C and 36.0±0.3 °C, respectively (Fig. 3). The post-exercise increase core temperature of 0.7 °C was the result of metabolic heating. However, the 1.8°C increase in skin temperature was more than
metabolic heating could produce and was likely a consequence of heating of the elephants’ skin by environmental radiation (Fig. 3).

**Seasonal Changes in Tissue Insulation**

Asian elephants’ adjusted effective tissue insulation in response to changing environmental conditions (Fig. 4). Over a range of ambient air temperatures, from 8 to 34.5 °C effective tissue insulation decreased by approximately 113%, from 0.08 to -0.01 m²·s⁻¹·°C⁻¹. At ambient air temperatures greater than approximately 30°C skin temperatures were often hotter than core body temperature (Fig. 3), indicating heating of the skin surface by direct solar radiation, and thus tissue insulation was minimized (Fig. 4).

**Net Radiant Heat Transfer**

During activity in full sun, seasonal differences in radiant environmental heat (Table 3) and skin temperature (Fig. 1) resulted in variations the magnitude and direction (i.e., positive, heat loss or negative, heat gain) of net radiant heat transfer in two Asian elephants (Table 4). Nocturnal activity, in the absence of solar radiation, would facilitate radiant heat loss in all seasons (Table 4). Avoidance of solar radiation has a functionally significant effect on radiant heat transfer in active elephants. For example, during the June trials, at an average air temperature of 31.4±1.7°C, activity in full sun resulted in a net radiant heat gain of -3971±1073 W, however, nocturnal activity would have resulted in an estimated net radiant heat loss of 1010±265 W (Table 4).

**Convective Heat Loss**

Differences in temperature gradient between elephants’ skin and ambient air temperature (Fig. 1), in combination with small variations in environmental wind and locomotion speed (Table 2 and 3), resulted in up to 2.4-fold seasonal variations in convective heat loss in
exercising elephants, from 1091±395W to 2664±871W in June and February, respectively (Table 4). With the exception of the November trials, when on average the elephants had a small net radiant heat loss of 107±640W (Table 4), convective heat transfer was the only heat loss mechanism available to elephants exercising in full sun (Table 4).

Heat Storage

Because active metabolic heat production (Table 2) could not all be transferred to the environment, and in some cases solar radiation created a net heat gain from the environment (Table 3), core body temperature increased following all exercise trials (Table 4). Assuming that post-exercise increases in core body temperature represent uniform heating in 100% of core tissues, heat storage ranged between 3617±1526W and 7831±4318W (Table 4), or 68% to 135% of dry active metabolic heat production (Table 2) in November and June, respectively. However, due to the large size of the elephants’ body core, and changes in tissue insulation (Fig. 4) regional heterothermy likely had an effect on the total amount of heat storage in tissues (Fig. 5).

Seasonal Thermal Energy Budgets

When elephants exercised in full sun during the February and June trials, net radiant heat from the environment (Table 4) combined with active metabolic heat production to produce total heat gains ($M_{ex} - E_b + Q_n$) of approximately 5988W and 9754W, respectively. In these conditions convection, $C_{ex}$, was often the only avenue of heat loss in exercising elephants, dissipating approximately 11% and 45% of $M_{ex} - E_b + Q_n$ during June and February trials, respectively.

Our results indicated that there was a functionally significant relationship between heat storage and locomotion in elephants, and that this relationship was affected by the level of radiant environmental heat. In the cool weather November and February exercise trials, at an
ambient air temperature of 13.7±1.7°C and 16.2±4.0°C, respectively, post-exercise increases in core temperature of 0.48±0.21°C in 52% and 0.38±0.19°C in 95% of the core tissue mass (Fig. 5) stored approximately 55% of total heat gain (Fig. 6A). During the June hot weather exercise trials, at an ambient air temperature of 31.4±1.7°C a post-exercise increase in core body temperature of 0.70±0.39°C in 100% of core tissue mass would store approximately 80% of the total heat gain (Fig. 6A). However, in hot conditions at the start of exercise trials, skin temperature was often equal to core body temperature at the start of exercise trails (Fig. 3 and 7A) due to vasodilatation and perfusion of peripheral tissues. Walking in full sun resulted in solar radiation heating the elephants’ skin surface (Fig. 7B). Thus, the remaining 8.5% of total heat gain, approximately 832W, can be accounted for by assuming solar radiation heated approximately 25% of the total skin surface area (i.e., approximately 6.5m², Table 1) of the elephants by 1.8 °C to a tissues depth of 2.5 cm. When exercised in full sun, the majority, 56%, 63% and more than 100%, of active metabolic heat production was stored in tissues during the November, February and June trials, respectively.

In the nocturnal environment, in the absence of solar radiation, dry metabolic heat production, \( M_{ex} - E_b \), would be the only avenue of heat gain in exercising elephants (Fig. 6B). The total amount of heat loss by net radiant and convective modes, \( Q_n + C_{ex} \), would dissipate a greater fraction of \( M_{ex} - E_b \). Therefore, an estimated 36% of \( M_{ex} - E_b \) in hot weather June trials, and greater than 90% of \( M_{ex} - E_b \) in cooler weather February and November trials could be dissipated by \( Q_n + C_{ex} \). The greater dissipation of \( M_{ex} - E_b \), during nocturnal exercise in the June trials would result in either a smaller portion, approximately 49% of core tissue mass, increasing in temperature by 0.70±0.39°C (Fig. 5) or a smaller increase in core temperature in a larger core. The storage of approximately 3682W, 64% of \( M_{ex} - E_b \), would balance heat gain and loss during...
nocturnal exercise in the June trials (Fig. 6B). Similarly, nocturnal exercise in the cool environmental conditions, in February and November, heat storage of approximately 252W and 556W, 5% to 9% of $M_{ex} - E_b$, would balance heat gain and loss (Fig. 6B).

DISCUSSION

Gigantothermy and the Functional Significance of Heat Storage

Asian elephants were a good model for endothermic gigantothermy. Over the range of ambient air temperatures, from 8 to 34.5 °C, Asian elephants used vascular adjustments to alter effective tissue insulation and regulate heat transfer from the core to the skin surface (Fig. 1 and 4), one of the defining characteristics of a gigantotherm (Spotila et al., 1973; Paladino et al., 1990; Spotila, et al., 1991; O’Connor and Dodson, 1999). Mathematical heat transfer models estimated that active endothermic gigantotherms would have rates of heat production that would exceed rates of heat loss (Spotila et al., 1991; O’Connor and Dodson, 1999). When active in full sun, even during the cool weather, November and February trials, mean ambient air temperatures of 13.7±3.4°C and 16.2±4.0°C, respectively, Asian elephants had active metabolic heat production rates (Table 2), which were 2.2- to 2.7-fold higher than total heat loss (Table 4). During activity in full sun, the hot weather June trials, mean ambient air temperatures of 31.4±1.4°C, metabolic heat production (Table 2) was approximately 5.3-fold higher than convective heat loss, which was the only functional heat loss mechanism available to elephants (Table 4).

Our results support the hypothesis that heat storage plays a functionally significant thermoregulatory role buffering metabolic heat production and solar radiation heating in active elephants. As a result of allometric constraints on heat loss, during exercise in full sun, only 19%, 38% and 44% of $M_{ex} - E_b$ (Table 2) was dissipated by total heat loss at the skin surface
during the June, February and November trials, respectively (Fig. 6A). In the coolest weather, trails in November at an average ambient air temperature of 13.7±1.7°C, environmental radiation did not contribute to total heat gain, yet 56% of metabolic heat production was stored in tissues (Fig. 6A).

Our results support the hypothesis that the level of radiant environmental heat has a functionally significant effect on the fraction of metabolic heat stored in tissues. Because walking speed (Table 2), and thus metabolic heat production, remained similar between seasons, the seasonal differences in heat storage (Fig. 6A) were likely due to variations in radiant environmental heat. During the June trials, radiant environmental heat was 36% to 48% greater than in the February and November trials, respectively (Table 3), and radiant environmental heat contributed to total heat gain, $M_{ex} - E_b + Q_n$ (Fig. 6A). The higher levels of radiant environmental heat resulted in a greater fraction of metabolic heat, 63% in the February trials, being stored in tissues (Fig. 6A). In the hottest conditions, during the June trials, approximately 2880W of radiant environmental heat was stored in tissues (Fig. 6A).

Behavioral Regulation of Heat Storage

The primary thermoregulatory challenge for endothermic gigantotherms is the dissipation of active metabolic heat production in a hot environment (Paladino et al., 1990; O’Connor and Dodson, 1999; Spotila et al., 1991). Our results indicated that in hot weather, ambient air temperature of 31.4±1.7°C, avoiding solar radiation by nocturnal locomotor activity would increased the total amount of heat loss, $Q_n + C_{ex}$ by approximately 92%, and reduced heat storage by approximately 57% (Fig. 6B) Therefore, it is not surprising that some elephants in tropical environments behaviorally select nocturnal activity (Elder and Rogers, 1975; Guy, 1976; Douglas-Hamilton et al., 2005; Kinahan et al. 2006; Graham et al., 2009; Joshi, 2009). Although
other factors, such as minimizing human contact, also favor nocturnal activity (Douglas-Hamilton et al., 2005; Graham et al., 2009), avoidance of high radiant heat loads (Kinahan et al., 2006) is likely a major consideration favoring nocturnal activity.

Thermoregulatory Constraints on Activity in Elephants And Dinosaurs

In tropical environments, heat storage in active elephants and endothermic dinosaurs might result in a potentially lethal rise in core body temperature (Spotila et al. 1991; O’Connor and Dodson, 1999). Elephants can experience ambient air temperatures that range from 0°C to above 40°C (Sukumar, 1989; Kinahan et al., 2006), and some elephants travel long distances. Home range size for elephants vary from approximately 50 km² to more than 2500 km², and some populations of elephants engage in seasonal migrations of up to 140 km (Guy, 1976; Leuthold, 1977; Sukumar, 1989; Lindeque and Lindeque, 1991; Tchamba, 1993; Thouless, 1995; Joshi, 2009). Similarly, Edmontosaurus is the “poster-boy” of presumably migratory dinosaurs (Bell and Snively, 2011). During the Late-Cretaceous, Edmontosaurus was widely distributed as far north as paleoartic Alaska, above 70° north latitude, and seasonal migrations of 2000 km to 3000 km were likely necessary to avoid exposure to prolonged (>3 months) darkness and reduced availability of food (Clemens and Nelms, 1993; Bell and Snively, 2011). The climate of the likely southern destinations for Edmontosaurus, located between 51° to 41° latitude, was similar to present day New Orleans, LA, USA, characterized by hot, humid summers and mild winters (Dodson, 1971). Therefore, it is highly likely that both active elephants and Edmontosaurus have experienced environmental conditions similar to those we recorded during the June trials (Table 3).

Indeed, heat storage may be a limiting factor for extended long duration diurnal locomotion in elephants and Edmontosaurus. A continuous diurnal walk of 16 km, which lasted
approximately 3.5 hours, was recorded in African elephants walking at a speed of 1.27 m.s\(^{-1}\) (Guy, 1976), a rate similar to walking speeds we report here (Table 2). We estimate that a potentially lethal increase core body temperature by about 8.0 °C, \(T_b\), of approximately 43°C, could occur in both elephants and endothermic *Edmontosaurus* after approximately 3.5 hours of locomotion in full sun (Fig. 8). An ectothermic metabolism would have reduced the rate of increase in core temperature in *Edmontosaurus* by about 18%. However, we estimate that ectothermic *Edmontosaurus* would experience a dangerously high increase in core body temperature after approximately 4 hours of diurnal locomotion (Fig. 8). In addition, our model assumes that the skin of *Edmontosaurus* had a solar absorptance similar to that of elephants, \(\approx 79\%\) (Table 1). While, we have no way of confirming the absorptance of dinosaur skin, the skin of reptiles generally has a higher absorptance for solar radiation, \(\approx 90\%\) (Gates, 1980). A higher rate of absorptance would increase the rate of heat storage and speed to onset of lethal core temperature by approximately 0.5 to 1 hours in *Edmontosaurus*. Therefore, as a means of reducing the chances of lethal heat storage, the lower metabolic heat production of the ectothermic assumption would have been of little thermoregulatory benefit to migratory *Edmontosaurus* in a hot tropical environment.

However, migratory routes in elephants are in often in close proximity to water (Lindeque and Lindeque, 1991; Tchamba, 1993; Joshi, 2009). Following exercise events in hot conditions one of the elephants, Panya, often chose to enter the pool, which despite a relatively warm water temperature of about 30 °C, increased the rate of convective cooling, about 8-fold. Although tail anatomy indicates that *Edmontosaurus* was not morphologically adapted for swimming, its preffered habitat was in close proximity to water (Bakker, 1986). Thus, like elephants, *Edmontosaurus*, might have used periodic bathing and wallowing as a behavioral
thermoregulatory option to increase cooling during activity in a hot environment. In addition, fossil evidence of gigantic feathered dinosaurs of northeastern China have recently been reported on (Xu et al., 2012). Like polar Edmontosaurus, these feathered dinosaurs inhabited cold environments for at least a portion of the year. While the distribution of feathers on the body of dinosaurs is not clear from the fossil record, the potential use of feathers as insulation from the cold or as solar shields in the heat (Bartholomew, 1966; Bakken, 1981) remains a possibility.

There is no evidence for or against nocturnal activity in Edmontosaurus. Because of its gigantic body size, thermal inertia would have permitted nocturnal activity even if they were ectothermic (McNab and Affenberg, 1976). As for elephants, our model indicates that endothermic Edmontosaurus could have reduced the potentially lethal heat storage by behaviorally selecting nocturnal locomotion. We estimate that nocturnal locomotion would reduce the rate of increase in core body temperature in elephants and endothermic Edmontosaurus by about 56%, prolonging the duration of locomotion up to approximately 8 hours (Fig. 6). At that point the challenge for both elephants and Edmontosaurus would be dissipation of stored heat either by wallowing or finding a shade microclimate. The models we present do not prove or dispute endothermic or ectothermic metabolism in Edmontosaurus. However, like behavioral choices made by elephants, the models we present do support the hypothesis that nocturnal activity and avoiding solar heat loads might have reduced potentially lethal increases in core body temperature in endothermic dinosaurs.

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Table 1. Physical characteristics of Asian elephants (*Elephas maximus*) and *Edmontosaurus* model.*Note: total skin surface of the body area (*A*) was estimated using the formula, *A* = 0.1(*M*<sub>b</sub>)<sup>0.67</sup>, where *A* is in m<sup>2</sup> (Benedict, 1936). † Note: body surface area projected perpendicular to the sun’s rays, approximated by the cross-sectional area of a spherical animal with total surface area *A*.

<table>
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<tr>
<th>Species</th>
<th>Elephants</th>
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<th>Mass (kg)</th>
<th>Body Surface Area* (m&lt;sup&gt;2&lt;/sup&gt;)</th>
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</tr>
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<td><em>Edmontosaurus</em></td>
<td>---</td>
<td>---</td>
<td>3655</td>
<td>24.4</td>
<td>0.0067</td>
<td>79</td>
<td>6.07</td>
</tr>
</tbody>
</table>

Table 2. Seasonal means (±s.d.) walking speed (*v*<sub>f</sub>), wet exercise metabolic heat production (*M*<sub>ex wet</sub>), respiratory evaporative heat loss (*E*<sub>b</sub>), dry exercise metabolic heat production (*M*<sub>ex dry</sub>), total distance traveled, and the number of exercise trials.

<table>
<thead>
<tr>
<th>Species</th>
<th>Season</th>
<th><em>v</em>&lt;sub&gt;f&lt;/sub&gt; (m.s&lt;sup&gt;-1&lt;/sup&gt;)</th>
<th><em>M</em>&lt;sub&gt;ex&lt;/sub&gt; (W)</th>
<th><em>E</em>&lt;sub&gt;b&lt;/sub&gt; (W)</th>
<th><em>M</em>&lt;sub&gt;ex&lt;/sub&gt; – <em>E</em>&lt;sub&gt;b&lt;/sub&gt; (W)</th>
<th>Total Distance (m)</th>
<th>Trials (n = )</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>E. maximus</em></td>
<td>February</td>
<td>0.95±0.18</td>
<td>6089±1107</td>
<td>754±107</td>
<td>5355±1056</td>
<td>19,251</td>
<td>14</td>
</tr>
<tr>
<td></td>
<td>June</td>
<td>1.03±0.17</td>
<td>6182±1094</td>
<td>292±33</td>
<td>5783±1056</td>
<td>18,582</td>
<td>14</td>
</tr>
<tr>
<td></td>
<td>November</td>
<td>1.04±0.17</td>
<td>6393±727</td>
<td>816±110</td>
<td>5577±685</td>
<td>10,512</td>
<td>9</td>
</tr>
<tr>
<td></td>
<td>Total</td>
<td>---</td>
<td>---</td>
<td>---</td>
<td>---</td>
<td><strong>48,345</strong></td>
<td><strong>37</strong></td>
</tr>
</tbody>
</table>
Table 3. Seasonal mean (± s.d.) environmental variable used to calculate heat transfer. Variables include: ambient air temperature \((T_a)\), wind speed \((v_s)\), direct solar radiation incident perpendicular to the body surface \((S_n)\), direct solar radiation falling on a horizontal surface \((S_h)\), diffuse solar radiation \((s)\), longwave thermal radiation from the atmosphere \((R_a)\) and longwave thermal radiation from the ground surface \((R_g)\).

<table>
<thead>
<tr>
<th>Species</th>
<th>Season</th>
<th>(T_a) (°C)</th>
<th>(v_s) (ms(^{-1}))</th>
<th>(S_n) (Wm(^{-2}))</th>
<th>(S_h) (Wm(^{-2}))</th>
<th>(s) (Wm(^{-2}))</th>
<th>(R_a) (Wm(^{-2}))</th>
<th>(R_g) (Wm(^{-2}))</th>
</tr>
</thead>
<tbody>
<tr>
<td>E. maximus</td>
<td>February</td>
<td>16.2±4.0</td>
<td>1.2±0.8</td>
<td>309.4±269</td>
<td>185±184</td>
<td>96.4±36</td>
<td>313.6±26.7</td>
<td>381.9±20</td>
</tr>
<tr>
<td>E. maximus</td>
<td>June</td>
<td>31.4±1.7</td>
<td>0.3±0.2</td>
<td>650.9±162</td>
<td>221±75</td>
<td>71.7±34</td>
<td>424.8±11.5</td>
<td>500.5±16</td>
</tr>
<tr>
<td>E. maximus</td>
<td>November</td>
<td>13.7±3.4</td>
<td>0.98±0.5</td>
<td>270.0±184</td>
<td>187±188</td>
<td>77.2±42</td>
<td>298.4±22.7</td>
<td>361.0±13</td>
</tr>
</tbody>
</table>

Table 4. Seasonal variations in estimated heat transfer and heat storage in two exercising Asian elephants, variables include: net radiant heat transfer in full sun \((Q_{n\ sun})\) and nocturnal \((Q_{n\ night})\) environments, convective heat transfer \((C_{ex})\) and heat storage \((X)\) assuming heat storage in 100% of the core.

<table>
<thead>
<tr>
<th>Species</th>
<th>Season</th>
<th>(Q_{n\ sun}) (W)</th>
<th>(Q_{n\ night}) (W)</th>
<th>(C_{ex}) (W)</th>
<th>(X) (W)</th>
</tr>
</thead>
<tbody>
<tr>
<td>E. maximus</td>
<td>February</td>
<td>-653±580</td>
<td>2439±416</td>
<td>2664±871</td>
<td>3617±1526</td>
</tr>
<tr>
<td>E. maximus</td>
<td>June</td>
<td>-3971±1073</td>
<td>1010±265</td>
<td>1091±395</td>
<td>7831±4318</td>
</tr>
<tr>
<td>E. maximus</td>
<td>November</td>
<td>107±640</td>
<td>2649±338</td>
<td>2372±526</td>
<td>5814±3811</td>
</tr>
</tbody>
</table>
Fig. 1. Illustration of vascular adjustments in effective tissue insulation \((I; \text{m}^2 \text{s} \circ\text{C} J^{-1}; \text{Eqn 4 in text})\) in gigantotherms exposed to (A) cold and (B) hot environments. In cold environments, peripheral vasoconstriction creates a layer of tissue \(I\) (Fig. A. grey area), which functions to regulate the transfer of dry metabolic heat production \((M_{\text{ex}} - E_b; \text{Wm}^2)\) from a warm and relatively small isothermal body core to the cooler skin surface \((T_r < T_b; \circ\text{C})\). In hot environments, maximum vasodilatation and perfusion of peripheral tissues with warm blood from the body core reduces effective tissue \(I\). However, perfusion of peripheral tissues in combination with exposure to direct solar radiation warms the skin surface (Fig. B. yellow area) to a temperature near or above core body temperature \((T_r \geq T_b)\), which minimizes effective tissue \(I\) and results in the storage of metabolic and radiant environmental heat in peripheral tissue.
Fig. 2. Illustrates all avenues of radiant heat transfer that contribute to net radiant heat transfer, $Q_n$ (W; Eqn 5 in text), at the skin surface (m$^2$) in elephants. Radiant heat loss, $R_s$ (W; Eqn 6 in text), occurs by longwave thermal radiation from the skin surface. The avenues of radiant environmental heat gain in full sun, $Q_a$ (W; Eqn 7 in text), include direct, $S_n$, diffuse, $s$, and reflected, $r(S_h + s)$, shortwave solar radiation (Wm$^{-2}$; Table 3), and longwave thermal radiation from the atmosphere, $R_a$, ground and surrounding surfaces, $R_g$ (Wm$^{-2}$; Table 3).
Fig. 3. Pre- (solid symbols and solid lines) and post-exercise (open symbols and dashed lines) measurements of core body temperature, $T_b$ (°C) and mean skin temperature, $T_r$ (°C), recorded in two Asian elephants (Panya, black circles and Jean, red circles) over a range of $T_a$'s from 8° to 34.5 °C (n = 37 trials). Linear regressions describing the pre- and post-exercise increases in $T_b$ with $T_a$ are, $T_b = 0.03 T_a + 34.3$, $R^2=0.27$ and $T_b = 0.05 T_a + 34.4$, $R^2=0.54$, respectively. Linear regressions describing the pre- and post-exercise increase in $T_r$ with $T_a$ are, $T_r = 0.59 T_a + 16.6$, $R^2=0.92$ and $T_r = 0.64 T_a + 16.8$, $R^2=0.93$, respectively.
Fig. 4. Effective tissue insulation, $I$ (m$^2$·s°C·J$^{-1}$), decreased with increasing ambient air temperature, $T_a$ (°C), in two Asian elephants (Panya, black circles; Jean, red circles) exercising in full sun. The decrease in $I$ with increasing $T_a$ is described by the linear regression, $I = -0.003 \times T_a + 0.09$, $R^2 = 0.88$. In elephants exposed to full sun, maximum vasodilatation and perfusion of peripheral tissues in combination with solar heating of the skin surface, $I$ was minimized at a $T_a \geq 30$°C.
Fig. 5. Linear regressions describing the seasonal relationships between the percent of core tissues mass (\(\%m_b\)) showing a changing in temperature and the amount of heat stored in tissues (W) during the, February (blue symbols), \(\%m_b = 0.028 \times X + 0.017\); June (red symbols) \(\%m_b = 0.013 \times X + 0.013\); and November (green symbols) \(\%m_b = 0.017 \times X + 0.007\).
Fig. 6. Estimated seasonal non-steady state heat balance, $M_{ex} - E_b = \pm Q_n + C_{ex} \pm X$ (W), in two Asian elephants during (A) exercise in full sun (Table 3) and (B) nocturnal conditions in the absence of solar radiation. Heat transfer variables include; heat gained by dry exercise metabolic rate ($M_{ex} - E_b$) and net radiant heat ($Q_n$), and heat loss by convection ($C_{ex}$), heat storage in 100% of core tissues ($X$), and heat storage adjusted ($X_{adj}$, Fig. 2. linear regressions) to balance heat gain and loss.
Fig. 7. Thermograms of an Asian elephant (Jean) during the June trials at an ambient air temperature of 32°C, with (A) pre- and (B) post-exercise mean (± s.d.) skin temperatures of 36.3±0.5 °C and 38.2±0.5 °C, and core temperatures of 36.0 °C and 36.3 °C, respectively. Note the effect of solar radiation on the skin temperature of the back.
Fig. 8. Estimated increases in core body temperature, $\Delta T_b$ (°C), resulting from continuous locomotion in hot weather conditions, at an ambient air temperature of 31.4±1.7°C, in Asian elephants (Elephas, red symbols), and Edmontosaurus with either endothermic (black symbols) or ectothermic metabolism (blue symbols), during diurnal (solid symbols) or nocturnal activity (open symbols).
CHAPTER 4

HEAT TRANSFER IN THE PINNAE OF EXERCISING ELEPHANTS: BEHAVIORAL CHOICES OPEN THERMAL WINDOWS FOR HEAT LOSS DURING ACTIVITY

M.F. Rowe, G.S. Bakken, J.J. Ratliff and D. Hagan

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ABSTRACT

Conspicuous vasodilatation has long been considered proof that elephants’ large pinnae are "thermal windows,” i.e. body surfaces where heat flow can be varied for thermoregulation. It is generally assumed that pinnae are "opened" by vasodilatation in order to dump metabolic heat. However, during daylight hours, environmental radiation can heat the pinnae surfaces so that heat would be gained rather than lost. In hot environments, one may predict that elephants would use behavioral thermoregulation, e.g. concentrating activity in the shade or at night, to facilitate heat loss. We sought to answer three questions. First, how does radiant environmental heat affect heat transfer in the pinnae of active Asian (Elephas maximus) and African elephants (Loxodonta africana)? Second, to what extent can behavioral options, such as microclimate choice, vary heat transfer from the pinnae of active elephants? Third, to what extent can such behavioral choices increase the portion of active metabolic heat dissipated via the pinnae? We performed pre- and post-exercise measures of pinnae skin surface temperatures using thermography to estimate radiative and convective heat gains and losses from the pinnae surfaces over a range of ambient air temperatures from 3°C to 34.5°C. In hot environments, walking in full sun resulted in radiant heat gain in vasodilated pinnae. Behavioral choices of shade seeking and nocturnal activity facilitate increased heat loss through vasodilated pinnae. We estimated heat loss from the pinnae during nocturnal activity would dissipate a maximum of 2.0% and 12.2% of active metabolic heat production in Asian and African elephants, respectively.
INTRODUCTION

The thermoregulatory significance of elephants’ large pinnae has been a topic interest for over 75 years, but the details of their thermoregulatory function remains poorly defined (Benedict, 1936; Buss and Estes, 1971; Sikes, 1971; Baldwin, 1974; Wright, 1984; Wright and Luck, 1984; Williams, 1990; Phillips and Heath, 1992 and 2001; Rowe, 1999; Narasimhan, 2008; Weissenböck et al., 2010). Vascular responses in the pinnae of elephants’ suggest that they are “thermal windows” that can be "opened" or "closed" to vary heat loss (Wright, 1984; Williams, 1990; Weissenböck et al., 2010). However, radiant environmental heat, particularly direct solar radiation, may inhibit transfer of heat from the pinna skin surface to the environment, rendering this thermal window ineffective. Therefore, in a hot environment, a behavioral response, such as shade seeking, nocturnal activity or pinna flapping is likely necessary to facilitate heat loss.

In natural conditions, locomotion accounts for 10 to 20% of elephants' daily activity budgets (Guy, 1976; Joshi, 2009). Activity is often greater at night or in the early morning hours (Guy, 1976; Douglas-Hamilton et al., 2005; Kinahan et al., 2006; Graham et al., 2009; Joshi, 2009). The timing of locomotor activity to coincide with minimum radiant environmental heat suggests that elephants, in some situations, use behavioral thermoregulation to facilitate heat loss. The only published data describing heat transfer in the pinnae of active elephants is a theoretical model of heat transfer in the pinnae of the fictional flying elephant, Dumbo (Phillips and Heath,
No published data is available describing heat transfer in the pinnae of active living elephants.

In the present study, we sought out to answer three questions, first, how does radiant environmental heat affect net heat transfer in the pinnae of active Asian (*Elephas maximus*) and African elephants (*Loxodonta africana*)? Second, to what extent can behavioral options, such as microclimate choice, vary heat transfer from the pinnae of active elephants? Third, to what extent can such behavioral choices increase the portion of active metabolic heat dissipated via the pinnae? These questions would be difficult, if not impossible to answer using elephants in their natural environment. However, the use of well-trained free-contact zoo elephants and biophysical modeling provided the means to answer the proposed questions.

To answer these questions we performed pre- and post-exercise measures of pinnae skin surface temperatures using thermography, and we recorded microclimate parameters necessary to estimate environmental radiant heat gains and losses from the pinna skin surfaces in elephants. To determine the functional significance of pinna heat loss, we compare it to the amount of metabolic heat produced during exercise using data from an earlier study (Langman et al., 2012) of the same adult Asian elephants we report here. We expect our results to provide insight into how pinnae vasodilatation and behavioral choices, in combination, can facilitate increased heat loss during activity in outdoor environments. In addition, our results will contribute to a better understanding of elephant ecology and husbandry.

METHODS

Elephants and Study Locations

Two adult female Asian elephants at the Audubon Zoo in New Orleans, LA, USA and three adult female African elephants at the Indianapolis Zoo in Indianapolis, IN, USA were used for
all of the measurements (Table 1). All elephants were managed in free-contact with keepers, and were very tractable and well trained. Their feeding schedules were unaltered, and water was available *ad libitum*, except during the exercise trials. All methods were approved by the Indiana State University, the Audubon Zoo and the Indianapolis Zoo Institutional Animal Care and Use Committees. As is commonly the case when working with large, rare animals, sample size was limited by availability. Thus, our results are strictly valid only for these five elephants, but we have no reason to believe they are not typical.

**Experimental Procedures and Data Analyses**

All of the Asian elephant exercise trials during the June 2009 study period were started before 1000 h (1500 UTC) or after 1720 h CDT (2220 UTC). During the February and November 2009 study periods, all trials were started before 1000 h CST (1600 UTC). All of the African elephant exercise trials during the July study period were started before 0945 h EDT (1345 UTC) or at 1430 h EDT (1830 UTC). During the November and March study periods, all trials were started after 1330 h EST (1830 UTC). At the start of each exercise trial, the elephant(s) were led by their keepers from the exhibit areas into the barn or to a shaded area outside of the elephant exhibits, where thermograms and rectal temperatures were recorded. Thermograms of the elephants and track were recorded using a FLIR ThermaCAM™ PM575 (FLIR inc., Portland, OR) radiometric thermal imaging camera (sensitivity of ca. ±0.1°C) fitted with a 45° lens. Images were taken from a distance of approximately 5 m from the elephants. The mean (±s.d.) temperature of the elephants’ skin, $T_i$ (°C), and the track surface temperatures, $T_g$ (°C), were measured using ThermaCAM™ Researcher Professional version 2.7 software (FLIR inc., Portland, OR). Thermal radiation was converted to surface temperatures using concurrently recorded ambient air temperature and relative humidity and assuming radiating surface

emissivities, $\varepsilon$, were 0.96 for elephant skin (Gates, 1980) and 0.93 for asphalt (www.engineeringtoolbox.com).

Rectal temperature, $T_b$ (°C), was measured for 5 to 7 minutes prior to the start of each exercise trial using a 35 cm thermocouple probe attached to a COMARK N9002 (COMARK, Ltd., Hitchin, United Kingdom) thermocouple thermometer (accuracy ±0.1°C). We mounted an accelerometer (SENSR, GPI programmable accelerometer, Elkader, IA) on the right rear leg of the elephants to provide a time stamp for determining walking speed. The length of the track was measured using a Bushnell (Yardage Pro Compact 800, Bushnell Corp. Overland Park, KS) range finder. Average walking speed was computed by dividing track length by time needed to complete the circuit. The Asian elephants either walked one lap (945 m) or two laps (1614 m) around a closed circuit at speeds ranging from 0.56 to 1.25 ms$^{-1}$ (Table 2). The African elephants walked either a short track (1782 m) or a long track (2616 m) at speeds ranging from 1.20 to 1.72 ms$^{-1}$. At the end of each trial thermograms and rectal temperatures were again recorded.

Environmental conditions needed for heat transfer calculation (Table 2) were recorded during exercise trials. Parameters were measured every 5-minutes, and averaged and recorded every 30-minutes using a HOBO® Micro-Station (Onset Computer Corp. Bourne, MA). The station was located in an exposed position on the periphery of the exercise track. A shielded thermistor measured ambient air temperature, $T_a$ (±0.2 °C), a capacitive humidity sensor measured relative humidity, RH% (±2.5%; used to correct thermograms), and a cup anemometer measured sustained wind speed, $u$ (±1.1ms$^{-1}$). A silicon pyranometer measured global solar radiation (±10 Wm$^{-2}$), and a second silicon pyranometer shielded from direct sunlight by a shade ring measured diffuse solar radiation (±10 Wm$^{-2}$). The sensors were set at elephant head height (i.e., 2 to 2.75 m above ground).
Net Radiant Heat Transfer From Pinnae

We approximated the elephants’ pinnae as vertical plates for radiation calculations. Net radiant heat transfer, $Q_n$ (W), was calculated by subtracting radiant environmental heat absorbed, $Q_a$ (W), from radiant heat loss at the pinna skin surface, $Q_l$ (W), so that net heat loss was positive and net heat gain was negative:

$$Q_n = Q_l - Q_a.$$  \hfill (1)

During locomotion African elephants generally hold the pinnae in close contact with their body (Buss and Estes, 1971; Moss, 1988). Asian elephants tended to hold the pinnae in a slightly extended position during locomotion (Fig. 1). For both species, we assumed that the pinnae were held close enough to the body surface that radiant heat transfer was exclusively between the posterior pinna and adjacent body skin surfaces, so that radiant heat transfer to the environment was negligible. Radiant heat loss from two anterior pinna surfaces, $Q_l$ (W), was therefore calculated from the mean of pre- and post-exercise skin surface of temperature $T_l$ of the two anterior pinna surfaces as,

$$Q_l = 2\sigma \varepsilon A_1 (T_l + 273)^4,$$  \hfill (2)

where $\sigma$ is the Stefan-Boltzmann constant $5.67 \times 10^{-8}$ Wm$^{-2}$K$^{-4}$ (Gates, 1980), $\varepsilon$ is skin emissivity of 0.96, and $A_1$ is the surface area of one-side of one-pinna (Table 1). Anterior $T_l$ during exercise was determined to be the average of pre- and post-exercise measurements (Fig. 3). The surface area of the individual elephants’ pinnae, were determined by tracing the pinnae onto cardboard marked with a cm$^2$ grid. The number of squares covered gave the surface area of the anterior-side of one pinna.

When the pinna were held close to the body (Fig. 1) the anterior surface of one pinna was exposed to direct solar radiation and the anterior surface of one pinna was shaded. The rate of
heat gain from environmental radiation, $Q_a$ (W), absorbed by the anterior skin surface of sunlit pinnae, $Q_{a\ sun}$ (W), is the sum of radiation absorbed from shortwave solar plus longwave thermal radiation from the atmosphere and ground,

$$Q_{a\ sun} = \alpha_1A_1s_1 + [\alpha_1A_2s + \alpha_1A_2r(\chi_0 + s) + \alpha_2A_2(R_a + R_g)].$$  

The absorptance of elephant skin for shortwave solar radiation is $\alpha_1$ (Table 1), $A_1$ is the total skin surface area of the anterior-side of one-pinna (m$^2$) (Table 1), and $A_2$ is 50% of the surface area of the anterior-side of one pinna (m$^2$), $S_h$ (Wm$^{-2}$) is the solar radiation falling on a horizontal surface, $s$ (Wm$^{-2}$) is diffuse solar radiation, $S_h + s$ (Wm$^{-2}$) is the total shortwave radiation falling on the horizontal surface, and $r$ is the reflectance of the asphalt track surfaces (0.15 at Audubon Zoo and 0.21 at Indianapolis Zoo). The pinnae were modeled as parallel vertical plates at an altitude, $\alpha_p$, of 90° to the horizon (Fig. 2A), so that the relation between direct solar radiation incident on the ears, $S_i$, and direct solar irradiance, $S_n$, on a plane normal to the sun’s rays (Gates, 1980) reduces to the simple relation,

$$S_i = S_n\sin \theta_z \cos(\phi_s - \phi_p).$$  

Here, the solar zenith angle is $\theta_z$ ($\theta_z = 0^\circ$ when the sun is directly overhead, $0^\circ \leq \theta_z \leq 90^\circ$) and $S_n = S_h/\cos \theta_z$. The ear assumes differing azimuth angles is $\phi_p (0^\circ = \text{north})$ relative to the azimuth angle of the sun $\phi_s (0^\circ = \text{north})$ as the elephants walked complete circuits of the tracks. During each ½ of the circuit only one anterior pinna surface was exposed to direct solar radiation while the other pinna was shaded (Fig. 2B). For the sunlit pinna, $-90^\circ \leq (\phi_s - \phi_p) \leq 90^\circ$ (Gates, 1980).

The solar zenith angle $\theta_z$ and the solar azimuth angle $\phi_s$ at the time of each trial were determined using the online solar position calculator available at www.esrl.noaa.gov. Azimuth angles of the pinnae $\phi_p$ at various positions along the tracks were determined using a Google Earth image of the track.
The shaded anterior pinna skin surface absorbs only diffuse solar radiation, so that

\[ Q_{\text{shade}} = \left[ \alpha_1 A_2 s + \alpha_1 A_2 r s + \alpha_2 A_2 s (R_a + R_g) \right]. \]  

(5)

Both the sunlit (Eqn 4) and shaded (Eqn 5) anterior pinna surfaces received longwave thermal radiation equally. For longwave thermal radiation, the absorptance and emittance of elephant skin are equal, \( \varepsilon = \alpha_2 \approx 0.96 \) (Gates, 1980). Atmospheric thermal radiation, \( R_a \) (Wm\(^{-2}\)), was estimated using the modified Swinbank (1963) relation,

\[ R_a = 1.22 \sigma (T_a + 273)^{\frac{4}{4}} - 171, \]  

(6)

where \( T_a \) is the air temperature recorded at the environmental station. Thermal radiation emitted by the ground (track), \( R_g \) (Wm\(^{-2}\)), was estimated as,

\[ R_g = \sigma \varepsilon (T_g + 273)^{\frac{4}{4}}, \]  

(7)

where \( T_g \), (°C) is the radiant temperature of the track as recorded in the thermograms, and \( \varepsilon \approx 0.93 \) for the asphalt tracks.

**Radiant Heat Transfer Models**

The \( Q_n \) in two pinnae of elephants walking in full sun, total shade and nocturnal environmental radiation (Table 4) were modeled by using \( Q_l \) and Eqns 2 – 4 as appropriate. For elephants walking in full sun, we assumed the anterior surface of one pinna was exposed to full sun and the anterior surface of one pinna was shaded. Elephants walking in total shade absorbed no direct or reflected solar radiation. Radiant heat transfer at night involved longwave radiation only.

**Convective Heat Transfer**

When the elephants were walking, both environmental wind, \( u \) (ms\(^{-1}\)), and wind created by walking speed, \( v_f \) (ms\(^{-1}\)), contributed to convective heat loss during exercise, \( C_{ex} \) (W).

Convective heat transfer in the pinnae was estimated using,
\[ C = h_c A_1 (T_1 - T_a), \] (8)

where \( h_c \) is the convective heat transfer coefficient, \( A_1 \) is the surface area of one anterior side of one pinna (Table 1), and \( T_1 - T_a \) is the difference between mean pinna skin temperature and air temperature. Convective heat loss was summed over two anterior pinna skin surfaces using the corresponding surface temperature \( T_1 \) and wind speed for each. We were unable to measure wind speed on the posterior pinna skin surface of moving elephants. Convective heat loss resulting from wind speed acting on the two partially shielded posterior surfaces of the pinnae was assumed to be 30% of the convective heat loss on the anterior surfaces. The convective heat transfer coefficient \( h_c \) is defined as,

\[ h_c = \frac{\text{Nu} \ k}{D} \] (9)

where Nu is the Nusselt number for vertical plate under turbulent flow, \( \text{Nu} = 0.032 \text{ Re}^{0.8} \), \( k \) is the thermal conductivity of the air at the mean air temperature recorded during each exercise trial (2.47 to 2.65 x 10^{-2} Wm^{-1}°C^{-1}), and \( D \) is the critical dimension of the pinna, which was determined to be the diameter of a circle with the same surface area as the pinna (Table 1). The Reynolds number, \( \text{Re} \) is,

\[ \text{Re} = \frac{u D}{\nu}, \] (10)

where, \( u \), represents the velocity of wind (ms^{-1}) moving over the pinna skin surface and \( \nu \) is the kinematic viscosity of ambient air (1.42 to 1.60 x 10^{-5} m^{2}s^{-1}) at the mean air temperature recorded during each exercise trial. The relation between wind and air movement due to locomotion varied around the circuit, sometimes causing velocities to add and sometimes to subtract.

Therefore, we chose to simply use the higher of the two wind speeds, i.e., environmental wind or the speed of locomotion, to estimate Re.
Active Metabolic Heat Production

The metabolic heat production during exercise, $M_{ex}$, was taken from an earlier study (Langman et al., 2012) of the same adult Asian elephants we report here. Langman et al. (1995) reported energy expenditure in smaller African elephants, with about one-half the body mass of the Asian and African elephants in the present study. Mass-specific energy expenditure for subadult African and adult Asian elephants is similar (Langman et al., 2012). Because the Asian and African elephants in the present study had similar body masses, we chose to use a single polynomial regression from Asian elephants (Langman et al., 2012) to estimate mass-specific metabolic heat production from walking speed,

$$M_{ex} = 0.35 \nu_f^2 + 0.42 \nu_f + 0.75, \quad R^2=0.88.$$ (11)

Here, mass-specific metabolic heat production $M_{ex} = M/m_b, \, (W/kg^{-1})$ and walking speed is $\nu_f, \, (ms^{-1}; \, Table \, 3)$. Mass-specific metabolic heat production for each exercise trial was converted to whole-animal heat production, $M_{ex} \, (W)$, in this study by multiplying the estimated mass-specific measurements by the current body mass of each elephant (Table 1). Seasonal mean ($\pm$s.d.) $M_{ex}$ (Table 4) was estimated by pooling whole-animal $M_{ex}$ estimates for individual elephant trails and dividing by the number of exercise trials conducted during a season (Table 3).

Evaporative Heat Loss

Evaporative heat loss ($E$) has both skin, $E_r$, and respiratory, $E_b$, components. Elephants may increase skin evaporative heat loss by wallowing and bathing (Lillywhite and Stein, 1987) but not by sweating, as African elephants do not have sweat glands (Eales, 1925; Luck and Wright, 1964; Spearman, 1970; Hiley, 1975) and the only sweat gland identified in Asian elephants are located interdigitally (Lamps et al., 2001). Despite the lack of sweat glands, the rate of evaporative water loss from the pinna skin surface of a young bull African elephant was reported
to be greater than that from human skin (Wright and Luck, 1984). However, recording accurate sweat capsule measurements can be challenging. The hot and humid test conditions (of 25°C to 27 °C and RH of 65%) in equatorial Africa, combined with the difficulty of making sweat capsule measurements on the flexible pinna skin surface of an uncooperative bull elephant, which had been rained on the previous night, introduces several possibilities for error in the results reported by Wright and Luck (1984). In addition, it should be noted that, following exercise during the June Asian elephant trials in the subtropical climate of New Orleans, LA, USA, the clothing of researchers and elephant keepers was completely saturated with sweat, yet no signs of water appeared on the elephants’ skin. Therefore, $E_r$ is assumed negligible as the elephants were dry at the start and end of the trials. Estimates of respiratory heat loss $E_b$ (W) were performed using Langman’s (1985) equation:

$$E_b = V*2*\left[c_p * (T_E-T_I) * \rho_E + (W_E-W_I) * \lambda_v\right].$$  \hspace{1cm} (10)

Here, $V$ is the estimated respiratory minute volume (ca. 5.2±1.1 l s⁻¹, Benedict, 1936) multiplied by two to account for the approximate two-fold increase in metabolic heat production during exercise, $M_{ex}$. The heat capacity of air is $c_p$ (1003.5 J °C⁻¹ kg⁻¹), $T_E - T_I$ is the temperature of exhaled minus inspired air (°C), $\rho_E$ is the density if air (0.0011 to 0.0012 kg l⁻¹), $W_E - W_I$ is the water content of exhaled air minus inspired air (mg l⁻¹), and $\lambda_v$ is the latent heat of vaporization (≈2.43 J mg⁻¹ H₂O). Exhaled air temperature $T_E$ was estimated to be approximately 31.3±0.95 °C based on the mean of the maximum $T_E$ recorded in elephants (n =3) exposed to $T_a$'s of 12.5° to 25.3 °C (Benedict, 1936).
RESULTS

Pinna Skin Temperature and Net Radiant Heat Transfer

Pinna skin temperature in Asian and African elephants increased slowly in response to increasing ambient air temperature, and increased rapidly in response to exercise (Fig. 3 and Table 3). Post-exercise increases in pinna temperature resulted from increased perfusion of pinna vasculature (Fig. 4).

Seasonal differences in radiant environmental heat (Table 2), influenced the magnitude and direction of net radiant heat transfer (i.e., positive heat loss or negative heat gain; Table 4). Walking in full sun often resulted in the pinnae gaining radiant heat from the environment. In hot environments (during June trials), at an average air temperature of 31.4±1.7 °C, the option of walking in the shade would reduce net radiant heat gain in the pinnae of Asian elephants by approximately 99.8%, from -211±72W to -0.4±13W. Similarly, in African elephants (during July trials), at an average air temperature of 25.3±1.7 °C, the option of walking in the shade would shift net radiant heat transfer in the pinnae from a net gain of -548±495W to a net loss of 27±52W. In all seasons, nocturnal walking, would maximize net radiant heat loss from the pinnae in both elephant species (Table 4).

Convective Heat Transfer During Exercise

Differences between skin temperature of the pinnae and ambient air temperature (Fig. 3), combined with variations in wind speed (Table 2), resulted in approximately 2.7-fold seasonal differences in convective heat transfer, from 23.6±9.5W to 62.5±19W in the pinna of Asian
elephants, and from 199±35W to 577±361W in the pinnae of African elephants. Due to high levels of radiant environmental heat (Table 2), during full sun exposure, convective heat loss was often the only functional mode of heat loss in the pinnae of active elephants (Table 4).

Dissipation of Active Metabolic Heat Production

Seasonal changes in radiant environmental heat influenced the ability of elephants to dissipate dry active metabolic heat via the pinnae (Table 4). During the June exercise trials (in New Orleans), at an average air temperature of 31.4±1.7°C, walking in full sun resulted in an average radiant environmental heat gain of -54.4±34W in vasodilated pinnae of Asian elephants (Fig 4.), a heat gain from the environment equivalent to approximately 1.0% of dry active metabolic heat production. During the July exercise trials (in Indianapolis), at an average air temperature of 25.3±1.7°C, walking in full sun resulted in an average total heat loss of 66±163W in vasodilated pinnae of African elephants (Fig 4.), a heat loss equivalent to approximately 0.6% of active metabolic heat production. It should be noted that the difference in total heat gain and loss between Asian and African elephants was influenced by higher levels of environmental radiation in New Orleans (Table 2) and increased convective cooling in the larger pinnae of African elephants (Table 4). The behavioral option of walking in the shade, rather than in full sun, would result in small increases in the amount of active metabolic heat dissipated via the pinnae, approximately 0.4% and 2.7% of dry active metabolic heat production in Asian and African elephants, respectively (Table 4). In the hottest conditions, reducing exposure to radiant environmental heat by switching from diurnal to nocturnal walking would result in a shift from heat gain to heat loss in the pinnae of active Asian elephants and a 4.5-fold increase in total heat loss in the pinnae of active African elephants (Table 4). The maximum total heat loss in the pinnae of 113±25W and 761±410W recorded in Asian and African elephants, respectively, was
equivalent to dissipation of 2.0% (Asian) and 12.2% (African) of dry active metabolic heat production (Table 4).

DISCUSSION

Behavioral Choices Facilitate Heat Loss in the Pinnae

Vasodilatation in the pinnae of elephants has long been assumed to be an open thermal window for heat loss (Wright, 1984; Williams, 1990, Weissenböck et al., 2010). Our results indicated that the level of radiant environmental heat has a functionally significant influence on heat transfer in the pinnae of active Asian and African elephants (Table 4). Indeed, during activity in full sun, radiant environmental heat loads can inhibit heat loss (Table 4) from vasodilated pinnae of elephants (Fig. 4). In hot environmental conditions, the behavioral choices of shade seeking and nocturnal activity (Guy, 1976; Douglas-Hamilton et al., 2005; Kinahan et al., 2006; Graham et al., 2009; Joshi, 2009) functionally open thermal windows of heat loss in the pinnae and facilitate increased transfer of heat to the environment (Table 4).

Dissipation of Active Metabolic Heat Production

Heat loss from the pinnae is often presented in relation to the amount of resting metabolic heat production that can be dissipated at the pinnae skin surface (Williams, 1990; Phillips and Heath 1992 & 2001; Narasimhan, 2008). However, our results indicate that, when walking in full sun, the pinnae are ineffective at dissipating active metabolic heat production. When walking in full sun, at seasonal mean ambient air temperatures ranging from 13.7±3.4°C to 31.4±1.7°C, heat loss in the pinnae of Asian elephants was equivalent to less than 1.0% of active metabolic heat production (Table 4). Similarly, when walking in full sun, at seasonal mean ambient air temperatures of 11.0±4.3°C to 25.3±1.7°C, heat loss in the pinnae of African elephants was less than about 11.1% of active metabolic heat production (Table 4). In addition, during the hottest
environmental conditions (in New Orleans), with an average air temperature of 31.4±1.7°C recorded during June exercise trials, a combination of vasodilatation and shade seeking was required for dissipate metabolic heat to occur in the pinnae of Asian elephants.

Evidence of Pinnae as Brain Cooling Structures

Our results indicate that the pinnae contribute only modestly to the dissipation of metabolic heat in hot conditions, and yet the conspicuous vasomotor responses in the pinnae (Fig. 4) indicate an important thermoregulatory function. Thus, the specific thermoregulatory function of the pinnae of elephants’ has yet to be adequately defined. A possible resolution to this paradox is that the pinnae may play a more localized thermoregulatory function.

Protecting the brain and central nervous system from overheating is of crucial importance for an animal’s survival (Simon, 1999), and the head and trunk region is often the hottest body surface of resting elephants (Williams, 1990; Rowe, 1999; Weissenböck et al., 2010). Similarly, following exercise, even in cool environmental conditions, the head and trunk was often the hottest body region, with skin temperatures approaching core body temperature (Fig. 5). Indeed, core body temperature in elephants increased (Table 3) following all short duration exercise trials (ranging from 14 to 31min.), with maximum increases in core body temperature of 1.2 and 1.4°C recorded in African and Asian elephants, respectively. In addition, an increase in arterial blood temperature of 6°C following short duration activity has been recorded in wild African elephants (Baldwin, 1974). Therefore, the large pinnae of elephants may play a localized thermoregulatory role buffering the brain from increases in temperature resulting from hot environmental conditions and activity.

The presence of anatomical structures that play a role in brain temperature regulation suggests that the pinnae may play a role in brain temperature regulation. Carotid rete, cavernous
sinus, and counter-current heat exchangers have been described in a variety of active mammals (Baker and Hayward, 1968; Baker, 1979; Baker and Nijland, 1993; Schroter et al., 1989; Mitchell et al., 2002, Lust et al., 2007), including elephants (Shoshani et al., 2006). Temperature differences of approximately 2.5 to 9°C between arterial and venous circulation in the pinnae of active elephants have been reported (Baldwin, 1974; Wright, 1984). Similarly, in our study, thermograms of the pinnae of elephants showed temperature differences of 1.5 to 5.5 °C between what we believe to be arterial and venous circulation (Fig. 6). Assuming that venous blood leaving the pinnae was delivered to the carotid rete and cavernous sinus, the pinnae of elephants might play a role in regulating brain temperature. However, this relationship is purely speculative until the destination of cooled venous blood exiting from the pinnae has been described, a topic worthy of further investigation.

Furthermore, our results suggest that, if the relevant anatomical structures exist, the pinnae could be effective brain coolers. Metabolic heat production in brain tissue is roughly 11.7 Wkg⁻¹ (Gallagher et al. 1998), and brain mass in adult elephant’s has been reported to be approximately 4.8 kg (Shoshani et al., 2006). Therefore, we estimate metabolic heat production in the brains of adult elephants’ to be approximately 56.2 W. In the hottest conditions we report here (Table 2), the combination of vasodilatation and nocturnal activity produced total heat loss in the pinnae ($Q_{n_{night}} + C_{ex}$; Table 4) of Asian elephants that could dissipate approximately 65% of metabolic heat production in the brain. Although it should emphasized that, compared to the Asian elephants in New Orleans, the African elephants in Indianapolis were exposed to reduced radiant environmental heat loads; while walking in full sun, the larger pinnae of African could dissipate 100% of metabolic heat produced in the brain. Conversely, while walking in full sun,
Asian elephants’ ability to dissipate metabolic heat produced in the brain via the pinnae would be negligible (Table 4).

ACKNOWLEDGMENTS

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REFERENCES


Table 1. Pinna characteristics of individual elephants used to calculate heat transfer. Asian elephants were weighed once at the start of the first study season, and African elephants were weighed seasonally; therefore the masses of African elephants are presented as the mean (±s.d.) recorded over the course of the study. Note: solar absorptance for African elephant skin came from previous measurements on three African elephants recorded at Zoo Atlanta, Atlanta, GA, USA (Rowe, 1999).

<table>
<thead>
<tr>
<th>Species</th>
<th>Elephant</th>
<th>Age (yr.)</th>
<th>Mass (kg)</th>
<th>Pinna Surface Area (m²)</th>
<th>Solar Absorptance (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>E. maximus</em></td>
<td>Jean</td>
<td>35</td>
<td>3447</td>
<td>0.26</td>
<td>78</td>
</tr>
<tr>
<td></td>
<td>Panya</td>
<td>45</td>
<td>4627</td>
<td>0.35</td>
<td>80</td>
</tr>
<tr>
<td><em>L. africana</em></td>
<td>Kubwa</td>
<td>32</td>
<td>3455±7</td>
<td>0.72</td>
<td>76*</td>
</tr>
<tr>
<td></td>
<td>Tombi</td>
<td>31</td>
<td>3532±96</td>
<td>0.94</td>
<td>76*</td>
</tr>
<tr>
<td></td>
<td>Sophi</td>
<td>40</td>
<td>4528±56</td>
<td>0.83</td>
<td>76*</td>
</tr>
</tbody>
</table>

Table 2. Seasonal mean (±s.d.) environmental conditions used to calculate heat transfer, including: ambient air temperature ($T_a$), wind speed ($u$), direct solar radiation ($S_n$), average direct solar radiation at an angle incident to the pinna skin surface ($S_i$), direct solar radiation falling on a horizontal surface ($S_h$), diffuse solar radiation ($s$), longwave thermal radiation from the atmosphere ($R_a$) and longwave thermal radiation from the ground surface ($R_g$).

<table>
<thead>
<tr>
<th>Species</th>
<th>Season</th>
<th>$T_a$ (°C)</th>
<th>$u$ (ms$^{-1}$)</th>
<th>$S_n$ (Wm$^{-2}$)</th>
<th>$S_i$ (Wm$^{-2}$)</th>
<th>$S_h$ (Wm$^{-2}$)</th>
<th>$s$ (Wm$^{-2}$)</th>
<th>$R_a$ (Wm$^{-2}$)</th>
<th>$R_g$ (Wm$^{-2}$)</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>E. maximus</em></td>
<td>February</td>
<td>16.2±4.0</td>
<td>1.2±0.8</td>
<td>309±269</td>
<td>138±128</td>
<td>185±184</td>
<td>96.4±36</td>
<td>314±27</td>
<td>381.9±20</td>
</tr>
<tr>
<td></td>
<td>June</td>
<td>31.4±1.7</td>
<td>0.3±0.2</td>
<td>651±162</td>
<td>276±107</td>
<td>375±150</td>
<td>71.7±34</td>
<td>425±12</td>
<td>500.5±16</td>
</tr>
<tr>
<td></td>
<td>November</td>
<td>13.7±3.4</td>
<td>0.98±0.5</td>
<td>270±184</td>
<td>146±101</td>
<td>138±110</td>
<td>77.2±42</td>
<td>298±23</td>
<td>361.0±13</td>
</tr>
<tr>
<td><em>L. africana</em></td>
<td>November</td>
<td>7.3±4.0</td>
<td>2.9±1.3</td>
<td>53.2±39</td>
<td>36.1±22</td>
<td>11.4±4.2</td>
<td>48.4±16</td>
<td>257±26</td>
<td>336.6±20</td>
</tr>
<tr>
<td></td>
<td>March</td>
<td>11.0±4.3</td>
<td>1.1±0.4</td>
<td>579±272</td>
<td>327±152</td>
<td>349±168</td>
<td>66.1±36</td>
<td>280±27</td>
<td>380.0±26</td>
</tr>
<tr>
<td></td>
<td>July</td>
<td>25.3±1.7</td>
<td>1.3±0.5</td>
<td>479±365</td>
<td>165±127</td>
<td>396±314</td>
<td>101±53</td>
<td>377±14</td>
<td>451.7±35</td>
</tr>
</tbody>
</table>
Table 3. Seasonal variations in mean (±s.d.) walking speed ($v_f$), exercise metabolic heat production ($M_{ex}$), respiratory evaporative heat loss ($E_b$), dry exercise metabolic heat production ($M_{ex} - E_b$), post-exercise change pinna skin temperature ($\Delta T_l$), post-exercise change core body temperature ($\Delta T_b$), total distance traveled, and the number of exercise trials.

<table>
<thead>
<tr>
<th>Species</th>
<th>Season</th>
<th>$v_f$ (ms$^{-1}$)</th>
<th>$M_{ex}$ (W)</th>
<th>$E_b$ (W)</th>
<th>$M_{ex} - E_b$ (W)</th>
<th>$\Delta T_l$ (°C)</th>
<th>$\Delta T_b$ (°C)</th>
<th>Total Distance (m)</th>
<th>Trials (n)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>E. maximus</strong></td>
<td>February</td>
<td>0.95±0.18</td>
<td>6089±1107</td>
<td>754±107</td>
<td>5335±1056</td>
<td>1.7±3.2</td>
<td>0.38±0.19</td>
<td>19,251</td>
<td>14</td>
</tr>
<tr>
<td></td>
<td>June</td>
<td>1.03±0.17</td>
<td>6075±1061</td>
<td>292±33</td>
<td>5783±1056</td>
<td>1.8±1.0</td>
<td>0.70±0.39</td>
<td>18,582</td>
<td>14</td>
</tr>
<tr>
<td></td>
<td>November</td>
<td>1.04±0.17</td>
<td>6393±727</td>
<td>816±110</td>
<td>5577±685</td>
<td>-0.7±1.4</td>
<td>0.48±0.21</td>
<td>10,512</td>
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<tr>
<td><strong>Total</strong></td>
<td></td>
<td>---</td>
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<td>---</td>
<td>---</td>
<td>---</td>
<td>---</td>
<td>48,345</td>
<td>37</td>
</tr>
<tr>
<td><strong>L. africana</strong></td>
<td>November</td>
<td>1.35±0.13</td>
<td>7572±1205</td>
<td>890±99</td>
<td>6682±1153</td>
<td>0.32±1.5</td>
<td>0.52±0.08</td>
<td>11412</td>
<td>5</td>
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<tr>
<td></td>
<td>March</td>
<td>1.59±0.10</td>
<td>8718±1024</td>
<td>869±66</td>
<td>7849±967</td>
<td>4.1±3.9</td>
<td>0.36±0.09</td>
<td>11412</td>
<td>5</td>
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<tr>
<td></td>
<td>July</td>
<td>1.50±0.05</td>
<td>8751±1260</td>
<td>427±39</td>
<td>8324±1256</td>
<td>2.3±1.3</td>
<td>0.36±0.09</td>
<td>19,260</td>
<td>8</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td></td>
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<td>---</td>
<td>---</td>
<td>---</td>
<td>---</td>
<td>---</td>
<td>42,084</td>
<td>18</td>
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</table>
Table 4. Net radiant heat transfer in three microclimates, full sun (\(Q_{n \text{ sun}}\)), total shade (\(Q_{n \text{ shade}}\)), nocturnal (\(Q_{n \text{ night}}\)), exercise convective heat transfer (\(C_{\text{ex}}\)), total heat transfer full sun (\(Q_{n \text{ sun}} + C_{\text{ex}}\)), total heat transfer shade (\(Q_{n \text{ shade}} + C_{\text{ex}}\)), total heat transfer nocturnal (\(Q_{n \text{ night}} + C_{\text{ex}}\)), and the percent of active metabolic heat production dissipated by the pinnae in full sun (% \(M_{\text{ex sun}}\)), shade (% \(M_{\text{ex shade}}\)) and at night (% \(M_{\text{ex night}}\)).

<table>
<thead>
<tr>
<th>Species</th>
<th>(Q_{n \text{ sun}}) (W)</th>
<th>(Q_{n \text{ shade}}) (W)</th>
<th>(Q_{n \text{ night}}) (W)</th>
<th>(Q_{n \text{ sun}} + C_{\text{ex}}) (W)</th>
<th>(Q_{n \text{ shade}} + C_{\text{ex}}) (W)</th>
<th>(Q_{n \text{ night}} + C_{\text{ex}}) (W)</th>
<th>((M_{\text{ex}}-E_b)) % (sun)</th>
<th>((M_{\text{ex}}-E_b)) % (shade)</th>
<th>((M_{\text{ex}}-E_b)) % (night)</th>
</tr>
</thead>
<tbody>
<tr>
<td>E. maximus</td>
<td>-23.0±35</td>
<td>18.0±12</td>
<td>45.7±9.0</td>
<td>53.3±42</td>
<td>30.3±55</td>
<td>71.3±43</td>
<td>99.0±47</td>
<td>0.6</td>
<td>1.4</td>
</tr>
<tr>
<td>February</td>
<td>-78.0±30</td>
<td>-0.4±13</td>
<td>22.7±6.8</td>
<td>23.6±9.5</td>
<td>-54.4±74</td>
<td>23.3±16</td>
<td>46.2±16</td>
<td>-1.0</td>
<td>0.4</td>
</tr>
<tr>
<td>June</td>
<td>-12.0±18</td>
<td>27.7±14</td>
<td>50.3±7.9</td>
<td>62.5±19</td>
<td>50.5±26</td>
<td>90.2±34</td>
<td>113±25</td>
<td>0.9</td>
<td>1.6</td>
</tr>
<tr>
<td>November</td>
<td>121±22</td>
<td>146±37</td>
<td>184±51</td>
<td>577±361</td>
<td>699±381</td>
<td>722±396</td>
<td>761±410</td>
<td>11.2</td>
<td>11.6</td>
</tr>
<tr>
<td>L. africana</td>
<td>---</td>
<td>---</td>
<td>---</td>
<td>---</td>
<td>---</td>
<td>---</td>
<td>---</td>
<td>---</td>
<td>---</td>
</tr>
<tr>
<td>March</td>
<td>-153±111</td>
<td>125±35</td>
<td>181±37</td>
<td>368±84</td>
<td>214±130</td>
<td>492±113</td>
<td>548±119</td>
<td>2.3</td>
<td>6.4</td>
</tr>
<tr>
<td>July</td>
<td>-133±159</td>
<td>27±52</td>
<td>105±39</td>
<td>199±35</td>
<td>66±163</td>
<td>226±61</td>
<td>305±53</td>
<td>0.6</td>
<td>2.7</td>
</tr>
</tbody>
</table>
Fig. 1. Common pinna position during exercise in (A) African and (B) Asian elephants.
Fig. 2. Illustrates the variables used in the calculation of fraction of direct solar radiation ($S_n$) incident to a sunlit pinna ($S_i$; Eqn 4.5). (A) The pinna, were assumed to be a vertical plates at an altitude, $a_p$, of 90° to the horizon. (B) The elephant’s body rotated 360° in relation to $S_n$ while walking on the relatively oval tracks. The $S_i$ was determined by the relationship $S_i = S_n \sin \theta_z \cos(\phi_s - \phi_p)$, where $\theta_z$ is the solar zenith angle (i.e. 90° minus solar altitude $\theta_{as}$) and $\phi_s - \phi_p$ is solar azimuth minus azimuth of the pinnae. At any give location on the exercise track, the anterior skin surfaces of the opposite pinna was assumed to be parallel to the sunlit pinna and thus shaded.
Fig. 3. Pre-(solid symbols) and post-exercise (open symbols) anterior pinna skin surface temperatures, $T_l$ (°C) in two adult Asian elephants (Panya; red and Jean; blue circles) and three adult African elephants (Sophi; black, Tombi; green and Kubwa; purple squares). The linear regressions describing the pre-exercise increases in $T_l$ with increasing ambient air temperature $T_a$ (°C) (solid lines) in Asian (red lines) and African elephants (black lines) were $T_l = 0.78T_a + 10.1$, $R^2 = 0.92$ and $T_l = 0.62T_a + 16.0$, $R^2 = 0.86$, respectively. The linear regressions describing the post-exercise (dashed lines) increases in $T_l$ with increasing $T_a$ in Asian (red lines) and African elephants (black lines) were $T_l = 0.87T_a + 9.2$, $R^2 = 0.92$ and $T_l = 0.68T_a + 17.5$, $R^2 = 0.84$, respectively.
Fig. 4. Pinnae perfusion increased following exercise at ambient air temperatures of 9.7 °C and 18°C in Asian (A and B) and African elephants (C and D), respectively. At higher air temperatures of 31.5°C and 21.5°C, respectively, perfusion of the pinnae in (E) Asian and (F) African elephants increased.
Fig. 5. Whole-body thermograms recorded prior to exercise in (A) Asian and (B) African elephants at ambient air temperatures of 11.5°C and 15°C, respectively, showed skin temperature of the head and body regions to be relatively uniform. Following exercise, thermograms showed skin temperature in the head region in (C) Asian and (D) African elephants that approached core body temperature. Note: the upper limit of the temperature scales were set 2°C below the post-exercise core body temperature.
Fig. 6. (A) Anterior view of vasoconstricted pinna in an African elephant prior to exercise at an air temperature of 25°C. (B) Following exercise skin temperature of the head region was close to post-exercise core body temperature of 35.3°C and the anterior view of the pinnae showed vasodilated. (C) The posterior view of a vasodilated pinna showed an average temperature difference of 3.3±1.5°C (n=40 spot measurements) between what appears to be hot arterial blood (light colored vessels) and cooler venous blood (dark colored vessels).
CHAPTER 5

BEHAVIORAL CHOICES AFFECT HEAT TRANSFER IN THE PINNAE OF ELEPHANTS:
A NEW PERSPECTIVE ON THE THERMOREGULATORY SIGNIFICANCE PINNA FLAPPING

M.F. Rowe, G.S. Bakken, J.J. Ratliff and D. Hagan

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ABSTRACT

The thermoregulatory significance of elephants’ large pinnae has long been a topic of study. Heat transfer has been proposed to dissipate 33% and 100% of resting metabolic heat production in Asian (Elephas maximus) and African elephants (Loxodonta africana), respectively. However, previous radiant heat transfer models excluded solar radiation and are valid only indoors. In the natural environment, solar radiation is a major factor affecting radiant heat transfer. Furthermore, previous convective heat transfer models are based on pinna flapping rates in excess of measured values. Therefore, previous models may have overestimated the amount of heat production that can be dissipated by the pinnae of elephants. Here, we constructed radiant and convective heat transfer models of the pinnae of elephants outdoors at rest. These animals were permitted to use microclimate choice and behavioral mechanisms including pinna positioning and flapping to regulate heat transfer. We performed thermography of the anterior and posterior pinna skin surfaces, and recorded environmental variables necessary to calculated heat transfer. Behavioral observations and heat transfer data were combined to build models that describe the seasonal variations in heat loss from the pinnae and the maximum amounts of metabolic heat dissipation. Under the conditions tested, Asian and African elephants dissipate a maximum of 5% and 48% of resting metabolic heat production, respectively, via the pinnae.
INTRODUCTION

The thermoregulatory significance of elephants’ large pinnae has been a topic of interest for over 75 years (Benedict, 1936; Sikes, 1971; Buss and Estes, 1971; Baldwin, 1974; Wright, 1984; Wright and Luck, 1984; Williams, 1990; Phillips and Heath, 1992 and 2001; Rowe, 1999; Narasimhan, 2008; Weissenböck et al. 2010). Each study has contributed to a better understanding of thermoregulation in the largest living terrestrial mammals, but all that we really know about the large pinnae of elephants is that they seem to be an important “thermal window” for heat dissipation (Wright, 1984; Williams, 1990; Phillips and Heath, 1992 and 2001; Weissenböck et al. 2010). Several studies have used the increase in radiant and convective heat transfer that accompanies vasodilatation of the pinnae and the increase in convective heat transfer that results from an increase in pinna flapping rate to estimate the percent of metabolic heat production that can be dissipated from the pinna skin surfaces (Williams, 1990; Phillips & Heath, 1992 and 2001; Narasimhan, 2008). However, their treatment of radiation and convection is not firmly based on field data.

First, these studies only considered longwave (\( \lambda = 3 – 30 \mu m \)) thermal radiation, and computed radiant heat transfer in the pinnae, \( Q_l \), as,

\[
Q_l = \sigma \varepsilon A_1 (T_1^4 - T_a^4)
\]

where \( \sigma \) is the Stefan-Boltzmann constant \((5.67 \times 10^{-8} \text{ Wm}^{-2}\text{K}^{-4})\), \( \varepsilon \) is the emissivity of animal skin \((\approx 0.96)\), \( T_1 (K) \), is mean pinna skin temperature, \( T_a (K) \), is air temperature, and \( A_1 (\text{m}^2) \) is the pinna skin surfaces area. However, radiant heat transfer in the outdoor environment includes
direct, diffuse and reflected shortwave (\(\lambda = 0.3-3 \, \mu m\)) solar radiation, as well as the exchange of longwave thermal radiation between the animals’ skin surface and the atmosphere or adjacent surfaces (Porter and Gates, 1969; Bakken and Gates, 1975; Gates, 1980). In addition, elephants change pinna orientation, particularly in relation to direct solar radiation. The position of the pinnae, either held in against the body or extended out away from the body will alter the amount of skin surface area exposed to environmental radiation. Such behaviors can significantly affect heat transfer and consequently, must be incorporated into radiant heat transfer models in the outdoor environment.

Convective heat transfer to the air is equally important and may be increased by pinna flapping. This behavior has been well documented in African elephants (\textit{Loxodonta africana}) (Buss and Estes, 1971; Phillips and Heath, 1992; Rowe, 1999). The combined effect of radiant and convective heat transfer in the pinnae of elephants has been estimated for African elephants to dissipate from 8% of resting metabolic heat production when no pinna flapping occurs (Williams, 1990) to 100% when pinna flapping occurs (Phillips and Heath, 1992) and for Asian elephants 33% (Narasimhan, 2008). However, these estimates are based on unrealistically large temperature differential between pinna skin and ambient air temperature (\(\Delta T_l - T_a \approx 16 \text{ to } 26^\circ \text{C}\)) and an equally unrealistic pinna movement speed of 5.0 m s\(^{-1}\). Therefore, these models likely overestimated the maximum amount of metabolic heat that can be dissipated by the pinnae.

No published studies have examined radiant and convective heat transfer mechanisms in the pinnae of elephants, in quasi-natural context, when elephants are subjected to a wide range of radiant environmental heat loads and are free to make behavioral choices that influence heat transfer. Therefore, here we present a rigorous radiant and convective heat transfer analysis of the pinnae of Asian and African elephants. Our analysis incorporates seasonal behavioral
observations of microclimate selection, pinna position, and pinna flapping rate, as well as anterior and posterior pinna skin surface temperatures measure by thermography. Microclimate parameters necessary to compute convective and radiative heat transfer were recorded concurrently with these observations. For comparison with prior studies, results are presented as the fraction of resting metabolic heat production dissipated by the pinnae. This computation uses metabolic data from an earlier study of the same individual adult Asian elephants used here (Langman et al., 2012). We expect our results will more clearly define the thermoregulatory significance of elephants’ large pinnae.

METHODS AND MATERIALS

Elephants and Study Locations

Two adult female Asian elephants at the Audubon Zoo in New Orleans, LA, USA and three adult female African elephants at the Indianapolis Zoo in Indianapolis, IN, USA were used for all of the measurements (Table 1). All elephants were managed in free-contact with keepers and were very tractable and well trained. Their feeding schedules were unaltered, and water was available ad libitum, except during the exercise trials. All methods were approved by the Indiana State University, the Audubon Zoo and the Indianapolis Zoo Institutional Animal Care and Use Committees. As is commonly the case when working with large, rare animals, sample size was limited by availability. Thus, our results are strictly valid only for these five elephants, but we have no reason to believe they are not typical.

Behavioral Observations

Behavioral observations of microclimate selection, pinna positioning, and pinna flapping were conducted over three seasons, in both elephant species (Table 2). Observations were made from public viewing areas on the periphery of the exhibits. Behavioral observations were
recorded in six consecutive 5-min. blocks over 30-min. periods. Microclimate selection, i.e. shade seeking or full sun exposure, was recorded. Partial shading, particularly of the head, was considered shade seeking. Pinna positioning was either classified as pinnae held in close proximity to the body, or extended away from the body at an angle ≥ 45°. During each 5-min. block, pinna flaps were recorded using a clicker counter and divided by 5 to give a flapping rate (flap min⁻¹).

Pinna Skin Temperature and Environmental Surface Temperatures

Thermograms (n = 110) of the elephants’ anterior and posterior pinnae skin surfaces and the ground surface were recorded using a FLIR ThermaCAM™ PM575 (FLIR inc., Portland, OR) radiometric thermal imaging camera (accuracy of ± 2%) fitted with a 45° lens. Thermograms were taken in shaded areas outdoors or in barns from a distance of approximately 5 m from the elephants. The mean (± s.d.) temperature of the elephants’ pinna skin $T_1 (°C)$, (Table 3) and the track surface temperatures $T_g (°C)$ were evaluated from the thermograms using ThermaCAM™ Researcher Professional version 2.7 software (FLIR inc., Portland, OR). Thermal radiation was converted to surface temperatures using concurrently recorded ambient air temperature and relative humidity and assuming radiating surface emissivity’s, $\varepsilon$, were 0.96 for elephant skin (Gates, 1980) and 0.92 for soil (www.infrared-thermography.com).

Environmental Conditions

Environmental conditions (Table 2) were measured every 5-min. and then averaged and recorded every 30-min. using a HOBO® Micro-Station (Onset Computer Corp. Bourne, MA) located in an exposed position on the periphery of the exhibit areas. The sensors were set at elephant head height (2 to 2.75 m above ground). A shielded thermistor measured ambient air temperature, $T_a (± 0.2 °C)$, a capacitive humidity sensor measured relative humidity, RH% (±
2.5%; used to correct thermograms) and a cup anemometer measured sustained wind speed, $u$ ($\pm 1.1\text{ms}^{-1}$). A silicon pyranometer measured global solar radiation ($\pm 10\text{ Wm}^{-2}$), and a second silicon pyranometer shielded from direct sunlight by a shade ring measured diffuse solar radiation ($\pm 10\text{ Wm}^{-2}$). The sensors were set at elephant head height (i.e., 2 to 2.75 m above ground).

**Data Analyses**

*Net Radiant Heat Exchange From Pinnae*

We approximated the pinnae as vertical plates for radiation calculations. Net radiant heat exchange, $Q_n$ in watts (W) was calculated by subtracting radiant environmental heat absorbed $Q_a$ from radiant heat loss at the pinna skin surface $Q_l$, so that net heat loss is positive:

$$Q_n = Q_l - Q_a.$$  \hspace{1cm} (2)

Radiant heat loss from the pinna $Q_l$ was calculated from $T_l$ of the anterior and posterior pinna skin surfaces,

$$Q_l = \sigma \varepsilon A (T_l + 273)^4,$$  \hspace{1cm} (3)

where $\sigma$ is the Stefan-Boltzmann constant $5.67 \times 10^{-8} \text{ Wm}^{-2}\text{K}^{-1}$ and $\varepsilon$ is skin emissivity of 0.96. The surface area $A_1$ of one side of the elephants’ pinna (Table 1) was determined by tracing the pinna onto cardboard marked with a 1 cm grid. The number of cm$^2$ squares enclosed by the tracing defined the surface area of one side of one pinna.

The estimated maximum environmental radiant heat gain by one pinna surface facing incident solar radiation, $Q_a$ (W), is the sum of absorbed shortwave solar plus longwave thermal radiation from the atmosphere and ground:

$$Q_a = A_1 \{ \alpha_1 S_i + (1/2) [\alpha_1 s + \alpha_1 r \cdot (S_h + s) + \alpha_2 (R_a + R_g)] \}. \hspace{1cm} (4)$$
The absorptance of elephant skin for short wave solar radiation is $\alpha_1$ (Table 1), $A_1$ (m$^2$) is the surface area of one side of one pinna (m$^2$), and $S_h$ (W/m$^2$) is the solar radiation falling on a horizontal surface. The pinnae were modeled as parallel vertical plates at an angle, $\alpha_p$, of 90° to the horizon, so that the relation between direct solar radiation incident on the ears, $S_i$, and direct solar irradiance, $S_n$ (Table 2), on a plane normal to the sun’s rays (Gates, 1980) reduces to the simple relation,

$$S_i = S_n \sin \theta_z \cos(\phi_s - \phi_p). \quad (4.5)$$

Here, the solar zenith angle is $\theta_z$ ($\theta_z = 0°$ when the sun is directly overhead, $0° \leq \theta_z \leq 90°$) and $S_n = S_h / \cos \theta_z$. The pinna surface facing the sun assumes an azimuth angle is $\phi_p$ ($0° = \text{north}$) equal to the azimuth angle of the sun $\phi_s$ ($0° = \text{north}$). The solar zenith angle $\theta_z$ and the solar azimuth angle $\phi_s$ at the time of each trial were determined using the online solar position calculator available at [www.esrl.noaa.gov](http://www.esrl.noaa.gov). Diffuse radiation is assumed to be half from the ground and half from the sky (Gates, 1980). The first term in brackets is diffuse solar radiation from the sky $s$ (W/m$^2$). The second term, $\alpha_1 \cdot r \cdot (S_h + s)$, is the total shortwave radiation falling on the asphalt track of reflectance ($r = 0.15$ at Audubon Zoo and 0.21 at Indianapolis Zoo). Diffuse thermal radiation from the sky, $R_a$ (W/m$^2$), was estimated from the modified Swinbank (1963) relation,

$$R_a = 1.22 \sigma (T_a + 273)^4 - 171. \quad (5)$$

Here $T_a$ is the air temperature recorded at the environmental station. Diffuse thermal radiation emitted by the ground (track) is $R_g$ (W/m$^2$),

$$R_g = \sigma \varepsilon (T_g + 273)^4, \quad (6)$$

where, $T_g$ (°C) is the radiant temperature of the track as recorded in the thermograms. For long-wave thermal radiation, the absorptance and emittance of elephant skin are equal, $\varepsilon = \alpha_2 \approx 0.96,$
The total rate of environmental radiant heat gain, in shaded pinna surfaces was estimated by omitting the direct solar radiation term ($\alpha_1 A_1 S_n$) in equation 4.

**Behavioral adjustments to radiant heat transfer**

We constructed five radiant heat transfer models based on microclimate selection and pinna positioning. Changing in pinna position changed the exposure of skin surfaces to direct solar radiation avenues of environmental radiation. Shade seeking eliminated exposure to direct solar radiation ($\alpha_1 A_1 S_n$). Descriptions of models 1 through 5 are as follows:

1) Model 1 describes an elephant standing in the shade with both pinnae held in close contact to the body. Therefore, the two anterior pinna skin surfaces are in radiant heat transfer with diffuse solar radiation and thermal radiation, while the posterior surfaces exchange thermal radiation with the body so there is no net transfer.

2) Model 2 describes an elephant standing in full sun with its body perpendicular to incident direct solar radiation, with the pinna in close contact with the body. Thus, one anterior pinna surface is in full sun and the other is shaded. Posterior surfaces have no net exchange, as in Model 1.

3) Model 3 describes an elephant standing in the shade with two pinnae extended. Therefore, all four pinna skin surfaces are exposed to diffuse solar and longwave thermal radiation.

4) Model 4 describes an elephant standing in full sun with two pinnae extended with direct solar radiation incident on one-surface while the other three surfaces are shaded and exposed to diffuse radiation.
5) Model 5 describes an elephant standing facing full sun with two pinnae extended so that two pinna surfaces receive direct solar radiation and two surfaces are shaded and exposed to diffuse radiation.

*Convective Heat Transfer*

Convective heat transfer in the pinnae was estimated as done by Phillips and Heath (1992),

\[ C = h_c A_1 (T_1 - T_a), \]  

where \( h_c \) is the convective heat transfer coefficient, \( A_1 \) is the surface area of one side of one pinna (Table 1), and \( T_1 - T_a \) is the difference between mean pinna skin temperature and ambient air temperature. The number of pinna surfaces exposed to convective transfers were adjusted depending on orientation to wind, pinna position and whether or not flapping occurred. The convective heat transfer coefficient \( h_c \) is defined as,

\[ h_c = \frac{Nu \ k}{D} \]  

where \( Nu \) is the Nusselt number for vertical plate under turbulent flow, \( Nu=0.032 \ Re^{0.8} \), \( k \) is the thermal conductivity of the air at the temperature recorded during each thermography trial, and \( D \) is the critical dimension of the pinna, which we defined as the diameter of a circle with the same surface area as the pinna (Table 1). The \( h_c \) was multiplied by 1.6 to account for turbulent wind conditions in the outdoor environment (Mitchell, 1976).

Reynold’s number, \( Re \), was defined as,

\[ Re = uD/\nu, \]  

where, \( V \) represents the velocity of wind (ms\(^{-1}\)) moving over the pinna skin surface and \( \nu \) is the kinematic viscosity of ambient air at the mean air temperature recorded during each exercise trial.
When the elephants were flapping their pinnae, the distance, $L$, (arc length) the pinna traveled in one flap, i.e. forward and back, was defined as,

$$L = 2\pi\left(\frac{2}{3}W\right)(100/360)*2,$$

where $W$ is the maximum width of the pinna, two-thirds $W$ was used as the radius of the arc because the width of the pinna varies from top to bottom and the outer portion of the pinna travels farther than the inner portions. It was assumed that the pinna traveled $\approx 100^\circ$ per flap. The average speed of the pinna during flapping $V$, was estimated from the pinna flapping rate $N$ (flap min$^{-1}$) and the arc length as,

$$V = L \cdot (N/60).$$

**Behavioral influences on convective heat transfer**

We constructed 6-convective heat transfer models based on pinna position and pinna flapping rate. Description of the convective heat transfer models are as follows:

1) Model 1 described an elephant with pinnae held in close contact with the body, with one anterior pinna surface exposed to environmental wind and three pinna surfaces exposed to a convection equivalent of 30% of the forced convection in the anterior surface.

2) Model 2 describes an elephant with pinnae extended out such that two surfaces were exposed to environmental wind and two surfaces were exposed to convection equivalent to 30% of the forced convective surfaces.

3) Model 3 mean pinna flapping model estimates convective heat transfer based on the wind created by the mean pinna flapping rates in full sun and adjusted to include both environmental wind $u$ and relative wind created by pinna flapping $V$.

$$V = \frac{\sqrt{|V+u|} + \sqrt{|V-u|}}{2}^2$$
4) Model 4 pinna flapping model estimates convective heat transfer based on the wind created by mean pinna flapping rates recorded in the shade and adjusted to include both environmental wind and wind currents created by pinna flapping (Eqn 12).

5) Model 5 pinna flapping model estimates the convective heat transfer resulting from the maximum pinna flapping rates recorded in full sun and adjusted to include both environmental wind and wind currents created by pinna flapping (Eqn 12).

6) Model 6 pinna flapping model estimates the convective heat transfer resulting from the maximum pinna flapping rates recorded in the shade and adjusted to include both environmental wind and wind currents created by pinna flapping (Eqn 12).

**Metabolic heat production**

Metabolic heat production \((M)\) was taken from an earlier study of the same individual Asian elephants (Langman et al., 2012). Resting mass-specific metabolic heat production \(M = M/m_b\) (Wkg\(^{-1}\)) recorded in the two Asian elephants was adjusted for body mass to estimate whole elephant resting metabolic heat production (Table 1). Resting metabolic rate is a function of body mass (Schmidt-Neilson, 1984). We estimated metabolic heat production in both the African and Asian elephants in the present study using data recorded on Asian elephants because the African elephants we report on here were 2.2 to 2.9 times larger than those used in the only available metabolic study of African elephants (Langman et al., 1995). Seasonal mean (±s.d.) \(M_{ce}\) (Table 4) was estimated by pooling whole-animal \(M_{ce}\) estimates for individual elephant trails and dividing by the number of thermography trials conducted during a season (Table 3).

**Evaporative heat loss**

Evaporative heat loss \((E)\) has both skin, \(E_r\), and respiratory, \(E_b\), components. Elephants may increase skin evaporative heat loss by wallowing and bathing (Lillywhite and Stein, 1987) but
not by sweating, as African elephants do not have sweat glands (Eales, 1925; Luck and Wright, 1964; Spearman, 1970; Hiley, 1975) and the only sweat gland identified in Asian elephants are located interdigitally (Lamps et al., 2001). Despite the lack of sweat glands, the rate of evaporative water loss from the pinna skin surface of a young bull African elephant was reported to be greater than that from human skin (Wright and Luck, 1984). However, recording accurate sweat capsule measurements can be challenging. The hot and humid test conditions (of 25°C to 27 °C and RH of 65%) in equatorial Africa, combined with the difficulty of making sweat capsule measurements on the flexible pinna skin surface of an uncooperative bull elephant, which had been rained on the previous night, introduces several possibilities for error in the results reported by Wright and Luck (1984). In addition, it should be noted that following exercise during the June Asian elephant trials in the subtropical climate of New Orleans, LA, USA, the clothing of researchers and elephant keepers was completely saturated with sweat, yet no signs of water appeared on the elephants’ skin. Therefore, $E_r$ is assumed negligible as the elephants were dry at the start and end of the trials. Estimates of respiratory heat loss $E_b (W)$ were performed using Langman's (1985) equation,

$$E_b = V^* [c_p \cdot (T_{E} - T_{I}) \cdot \rho_E + (W_{E} - W_{I}) \cdot \lambda_v].$$

(10)

Here, $V^*$ is the estimated respiratory minute volume (ca. 5.2±1.1 l s⁻¹, Benedict, 1936). The heat capacity of air is $c_p (1003.5 \text{ J°C}^{-1}\text{kg}^{-1})$, $T_{E} - T_{I}$ is the temperature of exhaled minus inspired air (°C), $\rho_E$ is the density if air (0.0011 to 0.0012 kg l⁻¹), $W_{E} - W_{I}$ is the water content of exhaled air minus inspired air (mg l⁻¹), and $\lambda_v$ is the latent heat of vaporization ($\approx 2.43 \text{ J mg}^{-1} \text{ H}_2\text{O}$). Exhaled air temperature $T_{E}$ was estimated to be approximately 31.3±0.95 °C based on the mean of the maximum $T_{E}$ recorded in elephants ($n =3$) exposed to $T_a$'s of 12.5° to 25.3 °C (Benedict, 1936).
Dissipation of metabolic heat production

We present heat loss from the pinnae as a fraction of metabolic heat production by dividing the maximum heat loss by radiation plus convection by the seasonally adjusted estimate of metabolic rate. The maximum amount of resting metabolic heat dissipated in the pinnae in Asian elephants (Table 5) was modeled using net radiant heat transfer in the shade with the pinnae extended (Fig. 4A, model 1) and convective heat loss estimated from maximum flapping rates (Fig. 6A, model 6).

RESULTS

Microclimate Choice, Pinna Position and Pinna Flapping Rate

Microclimate selection in elephants was correlated with environmental conditions. Shade seeking was recorded during 57% and 11% of the total behavioral observations in two Asian and three African elephants, respectively (Table 3). The frequency of shade seeking increased in both elephant species with increasing environmental temperature. In Asian elephants shade seeking ranged from 30% in November to 80% of behavioral observations in June. Conversely, shade seeking in African elephants ranged from a minimum of 0% of behavioral observations during the cool, November and March periods to a maximum of 14% during July. Reduced shade seeking behavior by African elephants in Indianapolis was likely influenced by both the availability of shade and cooler weather experienced.

Pinna positioning in two Asian elephants was not correlated with environmental conditions. Over a range of ambient air temperatures from 5.3 to 37.0°C, Asian elephants held their ears in the extended position during 72% of the total behavioral observations, and seasonal variation were small, ranging from 69% to 81% of seasonal behavioral observation. Microclimate choice had a small affect on pinna positioning in Asian elephants. Asian elephants held their pinnae in
the extended position during 66% and 80% of the behavioral observations recorded in full sun and shade, respectively (Table 2). Pinna positioning in African elephants was correlated with environmental conditions. When African elephants were exposed to cold weather (air temperatures from 4.6 to 32.4°C) during the November and March study periods, the pinnae were rarely held in the extended position (Table 2) and were in close proximity to the body during approximately 68% of the total behavioral observations. However, when exposed to hot weather during the July study, African elephants held in their pinnae in the extended position for approximately 56% of the behavioral observations. As for Asian elephants, microclimate choice seemed to have an effect on pinna positioning in African elephants. African elephants held their pinnae in the extended position during 7.7% and 25.0% of the behavioral observations recorded in shade and full sun, respectively (Table 2).

Pinna flapping rates (flaps.min⁻¹) recorded in Asian elephants were correlated with both environmental condition and microclimate selection (Fig. 1A). In all conditions pinna flapping rates recorded in the shade were approximately 2-fold greater than pinna flapping rates recorded in full sun. Seasonal maximum pinna flapping rates recorded in Asian elephants were 29.2 flaps min⁻¹ (June), 8.2 flaps min⁻¹ (November) and 6 flaps min⁻¹ (February). Pinna flapping rates recorded in African elephants were correlated with environmental condition, but not with microclimate selection (Fig. 1B). Pinna flapping rates increased with increasing air temperature; however the maximum flapping rates were less than those recorded in Asian elephants. Maximum pinna flapping rates in African elephants were 16.8 flaps min⁻¹ (July), 7.8 flaps min⁻¹ (November), and 0.4 flaps min⁻¹ (March). A reduced flapping rate recorded in African elephants was likely the result of cooler weather in Indianapolis rather than species related differences.
Pinna Skin Temperatures

In both Asian and African elephants, mean anterior and posterior pinna skin temperatures increased with increasing ambient air temperature (Fig. 2). With the exception of the June Asian elephant study, the mean temperature difference between the anterior and posterior pinna skin surfaces were small, < 1.0°C (Table 3).

Net Radiant Heat Transfer

Seasonal differences in environmental radiation (Table 4), microclimate choice, and pinna positioning influenced net radiant heat transfer in resting Asian and African elephants (Fig. 3A and B). When exposed to hot weather, the most common microclimate selection and pinna position in resting Asian elephants, shade seeking and holding the pinna extended (Fig. 5A), minimized radiant heat gain in the pinna (Fig. 3A, model 3). Similarly, when exposed to cooler weather, the same behavioral choices maximized radiant heat loss in the pinnae of Asian elephants. In contrast, full sun exposure on extended pinnae maximized radiant heat gain in Asian elephants during all study periods (Fig. 3A, model 5).

The most common microclimate selection and pinna position in African elephants, full sun and holding the pinna in close proximity to the body, minimized heat loss during the November study period and resulted in a moderate level of radiant heat gain during the March and July study periods (Fig. 3B, model 2). However, orienting the body facing directly into or away from incident solar radiation was observed in African elephants (Fig. 5B), which effectively shaded one or both pinnae by positioning them edge-on to the sun. Shade seeking and extending the pinnae (Fig. 3B, model 3), as was recorded in African elephants during the July study period, resulted increased radiant heat loss.
Pinna positioning and flapping influenced convective heat transfer in elephants (Fig. 5A and B). We estimate that, in resting Asian elephants, extending the pinnae (Fig. 5A, model 2) increased convective heat transfer by approximately 1.4-fold compared with holding the pinnae in close to the body. The maximum flapping rate recorded in Asian elephants standing in the shade (Fig. 1) during the June study period resulted in a 4-fold increase in convective heat transfer, from 6.1±2.9 W while holding the pinnae extended to 24.1±10.3W flapping (Fig. 5A, model 2 and 6). The maximum pinna flapping rates in the hot environmental conditions recorded during the June study period produced convective heat transfer that was 58% to 68% of the convective heat transfers (of 41.3±22 W and 35.4±34 W) that were achieved passively by holding the pinnae extended (i.e. the most common position recorded) during November and February, respectively (Fig.5A, model 2).

African elephants usually held their pinnae in close proximity to the body (Fig.5B, model-1). However, pinna extending during the July study period increased convective heat transfer by approximately 1.4-fold (Fig. 5B, model 2). The maximum pinna flapping rate recorded in African elephants during the July study period resulted in a 2.7-fold increase in convective heat transfer from 81±42 W while holding the pinna in close proximity to the body to 220±116W during maximum flapping (Fig. 5B, model l and 6). As was the case for Asian elephants, the maximum pinna flapping rates in the hot environmental conditions during July produced convective heat transfer in the pinna that were 68% to 150% of the convective heat transfer (of 330±227W and 145±58W) that was achieved passively with the pinna held close to the body (i.e. the most common position recorded) in November and March, respectively (Fig.5B, model-1).
Dissipation of Metabolic Heat

Estimated rates of dry resting metabolic heat production ($M_{\text{rest}} - E_b$) were similar between seasons, ranging from 2755 ± 357W to 2835±386W and from 2483 ± 270W to 2864 ±425W in Asian and African elephants, respectively (Table 5). The maximum total heat loss ($Q_{n\text{max}} + C_{\text{max}}$) in the pinnae of Asian elephants, 122±62 W, corresponds to dissipation of approximately 5% of dry resting metabolic heat production (Table 5). The maximum total heat loss in the pinnae of African elephants, 1193±637 W corresponds to dissipation of approximately 48% of dry resting metabolic heat production (Table 5). However, it should be noted that during daylight hours Asian and African elephants in nature rarely experience the cool weather conditions, average air temperatures of 13.8±3.4°C and 7.3±4.1°C that resulted in maximum heat dissipation in the pinnae. Therefore, in nature it is likely that during daylight hours elephants dissipate a smaller portion of metabolic heat production through the pinnae.

DISCUSSION

In the present study we have demonstrated that seasonal variations in radiant environmental heat (Table 3) have a functionally significant effect on heat transfer (Fig. 3 and 5) in the pinnae of Asian and African elephants. Similarly, we have demonstrated that elephants can use behavioral choices such as pinna positioning, pinna flapping and microclimate choice to affect heat transfer in the pinnae (Table 2 and Fig. 1). Vasodilatation in the pinnae of elephants (Fig. 6) is often referred to as “thermal windows” for heat loss (Wright, 1984; Williams, 1990, Weissenböck et al. 2010). However, radiant environmental heat loads can inhibit heat loss from vasodilated pinnae, in essence closing a thermal window. Opening the thermal window often requires a behavioral thermoregulatory choice (Fig. 3A and B).
Differences in pinna surface area between Asian and African elephants obviously result in differences in the total amount of heat transfer occurring at the pinna skin surface (Fig. 3 and 5; Table 5). Direct comparisons between the two species in the present study must be made with caution because of differences in environmental conditions, availability of shade, and management protocols, which might have influenced on our results. For example, the low frequency of shade seeking recorded in African elephants was probably due to cooler weather (Table 4) and the reduced shade availability in Indianapolis. Avoidance of radiant environmental heat by shade seeking (Fig. 7) sun has been documented in African elephants in natural conditions (Kinahan et al. 2006).

Dissipation of Resting Metabolic Heat

Our results indicated that the ability of elephants to dissipate metabolic heat via heat loss from the pinnae is a function of environmental conditions and behavioral thermoregulatory choices. In addition, our data indicated that the amount of dry metabolic heat dissipated by the pinnae of Asian and African elephants is a fraction of previous estimates. The maximum amount of resting metabolic heat production dissipated by the pinnae that we report here, 5% and 48%, in Asian elephants and African elephants, respectively (Table 5), is in contrast to previously estimated values of 33% and 100% in Asian and African elephants (Phillips and Heath, 1992; Narasimhan, 2008).

Differences between our results, which indicate a much smaller proportion of metabolic heat production can be dissipated in the pinnae than previously reported, are the result of: (1) The omission of solar radiation from the previous analyses, (2) The use of large temperature differentials between $T_i$ and $T_a$, of 16 to 26°C reported in the previous studies that did not occur in those or the present study, (3) The use of large $(T_i – T_a)$ differentials in combination with fast
pinna flapping rates to construct heat transfer models. In the present study, maximum flapping rates for both elephant species were recorded during the hottest study periods when mean \((T_i - T_a)\) was small, 3.3°C±1.3°C and 6.6±1.9°C in Asian and African elephants, respectively (Fig. 2) and (4) The maximum speed (Eqn 12) of the pinna of Asian elephants at 29.2 flaps min\(^{-1}\) was 0.68 ms\(^{-1}\) and African elephants at 16.8 flaps min\(^{-1}\) was 0.56 ms\(^{-1}\). However, the flapping speeds of 5.0 ms\(^{-1}\) as assumed previously (Phillips and Heath, 1992; Narasimhan, 2008) would require flapping rates of 217±5 flaps min\(^{-1}\) and 140±9.9 flaps min\(^{-1}\), 7.3 and 8.3 times greater than maximum values we report for Asian and African elephants, respectively.

Functional Significance of Elephant Pinna

The specific thermoregulatory function of elephants’ large pinnae remains poorly defined. The head and trunk is often the hottest body region in resting elephants (Williams, 1990; Rowe, 1999; Weissenböck et al. 2010). Maximum pinna flapping is likely serves two purposes; (1) pinna flapping maintains a baseline level of convective heat loss from the pinna in hot conditions, which is similar to the levels recorded in cooler conditions with no flapping (Fig. 3A and B), and (2) maximum pinna flapping maintains heat loss from the pinnae when a net radiant heat loss is not possible (Table 5).

Our results indicate that heat transfer from the pinna dissipate relatively small percentages of resting metabolic heat production. However, protecting the brain from overheating is of crucial importance for an animal’s survival (Simon, 1999). Anatomical brain cooling structures such as carotid rete, cavernous sinus, and counter-current heat exchangers have been described in a variety of mammals (Baker and Hayward, 1968; Baker and Nijland, 1993; Schroter et al., 1989; Mitchell et al., 2002; Lusk et al., 2007), including elephants (Shoshani et al., 2006). Temperature differences of approximately 2.5 to 9°C between arterial and venous circulation in the pinnae of
active elephants have been reported (Baldwin, 1974; Wright, 1984). Similarly, in our study, thermograms of the pinnae of elephants showed temperature differences of 1.5 to 5.5 °C between what we believe to be arterial and venous circulation (Fig. 6). Assuming that venous blood leaving the pinnae was delivered to the carotid rete and cavernous sinus, the pinnae of elephants might play a role in regulating brain temperature. However, this relationship is purely speculative until the destination of cooled venous blood exiting from the pinnae has been described, a topic worthy of further investigation.

Brain tissue has a high metabolic heat production approximately 11.7 W kg⁻¹, and the mass of an adult elephant’s brain is approximately 4.8 kg (Gallagher et al. 1998; Shoshani et al. 2006). Over the range of environmental test conditions (Table 2), pinna flapping in Asian could dissipate from 58% to 79% of metabolic heat produced in brain tissue (Table 5). Similarly, African elephants could dissipate greater than 100% of metabolic heat produced in the brain via maximum pinna flapping (Table 5).

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REFERENCES


Table 1. Physical characteristic of resting metabolic heat production ($M_{\text{rest}}$) and the pinna characteristics used to calculate heat transfer in individual elephants. *Note: Mean (±s.d.) $M_{\text{rest}}$ for Asian elephants (Langman et al. in press) was used to estimate $M_{\text{rest}}$ for African elephants.

<table>
<thead>
<tr>
<th>Species/Elephant</th>
<th>Age (yr.)</th>
<th>Mass (kg)</th>
<th>$M_{\text{rest}}$ (W.kg$^{-1}$)</th>
<th>Surface Area (m$^2$)</th>
<th>Maximum Width (m)</th>
<th>Arc Length (m.flap$^{-1}$)</th>
<th>Solar Absorptance (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>E. maximus/Jean</td>
<td>35</td>
<td>3447</td>
<td>0.77±0.1</td>
<td>0.26</td>
<td>0.580</td>
<td>1.35</td>
<td>78</td>
</tr>
<tr>
<td>Panya</td>
<td>45</td>
<td>4627</td>
<td>0.74±0.1</td>
<td>0.35</td>
<td>0.600</td>
<td>1.40</td>
<td>80</td>
</tr>
<tr>
<td>L. africana/Kubwa</td>
<td>32</td>
<td>3455±7</td>
<td>0.76±0.02*</td>
<td>0.72</td>
<td>0.860</td>
<td>2.00</td>
<td>76</td>
</tr>
<tr>
<td>Tombi</td>
<td>31</td>
<td>3532±96</td>
<td>0.76±0.02*</td>
<td>0.94</td>
<td>0.970</td>
<td>2.26</td>
<td>76</td>
</tr>
<tr>
<td>Sophi</td>
<td>40</td>
<td>4528±56</td>
<td>0.76±0.02*</td>
<td>0.83</td>
<td>0.940</td>
<td>2.19</td>
<td>76</td>
</tr>
</tbody>
</table>
Table 2. Seasonal changes in behavioral thermoregulation in Asian (*E. maximus*) and African elephants (*L. africana*), including; the range of air temperatures (*Tₐ*, °C) over which seasonal observations behavioral thermoregulation (Total Obs., Hrs), shade seeking (Shd. Micro, Hrs), pinnae extending in the shade (Pinnae Extd. Shd., Hrs.), full sun exposure (Sun Micro, Hrs.), Pinnae extended in full sun (Pinnae Extd. Sun, Hrs.) and the total number of 5-min trials (Trials, n=1284).

<table>
<thead>
<tr>
<th>Species</th>
<th>Season</th>
<th><em>Tₐ</em>  (°C)</th>
<th>Total Obs. (Hrs.)</th>
<th>Shd. Micro (Hrs.)</th>
<th>Pinnae Extd. Shd. (Hrs.)</th>
<th>Sun Micro (Hrs.)</th>
<th>Pinnae Extd. Sun (Hrs.)</th>
<th>Trials (n)</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>E. maximus</em></td>
<td>Feb. 2009</td>
<td>8.7–24.8</td>
<td>33.9</td>
<td>17.9</td>
<td>11.3</td>
<td>16.0</td>
<td>14.0</td>
<td>406</td>
</tr>
<tr>
<td></td>
<td>June 2009</td>
<td>29.8–37.0</td>
<td>30.3</td>
<td>24.1</td>
<td>16.1</td>
<td>6.2</td>
<td>4.7</td>
<td>363</td>
</tr>
<tr>
<td></td>
<td>Nov. 2009</td>
<td>5.3–23.6</td>
<td>20.7</td>
<td>6.3</td>
<td>4.3</td>
<td>14.4</td>
<td>10.4</td>
<td>248</td>
</tr>
<tr>
<td></td>
<td>Total</td>
<td>5.3 – 37</td>
<td>84.9</td>
<td>48.3</td>
<td>31.7</td>
<td>36.6</td>
<td>29.1</td>
<td>1017</td>
</tr>
<tr>
<td><em>L. africana</em></td>
<td>Nov. 2008</td>
<td>4.6–23.6</td>
<td>6.8</td>
<td>0</td>
<td>0</td>
<td>6.8</td>
<td>1.07</td>
<td>80</td>
</tr>
<tr>
<td></td>
<td>Mar. 2009</td>
<td>6.6–21.8</td>
<td>5.3</td>
<td>0</td>
<td>0</td>
<td>5.3</td>
<td>0.47</td>
<td>63</td>
</tr>
<tr>
<td></td>
<td>July 2009</td>
<td>20.4–32.4</td>
<td>10.2</td>
<td>2.3</td>
<td>1.6</td>
<td>7.9</td>
<td>4.1</td>
<td>124</td>
</tr>
<tr>
<td></td>
<td>Total</td>
<td>4.6–32.4</td>
<td>22.3</td>
<td>2.3</td>
<td>1.6</td>
<td>20.0</td>
<td>5.6</td>
<td>267</td>
</tr>
</tbody>
</table>
Table 3. Seasonal mean (±s.d.) anterior pinna skin temperature ($T_i$) and posterior pinna skin $T_i$, ground temperature ($T_g$) and the number of thermal imaging trial conducted (n = 55 trials, 110 thermographs).

<table>
<thead>
<tr>
<th>Species</th>
<th>Season</th>
<th>Anterior $T_i$ (°C)</th>
<th>Posterior $T_i$ (°C)</th>
<th>$T_g$ (°C)</th>
<th>Trials (n)</th>
</tr>
</thead>
<tbody>
<tr>
<td>$E. maximus$</td>
<td>February 2009</td>
<td>22.1±3.6</td>
<td>21.9±3.8</td>
<td>17.6±3.6</td>
<td>14</td>
</tr>
<tr>
<td></td>
<td>June 2009</td>
<td>31.7±1.5</td>
<td>35.1±0.88</td>
<td>39.1±2.6</td>
<td>14</td>
</tr>
<tr>
<td></td>
<td>November 2009</td>
<td>21.5±2.7</td>
<td>20.7±2.8</td>
<td>13.9±2.5</td>
<td>9</td>
</tr>
<tr>
<td></td>
<td>Total</td>
<td>---</td>
<td>---</td>
<td>---</td>
<td>37</td>
</tr>
<tr>
<td>$L. africana$</td>
<td>November 2008</td>
<td>20.3±2.5</td>
<td>19.4±2.8</td>
<td>9.5±4.2</td>
<td>5</td>
</tr>
<tr>
<td></td>
<td>March 2009</td>
<td>22.2±2.5</td>
<td>21.9±2.4</td>
<td>17.0±5.1</td>
<td>5</td>
</tr>
<tr>
<td></td>
<td>July 2009</td>
<td>32.3±1.7</td>
<td>32.2±1.3</td>
<td>31.0±5.9</td>
<td>8</td>
</tr>
<tr>
<td></td>
<td>Total</td>
<td>---</td>
<td>---</td>
<td>---</td>
<td>18</td>
</tr>
</tbody>
</table>
Table 4. Seasonal mean (±s.d.) environmental conditions used to calculate heat transfer, including: ambient air temperature ($T_a$), wind speed ($u$), direct solar radiation ($S_n$), average direct solar radiation at an angle incident to the pinna skin surface ($S_i$), direct solar radiation falling on a horizontal surface ($S_h$), diffuse solar radiation ($s$), longwave thermal radiation from the atmosphere ($R_a$) and longwave thermal radiation from the ground surface ($R_g$).

<table>
<thead>
<tr>
<th>Species</th>
<th>Season</th>
<th>$T_a$ (°C)</th>
<th>$u$ (ms$^{-1}$)</th>
<th>$S_n$ (Wm$^{-2}$)</th>
<th>$S_i$ (Wm$^{-2}$)</th>
<th>$S_h$ (Wm$^{-2}$)</th>
<th>$s$ (Wm$^{-2}$)</th>
<th>$R_a$ (Wm$^{-2}$)</th>
<th>$R_g$ (Wm$^{-2}$)</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>E. maximus</em></td>
<td>Feb. 09</td>
<td>15.9±4.0</td>
<td>1.20±0.80</td>
<td>288±267</td>
<td>246±198</td>
<td>165±178</td>
<td>92.7±41</td>
<td>311.5±26</td>
<td>377±19</td>
</tr>
<tr>
<td></td>
<td>June 09</td>
<td>31.5±1.7</td>
<td>0.32±0.20</td>
<td>621±162</td>
<td>487±238</td>
<td>358±126</td>
<td>89.9±37</td>
<td>423.5±13</td>
<td>501±17</td>
</tr>
<tr>
<td></td>
<td>Nov. 09</td>
<td>13.8±3.4</td>
<td>0.98±0.47</td>
<td>251±253</td>
<td>231±157</td>
<td>125±124</td>
<td>72.6±33</td>
<td>297.4±23</td>
<td>358±13</td>
</tr>
<tr>
<td><em>L. africana</em></td>
<td>Nov. 08</td>
<td>7.3±4.1</td>
<td>2.98±1.35</td>
<td>40±25</td>
<td>12±4.3</td>
<td>11±5</td>
<td>42.1±18</td>
<td>256.6±25</td>
<td>337±21</td>
</tr>
<tr>
<td>Mar. 09</td>
<td>10.7±4.1</td>
<td>1.37±0.42</td>
<td>567±263</td>
<td>350±168</td>
<td>354±164</td>
<td>67.4±36</td>
<td>277.8±26</td>
<td>374±26</td>
<td></td>
</tr>
<tr>
<td>Jul. 09</td>
<td>25.4±1.9</td>
<td>1.31±0.62</td>
<td>512±402</td>
<td>395±313</td>
<td>426±352</td>
<td>104±59</td>
<td>377.6±14</td>
<td>452±35</td>
<td></td>
</tr>
</tbody>
</table>
Table 5 lists seasonal variations in mean (±s.d.) estimated resting metabolic rate ($M_{\text{rest}}$), respiratory evaporative heat loss ($E_b$), maximum net radiant heat transfer ($Q_{n \text{ max}}$; model-3), maximum convective heat transfer ($C_{\text{max}}$; model-5 and 6), maximum total heat loss from the pinnae ($Q_{n \text{ max}} + C_{\text{max}}$), and the percent of $M_{\text{rest}} - E_b$ dissipated by $Q_{n \text{ max}} + C_{\text{max}}$. Positive values indicate heat loss and negative values indicate heat gain.

<table>
<thead>
<tr>
<th>Species</th>
<th>$M_{\text{rest}}$ (W)</th>
<th>$E_b$ (W)</th>
<th>$M_{\text{rest}} - E_b$ (W)</th>
<th>$Q_{n \text{ max}}$ (W)</th>
<th>$C_{\text{max}}$ (W)</th>
<th>$Q_{n \text{ max}} + C_{\text{max}}$ (W)</th>
<th>% $M_{\text{rest}} - E_b$</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>E. maximus</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>February</td>
<td>3094±395</td>
<td>302±43</td>
<td>2792±357</td>
<td>26.4±28</td>
<td>70.2±68</td>
<td>96.8±37</td>
<td>3.4</td>
</tr>
<tr>
<td>June</td>
<td>2952±388</td>
<td>117±13</td>
<td>2835±386</td>
<td>-34.8±25</td>
<td>24±10</td>
<td>-10.8±23</td>
<td>-0.3</td>
</tr>
<tr>
<td>November</td>
<td>3081±406</td>
<td>326±43</td>
<td>2755±366</td>
<td>54.2±26</td>
<td>82±45</td>
<td>136.2±62</td>
<td>5.0</td>
</tr>
<tr>
<td><em>L. africana</em></td>
<td>---</td>
<td>---</td>
<td>---</td>
<td>---</td>
<td>---</td>
<td>---</td>
<td>---</td>
</tr>
<tr>
<td>November</td>
<td>2898±419</td>
<td>356±40</td>
<td>2542±384</td>
<td>295±22</td>
<td>902±254</td>
<td>1197±637</td>
<td>48.0</td>
</tr>
<tr>
<td>March</td>
<td>2831±291</td>
<td>347±27</td>
<td>2483±270</td>
<td>106±72</td>
<td>397±157</td>
<td>503±222</td>
<td>21.0</td>
</tr>
<tr>
<td>July</td>
<td>3035±429</td>
<td>171±15</td>
<td>2864±425</td>
<td>-107±78</td>
<td>220±41</td>
<td>112±132</td>
<td>3.8</td>
</tr>
</tbody>
</table>
Fig. 1A and B illustrate ≈107 hours (n = 1227, 5-min trials) of pinna flapping (one ear) measurements recorded in full sun (closed symbols) and shade (open symbols) microclimates. (A) Asian elephants, Panya (red circles) and Jean (blue circles), were exposed to ambient air temperatures ($T_a$) that ranged from 5.3 to 37.0 °C. (B) African elephants, Sophi (black squares), Tombi (green squares) and Kubwa (purple squares), were exposed to $T_a$ that ranged from 4.6 to 32.4 °C. The figure also indicates that these elephants spent most of their time in the shade when $T_a$ exceeded 30.0°C.
Fig. 2. Increase in anterior (solid symbols) and posterior (open symbols) pinna skin temperatures ($T_l$, °C) with increasing ambient air temperature ($T_a$, °C) in two adult Asian elephants (blue and red circles) and three African elephants (black, green and purple, squares). The linear regressions describing the increase in $T_l$ with increasing $T_a$ in the anterior surfaces in Asian and African elephants (solid lines) were $T_l = 0.78 \, T_a + 10.1$, $R^2 = 0.93$ and $T_l = 0.62 \, T_a + 16.0$, $R^2 = 0.86$ respectively. The linear regressions describing increase in $T_l$ with increasing $T_a$ in the posterior surfaces in Asian and African elephants (dashed lines) were $T_l = 0.88 \, T_a + 9.4$, $R^2 = 0.93$ and $T_l = 0.67 \, T_a + 14.8$, $R^2 = 0.88$, respectively.
Fig. 3. Influence of microclimate choice and pinna positioning on mean (±s.d.) net radiant heat loss ($Q_n$) recorded in Asian elephants (A) and (B) African elephants, including: (1) pinnae held close to the body in the shade (solid dark grey), (2) pinnae held close to body with one pinna exposed to solar radiation (diagonal line grey), (3) pinnae extended and shaded (solid green), (4) pinnae extended with one surface in the sun and three shaded (diagonal line blue), and (5) pinnae extended with two surfaces in the sun and two shaded (cross-hatched red).
Fig. 4. Most common microclimate selection and pinna positioning recorded in (A) Asian elephants, shade seeking and pinna extended, and (B) African elephants full sun and pinna held close to the body.
Fig. 5. Influence of pinna positioning and pinna flapping on mean (±s.d.) convective heat loss recorded in (A) Asian elephants and (B) African elephants, including: pinnae (1) held close to the body (solid red), (2) extended (solid light grey), (3) mean flapping rate in the sun (cross-hatched yellow), (4) mean flapping in the shaded (cross-hatched grey), (5) maximum flapping in the sun (solid yellow), and (6) maximum flapping in the shade (solid dark grey). Maximum flapping rates in hot weather produced convective heat loss rates that were similar to pinnae held close to the body in cooler conditions (green shaded area).
Fig. 6. Thermograms of the anterior pinna skin surfaces of (A) Asian and (B) African elephants. The thermograms indicated a 2°C to 5°C temperature differential between arterial (light colored) and venous (dark colored) vessels in both elephant species. Note: the temperature scales are different due to different environmental conditions.
APPENDIX A: ABBREVIATIONS AND SYMBOLS FOR CHAPTER 2.

\( COT_{\text{net}} \)  Mass-specific net cost of transport in Jkg\(^{-1}\)m\(^{-1}\).
\( COT_{\text{min}} \)  Mass-specific minimum cost of transport in Jkg\(^{-1}\)m\(^{-1}\).
\( COT_{\text{tot}} \)  Mass-specific total cost of transport in Jkg\(^{-1}\)m\(^{-1}\).
\( EE_{\text{net}} \)  Mass-specific net energy expenditure in Wkg\(^{-1}\).
\( EE_{\text{tot}} \)  Mass-specific energy expenditure in Wkg\(^{-1}\).
\( Fr \)  Froude number, dimensionless speed.
\( g \)  Gravitational acceleration 9.8 ms\(^{-2}\).
\( M_b \)  Body mass in kg.
\( v_f \)  Walking speed in ms\(^{-1}\).
APPENDIX B: ABBREVIATIONS AND SYMBOLS FOR CHAPTER 3.

\( A \quad \text{Total skin surface area (m}^2\text{)) calculated from the relationship } A = 0.1 M_0^{0.67}. \)

\( A_1 \quad \text{Cross-sectional surface area of a spherical elephants (m}^2\text{).} \)

\( A_2 \quad 50\% \text{ of the total skin surface area (m}^2\text{).} \)

\( \alpha_1 \quad \text{Percent absorptance of elephants skin for shortwave solar radiation.} \)

\( \alpha_2 \quad \text{Percent absorptance of elephant skin for longwave thermal radiation.} \)

\( C \quad \text{Convective heat loss (W).} \)

\( C_{ex} \quad \text{Convective heat loss during exercise (W).} \)

\( c_p \quad \text{Heat capacity of air (1003.5 J}^\circ\text{C}^{-1}\text{kg}^{-1}). \)

\( \Delta T_b \quad \text{Change in core body temperature (}^\circ\text{C).} \)

\( \Delta t \quad \text{Change in time (s).} \)

\( E \quad \text{Evaporative heat loss (W).} \)

\( E_b \quad \text{Respiratory evaporative heat loss (W).} \)

\( E_r \quad \text{Evaporative heat loss from skin (W).} \)

\( \varepsilon \quad \text{Emissivity of elephant skin (0.96) and asphalt (0.93).} \)

\( h_c \quad \text{Convection coefficient (Wm}^{-2}\text{C}^{-1}). \)

\( I \quad \text{Tissue insulation (m}^2\text{s}^\circ\text{CJ}^{-1}) \)

\( K \quad \text{Conductive heat loss (W).} \)

\( k \quad \text{Thermal conductivity of air (2.47 to 2.65 x 10}^{-2}\text{ Wm}^{-1}\text{C}^{-1}). \)

\( \lambda \quad \text{Latent heat of water vaporization (\approx 2.43 J}\text{mg}^{-1}\text{H}_2\text{O).} \)
$M$  Resting metabolic heat production (W).

$M_{ex}$  Wet exercise metabolic heat production (W, Wkg$^{-1}$, Wm$^{-2}$).

$M_{ex-E_b}$  Dry exercise (active) metabolic heat production (W Wkg$^{-1}$, Wm$^{-2}$).

$m_b$  Body mass (kg).

$\rho_E$  Density of air (0.0011 to 0.0012 kgL$^{-1}$).

$\propto$  Proportional.

$Q_a$  Environmental radiation absorbed by a spherical elephant (W).

$Q_n$  Net radiant heat transfer (W).

$Q_{n_{sun}}$  Net radiant heat transfer in full sun (W).

$Q_{n_{night}}$  Net radiant heat transfer at night (W).

$R_a$  Long wave thermal radiation from the atmosphere (Wm$^{-2}$).

RH%  Relative humidity (%).

$R_g$  Long wave thermal radiation from the track surface (Wm$^{-2}$).

$R_s$  Radiant heat loss from a spherical elephant (W).

$r$  Reflectance of the asphalt track surface (15%).

$S_h$  Direct shortwave solar radiation falling on a horizontal plane (Wm$^{-2}$).

$S_n$  Direct shortwave solar radiation perpendicular to the body.

$s$  Diffuse shortwave solar radiation scattered in the atmosphere.

$\sigma$  Stefan-Boltzmann constant $5.67 \times 10^{-8}$ Wm$^{-2}$K$^{-4}$.

$T_a$  Ambient air temperature (°C).

$T_b$  Core body (rectal) temperature (°C).

$T_E$  Temperature of exhaled air (°C).

$T_g$  Radiant ground temperature (°C).
$T_1$ Temperature of inspired air (°C).

$T_r$ Mean radiant skin temperature (°C).

$u$ Sustained environmental wind speed (m.s$^{-1}$).

$V$ Respiratory minute volume (l.s$^{-1}$)

$v_r$ Walking speed (m.s$^{-1}$).

$W_E$ Water content of exhaled air (mg H$_2$O l$^{-1}$air)

$W_I$ Water content of inhaled air (mg H$_2$O l$^{-1}$air)

$X$ Heat storage in 100% core tissues (W).

$X_{adj}$ Adjusted heat storage (W).

$x$ Distance body core to skin surface (m).
APPENDIX C: ABBREVIATIONS AND SYMBOLS FOR CHAPTER 4.

$A_1$ Total pinna surface area (m$^2$).

$A_2$ 50% total pinna surface area (m$^2$).

$a_p$ Pinna altitude (vertical plate at 90° to the horizon).

$a_s$ Solar altitude.

$\alpha_1$ Percent absorptance of elephants skin for shortwave solar radiation.

$\alpha_2$ Percent absorptance of elephant skin for longwave thermal radiation.

$C$ Convective heat loss (W).

$C_{ex}$ Convective heat loss during exercise (W).

$c_p$ Heat capacity of air (1003.5 J°C$^{-1}$kg$^{-1}$).

$D$ Critical dimension, diameter of a circle with the surface area of the pinna (m).

$E$ Evaporative heat loss (W).

$E_b$ Respiratory evaporative heat loss (W).

$E_r$ Evaporative heat loss from skin (W).

$\varepsilon$ Emissivity (skin = 0.96, asphalt = 0.93).

$\sigma$ Stefan-Boltzmann constant, 5.673x10$^{-8}$ (Wm$^{-2}$K$^{-4}$).

$h_c$ Convection coefficient (Wm$^{-2}$°C$^{-1}$).

$k$ Thermal conductivity of air (2.47 to 2.65 x 10$^{-2}$ Wm$^{-1}$°C$^{-1}$).

$\lambda_v$ Latent heat of water vaporization (2.43 Jmg$^{-1}$H$_2$O).

$M$ Metabolic heat production (Wkg$^{-1}$ or W).
\( M_{\text{ex}} \) Exercise (active) metabolic heat production (Wkg\(^{-1}\) or W).

\( M_{\text{ex}}-E_b \) Dry exercise (active) metabolic heat production (W).

\( m_b \) Body mass (kg).

\( \text{Nu} \) Nusselt number.

\( \rho_E \) Density of air (0.0011 to 0.0012 kg\( \ell \)^{-1}).

\( \phi_p \) Pinnae azimuth (degrees clockwise from north).

\( \phi_s \) Solar azimuth (degrees clockwise from north).

\( Q_a \) Environmental radiant heat gain (W).

\( Q_{a\ sun} \) Environmental radiant heat gain in full sun (W).

\( Q_{a\ shade} \) Environmental radiant heat gain in shade (W).

\( Q_{a\ night} \) Environmental radiant heat gain at night (W).

\( Q_l \) Radiant heat loss in pinnae (W).

\( Q_n \) Net radiant heat transfer (W).

\( Q_{n\ sun} \) Net radiant heat transfer in full sun (W).

\( Q_{n\ shade} \) Net radiant heat transfer in shade (W).

\( Q_{n\ night} \) Net radiant heat transfer at night(W).

\( S_i \) Direct shortwave solar radiation incident to the pinna skin surface (Wm\(^{-2}\)).

\( S_h \) Direct shortwave solar radiation striking a horizontal surface (Wm\(^{-2}\)).

\( S_n \) Direct shortwave solar radiation incident perpendicular to the elephants body (Wm\(^{-2}\)).

\( s \) Diffuse shortwave solar radiation (Wm\(^{-2}\)).

\( R_a \) Longwave thermal radiation from the atmosphere (Wm\(^{-2}\)).

\( \text{Re} \) Reynolds number.

\( R_g \) Longwave thermal radiation from the ground (track) surface (Wm\(^{-2}\)).
RH%  Percent relative humidity.

\( r(S_{h+s}) \) Shortwave solar radiation reflected off the track surfaces (Wm\(^{-2}\)).

\( T_a \)  Ambient air temperature (°C).

\( T_b \)  Core body temperature (°C).

\( T_E \)  Temperature of exhaled air (°C).

\( T_g \)  Mean ground (track) temperature (°C).

\( T_i \)  Temperature of inhaled air (°C).

\( T_l \)  Mean pinna skin temperature (°C).

\( u \)  Sustained environmental wind speed (ms\(^{-1}\)).

\( V \)  Respiratory minute volume (l\( s^{-1}\)).

\( v_l \)  Walking speed (ms\(^{-1}\)).

\( v \)  Kinematic viscosity of air (1.42 to 1.60 \( \times 10^{-5} \) m\(^2\)s\(^{-1}\)).

\( W_E \)  Water content of exhaled air (mg l\(^{-1}\)).

\( W_i \)  Water content of inhaled air (mg l\(^{-1}\)).
APPENDIX D: ABBREVIATIONS AND SYMBOLS FOR CHAPTER 5.

A_1  Total pinna surface area (m^2).
A_2  50% total pinna surface area (m^2).
A_3  50% total pinna surface area (m^2).
C_{env}  Convective heat transfer in the pinnae from environmental wind (W).
C_{max}  Maximum convective heat loss from pinna flapping (W).
c_p  Heat capacity of air (1003.5 J°C^{-1}kg^{-1}).
\varepsilon  Emissivity of elephant skin (0.96) and soil (0.92).
\alpha  Stefan-Boltzmann constant, 5.673 \times 10^{-8}.
\lambda  Wavelength of light, micrometers (\mu m)
\lambda_v  Latent heat of vaporization (2.43 Jmg^{-1}H_2O).
M_{rest}  Resting metabolic heat production (W.kg^{-1} or W).
m_b  Body mass (kg).
Q_a  Environmental radiant heat gain (W).
Q_l  Radiant heat loss in pinnae (W).
Q_n  Net radiant heat transfer (W).
S_i  Direct shortwave solar radiation incident to the pinna skin surface (Wm^{-2}).
S_h  Direct shortwave solar radiation striking a horizontal surface (Wm^{-2}).
S_n  Direct shortwave solar radiation incident perpendicular to the pinna skin surface (Wm^{-2}).
s  Diffuse shortwave solar radiation (Wm^{-2}).
$R_a$  Longwave thermal radiation from the atmosphere (Wm$^{-2}$).

$R_g$  Longwave thermal radiation from the ground (track) surface (Wm$^{-2}$).

$r(S_{h+s})$  Shortwave solar radiation reflected off the track surfaces (Wm$^{-2}$).

$T_a$  Ambient air temperature ($^\circ$C).

$T_g$  Mean ground (track) temperature ($^\circ$C).

$T_l$  Mean pinna skin temperature ($^\circ$C).

$\nu$  Sustained environmental wind speed (m.s$^{-1}$).

$\nu$  Kinematic viscosity of air (1.42 to 1.60 x 10$^{-5}$m$^2$s$^{-1}$).

$W$  Maximum width of the pinna (m).

$W_E$  Water content of exhaled air (mg $l^{-1}$).

$W_I$  Water content of inhaled air (mg $l^{-1}$).