Do elephants need to sweat?

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An adequate rate of evaporative water loss is considered essential for the maintenance of thermal balance in the elephant in warm climatic conditions. Histological studies have failed to reveal the existence of sweat glands in elephant skin. Transepidermal water-loss rate has been measured and shown to be sufficiently high for possible thermal needs. The structure of elephant skin and the behaviour of elephants are seen to contribute towards maintaining skin permeability and the necessary level of transepidermal water loss.

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'n Toereikende tempo van waterverdamping word as noodsaaklik beskou vir die handhawing van hittebalans in olifante onder warm klimaatstoestande. Histologiese studies het tot nou toe nie die teenwoordigheid van sweetkliere in olifantvel bewys nie. Die tempo van transepidermale waterverlies is gemeet, en blyk hoog genoeg te wees om moontlike hittevereistes te dek. Daar word getoon dat die velstruktuur van die olifant, asook die olifant se gedrag, 'n bydrae lewer tot die handhawing van veldeurlaatbaarheid en die behoud van die vlak van transepidermale waterverlies.

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Radiative and convective channels of heat loss are likely to be very limited in many of the environments in which the African elephant, *Loxodonta africana*, is found. This leaves only the evaporative component and possible heat storage to maintain thermal balance under adverse conditions. Heat storage is an unknown factor but one which can only buffer heat transfer, not reduce it. In his experimental studies of elephant physiology Benedict (1936) estimated that 20% of metabolic heat was lost in the vaporization of water shared equally between lungs and skin. In spite of a histological report of the absence of sweat glands (Smith 1890), Benedict concluded from indirect evidence that 'sweat glands are undoubtedly present'. Since that time a number of authors have reported their inability to observe sweat glands in elephant skin but Sikes (1971) argues for their existence on the same unsatisfactory grounds as Benedict.

If the elephant does not secrete sweat, can its thick skin allow adequate water evaporation for thermoregulation in hot conditions? An answer to this question is sought from measurements of water loss from elephant skin now reported. Most observations were made on the ear which Wright (1984) has suggested plays an important role in elephant thermoregulation.

The structure of elephant skin is examined in relation to the known properties of skin which govern its permeability to water.

Materials and Methods

Measurements were made on a reasonably docile male elephant, about seven years old and with a body mass of 1 200 kg, at the zoo belonging to the Department of Agriculture and Fisheries of the Uganda Government, Entebbe, Uganda.

Initially evaporation of water from the skin surface was measured by circulating the air contained in a cylindrical aluminium capsule, 10 cm diameter × 10 cm high, through a container of anhydrous $CaCl_2$ by means of an electric fan. The capsule was held in place and sealed to the skin by a plastic foam washer. A blank to allow for the moisture in the air initially in the capsule was measured by holding it on to a dry wooden surface. It was necessary to absorb for about 4 min in order to obtain an adequate mass change.

Although the elephant was reasonably cooperative it was often difficult to keep the absorption capsule in position for the necessary time. An improved rapid technique was devised using electric-hygrometer sensors (Hygrodynamics, Inc.) to sense the humidity in a plastic chamber held manually onto the skin. The chamber had a depth of 130 mm and the upper

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part was occupied by a circular battery of eight Narrow-Range Hygrosensors mounted around an axial fan driven by a small electric motor. The air volume of the chamber was 1 200 ml and the surface area of skin exposed to the chamber was 908 mm^2. The fan speed chosen produced an air speed of about 60 m min^{-1} at the opening occupied by the skin. Via a selector switch, the hygrosensors provide a reading for humidity and air temperatures on a meter dial calibrated with 100 divisions. The readings are then converted to temperature and subsequently to humidity from calibrations individual to each sensor. The calibration curve for the meter reading against humidity is sigmoid but sensibly linear between meter readings of 20–60. The procedure adopted was to select the sensor appropriate to the atmospheric humidity giving an initial dial reading below 20. The chamber was then applied to the skin and the time taken for the reading to change from 20 to 60 measured with a stop watch. The chamber was removed and the contained air became replaced by atmospheric air. It was then moved to another site for a further determination. Depending on the rate of evaporation from the skin surface, the time for the humidity change ranged from 3 s to 3 min. As all variables are available, the amount of water moving from the skin surface to produce the observed change in humidity can be calculated and hence the rate of evaporation.

This technique has the virture of speed under field conditions but considerable variability in results can be expected as the natural state of the skin surface varies from place to place and from time to time. However, the order of magnitude of the measurements is more important than their individual values.

Results

Trial measurements with the CaCl$_2$ capsule technique were made on a recently dead elephant (E1); Luck & Wright (1964) found no change in evaporative water loss soon after death in another pachyderm. Similar measurements were then made on two separate occasions on the captive animal (E2). The results are shown in Table 1 together with a trial of the hygrometric technique. The values were of a similar order and

Table 1 Transepidermal water loss by absorbent capsule technique (g m^{-2} h^{-1})

Elephant	Anterior ear (pos. 6)	Posterior ear (pos. 6)	Shoulder (pos. S)	Flank (pos. F)
E1 (dead)	114	84	66	
E2	352		154	283
E2	152 (SD 9; n=2) *220(SD 90; n=3)	330 (SD 68; n=2)		259(SD 0; n=2)
Human thigh	22			

*Comparison by hygrometric technique

Figure 1 The approximate positions where the measurements in Tables 1 and 2 were made.

Table 2 Transepidermal water loss at sites shown in Figure 1

Site	g m^{-2} h^{-1}	Site	g m^{-2} h^{-1}
		Anterior ear	
Flank F	276	9	199
	140	10	169
	233	11	140
	117	12	115
$\bar{x}$	192 (SD 75; n=4)	13	169
Shoulder S	143		
Anterior ear		Posterior ear	
1	138	1	313
2	178	2	285
3	241	3	439
4	263	4	731
5	160	5	844
6	217	6	607
6	112	6	536
6	132	6	618
6	121	6	658
6	211	7	1185
6	188	8	537
6	69	9	559
6	169	10	174
7	245	11	128
8	240	$\bar{x}$	493 (SD 247; n=11*)
$\bar{x}$	185 (SD 48; n=13*)	Human thigh	7

Ambient temperature 25 °C, relative humidity 67%
*Includes mean value for position 6

much greater than for human skin measured by either technique. As both techniques gave results for man similar to those reported in the literature, we considered them adequate for this investigation and adopted the rapid hygrometric method to extend the number of sites investigated on a third occasion. Their positions are shown in Figure 1 and the values obtained, in Table 2. Repeated measurements at any one site were interspersed with those at other sites; intervals between
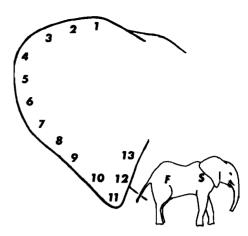
readings depended on the acquiescence of the subject.

The elephant was housed in an open grassed paddock with continual access to water. The measurements were made between 10h30 and noon when the ambient temperature was 25–27 °C and the relative humidity 67%. It had rained heavily on the previous evening and the skin surfaces were not cleaned before the observations were made.

Discussion

The African elephant occurs naturally in savannah which may be wet or dry, wooded or open grass, and which in some regions may verge on desert conditions. For the most part the environmental conditions must afford limited avenues for metabolic heat loss.

Radiative heat transfer, depending as it does on the temperature of a non-uniform environment (including the sun) relative to the body surface, will change from moment to moment as an elephant feeds; a process occupying some three-quarters of every day. Net heat transfer cannot be assessed accurately but the net loss can be expected to decline towards noon and may become a net gain. In two examples cited by Wright (1984) the mean radiant temperature of the surroundings during the experiments exceeded body temperature. It is normal elephant behaviour to seek shade under these conditions.

Convective heat transfer depends on the difference between the air and skin surface temperature and on the effective air velocity. The net heat transfer depends on the approximate square root of the air velocity so that under common climatic conditions air movement will contribute little; under hot air conditions a net gain may result. The fanning movement of the elephant ear produces an air velocity along the body of about 30 m min^{-1} (Wright & Luck 1964, unpublished); a two-knot breeze! Over the ear surface the velocity may be greater, particularly over the flexible margin (Figure 2).

It would seem therefore that under many common environmental conditions thermal balance will lean heavily on evaporative heat loss possibly ballasted by heat storage. In the absence of a continuous record of deep body temperature the existence of heat storage cannot be established although it probably occurs as in the other large pachyderm the white rhinoceros (Allbrook, Harthoorn, Luck & Wright 1958).

Under the cool ambient conditions of about 20 °C, 50% relative humidity and little air movement, Benedict (1936) estimated that about 20% of the total heat loss of his elephant was due to evaporation divided equally between lung and skin surfaces. In spite of the failure of Smith (1890) to find any sudoriferous glands in the skin from any part of *Elephas maximus* in a histological study, Benedict (1936) said that 'sweat glands are undoubtedly present'. His view was based on reports of apparent surface dampness on the removal of pack gear from working animals (Evans 1910). A similar view is expressed by Sikes (1971). Their observations, however, are no proof of sweat secretion. On the other hand since Smith's (1890) report, Eales (1925), Luck & Wright (1964), Horstmann (1966), and Spearman (1970) have consistently failed to find sweat glands on histological examination of the skin of both elephant species.

Under Benedict's (1936) experimental conditions with an ambient temperature of 17–20 °C, relative humidity about 50%, and a skin temperature of 22–25 °C, the estimated water loss from his elephant skin is about 20 g m^{-2} h^{-1}. Under similar conditions, which are well below the human sweating threshold of about 28 °C ambient temperature (Gagge, Winslow & Herrington 1938), human evaporative water loss from the skin is 2–10 g m^{-2} h^{-1} (Hertzman, Randall, Peiss & Seckendorf 1952; Grice, Sattar, Baker & Sharratt 1975). This transepidermal water loss in man (when not sweating) is doubled by an increase in skin temperature of 7–8 °C and with the onset of sweating can rise as high as 1 000 g m^{-2} h^{-1}. The values for transepidermal water loss which we have measured in the elephant are much greater than the estimates under the cold conditions of Benedict's (1936) experiments but fall short of the highest values attainable with the human sweating mechanism. Are our values adequate for the necessary evaporative contribution to thermal balance under adverse conditions without a sweat secretory mechanism?

The elephant from which the measurements detailed in Table 2 were obtained, had an estimated body mass of 1 200 kg. A total surface area of 11 m^2 can be estimated for it, of which 20% is ear surface. Using the mean values for trans-epidermal water loss from Table 2 it can be calculated that the evaporative heat loss is about 1,69 kW. The metabolic rate estimated from surface area and from Benedict's (1936) measurements is about 2,15 kW. Thus about three quarters of the heat loss requirements *could* be met by non-sweating transepidermal evaporation and the need to postulate the existence of sweat glands falls away.

A high level of evaporative water loss can only be maintained if body water is replenished. The loss rate calculated above amounts to 2,5 ℓ h^{-1} of water from 11 m^2 surface area which is equivalent to about 400 ml h^{-1} in a man; an evaporative rate which can readily be maintained when water is available. It is normal behaviour for elephant to drink at least once a day and more often under hot conditions. By general report elephant need a high water intake; when surface water is scarce they drink from holes dug in river beds, and in drought conditions they will drink foul water. Benedict (1936) measured a daily water intake of about 150 ℓ by his elephant of 3 672 kg under cool conditions. If heat storage exists in elephants, then this is a water-sparing mechanism.

The highest rates of evaporation recorded in Table 2 are from the outer edge of the posterior ear surface. This may be fortuitous owing to the necessarily limited sampling of the whole surface area but this organ is especially interesting. The elephant pinna, which weighs about 20 kg in an adult, contains an almost lace-like plate of cartilage supporting the vascular bed and the skin. The plate ends about 10–15 cm from the edge and the remaining tissue is stiffened by outwardly directed delicate fingers of cartilage. This makes for a very flexible structure well illustrated in Figure 2 which also shows the extensive vasculature. Smith (1890) wrote: 'The skin of the ear is remarkable for its extreme vascularity and the comparative thinness of the corium and epidermis'. Luck & Wright

Figure 2 Elephant ear, posterior surface, illustrating flexible margin and extensive vasculature.

(1964) noted that the stratum corneum of the posterior surface was thinner than that of the anterior surface where the primary papillae are abraded and the intervening crypts filled with detritus. This can be seen in Figure 3. However, neither Smith (1890) nor Luck & Wright (1964) could find sweat glands in the ear skin.
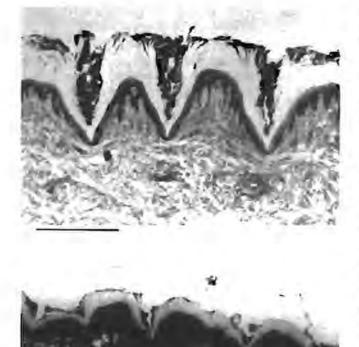
Figure 3 Skin from anterior surface of elephant ear (top), and skin from posterior surface of elephant ear (bottom). Both are stained with haemotoxylin eosin. Note the primary and secondary dermal papillae, the different thicknesses of the stratum corneum, the abraded anterior surface and the debris-filled crypts between the primary papillae. The calibration bar is 1 mm.

Properties of skin which influence water permeability

The barrier to water movement through skin is the stratum corneum; both the cellular and the intercellular components (Scheuplein 1978a). Investigations in man have defined a number of factors influencing the water permeability of this material which are relevant to a consideration of skin permeability in elephant.

The stratum corneum varies in thickness averaging 60 µm on the flank (Spearman 1970), 320 µm on the anterior ear and 500 µm on the trunk (Luck & Wright 1964). This thick horny layer overlies an arrangement of primary and secondary dermal papillae (Smith 1890) similar to papillae in hippopotamus, rhinoceros, and in the Cetacea and Sirenia (Luck & Wright 1964; Spearman 1970). These dermal papillae are finger-like projections into the epidermis and the arrangement results in an extensive undulating basal layer of proliferating epidermal cells. Spearman (1970) showed that elephant stratum corneum contained structural and chemical components which in man are associated with coherence of corneal cells (Brody 1962) and thus thickening of the horny layer. When this occurs in conjunction with extensive epidermal proliferation, as described above, then water loss is greatly increased (Grice & Bettley 1967).

The thickness of the stratum corneum need not of itself militate against rapid water movement. Although the diffu-

sion distance is increased, the diffusion constant of thick corneum in man so exceeds that of thin corneum that the water flux is higher in the thick tissue (Scheuplein 1978b).

The hydration of stratum corneum is important for two reasons; it affects both the pliability of skin and its permeability. Blank (1952) showed that the water content of corneum varied with relative humidity and that below a humidity of 60% its plasticity was reduced.

Corneal water content is increased by increased humidity and this process is enhanced by an increased temperature (Spencer, Linamen, Akers & Jones 1975). When in contact with liquid water, stratum corneum takes up water (Scheuplein & Morgan 1967); these authors and Scheuplein & Ross (1970) showed that the increased hydration raised the permeability constant of the tissue considerably. Both an increased skin temperature (Grice, Sattar, Sharrart & Baker 1971) and a raised relative humidity (Grice, Sattar & Baker 1972) were shown to increase transepidermal water loss in man.

Evaporative water loss will also depend on air movement displacing water molecules at the surface. Johnson & Shuster (1969) at a low air velocity (below 16 m min^{-1}) showed an increase of about 25% in non-sweating transepidermal water loss for an approximately four-fold increase in air speed. The evaporative loss from a fully wet sweating skin measured at air speeds from 35–241 m min^{-1} showed a proportionately higher increase (Clifford, Kerslake & Waddell 1959).

Thus a number of factors studied under laboratory conditions in non-sweating human skin are pertinent to this consideration of evaporative water loss from elephant skin and we have shown that the evaporative loss could provide the heat transfer necessary for thermal balance. It is apparent that the properties of stratum corneum, its thickness and its hydration, are of considerable importance in affecting water movement through skin. The dermal papillae with the large surface area of the acanthotic basal layer and its proximity to the capillary circulation will ensure a fluid driving force to maintain hydration. However, a characteristic component of elephant behaviour will serve the same purpose and at the same time contribute to economy in water balance. Bathing, mud-wallowing and spraying the skin will promote hydration of the stratum corneum and thus indirectly and directly increase evaporative loss. Ingram (1965) showed that when the flank of a pig was soaked with water, the evaporative loss from the flank rose from 30–40 g m^{-2} h^{-1} to about 800 g m^{-2} h^{-1} but declined again after 15 min. When the flank was smeared with mud the same increase occurred but it now persisted for more than 2 h. The pig is an animal without sweating ability which under hot conditions wallows in water, urine, mud and faeces. The wet surface layer raises the evaporative loss rate to levels comparable with sweating man and with those we have measured in the elephant. As an alternative to a mud wallow, elephant frequently wet the body surface and then spray dust over the wet surface producing mud *in situ*. Sikes (1971) says this behaviour seems more common in savannah elephant than in those in forested or montane habitats where there is higher humidity. Sikes (1971) also comments that elephant choose humid shelter in preference to equally shaded dry cover and that those living in humid environments seem to thrive better than those restricted to dry areas.

Conclusions

Under warm climatic conditions evaporative water loss from the skin seems to be essential for thermal balance to be achieved in the elephant but a number of histological studies

have failed to demonstrate the existence of sweat glands in elephant skin. Transepidermal water loss has been measured and is of sufficient magnitude to satisfy the evaporative heat loss requirement.

From studies on non-sweating human skin it is apparent that the thickness of the horny layer in this pachyderm need be no hindrance to water loss by diffusion. The hydration of the stratum corneum is important in determining its water permeability; the extensive surface area of the underlying basal layers with their attendant blood vessels in elephant skin, and elephant behavioural activity directed at wetting the skin surface are seen as essential factors in maintaining the hydration of the horny layer in this animal. The known drinking habits of elephant are consonant with the need to maintain water balance in the face of a high loss rate from the skin.

It is concluded that evaporative water loss from the skin can be adequate to meet heat-loss requirements without the need to postulate the existence of sweat glands in elephant.

Acknowledgements

References

ALLBROOK, D.B., HARTHOORN, A.M., LUCK, C.P. & WRIGHT, P.G. 1958. Temperature regulation in the white rhinoceros. *J. Physiol.* 143: 51 – 52

BENEDICT, F.G. 1936. The physiology of the elephant. Carnegie Institution of Washington, New York.

BLANK, I.H. 1952. Factors which influence the water content of the stratum corneum. *J. invest Derm.* 18: 433 – 440.

BRODY, I. 1962. The ultrastructure of the horny layer in normal and psoriatic epidermis as revealed by electron microscopy. *J. invest. Derm.* 39: 518 – 528.

CLIFFORD, J., KERSLAKE, D.McK. & WADDELL, J.L. 1959. The effect of windspeed on maximum evaporative capacity in man. *J. Physiol.* 147: 253 – 259.

EALES, N.B. 1925. External characters, skin, and temporal gland of a foetal African elephant. *Proc. zool. Soc. Lond.* 445 – 456.

EVANS, G.H. 1910. Elephants and their diseases. *Rangoon.* Cited in Benedict (1936).

GAGGE, A.P., WINSLOW, C.E.A. & HERRINGTON, L.P. 1938. The influence of clothing on the physiological reactions of the human body to varying environmental temperatures. *Amer. J. Physiol.* 124: 30 – 50.

GRICE, KATHERINE & BETTLEY, F.R. 1967. Skin water loss and accidental hypothermia in psoriasis, ichthyosis and erythrodermia. *Br. med. J.* 4: 195 – 198.

GRICE, KATHERINE, SATTAR, H. & BAKER, H. 1972. The effect of ambient humidity on transepidermal water loss. *J. invest. Derm.* 58: 343 – 346.

GRICE, KATHERINE, SATTAR, H., BAKER, H. & SHARRATT, M. 1975. The relationship of transepidermal water loss to skin temperature in psoriasis and eczema. *J. invest. Derm.* 64: 313 – 315.

GRICE, KATHERINE, SATTAR, H., SHARRATT, M. & BAKER, H. 1971. Skin temperature and transepidermal water loss. *J. invest. Derm.* 57: 108 – 110.

HERTZMAN, A.B., RANDALL, W.C., PEISS, C.N. & SECKENDORF, R. 1952. Regional rates of evaporation from the skin at various environmental temperatures. *J. app. Physiol.* 5: 153 – 161.

HORSTMANN, E. 1966. Die epidermis des elefanten. *Z. Zellforsch* 75: 146 – 159.

INGRAM, D.L. 1965. Evaporative cooling in the pig. *Nature.* 207: 415 – 416.

JOHNSON, C. & SHUSTER, S. 1969. The measurement of transepidermal water loss. *Br. J. Derm.* 81: Supplement 4, 40 – 46.

LUCK, C.P. & WRIGHT, P.G. 1964. Aspects of the anatomy and physiology of the skin of the hippopotamus (*H. amphibius*). *Quart. J. exp. Physiol.* 49: 1 – 14.

SCHEUPLEIN, R.J. 1978a. The skin as a barrier. In: The Physiology and Pathophysiology of the skin, (ed.) Jarrett, A. Vol.5, pp 1669 – 1692. Academic Press, London.

SCHEUPLEIN, R.J. 1978b. Site variations in diffusion and permeability. In: The Physiology and Pathophysiology of the Skin, (ed.) Jarrett, A. Vol.5, pp 1731 – 1752. Academic Press, London.

SCHEUPLEIN, R.J. & MORGAN, L.G. 1967. 'Bound water' in keratin membranes measured by a microbalance technique. *Nature (Lond)* 214: 456 – 458.

SCHEUPLEIN, R.J. & ROSS, L. 1970. Effects of surfactants and solvents on the permeability of epidermis. *J. Soc. Cosmet. Chem.* 21: 853 – 873.

SIKES, SYLVIA K. 1971. The natural history of the African elephant. Weidenfeld and Nicholson, London.

SMITH, F. 1890. The histology of the skin of the elephant. *J. Anat. Physiol.* 24: 493 – 503.

SPEARMAN, R.I.C. 1970. The epidermis and its keratinisation in the African elephant. *Zool. Afr.* 5: 327 – 338.

SPENCER, T.S., LINAMEN, C.E., AKERS, W.A. & JONES, H.E. 1975. Temperature dependence of water content of stratum corneum. *Br. J. Derm.* 93: 159 – 164.

WRIGHT, P.G. 1984. Why do elephants flap their ears? *S. Afr. J. Zool.* 19: 266 – 269.