

Heat transfer in elephants: thermal partitioning based on skin temperature profiles

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(With 4 figures in the text)

The elephant with its low surface-to-volume ratio presents an interesting problem concerning heat dissipation. To understand how such large mammals remain in thermal balance, we determined the major avenues of heat loss for an adult African elephant and an immature Indian elephant. Because conventional physiological measurements are difficult for these animals, the present study used a non-invasive technique, infrared thermography, to measure skin temperatures of each elephant. Detailed surface temperature profiles and surface area measurements of each elephant were used in standard equations for convective, conductive and radiant heat transfer. Results demonstrated that heat transfer by free convection and radiation accounted for 86% of the total heat loss for the elephants at $T_a = 12.6$ °C. Heat transfer across the ears, an important thermal window at high ambient temperatures, represented less than 8% of the total heat loss. Surface area of the animals, and metabolic heat production calculated from total heat loss of the African elephant, scaled predictably with body mass. In contrast, the thermal conductance of the elephants (71.6 W/°C, African; 84.5 W/°C, Indian) was three to five times higher than predicted from an allometric relationship for smaller mammals. The high thermal conductance of elephants is attributed to the absence of fur and appears to counteract reduced heat transfer associated with a low surface-to-volume ratio.

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Introduction

The large size of elephants results in a comparatively small surface-to-volume ratio as well as a small surface area available for heat transfer. Many studies have suggested that elephants facilitate

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heat transfer by using thermal windows (Buss & Estes, 1971; McKay, 1973; Wright, 1984). Hyperthermia caused by inadequate heat loss across the body surface may be avoided by increasing heat transfer across the elephant's highly vascularized ears. On the basis of blood flow rates and arterio-venous temperature differences, Wright (1984) determined that heat loss from the ears of the African elephant could account for 20–50% of the calculated metabolic heat loss requirements. Ear-spreading and flapping also facilitate heat dissipation in these animals (Buss & Estes, 1971). The Indian elephant does not share the distinctive ears of the African elephant. Despite this, the extensive vasculature of the ears and the correlation between ear-flapping rates and ambient temperature indicate a thermoregulatory role for the Indian elephant's small pinnae as well (McKay, 1973).

Although the ears provide an important area for heat transfer during periods of high heat production or environmental heat loads, we know little about the thermal properties of the remaining body surfaces of elephants. In view of this, the present study measured skin temperature and calculated convective, radiant and conductive heat losses for different anatomical sites of an African and an Indian elephant. Heat losses were determined from the temperature differential between the skin and the surrounding environment (Clark, 1981). Recent technological advances in infrared thermography and system-compatible computer analysis permitted the temperature profile of a complex surface such as an elephant to be examined, and the surface area occupied by specific isotherms to be quantified. By summing the different avenues of heat transfer, the contribution of various anatomical areas to total heat loss was determined for each species of elephant.

Methods

Animals and protocol

Two captive-raised female elephants, one Indian (*Elephas maximus*; immature; 2000 kg) and one African (*Loxodonta africana*; adult; 3500 kg), were studied at the San Diego Zoo. A routine schedule was followed: both animals were fed *ad libitum* during the night, and were housed in individual indoor stalls. Their diet consisted of a combination of hay, grain, vegetables and fruit. Before releasing it outdoors, keepers walked each elephant into the large central court (14 m × 15 m) of the elephant barn. Animals were a minimum of 7 m away from any structure during all tests. Using signals, the keepers maintained each elephant in a stationary position as different viewing angles were presented to an infrared thermographic camera. To define specific thermal windows, close-up views obtained with a 7 × 7 magnifying lens were recorded for axillary and ventral regions, inner (posterior) and outer (anterior) ear surfaces, and the side of the neck behind the ears. Distance between the camera and subject was constant for each viewing angle and each elephant.

Following thermographic analysis, morphological measurements were taken for each elephant. Measurements included height at the shoulder, chest width, circumferences of the front and hind feet and ear and trunk dimensions. Photographs taken at this time were used to calculate other body dimensions. Surface area of each elephant was calculated by dividing the body into cylinders (Fig. 1). Surface areas of all cylinders were summed with appropriate corrections made for adjoining cylinders. Total body surface area, excluding the ears, of the African elephant was within 3.4% of predicted values (Calder, 1984). The surface area of the Indian elephant was 7.3% higher than predicted.

Infrared thermography

Thermographic images representing skin temperatures were generated by an Agema 728 Infrared Thermography System, and recorded on a system-compatible videotape recorder. Reference temperature for

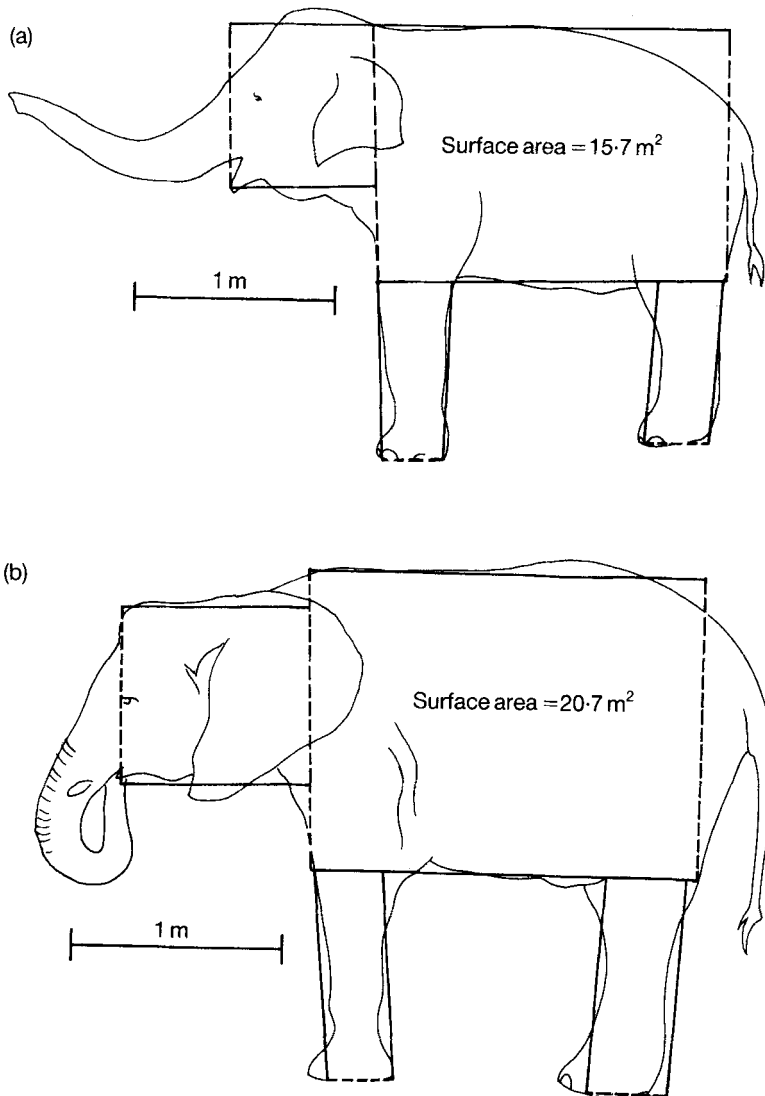


FIG. 1. Division of Indian (a) and African (b) elephant profiles into simple geometric shapes. Each box dimension represents the height (—) and diameter (---) of cylinders used in surface area determinations. Surface areas of the ears and trunk were measured directly. Total body surface area excluding the ears and bottom surface of the feet is indicated for each elephant.

the Agema system was a liquid nitrogen source. Fields of view were subdivided into 8 isotherms with $0.1\text{ }^{\circ}\text{C}$ resolution between adjoining isotherms. Thermal readings were calibrated against skin surfaces of known temperatures. Calibration temperatures ($13.3\text{--}30.6\text{ }^{\circ}\text{C}$) spanned the range of skin temperatures of the elephants. Skin temperatures indicated by the thermographic system and a calibrated thermocouple thermometer (Cole-Palmer) varied by less than $0.2\text{ }^{\circ}\text{C}$. Thermographic tests were performed between 07:00 and 08:00 h at T_{air} and $T_{\text{blackbody}} = 12.6\text{ }^{\circ}\text{C}$. Because of these conditions and an indoor test location, the effects of incident solar radiation and wind speed were considered negligible.

Heat-transfer analysis

Convective, radiant and conductive heat transfer were determined from skin temperature isotherms. Temperature artefacts resulting from surface curvature of the elephants (Cena, 1984; Ring, 1984) were avoided by analysing thermographic images representing anatomical planes facing the camera lens. Angles between the thermographic scanner axis and the normal to the surface to be analysed were less than 40° (Steketee, 1984). By changing the viewing angle or position of the elephant, we were able to determine isotherms for anterior, posterior, ventral and lateral surfaces. Only the mid-dorsal surface of the elephant was not imaged directly. The percentage of body surface area occupied by individual isotherms was measured by digitizing (HiPad, Inc.) thermographic images of the elephants. These percentages were converted to skin surface area by using dimensional information from morphological measurements. Heat-transfer analysis was simplified by converting body segments into geometric shapes. The trunk, head, torso and legs were analysed as vertical or horizontal cylinders, while the ears were analysed as flat, vertical plates. Standard expressions describing heat loss as a function of temperature gradients at the surface of geometric objects were applied. Similar analyses have been used to examine heat loss from different areas of the human body (Draper & Boag, 1971; Clark & Edholm, 1985). Heat transfer was determined from the following equations:

1. Free convective heat transfer = $h_c A (T_s - T_a)$ where h_c = free convective heat transfer coefficient of plates or cylinders ($\text{W/m}^2 \text{ } ^\circ\text{C}^{-1}$) from Clark & Edholm (1985); A = isotherm area (m^2); T_s = skin temperature represented by the isotherm ($^\circ\text{C}$); and T_a = ambient temperature ($^\circ\text{C}$).

2. Net radiant energy transfer = $\sigma \varepsilon (T_s^4 - T_a^4) \times 0.85A$ where σ = Stefan-Boltzmann constant, $5.7 \times 10^{-8} \text{ W/m}^2 \text{ } ^\circ\text{K}^4$, and ε = emissivity factor for skin, 0.98 (Clark & Edholm, 1985); T_s and T_a = skin and ambient temperatures ($^\circ\text{K}$), respectively. Because of the complex exchange of radiant heat between different body areas, we assumed that only 0.85 of the total surface area of the animal was involved in radiant energy transfer with the enclosure. This simplified version of Christiansen's equation was chosen since the barn enclosure was much larger than the test subjects.

3. Conductive heat flow = $kA (T_s - T_{\text{foot}})/b$ where k = thermal conductivity of tissue, $0.39 \text{ W/m } ^\circ\text{C}$ (Clark & Edholm, 1985); and b = gradient length across the foot, 0.05 m.

The two remaining components of the thermal energy budget, heat storage and evaporative water loss, were estimated for the elephants. Under the conditions of this study we considered heat storage to be negligible. Calculations of transepidermal evaporative water loss from elephants have ranged from 10% of total heat loss at $T_a = 17\text{--}20 \text{ } ^\circ\text{C}$ (Benedict, 1936) to 75% at $T_a = 25\text{--}27 \text{ } ^\circ\text{C}$ (Wright & Luck, 1984). We conducted the present study at ambient temperatures below this range. Therefore, on the basis of Benedict (1936) we assumed that transepidermal and respiratory evaporative water losses represented less than 12% of the total heat loss.

Results*Skin temperature*

Mean skin temperatures for six major anatomical sites of the African and Indian elephant are presented in Fig. 2a. With the exception of the ears, skin temperatures (T_{skin}) for the Indian elephant were significantly different (Student's t at $P < 0.01$) from the African elephant. At $T_a = 12.6 \text{ } ^\circ\text{C}$ mean T_{skin} for the body, legs, head and trunk were each higher for the Indian elephant. In contrast, T_{skin} of the neck behind the ears was more than $10 \text{ } ^\circ\text{C}$ higher for the African elephant. This represented the site of the greatest temperature difference between the two species of elephant. Mean T_{skin} for the body, trunk and legs of the Indian elephant in this study was $2\text{--}3 \text{ } ^\circ\text{C}$ higher than measured by Benedict (1936) using a thermo-electric probe on the same species at $T_a = 16.0 \text{ } ^\circ\text{C}$. Under outdoor conditions (wind speed = 5 m/s , solar irradiance = $100\text{--}700 \text{ W/m}^2$, $T_a = 15 \text{ } ^\circ\text{C}$)

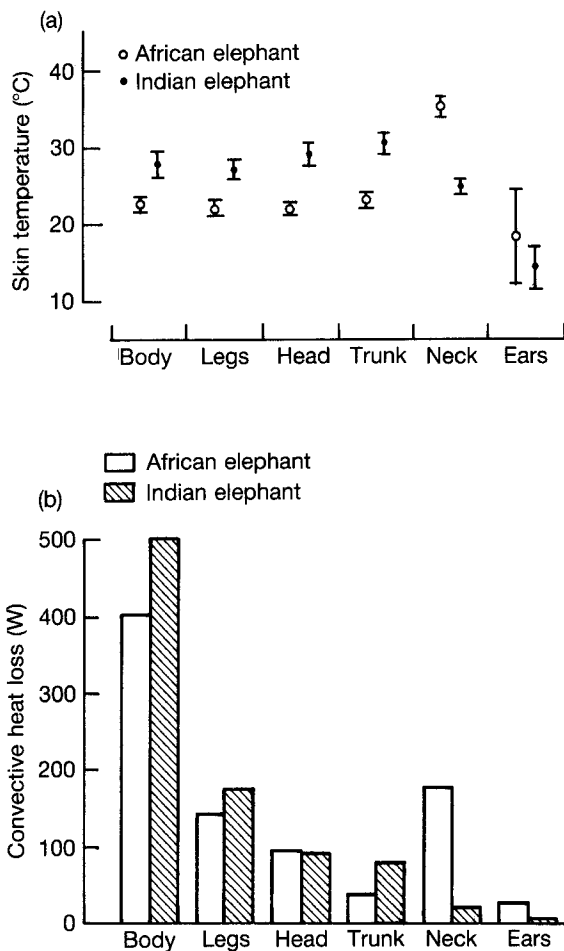


FIG. 2. Skin temperature (a) and free convective heat loss (b) for different anatomical sites. Shaded symbols denote values for the Indian elephant and open symbols represent values for the African elephant. Skin temperatures are based on isotherms for each anatomical area and are presented as mean \pm 1 S.D. ($n=10$). Convective heat loss was calculated from these isotherms (see text).

Cena & Clark (1973) found that skin temperatures for an African elephant ranged from 24.0 to 27.5 °C. As reported in the earlier studies, mean temperatures at these sites are quite uniform for individual African or Indian elephants.

Thermal profiles of the anterior ear surface of the African elephant differed from profiles of the Indian elephant in this study (Fig. 3) and an African elephant thermogram presented in Cena & Clark (1973). For both animals lower skin temperatures were concentrated distally and higher temperatures were located proximally to the auditory canal. Ear isotherms ranged from 13.1 to 26.6 °C for the Indian elephant. The African elephant ear demonstrated a greater range of skin temperatures. Although mean T_{skin} of the ears calculated from isotherm area was not significantly different (at $P < 0.01$) for the two species, the highest temperature recorded for the African elephant ear (34.0 °C) was more than 7 °C higher than measured for the Indian elephant.

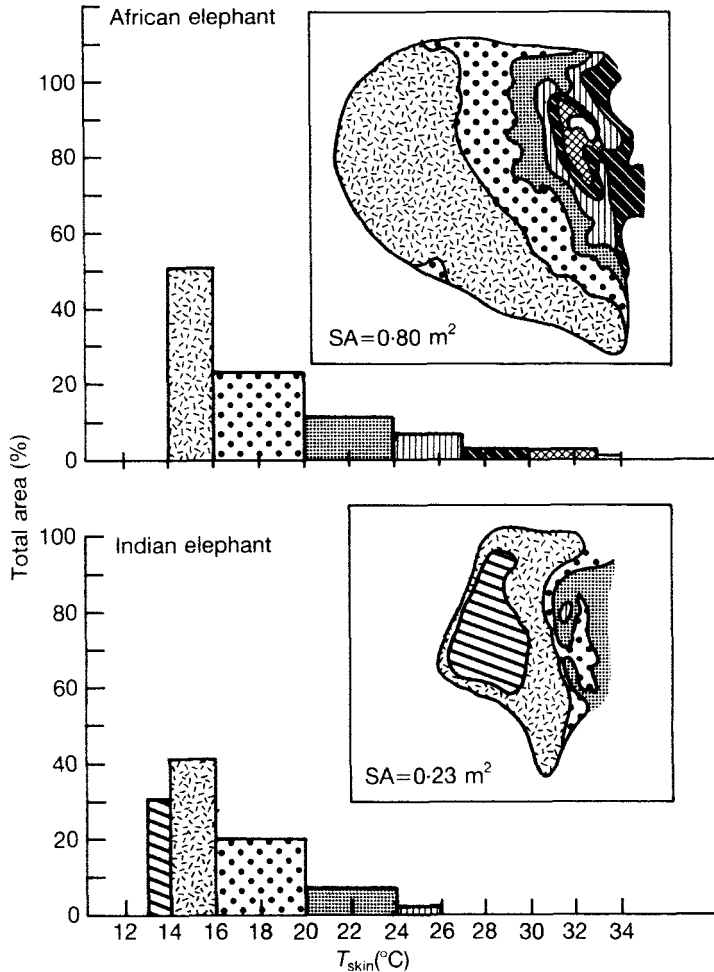


FIG. 3. Thermal patterns and surface area (SA) for the anterior surface of the African and Indian elephant ear at $T_a = 12.6$ °C. Shading in the illustration corresponds to temperature bars on the abscissa. Note the greater range of surface temperatures for the African elephant in comparison to the Indian elephant. The ordinate shows the percentage of ear surface area occupied by each isotherm.

Heat transfer

Free convective heat loss of the elephants varied with anatomical site (Fig. 2b). The two elephants demonstrated similar patterns of convection across comparable sites with the exception of the neck and ears. Convective transfer across the body accounted for 45% of the total convective heat loss of the African elephant and 59% of the total for the Indian elephant. The neck was an important site of convective heat transfer for the African elephant: 20.1% of the total convective heat loss occurred at this site for this animal. In comparison, only 2.5% of total convective heat loss of the Indian elephant was across the neck. Heat loss by convection from the anterior surface of the ears of the African elephant (13.9 W) was 10 times the value for the Indian

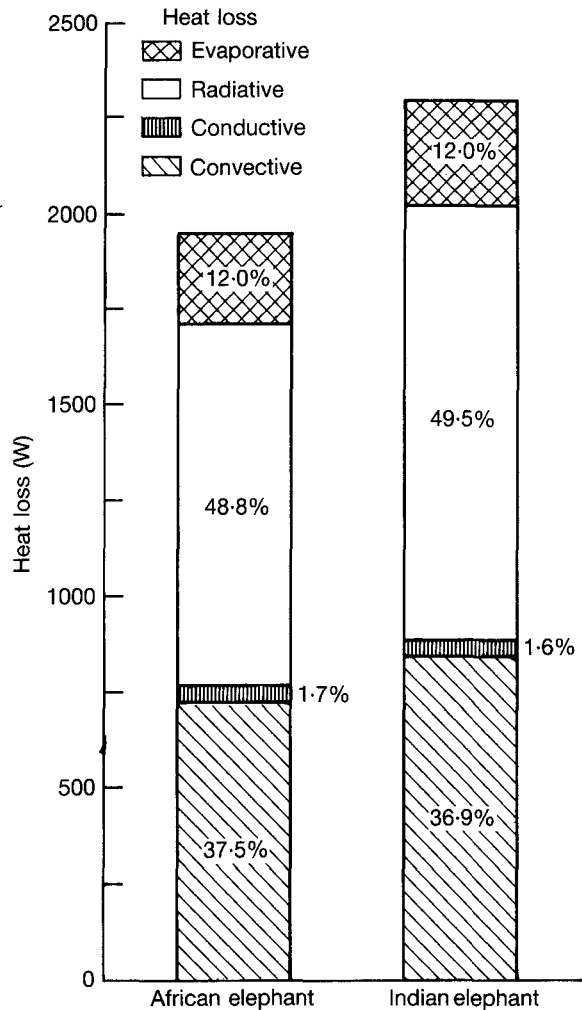


FIG. 4. Thermal budgets for the African and Indian elephant. Radiative, conductive and convective heat losses were calculated from skin temperatures measured by infrared thermography. Heat loss by evaporative pathways was estimated. Total heat loss (column height) corresponded well with predicted heat production for the African elephant, but exceeded predictions for the immature Indian elephant.

elephant (1.4 W). For both species, this represented less than 4% of the total convective heat transfer.

Total radiant heat exchange was 948.9 W for the African elephant and 1134.0 W for the Indian elephant (Fig. 4). Radiant exchange at different anatomical sites paralleled convective heat loss. For example, as found for convective pathways, radiant heat exchange across the ears of the African elephant (37.0 W) represented less than 4% of the total radiant transfer, and was 10 times greater than the value for the Indian elephant's ears.

Conduction of heat from the feet to the ground represented the smallest avenue of heat transfer

measured for the two elephants. Total foot surface area for the African elephant was 0.42 m². Conductive transfer across this area was 32.1 W. In comparison, the total foot area of the Indian elephant, 0.36 m², was associated with a conductive heat loss of 37.4 W.

Thermal energy budgets

The sum of heat transfer from convection, radiation and conduction was 1712.0 W for the African elephant, and 2018.7 W for the Indian elephant (Fig. 4). If evaporative water loss accounts for approximately 12% of the total heat loss of the elephant (as calculated for this T_a from Benedict, 1936), then total heat loss is 1945.5 W and 2293.9 W for the African and Indian elephant, respectively. From these results, at $T_a = 12.6$ °C approximately 86% of the heat transfer for both species of elephant was divided between free convective and radiant pathways. Less than 2% of the total heat transfer occurred by conduction to the ground.

Discussion

Like other biological systems, the thermal balance of the elephant depends on an equilibrium between heat production and heat loss. The equation for heat balance can be written as:

$$M - W = R + G + C + E + S \quad (1)$$

where M denotes metabolic heat production, W denotes work performed by the subject and S represents heat stored by the body. R , G , C and E represent net heat transfer by radiant exchange, conduction, convection and evaporation, respectively. Except for evaporative pathways, the magnitude of heat loss by these different avenues depends primarily on the total surface area available for transfer, as well as on the thermal gradient between the body surface and the environment.

In view of these principles of heat transfer and the elephant's small surface-to-volume ratio, this large mammal could experience difficulty in dissipating excess metabolic heat (Eltringham, 1982; Schmidt-Nielsen, 1984). The rationale for this suggestion becomes apparent when allometric relationships for metabolic heat production, thermal conductance and surface area are examined. In mammals, metabolism increases with body mass to the exponent 0.75; that is, $M_b^{0.75}$. Thermal conductance and surface area also scale with body mass, but with lower exponents. For mammals, thermal conductance is proportional to $M_b^{0.57}$, and surface area is proportional to $M_b^{0.67}$ (Peters, 1983). Schmidt-Nielsen (1984) argued that if these parameters scale predictably for elephants, then metabolic heat production may exceed the ability of the animal to transfer heat across the body surface, unless physiological or behavioural adjustments are made.

The results of the present study permit heat production, thermal conductance and the surface area available for heat transfer to be calculated for elephants. By comparing these values to allometric predictions, the thermal lability of these large mammals can be assessed.

Metabolic heat production, as calculated from Equation 1, scaled as predicted for the African elephant. We assumed that heat storage and external work were insignificant in quiescent elephants examined at low ambient temperatures. Therefore, the sum of convective, conductive, radiant and evaporative heat loss approximates heat production (Cena, 1984). In this study, total heat production of the African elephant with ears pressed against the body was 1945.5 W. This corresponds well with the predicted value of heat production based on body mass (2065.7 W from Robinson *et al.* (1983) in Peters, 1983) and with metabolic rates measured using a trunk breathing

respirometer on a 3672 kg Indian elephant at $T_a = 17^\circ\text{C}$ (2219.4 W; Benedict, 1936). Unfortunately, because metabolic rate is influenced by growth of the animal (Guyton, 1986), similar comparisons could not be made for the immature Indian elephant examined in the present study.

Surface area of both elephants also scaled predictably with body mass. The measured surface area of the body of the African elephant, 20.7 m², is similar to the predicted area of 21.8 m² based on cattle (Calder, 1984). Likewise, surface area of the Indian elephant is within 7.3% of the predicted value calculated from body mass.

The agreement between measured and predicted values of heat production and of surface area supports the argument that large size predisposes the elephant to hyperthermia. However, the same is not true for thermal conductance. For a resting animal heat exchange (H) by convection, conduction and radiation is related to thermal conductance (c) by the expression:

$$H = c (T_b - T_a) \quad (2)$$

where T_b = core body temperature, and T_a = ambient temperature (Tracy, 1972). For the African elephant in this study $H = 1712.0$ W (Fig. 4), $T_b = 36.5^\circ\text{C}$ (from Benedict, 1936), and $T_a = 12.6^\circ\text{C}$. From the above equation thermal conductance of the African elephant is 71.6 W/°C (3.2 W/m² °C). At $H = 2018.7$ W, thermal conductance of the immature Indian elephant is 84.5 W/°C (5.1 W/m² °C). Similarly, conductance calculated for the Indian elephant examined by Benedict (1936) was 92.0 W/°C (3.9 W/m² °C). These values are 3.0 to 4.8 times greater than thermal conductances predicted from a relationship for mammals ranging in mass from 0.0035 kg to 150 kg (Bradley & Deavers, 1980). If such an extrapolation is valid, the elephant demonstrates an enhanced ability to move heat across the body surface. As a result, reduced heat transfer associated with a low surface-to-volume ratio appears to be offset by a high thermal conductance.

The absence of fur distinguishes the elephant from many mammals and undoubtedly contributes to its thermal balance. Other relatively hairless mammals include man, pigs and whales. The small size or aquatic habitat of these mammals switches the primary thermoregulatory problem from one of heat dissipation to heat conservation. Thus, man, pigs and whales use alternative forms of insulation (i.e. clothing, fat, blubber) to prevent excessive heat loss. Under cold and variable climatic conditions, early Pleistocene ancestors of modern elephants, the mammoths, also depended on an insulating layer or exceptionally large size to maintain a stable core temperature. Calculations based on the shoulder height of African elephants (Laws & Parker, 1968) demonstrate that while the giant steppe mammoth (*Mammuthus trogontherii*) would have had a surface area almost double that of modern elephants, its surface-to-volume ratio and available area for heat loss would have been relatively lower. In comparison, the woolly mammoth (*Mammuthus primigenius*) was no larger than modern elephants. This prehistoric animal relied on insulation in the form of fur and subcutaneous fat deposits to prevent hypothermia under the severe climates characteristic of its subarctic distribution (Kurtén, 1968).

It is apparent from this study that despite their large size, heat losses across the general body surface readily balance metabolic heat production of inactive African and Indian elephants under relatively cool environmental conditions. This balance occurs without the use of specialized thermal windows. With increased intrinsic or extrinsic heat loads, these large mammals may facilitate heat loss by behavioural and vascular modifications. In the wild, thermoregulatory mechanisms include ear-flapping (Buss & Estes, 1971; McKay, 1973; Wright, 1984), increased blood flow to thermal windows (Wright, 1984), and the use of shade, wind, water and dust (McKay, 1973). Through vasodilation, heat loss from the anterior surface of the ear of the African

elephant can increase from 8% (present study) to 53% (Wright, 1984) of the total metabolic heat production. Forced convection resulting from increased air flow across the warm skin located behind flapping ears (Fig. 2) may be especially important for facilitating heat dissipation in the African elephant. In addition, surface sculpturing of the elephant's integument enhances water retention which facilitates evaporative heat loss in these animals (Lillywhite & Stein, 1987). Until further investigations are conducted it is difficult to predict changes in skin temperature and, therefore, the contribution of convective, conductive and radiant pathways to the thermal balance of elephants in their natural environment. Wright & Luck (1984) suggest that the typical environmental conditions of the African elephant prohibit heat loss by these pathways. As a result, heat loss across the body surface will have to be supplemented with evaporative heat loss, behavioural thermoregulation and heat storage.

Summary

Calculations of heat transfer demonstrated that convection and radiation account for almost 90% of the total heat loss of the Indian and African elephant at $T_a = 12.6$ °C. Heat loss from the ears by these two pathways was 10 times greater for the African elephant and represented less than 8% of the total heat loss. Surface area and metabolic heat production determined from total heat loss scaled as predicted from allometric relationships. In contrast, thermal conductance was three to five times expected values. This increased thermal conductance counterbalances reduced heat transfer associated with a low surface-to-volume ratio, and contributes to the thermal balance of the elephant.

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