

Heat loss in relation to plane of nutrition and thermal environment

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Some of the valuable information which can be derived from the measurement of heat loss from the pig lies in the estimates which can be made of energy retention by the animal from the relation: $ME \text{ intake} = H + ER$, where ME is metabolizable energy, H is heat loss, and ER is energy retention. Such measurements are most useful when they are made throughout 24 h periods, because then the mean energy intake and heat loss can be determined. Measurements made only at particular times during the 24 h may be affected markedly by feeding, activity or other relatively short-term factors (Mount, 1968; Neergaard & Thorbek, 1969). Consequently these observations may not be representative of the mean rates, and may therefore fail to give an accurate indication of energy retention. Short-term measurements are permissible for the determination of acute metabolic responses to given thermal environments or other stimuli, but when plane of nutrition is to be taken into account in addition to thermal environment, which is the present purpose, isolated measurements may be misleading. In this paper, therefore, all results are 24 h values. This longer period of measurement ensures also that any difference in heat stored in the animal between the beginning and end of the measurement period (due to difference in mean body temperature) is of decreasing significance. Such heat-storage effects are anyway minimized by 24 h measurements, since the latter are always made at the same phase of any cycles involved with feeding, activity and body temperature (Ingram & Mount, 1973).

Nutrition–environment interactions

Factors which are of central importance in the consideration of the interplay of nutritional and environmental factors, as these bear on an animal's heat loss and energy retention, are the critical temperature (CT) and the zone of thermal neutrality. CT is defined as the environmental temperature below which it is obligatory for an animal to increase its rate of heat production if it is to maintain its body temperature at the usual level. The CT lies at the lower end of the zone of thermal neutrality, which for general purposes may be defined as the range of environmental temperature in which heat production is constant, at a minimum, and independent of temperature; other definitions may also be used, but these also include minimal metabolism (Mount, 1974).

The CT is often referred to as if it were a precisely defined temperature below which the animal's heat production suddenly begins to rise at a uniform rate from

a level which is constant throughout the thermoneutral zone. Although such a well-defined CT can be obtained under some conditions, particularly with an immobile animal, more often the relation between heat production and environmental temperature is curvilinear, so that it becomes necessary to resort to making an estimate of 'effective CT' as described later. With the larger unrestrained pig, and particularly with groups of pigs, the curvilinearity is increased, so making the CT even less definite.

There are several reasons for the departure of actuality from a sharply defined CT. These include changes in posture by the conscious animal as the temperature falls through the critical level, so extending the change in over-all insulation brought about by peripheral vasomotor control in the thermoneutral zone, variations in activity, and, with groups of pigs, the tendency to huddle as the temperature falls, with further increase in over-all thermal insulation of the group (Mount, 1960, 1968).

In addition to effects of body size and thermal insulation, an animal's rates of heat production and heat loss are determined principally by the plane of nutrition and the environmental temperature. Under warm conditions, that is at or above CT and within the zone of thermal neutrality, the plane of nutrition is the chief determinant; under cool conditions, below CT, the environmental temperature is the principal factor. Following the earlier demonstration of this relationship in individual clipped sheep (Graham, Wainman, Blaxter & Armstrong, 1959), an approximation to this relationship has also been shown to hold for groups of pigs (Close, Mount & Start, 1971; Versteegen, 1971; Versteegen, Close, Start & Mount, 1973).

Warm conditions. In the thermoneutral zone one effect of the increased rate of heat loss which accompanies a higher plane of nutrition is to lower the CT (Fuller, 1969). This effect is sometimes partially obscured by the curvilinearity in the region of the CT, but one result is that animals on higher planes of nutrition approach maximum productivity at temperatures below the optimum temperatures needed by animals on lower planes of nutrition. Maintaining higher temperatures for animals on high planes is therefore not only pointless as an attempt to increase energy retention, but also provides an obstacle to the dissipation of the increased amount of heat produced on high food intakes, and may limit food intake (Bianca & Blaxter, 1961).

Evidence from operant conditioning experiments indicates the animals' own preferences for lower environmental temperatures when the plane of nutrition is high. Pigs trained to operate a switch to control the radiant heating of their environment took 300 heat reinforcements/h when they were fed at 400 g food/d, and only 200 reinforcements/h when they were fed at 900 g/d, at 10° environmental temperature (Baldwin & Ingram, 1968).

Animals on higher planes of nutrition become hyperthermic at lower environmental temperatures than animals on lower intakes. From measurements of heat loss from individually caged pigs of 25–35 kg body-weight, 30° is in the hyperthermic zone for all levels of feeding above maintenance, with more marked effects at the higher levels, using an increased heat production as the criterion of

heat stress (Close & Mount, 1976). Gray & McCracken (1974) found that 29° was close to the hyperthermic zone of the full-fed 20 kg pig housed in a metabolism cage, using a reduction in energy retention as the criterion.

When the plane of nutrition is increased under warm conditions the additional heat produced is dissipated primarily by evaporative means, with a smaller contribution through the non-evaporative or sensible modes of transfer of radiation, convection and conduction as a consequence of prolongation of the period in which skin temperature is increased following feeding (Sørensen, 1962). Evaporative heat loss from the pig is markedly limited as a result of the animal's inability to sweat to any effective extent (Ingram, 1965), and increased evaporative cooling is usually achieved by the animal wetting its surface with any available water from wallows, urine or faeces. Increased evaporative loss accompanies the rise in respiratory rate exhibited by pigs exposed to warm conditions (Holmes, 1966; Mount, 1968; Morrison & Mount, 1971). The proportion of total heat lost by evaporation by a group of pigs living in a pen built into a direct calorimeter was about 30% at 20° and 60% at 30° (Holmes & Mount, 1967). This included evaporative loss from the floor of the pen in addition to evaporative loss from the animals themselves.

From measurements made on pigs living in metabolism cages, Fuller & Boyne (1972) calculated that at 30 kg body-weight the production of water vapour increased by a mean value of 5.3 g/d with each increase in daily food intake of 1 g/kg body-weight^{0.73}; at 55 kg the water vapour increased by 5.8 g/d and at 80 kg by 6.2 g/d. These values did not vary between environmental temperatures of 5, 13 and 23°.

Cool conditions. At lower temperatures, heat loss tends to be independent of plane of nutrition, and increases progressively as the temperature falls. For this reason the partial efficiency of energy retention (k_f) associated with an increment of feed can be expected to approximate to unity in the cold, and this was found to be so with groups of pigs studied at 8° and 20° environmental temperatures (Verstegen *et al.* 1973). At 8°, k_f was 0.99 whereas at 20°, which was above CT, it was 0.67. Above the CT, the extra heat production associated with a higher plane of nutrition is dissipated. Below the CT, however, this extra heat production can take the place of some of the extra thermoregulatory heat (ETH) needed, and it is this factor which accounts for the higher k_f in the cold.

Partial efficiency (k_f) and critical temperature (CT)

k_f can be defined as the ratio, increment of ER (ΔER) : increment of ME (ΔME) which accompanies an increase in food intake above the maintenance level (Kielanowski & Kotarbińska, 1970; Sharma, Young & Smith, 1971; Burlacu, Bina, Ionides & Moisa, 1973). At thermal neutrality, ΔER is less than ΔME by an amount ΔH , the increment of heat production. Calorimetric determination of the energy costs of deposition of protein and fat inclusive of their energy values in one series of experiments gave these as 38.1 kJ/g for protein and 46.7 kJ/g for fat (Close, Verstegen & Mount, 1973).

At thermal neutrality on a given ME intake, the total heat production is:

$$H = H_m + H_p, \quad (2)$$

where H_m is the heat production at the maintenance ME intake (ME_m), when

$$H_m = ME_m, \text{ since } ER = 0;$$

H_p is the additional heat production, above that of the maintenance level, associated with ME intakes above the maintenance level and positive values of ER.

From the definition of k_f ,

$$ER = k_f (ME - ME_m). \quad (3)$$

From equations (1) (p. 81), (2) and (3) and since $ME_m = H_m$:

$$H_p = \frac{ER (1 - k_f)}{k_f}. \quad (4)$$

At temperatures below thermal neutrality,

$$H = H_m + H_p + ETH.$$

From equations (1) and (4):

$$ME = ME_m + \frac{ER}{k_f} + ETH. \quad (5)$$

The occurrence of ETH can be used to determine whether the animals are below their CT and, knowing the slope of the curve of heat production against environmental temperature, to determine an effective CT. In the experiments of Close *et al.* (1973), and referring to equation (5), of the ME intake at 8°, ER/0.67 was that part associated with energy retention. The value of 0.67 for k_f is used on the assumption that the total energy associated with the process of retention, as distinct from thermoregulatory responses, is the same both at thermoneutrality and under cold conditions. Any excess of $(ME - \frac{ER}{0.67})$ over ME_m was then due to

ETH production at 8°; ETH production was found to occur at 8°. The slope of the heat production curve derived from a series of experiments proved to be close to 12 kJ/body-wt^{0.75} per d for each ° below CT, so that CT could be estimated as $(8 + \frac{ETH}{12})^\circ$, indicating 17° for groups of pigs given 45 g food/kg body-wt per d and 11° for pigs given 52 g food/kg body-wt per d (Mount, Close & Versteegen, 1973).

There are not always clear-cut differences between the k_f under warm and that under cold conditions, particularly when the calculation is based on regressions of ER on ME. Fuller & Boyne (1972) found a mean k_f of 0.72 with pigs between 25 and 85 kg body-weight at 23° and 0.78 at 5°, from regression analysis. Their Table 3, however, indicates a proportionately smaller range of heat loss for a given range of planes of nutrition at 5° compared with 23°. During those parts of the day which follow feeding it might be expected that the effects of heat increment tend to depress the animals' CT below the constant pen temperature, so that k_f falls to the level characteristic of warm conditions, with the result that the mean 24 h k_f is less than unity.

Fasting metabolism. Fasting heat loss in the 25–40 kg pig was found to be higher at 20° environmental temperature (457 kJ/kg body-wt^{0.75} per d) than at 30° (380 kJ/kg body-wt^{0.75} per d), and it was not significantly dependent on the preceding level of feeding (Close & Mount, 1975). Results on fasted 26–60 kg pigs

taken from another study (Thorbek, 1974) gave 478 kJ/kg body-wt^{0.75} per d at 18°, and 380 kJ/kg body-wt^{0.75} per d at 26°. These values suggest that the CT for the individual fasted pig of this body size is approximately 25°.

The assessment of thermal environment in relation to heat loss and pig production

The thermal environment has so far been characterized quantitatively in this discussion only in terms of the environmental temperature. Under controlled laboratory conditions an environment can be produced in which the air and mean radiant temperatures are equal to each other, in a regimen of free convection and with an insulated floor. This constitutes a standardized environment, in which the air temperature equals the environmental temperature. Heat losses from pigs are usually measured in the laboratory under such standardized conditions; however, usually there are departures from a standardized environment under farming conditions, so that air temperature by itself is no longer an adequate assessment of the thermal environment. An equivalent standardized environmental temperature (ESET) can then be calculated by adding algebraically to the air temperature experimentally determined variations which allow for deviations of the radiant, convective and conductive components of the environment from the standardized situation. ESET allows laboratory determinations of heat loss and effective CT to be referred to complex thermal environments which are characterized by differences between air temperature and mean radiant temperature, draughts of air, and floors which may be wet and of varied thermal insulation (Mount, 1976).

When ESET for particular circumstances falls below the effective CT corresponding to a given plane of nutrition and size of group, production losses may occur because the animals' heat production is likely to be above the level characteristic of thermal neutrality. The increased rates of heat loss occurring at sub-critical temperatures, and the corresponding increases in food intake required to offset the increases in heat loss, are given for pigs in the weight range 20–50 kg in Table 1, which also includes mean approximations to heat losses and effective

Table 1. *Relation of effective critical temperature (CT) to feeding level and number of pigs/group for 35 kg pigs, and the rate of increase in heat loss below the CT*

Feeding level (/kg body-wt per d)*		Heat loss at temperatures above CT (kJ/kg body-wt per d)	CT (°) with no. of pigs/group:		
kJ	g		1	4	9
500	42	270	20	17	16
540	45	290	19	16	14
575	48	310	18	14	12
620	52	330	17	12	10
Rate of increased heat loss below CT (kJ/° per kg body-wt per d)			8	5	4
Equivalent increase in food intake (g/° per kg body-wt per d)			0.7	0.4	0.3

*Assuming a food metabolizable energy content of 12 kJ/g.

CT in relation to plane of nutrition and size of group. However, too precise an estimate of the optimum temperature for growth is not realistic because adaptation, particularly behavioural adaptation, reduces metabolic responses to environmental change (Bianca & Blaxter, 1961).

REFERENCES

- Baldwin, B. A. & Ingram, D. L. (1968). *Physiol. Behav.* **3**, 395.
 Bianca, W. & Blaxter, K. L. (1961). *Proc. VIIIth int. Congr. Anim. Prod., Hamburg.*
 Burlacu, G., Bina, G., Ionides, D. & Moisa, D. (1973). *J. agric. Sci., Camb.* **81**, 295.
 Close, W. H. & Mount, L. E. (1975). *Br. J. Nutr.* **34**, 279.
 Close, W. H. & Mount, L. E. (1976). *Proc. Nutr. Soc.* **35**, 60A.
 Close, W. H., Mount, L. E. & Start, I. B. (1971). *Anim. Prod.* **13**, 285.
 Close, W. H., Verstegen, M. W. A. & Mount, L. E. (1973). *Proc. Nutr. Soc.* **32**, 72A.
 Fuller, M. F. (1969). In *Animal Growth and Nutrition*, p. 82 [E. S. E. Hafez and I. A. Dyer, editors]. Philadelphia: Lea and Febiger.
 Fuller, M. F. & Boyne, A. W. (1972). *Br. J. Nutr.* **28**, 373.
 Graham, N. McC., Wainman, F. W., Blaxter, K. L. & Armstrong, D. G. (1959). *J. agric. Sci., Camb.* **52**, 13.
 Gray, R. & McCracken, K. J. (1974). *Publs Eur. Ass. Anim. Prod.* no. 14, p. 161.
 Holmes, C. W. (1966). Studies on the effects of environment on heat losses from pigs. PhD Thesis, The Queen's University of Belfast.
 Holmes, C. W. & Mount, L. E. (1967). *Anim. Prod.* **9**, 435.
 Ingram, D. L. (1965). *Res. vet. Sci.* **6**, 9.
 Ingram, D. L. & Mount, L. E. (1973). *Pflügers Arch. ges. Physiol.* **339**, 299.
 Kielanowski, J. & Kotarbińska, M. (1970). *Publs Eur. Ass. Anim. Prod.* no. 13, p. 145.
 Morrison, S. R. & Mount, L. E. (1971). *Anim. Prod.* **13**, 51.
 Mount, L. E. (1960). *J. agric. Sci., Camb.* **55**, 101.
 Mount, L. E. (1968). *The Climatic Physiology of the Pig*. London: Edward Arnold.
 Mount, L. E. (1974). In *Heat Loss from Animals and Man*, p. 425 [J. L. Monteith and L. E. Mount, editors]. London: Butterworths.
 Mount, L. E. (1976). *Livestock Prod. Sci.* (In the Press.)
 Mount, L. E., Close, W. H. & Verstegen, M. W. A. (1973). *Proc. Nutr. Soc.* **32**, 71A.
 Neergaard, L. & Thorbek, G. (1969). *Publs Eur. Ass. Anim. Prod.* no. 12, p. 291.
 Sharma, V. D., Young, L. G. & Smith, G. C. (1971). *Can. J. Anim. Sci.* **51**, 761.
 Sørensen, P. H. (1962). In *Nutrition of Pigs and Poultry*, p. 88 [J. T. Morgan and D. Lewis, editors]. London: Butterworths.
 Thorbek, G. (1974). *Publs Eur. Ass. Anim. Prod.* no. 14, p. 147.
 Verstegen, M. W. A. (1971). *Meded. LandbHoogesch. Wageningen* no. 71.
 Verstegen, M. W. A., Close, W. H., Start, I. B. & Mount, L. E. (1973). *Br. J. Nutr.* **30**, 21.