The metabolism and thermal regulation of calves in the first month of life

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The object of these experiments was to examine the effect of environmental temperature on the energy exchange of the calf during its early life and, in particular, to determine the environmental temperature below which heat production increases in response to increasing cold. This latter temperature is called the critical temperature. The range of temperature between the critical temperature and that higher environmental temperature when heat production increases is called the thermoneutral zone. There is evidence that the mortality and morbidity of calves is greater in winter than in summer and is greater in the more northern and hence colder parts of Britain (Withers, 1952). This evidence suggests, but does not prove, that cold conditions in calfhouses are undesirable. Most farmers concur in their opinion that calves require a warm environment in early life, but no quantitative information about the conditions optimal for their growth and well-being is available.

EXPERIMENTAL

Animals and food. Four Ayrshire bull calves (A, B, C and D) were used as experimental animals. They were given either 4 l. or 6 l. cow's whole milk each day in two meals. The milk was always given at body temperature. Experimental measurements began on or shortly after the 2nd day of life and continued for about 4 weeks.

Sequence of experiments. Each calf was kept throughout the experiments in a respiration chamber, and measurements of metabolism were made at environmental temperatures of about 3°, 13° and 23°. Initially, measurements were restricted to periods of 12 h because the calves had not learned to drink from a bucket and the chamber had to be opened to feed the calf. Once the calves had learned to drink, 24 h periods of measurements were used with the exception that with calf A all experiments were of 12 h duration. The details of all experiments are given in Table 1. In addition, on six occasions with calves C and D, heat production was measured at hourly intervals during the cooling of the chamber, over periods of 8–9 h, from temperatures of from over 30° to 3°. With the same two calves, rectal, skin surface and hair surface temperatures were measured throughout all experiments. The losses of energy in the faeces and the urine of calves B and D were measured when they were given 4 l. and when they were given 6 l. milk and the heat of combustion of the milk

was also determined. The energy retained by these animals could thus be calculated.

Methods. The respiration chamber was that of Wainman & Blaxter (1958) modified to enable the quantitative admission of milk. Heat production (H) was calculated from oxygen consumption, carbon dioxide production and urinary nitrogen excretion by means of the equation:

$$H = 3 \cdot 998 \; O_2 \; (l.) + 1 \cdot 026 \; CO_2 \; (l.) - 1 \cdot 602 \; N \; (g).$$

The equation was based on the calorific values and C and N contents of milk fat, casein and lactose. The error in estimating heat production from a similar equation developed by Brouwer (1958) which uses starch, body fat and meat protein as reference

Table 1. *Details of metabolism experiments with four calves, and their heat production*

Age (days)	Milk intake (l./day)	Weight (kg)	Environmental temperature (°C)	Heat production (kcal/m² 24 h)*	Age (days)	Milk intake (l./day)	Weight (kg)	Environmental temperature (°C)	Heat production (kcal/m² 24 h)*
Calf A (12 h observations)					Calf B (24 h observations except those marked†)				
4	4	39·3	4·5	2483	2†	4	39·2	24·9	2379
5	4	38·7	23·4	2310	3†	4	37·7	5·0	3033
8	4	38·2	23·5	2331	4†	4	37·7	23·8	2367
9	4	38·5	3·2	2475	8†	4	40·3	23·5	2051
11	4	38·6	24·0	2152	9†	4	40·6	2·8	2488
12	4	38·8	3·0	2499	10†	4	41·0	23·5	2074
13	4	39·4	23·3	2205	11	4	41·4	2·7	2292
16	6	41·6	5·2	2684	15	4	42·0	3·2	2096
17	6	42·3	23·4	2388	16	4	42·6	23·1	1764
22	6	45·1	4·6	2645	17	4	43·3	2·2	2032
23	6	45·7	23·4	2296	18	4	43·7	24·1	1755
					24	6	44·2	22·7	1952
					25	6	45·0	3·2	2418
					29	6	49·6	23·6	2117
					30	6	50·4	3·2	2299
Calf C (24 h observations)					Calf D (24 h observations)				
5	4	37·3	23·4	1916	4	4	37·5	24·9	1928
8	4	38·8	2·8	2294	6	4	37·9	4·3	2403
11	4	40·0	24·5	1824	8	4	38·3	23·4	1996
13	4	40·5	2·9	2039	9	4	38·5	3·6	2400
17	4	43·1	12·1	1700	11	4	38·7	23·8	1971
18	4	43·3	23·0	1741	12	4	39·1	13·8	1969
22	4	44·7	2·8	2044	14	4	39·5	3·9	2241
					18	6	42·2	24·1	2155
					19	6	43·0	13·3	2235
					22	6	44·1	2·8	2418

* Surface area was estimated from the formula: surface area = $0 \cdot 09 \times$ weight $(kg)^{0 \cdot 667}$ (Mitchell, 1928).
† 12 h observations.

bases is, however, very small. On occasions calf C produced small amounts of a combustible gas which was identified as a mixture of H_2 and CH_4. It was ignored in calculation of the heat production.

The analytical methods for determination of the C, N and calorific values of food

and excreta were those of Graham, Armstrong & Blaxter (1958). The temperature measurements were made with copper–constantan thermocouples and were recorded potentiometrically. The heat lost by the animal in vaporizing water from its skin and respiratory passages was determined by absorbing and weighing the water vapour in the air leaving the chamber and multiplying the weight by the heat required to vaporize unit weight of water. A correction was made to the determined water vapour loss because it includes water vaporized from the urine. The correction was arrived at before the experiments began by simulating urination in the chamber and weighing the water vaporized. These measurements were made at the environmental temperatures subsequently used in the experiments and the resultant correction was a very small proportion of the total water lost from the chamber. The sensible loss of heat was estimated as the difference between the heat produced and the heat lost by vaporizing moisture.

<div align="center">RESULTS</div>

Heat production at 23° in relation to the age of the calf. When 4 l. milk were given, analysis of the observations made at 23°, a temperature well above the critical temperature, showed that metabolism declined with age. Observations over 24 and 12 h periods (Table 1) were analysed separately and the regression equations obtained were

$$H = 1963 - 8 \cdot 8t, \text{ for 24 h observations,} \qquad (1a)$$
$$H = 2485 - 33 \cdot 2t, \text{ for 12 h observations,} \qquad (1b)$$

where H is heat production (kcal/m² 24 h) and t is age in days. In these regressions variation due to calves was removed and the standard errors of estimate were ± 48 and ± 83 kcal/m² 24 h respectively. Heat production measured over 24 h was lower

Table 2. *Energy retained at environmental temperature of 23° by two calves when given daily 4 l. or 6 l. milk*

		Energy (kcal/24 h)					
Calf	Milk intake (l.)	Intake as milk	Excreted in faeces	Excreted in urine	Lost as heat	Total retained in body	Retained as protein
B	4	2976	45	78	1951	902	276
B	6	4463	60	72	2386	1945	671
D	4	2897	20	72	2028	777	449
D	6	4246	104	88	2412	1842	756

than that measured over 12 h, suggesting that a diurnal variation in metabolism occurred. It could have arisen from the small inequality of feeding intervals (13 h and 11 h), but the calves were more active during the daylight hours. The regression coefficient was significant statistically ($P < 0 \cdot 05$) for the 12 h measurements but not for the 24 h measurements. No differences of any significance were noted when observations on heat production made at 13° were compared with those predicted from equation (1a).

Utilization of the energy of milk. The results in Table 2 were obtained in experiments made at an environmental temperature of 23°, that is above the critical tempera-

ture of the calves. They show that losses of energy in faeces and urine were very small, the metabolizable energy being on average 95·1 % of the gross energy of the milk. This value agrees precisely with that determined a few years ago (Blaxter, 1952). The net availability of the metabolizable energy of the milk was estimated after dividing both the values for the metabolizable energy and the energy retentions by the body-weight of the calf raised to the power 0·73 to equate for differences in their body size. The net availability of the metabolizable energy of milk was 77·0 % with calf B and 82·0 % with calf D. Previous trials with calves in an open-circuit respiration apparatus had given a value of 84·5 % (Blaxter, 1952). The two sets of observations are thus in agreement and they emphasize the very high efficiency with which the calf uses its natural food as an energy source.

Heat production at 3°. When 4 l. milk were given and the environmental temperature was 3°, heat production was greater than that measured at 23°. The values obtained are given in Table 1 and they also reveal a decline of metabolism with age. The regressions for both 24 h and 12 h observations were:

$$H = 2419 - 17\cdot3t, \text{ for 24 h observations,} \tag{2a}$$
$$H = 2823 - 30\cdot7t, \text{ for 12 h observations.} \tag{2b}$$

Differences between calves have been removed in arriving at these regressions.

As with observations made at 23°, heat production was higher when determined in 12 h observation periods. A fall in metabolism with time is apparent with both sets of observations, though in neither set were the regressions significant statistically. Equations (1a), (1b), (2a) and (2b) all reveal a decline in metabolism with age, differences between calves having been discounted. The pooled value of the regression coefficient was −19·9 kcal/m² 24 h, which was statistically significant ($P < 0\cdot01$).

Partition of heat losses. The heat loss of each calf was partitioned into the evaporative loss and the sensible loss of heat, the latter including losses of heat by radiation, convection and conduction. The mean of eight 24 h determinations of the loss of heat as water vapour made at an environmental temperature of 3° when 4 l. milk were given was 340 ± 15 kcal/m² 24 h. When 6 l. milk were given and the environmental temperature was 23° the mean loss of heat by evaporation was 344 ± 25 kcal/m² 24 h. Age had no effect on these losses and the mean of all observations was 341 ± 12 kcal/m² 24 h. This last value, since it was measured below the critical temperature, represents the minimal loss of heat by evaporation and it is of some interest to compare this value for the calf with values obtained with other species. In man the minimal loss is 288 kcal/m² 24 h (Winslow & Herrington, 1949), in sheep 312 kcal/m² 24 h (Blaxter, Graham, Wainman & Armstrong, 1959) and in adult cattle 348 kcal/m² 24 h (Blaxter & Wainman, 1961). The minimal loss of heat by evaporation under cold conditions thus appears to be fairly constant irrespective of body size and species.

The virtual constancy of the evaporative loss of heat by the calves at 3° coupled with the fall in their heat production with increasing age must imply that the loss of heat by sensible pathways decreased with increasing age. The sensible heat loss thus falls at a rate of 19·9 kcal/m² 24 h from an initial value which is 341 kcal less than the initial heat production.

Conductance of sensible heat. The overall conductance of sensible heat from the body (K) is defined as

$$K = \frac{H_N}{T_R - T_A},\tag{3}$$

where H_N is the sensible loss of heat and T_R and T_A the temperature of the rectum and that of the air respectively. It is in some ways more convenient to deal with the reciprocal of the conductance, that is the overall insulation or the resistance of the

Table 3. *Cooling resistances* $(1/K = °C \times 10^{-3}/kcal\ m^2\ 24\ h)$, *determined at about* 3°, *in relation to the age of calves given 4 l. or 6 l. milk daily*

Milk intake (l.)	Calf A		Calf B		Calf C		Calf D	
	Age (days)	Cooling resistance (1/K)	Age (days)	Cooling resistance (1/K)	Age (days)	Cooling resistance (1/K)	Age (days)	Cooling resistance (1/K)
4	4	18·0	3	14·5	8	18·3	6	16·8
	9	18·1	9	18·6	13	21·0	9	17·3
	12	18·8	11	21·5	22	20·7	14	18·5
	—	—	15	20·7	—	—	—	—
	—	—	17	21·0	—	—	—	—
6	16	15·7	25	17·3	—	—	22	17·0
	22	17·5	30	18·4	—	—	—	—

animal to cooling. The values obtained at about 3° are given in Table 3 and an effect of age is apparent. The effect of age on the cooling resistance of the calves when given 4 l. milk can be approximated by the equation

$$1/K = 15·8 + 0·28t,\tag{4}$$

where $1/K$ is measured in $°C \times 10^{-3}/kcal\ m^2\ 24\ h$. In determining this equation differences due to calves were removed. The standard error of estimate was $\pm 1·4\ °C \times 10^{-3}/kcal\ m^2\ 24\ h$. In adult beef cattle $1/K$ is $20·2 \times 10^{-3}\ °C/kcal\ m^2\ 24\ h$ (Blaxter & Wainman, 1961) which suggests that during the first 16 days of life the calf is not as well insulated as the adult steer. Measurements of insulation of calves made after 16 days of age agreed with those obtained with adult steers.

The critical temperature (C_T) of the calf is defined by the equation

$$C_T = 39·3 - 1/K\ (H - H_V).\tag{5}$$

The constant 39·3 is the mean rectal temperature of calves in a thermoneutral environment obtained from measurements made at 23°, H is the total heat production in $kcal/m^2\ 24\ h$ also measured in a thermoneutral environment, H_V the minimal heat loss by vaporizing water and $1/K$ the resistance to cooling as defined above.

By inserting in equation (5), first, heat production at 23° when 4 l. milk were given daily as estimated from equation (1 *a*) and, second, the resistance to cooling estimated from equation (4), the critical temperature during the 1st month of life can be related to age by the following expression in which t is the age of the calf in days

$$C_T = 13·7 - 0·315t + 0·0024t^2.\tag{6}$$

Equation (6) shows that on the 3rd day of life the critical temperature of the calf given 4 l. milk is about 12·8° and falls with age. At 10 days of age the critical temperature is 10·8° and at 20 days 8·2°.

When 6 l. milk were given, heat production in the thermoneutral zone was 2034 kcal/m² 24 h for calf B and 2195 kcal/m² 24 h for calf D. These values, if combined with cooling resistances measured when 4 l. of milk were given, suggest that the critical temperature when 6 l. of milk were consumed should be about 1°. However, determinations of metabolism at 3° showed that it was 2358 kcal/m² 24 h in calf B and 2418 kcal/m² 24 h in calf D, that is in both animals it was higher than the values obtained in the thermoneutral zone. It thus appears that the resistance to cooling of calves given 6 l. milk is less than that of those given 4 l. The observations on resistance to cooling both when 4 l. and 6 l. milk were given confirm this supposition as shown in Table 3. The critical temperature of calves aged 3–4 weeks given 6 l. milk is thus 7–8° rather than 1·0°. The reason for this difference is not known.

Roy, Huffman & Reineke (1957) have determined the heat production of calves up to 3 weeks of age using mask techniques. Measurements were made 15 h after food. When the results of a series of such observations were examined an initial rise and subsequent fall in metabolism were noted. Many of their determinations appear from our results to have been made below the critical temperatures of the animals. Of the four observations made on the 2nd day of life not one was above the critical temperature as predicted from equation (6) for calves given 4 l. milk. On the 5th day, however, all observations were above the critical temperature. This suggests that the peak in metabolism they noted at 2–3 days of age may well have been a response to cold.

The magnitude of insulation terms. In two calves, C and D, measurements of the temperature of the skin and the hair coat surfaces were made. These permit estimation of the insulation provided by the tissues, the hair coat and the air interface at the surface of the hair coat. The terms are defined as:

$$\text{Insulation of the tissues} \quad I_T = \frac{T_R - T_S}{H},$$

$$\text{Insulation of the coat} \quad I_F = \frac{T_S - T_H}{H_N},$$

$$\text{Insulation of the air interface} \quad I_A = \frac{T_H - T_A}{H_N},$$

where H is total heat produced (kcal/m² 24 h), H_N the sensible heat loss (kcal/m² 24 h) and T_R, T_S, T_H and T_A are the temperatures (°C) of the rectum, the skin surface, the hair surface and the environment.

Insulation of the air interface. Seven determinations were made at environmental temperatures of 3° and 23° and three at 13°. They are summarized in Table 4.

There were no significant differences in the insulation of the air interface due to environmental temperature, and inspection of the values showed that the insulation of the air interface did not change with age of the calf. The mean value of $5\cdot7 \times 10^{-3}$ °C/kcal m² 24 h is in good agreement with observations made with other species. In man, Burton & Edholm (1955) have recorded the insulation of the air interface as

$6 \cdot 0 \times 10^{-3}$ °C/kcal m² 24 h. In sheep with fleeces the insulation is $7 \cdot 1 \times 10^{-3}$ °C/kcal m² 24 h (Blaxter, Graham, Wainman & Armstrong, 1959), and in steers appears from our unpublished work to be from $5 \cdot 1$ to $6 \cdot 0 \times 10^{-3}$ °C/kcal m² 24 h.

Table 4. *Insulation of the air interface and of the hair coat of calves C and D kept at different environmental temperatures for 24 h*

Environmental temperature (°C)	No. of observations	Insulation of air interface*	Insulation of hair coat*
		(°C $\times 10^{-3}$/kcal m² 24 h)	
3	7	$5 \cdot 99 \pm 0 \cdot 17$	$7 \cdot 73 \pm 0 \cdot 56$
13	3	$5 \cdot 97 \pm 0 \cdot 67$	$6 \cdot 06 \pm 0 \cdot 39$
23	7	$5 \cdot 37 \pm 0 \cdot 22$	$5 \cdot 55 \pm 0 \cdot 47$
Mean		$5 \cdot 73 \pm 0 \cdot 33$	—

* Mean values with their standard errors.

Insulation of the coat. Measurements of the mean thickness of the hair coat at different sites on the body were made with calf D by means of a probe. These showed that at an environmental temperature of 23° the mean depth of the coat was $12 \cdot 2$ mm, and that when piloerection had occurred in response to cold the mean depth was $23 \cdot 3$ mm. Table 4 also shows the insulation of the coat in the different environments. Insulation increased from $5 \cdot 5 \times 10^{-3}$ to $7 \cdot 7 \times 10^{-3}$ °C/kcal m² 24 h, that is a gain of $2 \cdot 2$ units of insulation occurred for an increase in coat depth of about 11 mm. The insulation of still air such as that in a blanket or a wool cloth is about 10×10^{-3} °C/kcal m² 24 h cm. Comparison with the results with calves shows that the insulation of an unerected coat in the calf is about half that of still air, and that the additional insulation provided by piloerection is only about one-fifth of the insulation of a still-air barrier. The low efficiency of the insulation of the hair coat when erected can be accounted for in part by the physics of radial heat flow and the increase in surface area when the coat is erected (Blaxter, Graham & Wainman, 1959). It seems, however, that considerable natural convection must occur in erected coats.

Insulation of the tissues. The mean insulation of the tissues in the cold was $4 \cdot 4 \times 10^{-3}$ °C/kcal m² 24 h and fell to $1 \cdot 8$ units at 23°. These values may be compared with those obtained with adult cattle. In the cold the tissue insulation of steers was $6 \cdot 7$ units and in warm conditions $2 \cdot 0$ units. The comparison suggests that the young calf is less well insulated than the adult steer. The same increase in insulation with age is seen in pigs which at birth have tissue insulations in the cold which can be calculated to be $1 \cdot 0 \times 10^{-3}$ °C/kcal m² 24 h (Mount, 1959) and in adult life of $7 \cdot 0 \times 10^{-3}$ °C/kcal m² 24 h (Irving, Peyton & Monson, 1956). The higher values in adult steers than in calves may reflect the greater thickness of the skin of adult animals and their greater amount of subcutaneous fat. On the other hand, control of the blood supply to the skin may be better developed in the older animal. The regression of tissue insulation on age was

$$I_T = 2 \cdot 68 + 0 \cdot 15t, \tag{7}$$

which was statistically significant. This suggests that one of the main reasons why the overall resistance to cooling of the calf increases with age and why its critical tempera-

ture simultaneously falls is because its tissue insulation increases. This phenomenon seems likely to be due to changes in the blood supply to the skin rather than to morphological changes in skin thickness which could hardly change so rapidly with age.

Oxygen consumption and temperature measurements during experimental cooling. Fig. 1 shows the results of a series of experiments with calf D, given 4 l. milk, at ages of 1, 5, 10 and 13 days in which oxygen consumption was measured over hourly intervals during cooling. The results show that oxygen consumption was minimal at temperatures between 18 and 29°. Above 29° metabolism increased slightly. Oxygen consumption also increased slightly when environmental temperature fell from 18° to 15° and more markedly when it fell still more to 11°. At temperatures of about 7° metabolism was reduced and then at still lower temperatures increased to values which in
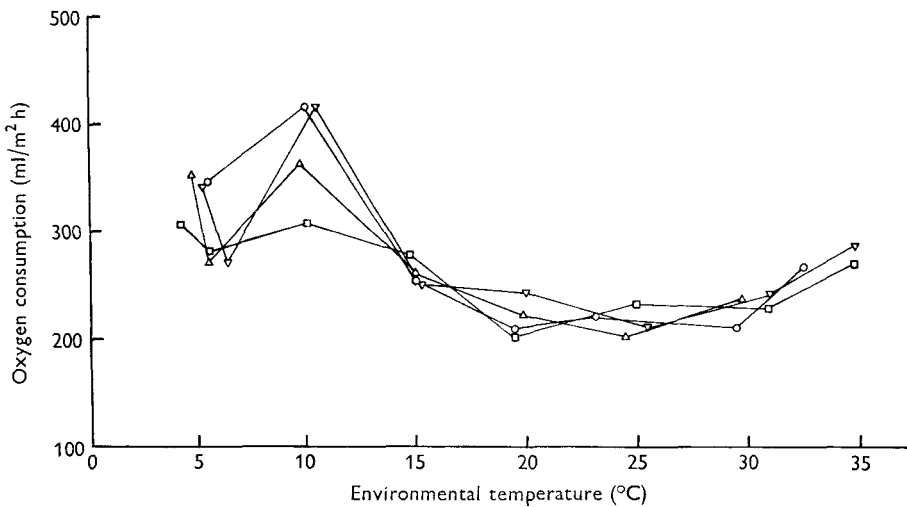

Fig. 1. Oxygen consumption of calf D during experimental cooling in four experiments on days 1 (○—○), 5 (□—□), 10 (△—△) and 13 (▽—▽) of life.

three instances were less than the peaks observed at 11°. Similar results were obtained with calf C when 21 and 25 days of age as shown in Fig. 2, but the events occurred at slightly lower temperatures. Calf C was older than calf D when the measurements were made and its tissue insulation was higher. Fig. 1 shows that a small increase in oxygen consumption occurred at 15°. It coincided with the onset of piloerection, and in each trial with each animal when piloerection commenced, the calf immediately rose to its feet. The increased oxygen consumption observed at 15° no doubt reflects in great measure the increase in metabolism due to standing. Shivering began at about 10–11° in calf D and it appears from Fig. 1 that some overcompensation for previous cooling occurred, in that oxygen consumption was greater at 10–11° than at lower temperatures. Fig. 2 shows that with calf C the temperature corresponding to this elevation was lower. This same phenomenon of overcompensation of the metabolic response to cold during experimental cooling was observed in pigeons by Metz & Kayser (1948). Benzinger, Pratt & Kitzinger (1961) have also demonstrated

on 'overshoot' in the metabolic response of man to cold. The short-term measurements of oxygen consumption made at 3° showed that oxygen consumption was then the same as that measured during the 24 h periods. The above results indicate that the major response to cold is relatively abrupt and the temperature at which it occurs coincides with the critical temperature calculated from the heat production and resistance to cooling determined during periods of 24 h duration.

Peripheral cooling. During periods of cooling and also during observations at fixed temperatures, skin surface temperatures were recorded and mean values for calf D are given in Fig. 3. The surface temperatures of different sites responded very differently to cooling. For example, Fig. 3 shows that at temperatures below 10° the pattern of surface temperature was very different from that in warm environments. The values in
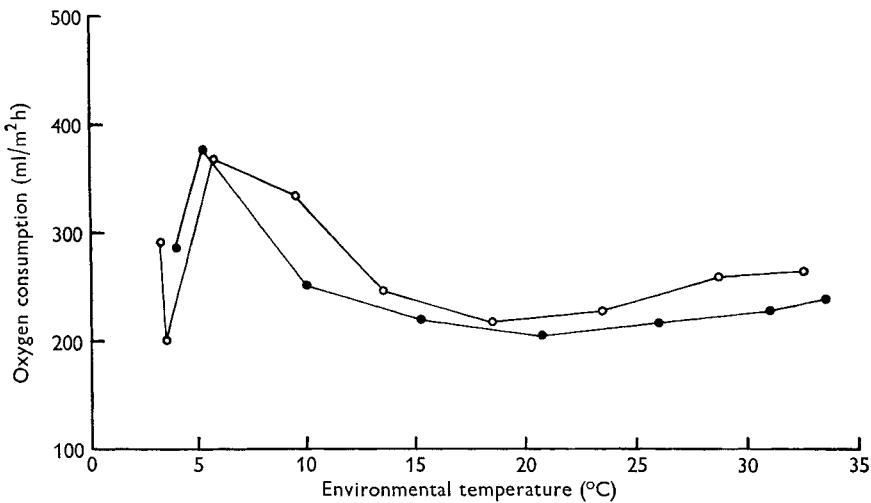

Fig. 2. Oxygen consumption of calf C during experimental cooling in two experiments on days 21 (○—○) and 25 (●—●) of life.

Fig. 3 can be analysed conveniently by computing the rate of change of skin or other body temperature with air temperature during different environmental temperature ranges defined by recognizable events occurring in the animal. Thus the beginning of piloerection in this calf occurred at 19°. It was apparently completed at 14°, and shivering began at the critical temperature of 10°. An environment between 20 and 30° was certainly thermoneutral and there was probably a little heat storage in the body above 32°. The results of the calculations are given in Table 5.

In the thermoneutral zone rectal temperature fell by 0·05 °C/°C fall in environmental temperature. This rate of fall was markedly reduced by piloerection and by constriction of the blood supply to the limbs (see p. 209). When shivering commenced the rectal temperature rose at the rate of 0·04 °C/°C fall in environmental temperature. This same phenomenon of an increase in rectal temperature at 'shivering point' has been noted in sheep (Blaxter, Graham & Wainman, 1959).

In the thermoneutral zone the surface temperature of the trunk fell at the rate of

0·2–0·3 °C/°C fall in environmental temperature. During piloerection this rate of fall was checked; in fact the temperature of the chest wall, which is well covered with hair, rose. Between the temperature at which piloerection was virtually complete and the shivering point, trunk surface temperatures fell at rates of 0·8 °C/°C fall in environmental temperature. These rates suggest that the blood supply to the skin was con-
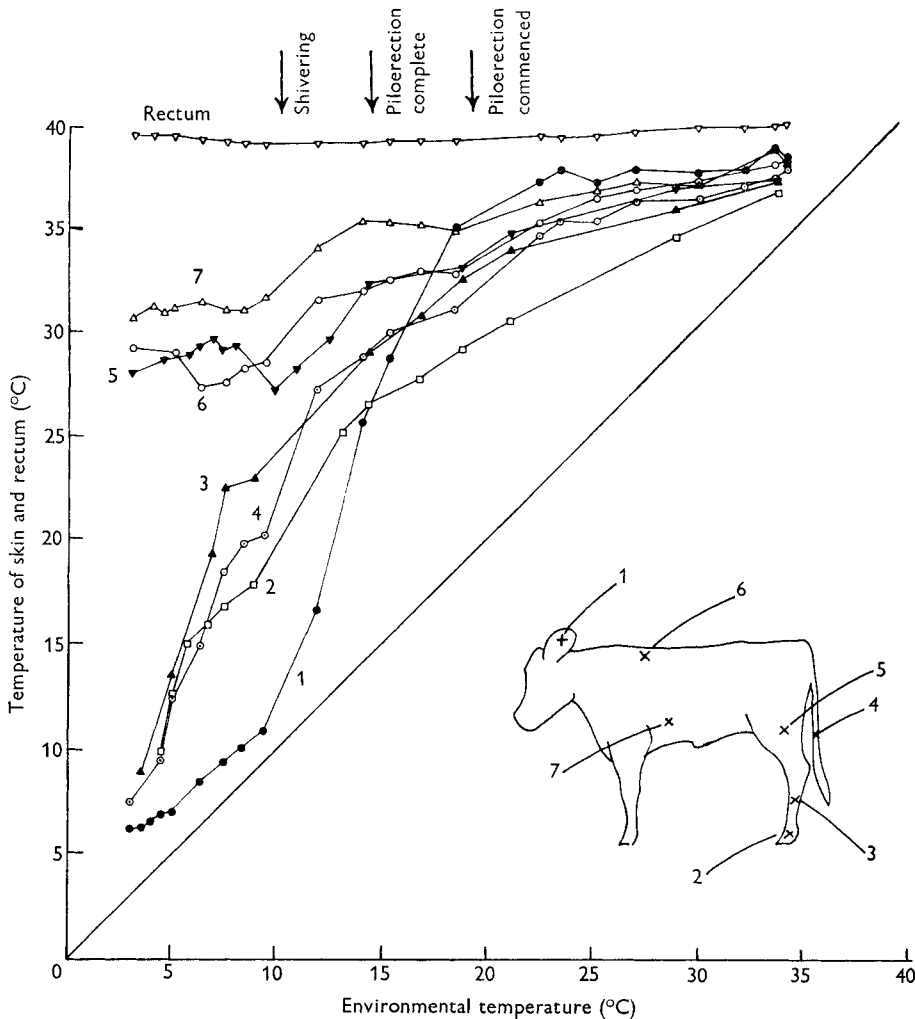

Fig. 3. Mean temperatures of the rectum and skin surfaces of calf D during experimental cooling. The positions of the thermocouples are marked in the diagram with numbers corresponding to the values shown.

siderably reduced. Below the critical temperature, the chest wall continued to cool at a very slow rate, but the temperature of the skin of the centre of the back rose. It is in this region that muscular activity in shivering is most severe, and a local gain of heat by the skin from heat produced in the muscles is understandable.

The skin surfaces of the hind limb also revealed a regular pattern of change. In the

thermoneutral zone, the rate of fall of skin temperature with fall of environmental temperature was greatest for the foot, and smallest for the thigh. During piloerection, the thigh cooled least, which is understandable because the coat on the thigh is thick and when erected provided considerable insulation. Between completion of pilo-erection and shivering, vasoconstriction occurred in the whole limb, including the thigh. The evidence for vasoconstriction in the limb is unequivocal because in every instance the rate of fall of skin temperature with falling environmental temperature exceeded 1 °C/°C. This vasoconstriction continued at temperatures below the shiver-ing point for the shin and foot, but the temperature of the thigh rose, this being accompanied by shivering of the underlying muscles. The rise in the temperature of

Table 5. *Rates of change of rectal and surface temperatures of calf D between different environmental temperatures* (°C *change in skin temperature*/°C *decrease in environmental temperature*)

Site of measurement	In thermo-neutral zone, 20°–35°	During piloerection, 14°–19°	From completion of piloerection to critical temperature (shivering point), 10°–14°	Below critical temperature, 3°–10°
Rectum	−0·05	−0·02	0·0	+0·04
Trunk:				
Centre of back	−0·23	−0·16	−0·75	+0·03
Thorax wall	−0·31	+0·12	−0·85	−0·02
Limbs and extremities:				
Muscular part of thigh	−0·36	−0·22	−1·25	+0·01
Shin	−0·38	−0·76	−1·20	−2·70
Foot (pastern)	−0·73	−0·58	−1·69	−1·59
Tail	−0·48	−0·48	−1·95	−1·91
Ears	−0·25	−1·90	−3·35	−0·86

the trunk surface and the limb root surface at the onset of shivering has also been observed in sheep in long-term experiments (Blaxter, Graham & Wainman, 1959). The tail responded in a very similar way to the foot. The ear, however, showed a fall in its surface temperature characteristic of vasoconstriction at the time piloerection com-menced. The temperature of the skin of the ear immediately before vasoconstriction occurred was 35°. Vasoconstriction of the tail did not occur until its surface tempera-ture was 27°, and vasoconstriction of the foot did not occur until its surface temperature was 25°. The initial constriction of the blood vessels underlying different surfaces of the body occurred at quite different environmental temperatures and surface tempera-tures. The neural control mechanisms involved in physical temperature regulation in response to cold can be inferred from these differences to be complex.

DISCUSSION

The results obtained in these experiments show that in early life calves given an allowance of milk which is about 10 % of their body-weight have a critical temperature of 13° and that this critical temperature falls to about 8° when the animal is 3 weeks

old. With 6 l. milk the critical temperature in the 3rd–4th week of life is about 7°. The environment in which these measurements were made had a low air movement, a low humidity (50 % saturation), and its radiant temperature was the same as the ambient temperature. These characteristics of the environment other than air temperature are similar to those found inside most animal houses and so estimates of the critical temperature of calves obtained in the respiration chamber are applicable to buildings for calves. It appears from this study and work reviewed by Bianca & Blaxter (1961) that the young calf is considerably more sensitive to cold than either the adult cow or the steer. It can be argued that the optimal environmental temperature in a calf house is one which causes the calf minimal discomfort, and it can be argued that piloerection and vasoconstriction are evidence of discomfort. Calves are kept for economic reasons, however, and discomfort is only of economic importance if it leads to a reduction in productivity. There is no reason to suppose that the physiological responses of pilo-erection and initial vasoconstriction lead to any significant decline in productivity. It is true that in short-term experiments at the onset of piloerection the calf rises to its feet, which results in a small increase in energy expenditure as measured by oxygen consumption. The calf subjected to continued cold, however, does not continue to stand, and 24 h measurements of metabolism in calves which had erected coats in an environment of 13° showed that any elevation in metabolism over that measured at 23° (an environment which evokes no defence mechanisms to cold) was negligibly small. It does not seem reasonable therefore to take as the lower limit of the comfort zone that environmental temperature at which physiological mechanisms of defence against cold come into operation. Rather the lower limit should be that at which increases in heat production and in consequence declines in energy retention occur. This means that the lower limit of optimal temperature in a calf house should be 13° (55 °F).

The studies of metabolism, temperature and insulation in cold environments show the relative importance of the various thermoregulatory responses made by the calf. Firstly, the calf has a temperature sense similar to what Benzinger (1960) has termed the 'Pavlovian temperature sense' of man. Thus in all the experiments in which the animal was cooled, the immediate voluntary reaction to an environmental temperature inducing piloerection was for the calf to stand. Similarly, in acute cold the animal's posture on lying was very typical, the limbs being tucked under the body, the tail held close to the side and the head buried in the flank. This posture was rarely observed at environmental temperatures of 23°. These are behavioural responses to cold, similar to man's search for shelter and his adjustment of clothing. Secondly, piloerection in these calves resulted in an increase of 40 % in the insulation provided by the hair coat. This is considerably less than the gain of insulation to be expected on theoretical grounds and it seems likely that the sparse hair fibres in the erected coat allow some free convection within the coat. Thirdly, the constriction of the blood vessels of the skin appeared to enable the calf to withstand a fall in environmental temperature of about 4° before it began to shiver. The whole range of physical temperature regulation in response to cold, commencing with piloerection and constriction of the blood supply to the ears and ending at the onset of shivering, appeared to be about 8°, that is from 19° to 11°. Finally, shivering when it occurred appeared to overcompensate at first for

the increased heat demand of the environment. This, as previously noted, is a phenomenon also seen in man and in pigeons. There is also evidence of some overlap of vasoconstrictor responses. Thus the limbs continue to cool at rates so high that they must imply a vasoconstriction even when the 'chemical regulation' of shivering has taken place.

These responses to cooling obtained in the respiration apparatus are probably those which occur under farm conditions in poorly insulated buildings on cold nights. Whether the responses become more highly integrated with continued cooling, that is whether there is an acclimation to cold, is not known. From the experiments described, in which the same animal was cooled at intervals, however, no such acclimation was observed. On the other hand, the increase in the overall resistance to cooling and in particular the increase in the insulation of the tissues with increasing age might indicate that some acclimation occurred. The effect of age was not separated from that of any possible acclimation in these experiments.

SUMMARY

1. Forty-three calorimetric experiments were made with four Ayrshire calves in which heat production and heat losses were determined at different environmental temperatures. Six experiments were also made in which oxygen consumption was determined during the cooling of the respiration apparatus from 30° to 3°.

2. Measured in the thermoneutral zone during the 11th to the 29th day of life, the metabolizable energy of cow's milk was 95 % of the gross energy, and the net availability of the metabolizable energy 77 % in one calf and 82 % in another.

3. Heat production per unit surface when measured at environmental temperatures of 23° and of 3° declined with age. The mean decline was about 1 % per day.

4. Heat losses due to vaporization of water were 344 kcal/m² 24 h at low environmental temperatures, and invariant with the amount of food consumed. Sensible heat losses per unit surface declined with age, and the cooling resistance of the calf increased from values of $16 \cdot 1 \times 10^{-3}$ °C/kcal m² 24 h on the 1st day of life to $21 \cdot 2 \times 10^{-3}$ °C/kcal m² 24 h at 20 days of age.

5. The critical temperature of calves given 4 l. milk daily was $12 \cdot 8$ ° on the 3rd day of life and declined to $8 \cdot 2$° on the 20th day. For those given 6 l. milk daily the critical temperature was not below 7–8° despite the higher heat production.

6. The insulation of the air-interface was $6 \cdot 0 \times 10^{-3}$ °C/kcal m² 24 h, and invariant with the environmental temperature. The insulation of the hair coat was $7 \cdot 7 \times 10^{-3}$ °C/kcal m² 24 h when erected and $5 \cdot 5 \times 10^{-3}$ °C/kcal m² 24 h when unerected. Measurements of tissue insulation in the cold and in warm conditions showed that it was initially considerably below adult values and increased with increasing age. It is thought that this pattern reflects an immaturity of vasoconstrictor responses to cold.

7. Overcompensation of the metabolic response to cold was observed during experimental cooling. The first response to cold was piloerection associated with constriction of the blood supply to the ears which was followed by vasoconstriction of the limbs. Constriction of the blood vessels of the limbs was not complete when shivering began.

8. The results are discussed in relation to the design of calf houses and it is concluded that the temperature of calf houses should not be allowed to fall below 13° (55 °F).

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