The lateral buccal pockets and three or four elongate compound buccal floor arena papillae comprise the lateral margins of the buccal floor arena. The ventral velum is moderately scalloped with marginal projections and a small medial notch.

Buccal roof

The prenarial arena possesses a transversely arranged row of pustulations. The choanae open laterally into the buccal cavity and are not visible ventrally. A pair of infralabial papillae are present on each side. Two elongate postnarial papillae form the anterior border of the buccal roof arena. The buccal roof arena is subcircular, and covered posteriorly by many pustulations. The lateral and posterior margins of the buccal roof arena are bounded by six to eight compound papillae.

Discussion

These tadpoles key out easily as *Hyperolius* using Van Dijk's (1966) key. The rostral papillae are an unusual feature and may prove to be useful for identification. The function of these external papillae may be related to that of the dense curtain of lingual and prelingual papillae present in these tadpoles; both may serve a tactile function.

Hyperolius tadpoles swim with their mouths open (judging from the position of the keratodonts in preserved specimens). The rostral papillae and lingual papillae are ideally situated to detect food items or large particles which are potential feeding hazards. The lingual papillae could possibly prevent large particles from entering the mouth and clogging the gill filters in this species, but Hammerman (1967) has shown that they are chemoreceptive structures in other ranid tadpoles.

It is too early in the study of *Hyperolius* larvae to be able to distinguish morphological trends, or to construct an identification key to the various species.

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References

CHANNING, A. 1972. A description of *Bufo pusillus* tadpoles (Anura: Bufonidae). *Ann. Natal Mus.* 21: 509–511.

CHANNING, A. 1974. A description of *Bufo pardalis* tadpoles (Anura: Bufonidae). *Zool. Afr.* 8:153–156.

CHANNING, A. 1976. *Rana johnstoni inyangae* tadpoles from Rhodesia. *Arnoldia Rhod.* 8: 1–4.

CHANNING, A. 1978. A new bufonid genus (Amphibia: Anura) from Rhodesia. *Herpetologica* 34: 394–397.

FROST, D.R. 1985. Amphibian species of the world. Allen Press and The Association of Systematics Collections. Lawrence, Kansas.

GOSNER, K.L. 1960. A simplified table for staging anuran embryos and larvae with notes on identification. *Herpetologica* 16: 183–190.

HAMMERMAN, D.L. 1967. Lingual premetamorphic papillae as larval taste structures in frogs. *Nature, London* 215: 98–99.

SCHIØTZ, A. 1975. The Treefrogs of Eastern Africa. Steenstrupia, Copenhagen.

VAN DIJK, D.E. 1966. Systematic and field keys to the families, genera and described species of southern African tadpoles. *Ann. Natal Mus.* 18: 231–286.

WASSERSUG, R.J. 1976. Oral morphology of anuran larvae: terminology and general description. *Occ. Papers Mus. Nat. Hist. Univ. Kansas* 48: 1–23.

Thermoregulation in the hippopotamus on land

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Restriction of a hippopotamus to the land under hot environmental conditions during the day resulted in an increase of no more than 1°C in core temperature. The rising adverse radiation and convection heat load was met by increase in evaporative water loss from the skin. The increased water loss was brought about by secretion from subdermal glands which wetted the skin surface and increased water movement through the integument. The hippopotamus normally avoids thermal stress on land by taking to the water for most of the day but it can restrain its core temperature under adverse conditions on land.

'n Seekoei, tydens die dag tot die land beperk onder warm omgewingstoestande, se kerntemperatuur het gestyg met niks meer as 1°C. Die toenemend ongustige uitstralings- en konveksie-hittelading is teëgewerk deur 'n vermeerdering in die verdampingsverlies van water deur die vel. Die verhoogde waterverlies is die gevolg van die benatting van die veloppervlak deur subdermale kliere wat ook vermeerderde waterbeweging deur die huid veroorsaak het. Die seekoei vermy hittespanning op land nomaalweg deur in water te bly vir die grootste deel van die dag maar hy kán sy kerntemperatuur in ongunstige landtoestande beheer.

The bodycore temperature of the hippopotamus (*Hippopotamus amphibius* Linn.) sampled in individuals culled from a wild population under natural conditions showed a remarkable uniformity with no obvious 24-hourly rhythm (Luck & Wright 1959; Wright 1964). Consideration of heat loss mechanisms apparently available to this animal led Wright (1964) to suggest that autonomic control was limited but that the behavioural pattern minimized thermoregulatory problems. Luck & Wright (1964) demonstrated the high basal rate of transepidermal water loss on land and considered possible implications of this in relation to the structure of the skin.

These observations were all made under field conditions in the Queen Elizabeth (now Ruwenzori) National Park in Uganda. The temperature measurements were made in 40 individual animals at various times during 24 h and throughout a year. The *SD* of the mean was 0,4°C and no 24-hourly pattern was obvious in the population (Wright 1964). However it was not possible to follow the core temperature of any individual throughout a day nor to detect changes in rate or distribution of water loss under varying environmental conditions in an animal unrestrained by drugs. Measurements of core temperature and transepidermal water loss were later extended under natural environmental conditions in an animal used to the proximity of humans, restricted only by an enclosure, and unaffected by drugs, in order to study the nature and extent of thermoregulatory control on land. They were made in the Department of Physiology, Makerere University, Kampala.

Methods

All the observations reported here were made on a young male hippopotamus, about 7 years old weighing about 860 kg and in excellent physical condition. He had lived for 3 years in the experimental enclosure belonging to the department, was accustomed to humans and amenable to the minor investigation procedures used in these experiments. The enclosure had a narrow stall at one end in which the animal was accustomed to be fed early each morning. The stall was normally closed behind him so that the enclosure and pool could be cleaned; on the experimental days it remained closed. It was constructed of widely spaced wooden poles which interfered little with the ambient environment. It was roofed 4 m above the ground to provide shelter from rain but the roof could be removed to allow full insolation.

Provided the head was occupied by feeding, a well-oiled thermistor could be inserted 300 mm into the rectum without difficulty and with minor attention could be kept in place for the 9 h of observations. The rectal thermistor was a Standtel Type F enclosed snugly within a brass tube 70 mm in length with 0,1 mm wall thickness. The tube was connected to a polyvinyl tube 400 mm long which protected the connecting wires and provided the rigidity necessary to insert the device to the required depth. The thin sheath whilst protecting the thermistor was of negligible thermal capacity in relation to the mass of tissue surrounding it but effectively sampled the temperature of that tissue while avoiding errors which might result from the lodgement of the thermistor tip in faecal material whose temperature could be locally unrepresentative. Temperature was measured by a Wheatstone Bridge null-point method and the thermistor was calibrated against a standard thermometer. The skin temperature was measured by a Standtel Type M thermistor closely attached to a copper disc of 25 mm diameter, 0,2 mm thickness, mounted on a wooden holder. This was hand-held when readings were taken and calibrated against a standard thermometer by fixing it against the flat side of a water bath. Again the metal was of negligible thermal capacity but sampled the temperature of a representative area of skin without artefacts arising from local placement of the tiny thermistor element.

Evaporative water loss was measured using an Electric Hygrometer (Hydrodynamics Inc.,) as described by Wright & Luck (1984).

Air velocity was assessed with a Silvered Kata Thermometer (Casella) and radiation with a 150 mm diameter Vernon Globe Thermometer (Casella). They were each situated about 2 m from the animal to sample as closely as possible the values relevant to the animal. The globe thermometer was 20 cm and the Kata thermometer was 40 cm above the floor. The mean radiant temperature was then estimated from charts (Bedford 1946). The wet bulb depression was measured with a Whirling Hygrometer (Casella) and the ambient water vapour pressure calculated at the altitude of 1200 m.

Occasional samples of subdermal gland secretion for chemical analysis were collected by hypodermic syringe from run-off channels provided by skin creases at the neck.

The object of these experiments was to measure core and surface temperatures and evaporative water loss in a healthy contented animal under varied environmental conditions with imposed restraint minimized to that necessary for successful measurements. For these reasons the natural environmental conditions could not be predetermined and only shelter against the sun and rain could be provided or withheld. Observations were limited to daylight hours because the animal was alert and restless after dark. Climatic stress could not be imposed in excess of that caused by the somewhat artificial surroundings and restrictions nor could water and food be denied beyond the end of the day. As the experimental site latitude was 0° 38′ North the sun was effectively vertically overhead at noon.

Results

The animal lay prone on the concrete floor of the pen for most of the observation time. Approximately 2 m^2 of the body surface was in contact with a concrete slab 30 cm thick which had an initial morning temperature of 20°C. The respiration rate remained below 10 per min throughout except during occasional vocalization at the end of the day. Under normal routine conditions the animal spent several daylight hours submerged in the pool but he remained placid during the experimental deviations, getting up occasionally and sleeping periodically.

The observations in Figures 2–5 are selected as examples of 4 different environmental patterns. The environmental parameters were measured at the time of each set of temperature and evaporative water loss measurements. The skin temperature ($\overline{T_s}$) plotted was the mean of about 25 measurements taken all over the available skin surface as illustrated in Figure 1. This comprised about 75% of the total skin surface and was the radiation area considered in this paper. It can be seen that there is often a range of skin temperatures but no form of weighting seems applicable in the calculation of $\overline{T_s}$. The S.E. of mean is plotted in each instance when

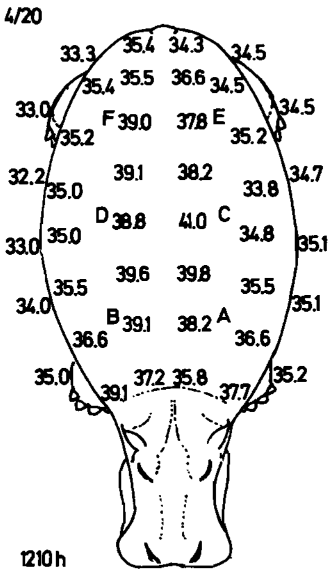

Figure 1 Distribution of skin temperature (°C) at 12h10 in hippopotamus resting in full sun. (Used to calculate $\overline{T}_s$ in Figure 3). A – F, sites of measurement of evaporation.

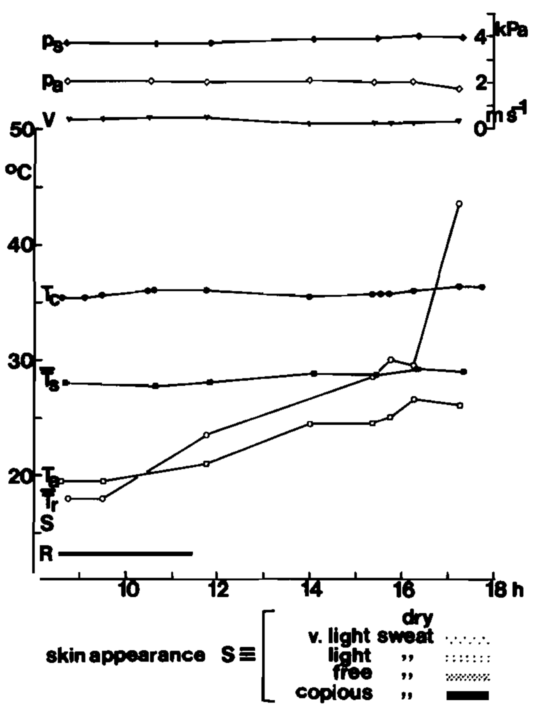

Figure 2 Hippopotamus body temperature and environmental parameters during daytime. ◆ p_s saturated water vapour pressure at mean skin temperature; ◇p_a ambient water vapour pressure; ▼ V wind speed; ● T_c body core temperature; ■ $\overline{T}_s$ mean skin temperature and standard error of mean; □ T_a ambient temperature; ○ $\overline{T}_r$ mean radiant temperature; S visual assessment of general skin appearance. Overcast sky until 15h30, R rain until 11h30 as shown by bar.

it exceeds the symbol height.

The plot of evaporative water loss (m) shows the mean and S.E. of mean of six measurements at each of six positions on each occasion. The appearance of the skin surface in relation to sweat secretion was noted according to the key shown in Figure 2.

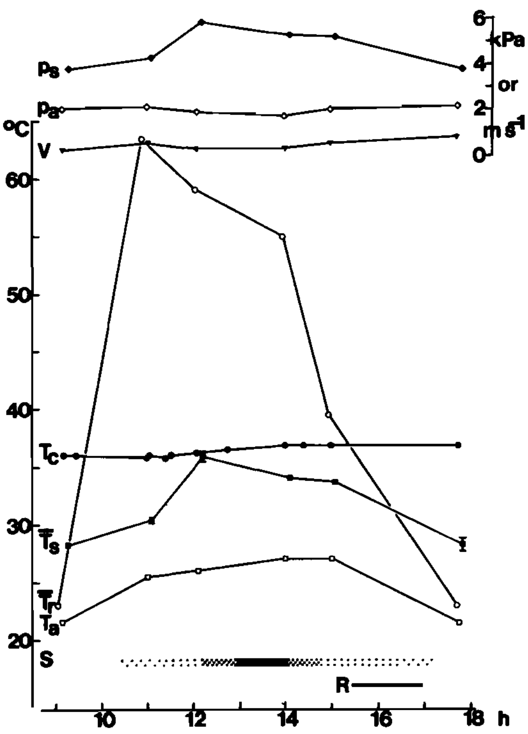

Figure 3 As in Figure 2. Full sun until 13h00, full cloud from 14h00, rain from 15h30 to 17h00.

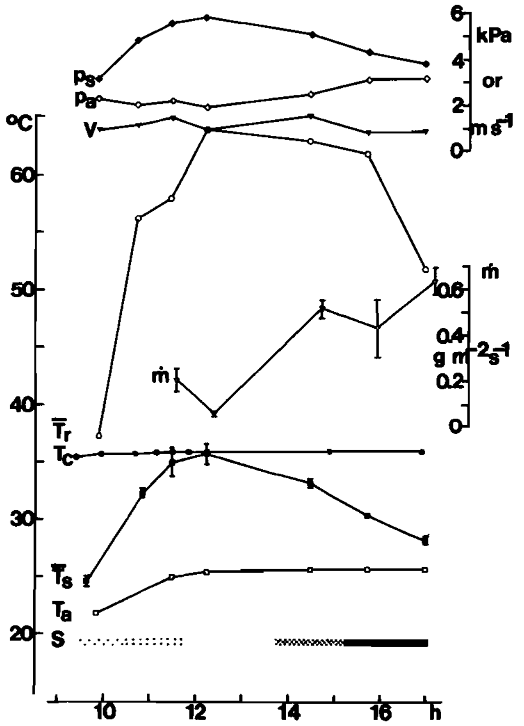

Figure 4 As in Figure 2. $\dot{m}$ of evaporation and standard error of mean. Full sun throughout.

Discussion

In the estimation of mean radiant temperature the 150

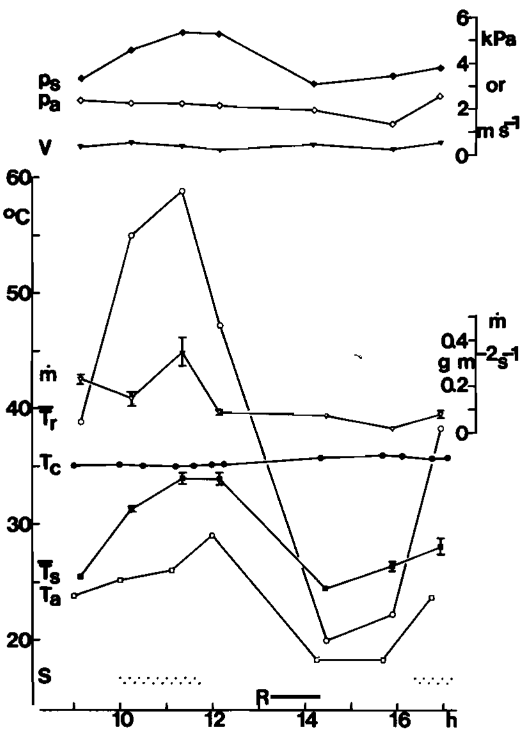

Figure 5 As in Figure 4. Full sun until 11h30, rain between 13h15 and 14h15 but animal was sheltered. Sun after 15h00.

mm Vernon Globe weights air and radiant temperatures satisfactorily for a human subject. The contribution of direct sunlight depends on posture and orientation but the contribution of reflected sunlight affects both man and globe similarly.

The emittance of a large enclosure makes little contribution to radiant heat exchange (Kerslake 1972a). The shape of the pronate hippopotamus is relatively symmetrical and its projected area will change less with sun movement than in the case of man. The ratio of the radiant area to the total surface area is 0,75 which is similar to that for an erect man (Guibert & Taylor 1952). Because of size and shape differences the convection coefficient will differ but the wind speed during these experiments was low (1 m s^{-1} or less) and changed little. Therefore, the measure of mean radiant temperature used in these experiments, though derived as for man, is considered sufficiently meaningful to provide an estimate of the radiation – convection heat load on the animal and of changes in it. If the hippopotamus skin is considered a black body with an absorbance of one then the radiant heat flux down the gradient, mean radiant temperature to mean skin temperature ($\overline{T}_r$ to $\overline{T}_s$), can be obtained (Kerslake 1972b).

Under cloudy conditions shown in Figure 2 $\overline{T}_s$ exceeded $\overline{T}_r$ so that heat loss by radiation – convection was possible. Under such conditions hippopotami commonly remain on the shore at the water's edge for most of the day. In the other situations illustrated $\overline{T}_r$ rapidly overtook $\overline{T}_s$ in the morning and remained higher until sunset (Figure 4) or until cloud and rain intervened (Figures 3 & 5). In these circumstances $\overline{T}_s$ increased initially with $\overline{T}_r$ but this increase minimized heat gain from the environment. For instance, at 12h15 in Figure 4 the radiant gain was 217 W m^{-2} but this would have been 23% higher if $\overline{T}_s$ had not increased along with $\overline{T}_r$. In this example the increased evaporation lowered $\overline{T}_s$ and this had the effect of increasing radiation transfer slightly to a maximum of 228 W m^{-2} at 15h00.

The thermal conductivity of stone-mix concrete is 0,92 W $m^{-1}{}^{\circ}C^{-1}$ (Norton 1948) and if it is assumed that the temperature of the skin in contact was as high as core temperature (36°C) the heat flow to the floor calculated under steady state conditions was 2842 kJ over an 8-h period. If the skin contact temperature was less than core temperature or the concrete base temperature rose, this heat flux would be reduced.

The technique used to measure evaporative water loss attempted to simulate natural environmental conditions in that it measured the rate of change in humidity within a capsule from the ambient level at the ambient air velocity. Saturation of the air in the capsule was not reached and the actual amount of water moving from the skin surface would not affect its hydration. The values obtained ranged from 68 g m^{-2} h^{-1} when the skin was visibly dry to 2280 g m^{-2} h^{-1} when it was wet with secretion. These maximum evaporative rates are similar to the values obtained when the hygrometric chamber was placed on a filter paper soaked in 250 mmol dm^{-3} KCl solution on a surface maintained at 37°C. They represent therefore the maximal evaporative rates measurable by this technique under the experimental conditions but because the measured time intervals are short no great accuracy can be claimed for them.

As $\overline{T}_s$ increased with increasing $\overline{T}_r$ the vapour pressure at the skin surface increased and thus the driving force for evaporation. As $\overline{T}_s$ fell as a consequence of evaporation the vapour pressure difference between skin and ambient ($p_s - p_a$) was reduced and this probably contributed to the accumulation of unevaporated secretion seen in Figure 4. A difference in evaporative rates at different locations on the body surface must be expected as a result of local variations in radiation and convection. This may be both the cause and the consequence of the variations in skin temperature as illustrated in Figure 1. The initial decline in evaporative water loss in Figures 4 & 5 may be due to the drying out of water gained by the skin during previous submersion as has been found in man and pig (Ingram 1965a). It is apparent in Figure 5 where initially evaporative water loss was increasing with $\overline{T}_r$ and $\overline{T}_s$ (as in Figure 4), that the abrupt fall in $\overline{T}_r$ owing to cloud and rain was accompanied by a rapid reduction in water loss and visible secretion disappeared.

The fluid sampled from the copious secretion occuring at 14h00 in Figure 3 had the composition

Na^+	1,2	mmol dm^{-3}
K^+	140,0	mmol dm^{-3}
Cl^-	18,4	mmol dm^{-3}
HCO_3^{--}	99,5	mmol dm^{-3}
pH	9,55	mmol dm^{-3}

No measurements of vapour pressure were made but this concentration of solutes would lower the water vapour pressure by about 0,5 kPa whereas in the sample discussed by Luck & Wright (1964) the reduction would be 1 kPa. In all the experimental records the value p_s calculated at $\overline{T}_s$ always exceeded the observed p_a and if p_s is reduced by 1 kPa there will still be a margin for continued evaporation. Furthermore, when fluid runs off the surface it will carry with it solutes which have accumulated as a result of evaporation.

These observations support the suggestion by Luck & Wright (1959) and Wright (1964) that the hippopotamus has a stable core temperature under natural conditions. They show a maximum variation of 1°C under environmental conditions in these experiments which were more severe than those usually experienced in the daytime by a hippopotamus in the wild. The normal behavioural pattern takes the animal into the water when full sunshine in the tropical savanna, which is its habitat, may produce a total solar radiation flux calculated for a horizontal hemispherical surface of 935 W m^{-2} at 14h00 (Roller & Goldman 1968).

An increase of 1°C in core temperature in this animal of 860 kg represents heat storage of approximately 3010 kJ during about 8 h in these experiments. The metabolic heat production calculated from oxygen consumption measured in this animal under similar conditions on land was 2,575 kJ kg^{-1} h^{-1} (Wright, P.G. 1966, unpublished) which is 17 715 kJ over an 8-h period. The observed increase in core temperature represents storage of about 17% of the daytime metabolic heat production. It is reasonable to say that heat loss by conduction to the ground surface in these experiments will account for no more than 16% of the daytime metabolic heat production. As the animal does not pant, heat loss from the respiratory tract will be small and change little. Therefore evaporative heat loss from the exposed 75% of the body surface must be adequate to account for about 66% of the metabolic heat production in the face of the adverse radiation – convection heat load in these experiments.

Hippopotamus skin is devoid of the more usual type of eccrine sweat glands but large subdermal glands discharging on to the surface are a conspicuous feature of the integument. The distribution of these glands and their ducts is regular but very sparse being less than 1 / cm^2. However, as each subdermal gland may be up to 1 g in weight it should be capable of elaborating a considerable volume of secretion. Luck & Wright (1964) demonstrated that in hippopotamus immobilized with succinyldicholine and then atropinized there was a high rate of transepidermal water loss which ranged between 108 and 191 g m^{-2} h^{-1}. Atropine stopped the secretory activity of the subdermal glands but the presence of a film of dried secretion on the skin surface increased the water loss by as much as 50% on average. Similar high values were obtained from recently dead animals. As all measurements were made in the shade and the skin was visibly dry, the values reflected a basal condition of the skin. These results for dry skin are now confirmed and the higher observed rates must be due to subdermal gland activity and possibly changes in water movement through the skin between the ducts. Hydration of intercellular mucopolysaccharides and of the ground substance of the epithelium and corium is important in controlling water movement; this aspect is reviewed in detail by Bettelheim (1971) and by Yates (1971). Luck & Wright (1964) suggested that the mucopolysaccharide component of the subdermal gland secretion was responsible for enhancing water lost from the dry surface. It is not possible to say whether the mucopolysaccharide component of the secretion itself makes any contribution when the surface becomes wet.

It would be presumptuous to attempt to equate the channels of heat transfer under these experimental conditions but it is possible to say that estimates for radiation – convection gain and metabolic production on the one hand and evaporative heat loss on the other are of the same order. Certainly evaporative water loss from the skin does change considerably and is adequate to counter the adverse radiation load. It is interesting that Ingram (1965b) showed that the pig which does not sweat, can, by wallowing in wet mud and urine, raise its evaporative cooling to levels comparable with the hippopotamus. In the other pachyderm, the elephant, which has neither sweat nor subdermal glands, the importance of evaporative heat loss has been stressed (Wright & Luck 1984).

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References

BEDFORD, T. 1946. Environmental warmth and its measurement. *Medical Research Council War Memorandum*. No. 17, HMSO, London.

BETTELHEIM, F.A. 1971. Structure and hydration of mucopolysaccharides. In: Biophysical properties of the skin, (ed.) Elden, H.R. John Wiley, London.

GUIBERT, A. & TAYLOR, C.L. 1952. Radiation area of the human body. *J. Appl. Physiol.* 5: 24–37.

INGRAM, D.L. 1965a. The effect of humidity on temperature regulation and cutaneous water loss in the young pig. *Res. Vet. Sci.* 6: 9–17.

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

KERSLAKE, D.McK. 1972a. The stress of hot environments, pp. 47–73. University Press, Cambridge.

KERSLAKE, D.McK. 1972b. The stress of hot environments, appendix 5. University Press, Cambridge.

LUCK, C.P. & WRIGHT, P.G. 1959. The body temperature of the hippopotamus. *J. Physiol.* 147: p.53.

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.

NORTON, 1948. Cited in Handbook of chemistry and physics, 31st edition, p. 1892. Chemical Rubber Publishing Co., Cleveland.

ROLLER, W.L. & GOLDMAN, R.F. 1968. Prediction of heat load on Man. *J. Appl. Physiol.* 24: 717–721.

WRIGHT, P.G. 1964. Wild animals in the tropics. *Symp. Zool. Soc. Lond.* 13: 17–28.

WRIGHT, P.G. & LUCK, C.P. 1984. Do elephants need to sweat? *S. Afr. J. Zool.* 19: 270–274.

YATES, J.R. 1971. Mechanism of water uptake by skin. In: Biophysical properties of the skin, (ed.) Elden, H.R. John Wiley, London.