

Why do elephants flap their ears?

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The blood flow in the ear of the African elephant *Loxodonta africana* was measured in anaesthetized animals using the dye dilution technique at the same time as the arterio-venous temperature difference. The calculated heat loss from the ear is shown to be a substantial proportion of the total metabolic heat-loss requirement calculated from body surface area estimations. Reasons are advanced for believing that ear blood flow is controlled in the interests of thermoregulation. Behavioural fanning activity and the large ear surface area and surface to volume ratio suggest that this organ is of major importance in thermoregulation under warm environmental conditions.

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Die bloedvloei in die oor van die Afrika-olifant *Loxodonta africana* is gemeet in genarkotiseerde diere deur middel van die kleurstofverduunningsmetode. Terselfdertyd is die arteriovenese temperatuurverskil bepaal. Die berekende hitteverlies deur die oor vorm blykbaar 'n substansiële gedeelte van die totale metaboliese hitteverliesvereiste soos bereken van liggaamsoppervlaktebepalings. Daar word voorgestel dat oorbloedvloei gereguleer word in belang van termoregulering. Die groot ooroppervlakte, die oppervlakte/volume verhouding en oorbewegings dui aan dat hierdie orgaan van groot belang is vir termoregulering tydens warm omgewingstoestande.

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Although the pinnae of *Loxodonta africana* are notably larger than those of *Elephas maximus*, three characteristics are common to both. The ears have a high surface to volume ratio, a prominent and extensive vascular supply, and they are frequently in motion especially under warm ambient conditions. Several writers have speculated that the ears may serve a heat-loss function but Benedict (1936), in his monograph on elephant physiology, said: 'We believe that the theory that the elephant's ears serve as an important heat-regulating mechanism is not tenable'. However, no quantitative estimates have hitherto been made of the contribution to heat loss that elephant ears may make.

The possible contribution to heat loss that the pinnae of *Loxodonta africana* could make has now been assessed by the simultaneous measurement of ear blood flow and arterio-venous temperature difference in anaesthetized animals.

Material and Methods

Measurements were made on two male and two female elephant which were free-ranging in the Queen Elizabeth National Park (now Ruwenzori) in south-western Uganda. They were immobilized and anaesthetized with etorphine HCl (M99, Reckitt, 1 mg/1000 kg) and acetylpromazine maleate (Smith, Kline & French, 1,2 mg/1000 kg) delivered by hypodermic dart. Necessarily the administered doses were estimates and they were supplemented as required by intravenous injection to maintain the animal during subsequent manipulations. As soon as an animal was recumbent in the 'brisket' position, the head was shaded to obviate abnormal heating of the ear by the sun. A small superficial incision was made over the main central artery and vein of the right pinna, near the basal fold, to facilitate access to the vessels. The tissue edges were treated with 4% xylocaine (Astra-Hewlett) and a pledget of cotton wool soaked in 2% papaverine HCl (Merck) was applied to each vessel; these were precautions to obviate local vascular spasm, particularly of the artery. Using a trochar and needle a heparin-saline-filled catheter was introduced into the artery and advanced centrally until its tip was 20 cm beyond the edge of the cartilage at the basal fold of the ear; dissection on culled animals had established that the tip would then lie before the first branches of the pinnal arteries. Similarly a catheter was introduced and secured so that its tip lay freely in the vein. About 50 ml of blood was collected, heparinized, centrifuged, and the plasma stored for the preparation of standard dye dilutions.

Free-flowing blood from the venous catheter was collected into tubes containing heparin at 1-s intervals timed by a

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metronome. A bolus of 4% Evans blue (T1824) was injected into the artery and venous collection continued for 30 tubes. About 0,7 ml dye solution was injected; the actual quantity being determined by weighing the syringe, due allowance being made for the dead space.

After centrifugation of the venous samples the dye coloration of the plasma was measured on a spectrophotometer (Zeiss PMQ) at 625 nm and the concentration estimated from the standard curve constructed from the original plasma. The venous haematocrit was determined before and after each determination. The blood flow in the pinna was then calculated from the dye-dilution time curve (Zierler 1962).

While the blood samples were being collected the arterio-venous temperature difference was measured by means of copper constantan thermocouples applied to the surface of each vessel and connected to a sensitive oil-suspension mirror galvanometer. The thermocouples were calibrated against an NPL certified mercury-in-glass thermometer. For several reasons we decided against an attempt to use intravascular thermocouples; the cleaned vessel surface temperature was considered adequate because of the large blood flow within.

On completion the catheters were withdrawn and the incisions closed. Two animals were killed under the Parks Board management programme, the other two received cyprenorphine HCl (M285, Reckitt) to reverse the action of the M99 and they resumed their normal existence.

Results

Two examples of dye-dilution curves are shown in Figure 1. The irregular appearance of one of them is presumably due to uneven perfusion and clearance in the widespread vascular bed. The results of eight determinations made in four animals are given in Table 1. Successive determinations were made on the same occasion but should not be regarded as replicates for statistical purposes. They were made after variable intervals against an uncertain homeostatic background in the anaesthetized animal. It is unlikely that results from this technique under field conditions can be more accurate than 0,5 $\ell \text{ min}^{-1}$; the calculations of whole blood flow in Table 1 are

Table 1 Ear blood flow (right ear)

	Sex	F plasma ($\ell \text{ min}^{-1}$)	Haematocrit (%)	F blood ($\ell \text{ min}^{-1}$)
E1	M	7,1	35	11
E2	M	3,1	43	5
		3,6	43	6
E3	F	4,1	46	8
		6,4	46	12
E4	F	6,3	41	11
		3,5	41	6
		6,8	41	12

Table 2 Heat loss from right ear and estimated metabolic rate

	Mass (kg)	Surface area (m^2)	F blood ($\ell \text{ min}^{-1}$)	a - v Δt ($^{\circ}\text{C}$)	Heat loss (kW)	Metab. rate (kW)
E1	4200	26	11	2	1,51	5,12
E2	3900	25	5	2	0,70	4,88
			6	2	0,81	
E3	2600	19	8	3	1,63	3,72
			12	3	2,44	
E4	2400	18	11	2,5	1,86	3,49
			6	2,5	1,05	
			12	2,5	1,98	

Table 3 Environmental warmth

	t dry ($^{\circ}\text{C}$)	t wet ($^{\circ}\text{C}$)	t globe ($^{\circ}\text{C}$)	RH (%)	v (m min^{-1})	t _s ($^{\circ}\text{C}$)
E3	29,4	23,3	34,4	60	32	42
E4	27,5	22,5	32,9	65	268	54

Relative humidity, RH.
Air velocity, v.
Mean temperature of the surroundings, t_s, Bedford (1946).

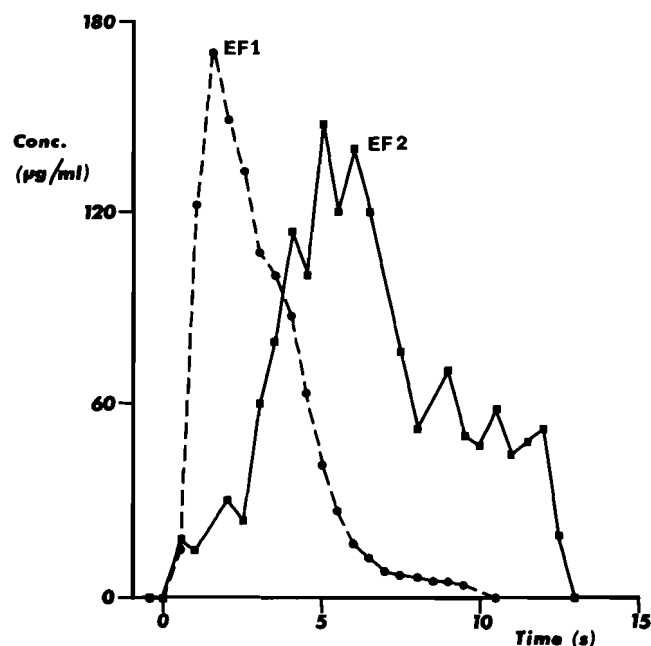


Figure 1 Dye-dilution curves obtained from elephants E1 and E2. Ordinate; concentration of Evans blue in plasma.

thus shown to this significant figure. Similarly the arterio-venous temperature difference as measured could not be more precise than 0,5 $^{\circ}\text{C}$ therefore the heat-loss values calculated using a specific heat 0,96 (Altman & Dittmer 1971) are expressed to the nearest 100 kcal h^{-1} (0,12 kW) in Table 2. The metabolic heat-loss requirements have been calculated from Benedict's (1936) determinations and the estimated surface areas of the animals are based on their body mass predictions from shoulder height measurements (Johnson & Buss 1965). The environmental conditions during the measurements on elephants 3 and 4 are shown in Table 3. Conditions were similar for the first two animals but environmental measurements were incomplete.

Discussion

The combined surface area of both sides of both ears in *Loxodonta africana* has been estimated (Luck & Wright 1964, unpublished) at not less than about 20% of the total skin surface area. This proportion based on measured ear area and body surface area derived from Vierordt's formula using a body mass estimated from measured shoulder height (Johnson & Buss 1965), can be little more than an informed guess but it emphasizes the contribution made by the ears to the

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total surface area!

The ear blood-flow rate measured by the dye-dilution technique reveals a magnitude far in excess of the conceivable metabolic requirements of the tissues of the pinna which weigh about 20 kg each. These measurements were made in anaesthetized animals but the size and distribution of the ear vasculature and its prominent appearance in undisturbed animals under natural conditions, suggest that such high flow rates are feasible.

Benedict (1936) measured the metabolic rate of a female Indian elephant of 3 672 kg, standing, on feed, in a respiration chamber with an ambient temperature of about 20 °C and about 50% relative humidity. Under those conditions the heat output was estimated at 3,14 kW.

The ambient temperature at the time of our experiments was about 29 °C with a relative humidity of about 65% and little wind; slightly more onerous conditions than in Benedict's experiments. Brody (1945) measured a 37% increase in metabolic rate in cattle and horses when they walked at 0,5 mile h⁻¹. It should therefore seem reasonable to suggest that an elephant of larger mass, moving and feeding under the ambient conditions of our experiments, would need to maintain an estimated heat loss of at least 4,65 kW and probably more.

The arterio-venous temperature difference measured in these experiments combined with the flow rates, reveal a heat loss which represents a substantial proportion of such an estimated metabolic rate. An arterio-venous temperature difference of two or three degrees can readily be measured from the skin surface overlying the major ear vessels under these conditions and if the ear is exposed to direct sunlight, the difference can be reduced and even reversed, clearly indicating a heat exchange phenomenon. Since the ears are the only region of the body surface to have an extensive vascular network, a very high surface to volume ratio, and a large surface area, they may be expected to make a major contribution to heat loss. The measurements now reported indicate the possible magnitude of that contribution. The pathways for this transfer must be largely convective and evaporative because an assessment of the mean radiant temperature of the surroundings made during measurements on two of the animals from globe thermometer, air temperature and air velocity readings (Bedford 1946) yielded values in excess of deep body temperature (Table 3). The possible heat losses and gains by radiation will vary continually as the animal moves through vegetation and it is usual elephant behaviour to seek shade during the hottest part of the day.

The elephant does not possess sweat glands (Wright 1984) so that evaporative loss from the skin will depend on epithelial hydration and therefore on blood flow. Both evaporative and convective heat loss will be increased by ear movement and the resultant air movement will facilitate heat loss from the rest of the body. Under his experimental conditions Benedict (1936) estimated that about 20% of the metabolic heat was lost by evaporation divided equally between respiratory tract and body surface.

The present considerations refer to the recumbent anaesthetized animal. How valid may they be under normal conditions? Benedict, Fox & Baker (1921) and Benedict (1936) recorded a number of overall skin temperatures on Indian circus and zoo elephants and on two African zoo elephants. Despite many point variations, the temperatures appeared to be about 5 °C above the moderate ambient of 17 to 25 °C. Benedict (1936) concluded that there was 'reasonable uniform

heat loss from radiation'. Benedict *et al.* (1921) and Benedict (1936) noted that considerable changes in ear temperature could occur and that there was an increase in ear temperature and ear flapping after muscular work. It was also noticed that frostbite frequently mutilated the ears of circus elephants (this presumably is the consequence of intense vasoconstriction under cold conditions). However Benedict felt that changes in ear temperature and flapping were caused by 'nervousness, fright, or apprehension' and the idea 'that a large, hairless animal, unprotected by fur, needs any special temperature-regulating device in its ears is inconceivable'.

Cena (1974, Figure 3.8) shows a thermogram of an African elephant outdoors in an English zoological garden (a thermogram is the thermal image of a field viewed by a camera sensitive to radiative flux). The day is described as windy with an air temperature of 15 °C; conditions under which a reduced ear blood flow would be expected if the ears serve a thermoregulatory function. In conformity with this idea the pinna is seen to have a surface temperature of 20–23,5 °C, the same as the ground, while the visible body surface has a temperature of 24–27,5 °C.

While skin temperature says little about quantitative heat transfer, these observations on ear temperature do indicate a considerable degree of vasomotor control over the ear vessels. In our own experience elephant ear arteries constrict under cool conditions and go into spasm if roughly manipulated or in response to local injury, indicating the capacity for constriction possessed by these large vessels. Such a capacity to control blood flow is an essential feature in an organ serving thermoregulation.

Conclusions

In spite of the inaccuracies inherent in these observations made under field conditions and the abnormal conditions imposed by sternal recumbency and anaesthetization, it is possible to conclude with some assurance from these measurements that ear blood flow in the African elephant can constitute a substantial and controllable avenue of heat loss.

Seeking shade, bathing, and wallowing are normal behavioural practices reducing heat gain and promoting heat loss. It is probable that convection and evaporation from the ear skin, and to a lesser extent from the remaining body skin, constitute the major routes for heat loss under adverse environmental conditions. The characteristic ear-fanning behaviour under these conditions will promote heat loss by these routes.

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