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THE ENERGY COST OF REPRODUCTION IN SHEEP

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Much has been written on different systems of feeding for pregnant and lactating ewes; the subject has been reviewed by Guyer & Dyer (1954) and by Thomson & Aitken (1959). Very little work has been done, however, on the energy *cost* of pregnancy and lactation in the ewe, apart from that of Ritzman & Benedict (1931) and of Brody (1938).

In the present experiment the energy expenditure of a group of Blackface ewes during pregnancy, parturition and lactation was compared with that of a similar group of reproductively inactive ewes. The energy expenditure was measured by direct calorimetry. An account of the heat output during parturition of two Swaledale ewes has been published previously (Brockway & Pullar, 1961).

METHODS

Animals. 5- to 6-year-old Scottish Blackface ewes were used for this experiment. Little was known of their previous history, but they had certainly all borne lambs in previous years. Three ewes were mated to a ram of the same breed at approximately 14-day intervals in late October and November 1961. Three similar ewes were selected as non-pregnant control animals.

Housing. Mating took place out of doors, but immediately afterwards the ewes were moved into indoor accommodation. This consisted of three pens each about 8 ft. (2·5 m) square and centrally divided by a wire mesh partition. Each pen housed one pregnant and one non-pregnant ewe. Ambient temperature was thermostatically maintained at 10° C, while the relative humidity was generally in the range 50–60 %. Lighting was artificial, by electric bulbs switched on and off to simulate the day length appropriate for the time of year.

Feeding. Both pregnant and non-pregnant ewes were offered the same amounts of food throughout the experiment. Water was available *ad lib.* The ration of food was 600 g hay per day, given in two meals, at 8.30 a.m. and 5.00 p.m., and 250 g concentrate mixture, consisting of 2 parts linseed cake meal and 1 part crushed oats, given at noon. About 3 weeks before lambing was due the concentrate allowance was increased to 500 g per day. This increase was also given to the control ewes. The initial daily intakes of crude protein, and the gross energy, were approximately 120 g and 3300 kcal respectively. These increased to 180 g and 4500 kcal after the ration of concentrate mixture was doubled. The energy available to the ewes would be about half the gross intake. Except in the first few weeks after mating the pregnant ewes always ate all the food offered to them; frequently the non-pregnant animals did not consume all the hay, but generally they ate all the concentrate mixture.

Calorimetry. All measurements of heat loss were carried out in the large gradient-layer calorimeter described by Pullar (1958). The animal chamber of this calorimeter has a floor space of 5 ft × 4 ft. (1·5 m × 1·2 m) and no form restraint of was imposed on the sheep. The ambient temperature in the calorimeter was 10° C and the relative humidity of the incoming air was 50 %. A cycle of artificial lighting similar to that in the pens was in operation. Preliminary training measurements were made on each ewe to accustom her to the experimental conditions. From the time of mating onwards measurements of heat loss were made on each ewe at intervals of approximately 3 weeks. Each measurement lasted just under 24 hr. During these measurements the ewes appeared to behave normally, and ate amounts of food similar to those consumed when not in the calorimeter.

RESULTS

Body weights. Table 1 shows the body weights of the individual animals at various stages of the experiment. The mean body weight of each group of ewes and of the lambs is shown in Fig. 1. No differences are apparent in the mean body weights of the two groups of ewes in the first 3 months of gestation. At the time of parturition of the pregnant ewes the mean body weight of the non-pregnant group was the same as it had been at the start of the experiment; in the following 2 months on the increased ration of concentrate these ewes gained about 3 kg.

TABLE 1. Body weights (kg) of sheep. Ewe *F* gave birth to twin lambs

	Non-pregnant control ewes			Pregnant ewes			Lambs			
	A	*B*	*C*	*D*	*E*	*F*	*d*	*e*	f_1	f_2
At mating	40·5	50·5	55·4	41·8	45·9	54·5	—	—	—	—
100 days antepartum	41·4	50·5	54·1	42·7	48·2	54·5	—	—	—	—
50 days antepartum	39·5	49·5	50·9	45·5	50·5	59·5	—	—	—	—
At term	42·3	51·4	52·3	52·3	54·5	70·9	—	—	—	—
1 day post-partum	—	—	—	43·6	48·6	56·8	4·6	4·4	2·9	3·2
50 days post-partum	44·5	53·6	56·8	38·6	40·0	46·8	13·4	16·4	7·4	11·4

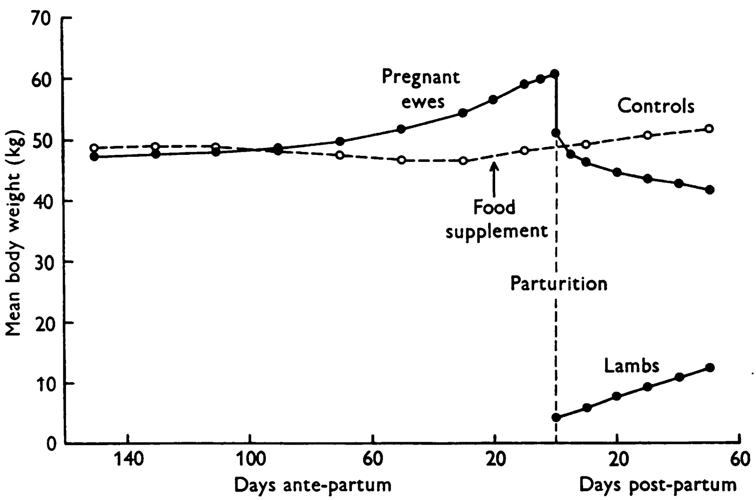

Fig. 1. Mean weights of ewes and lambs.

Course of pregnancy. The course of pregnancy was uneventful for all the ewes, the gestation period being 144 days for ewes *E* and *F* and 148 days for ewe *D*. Ewes *D* and *E* gave birth to single lambs and ewe *F* to twin lambs. Ewe *D* required mild obstetrical assistance in the final stages of parturition. The head of the lamb was delivered by the ewe but a mal-presentation of the forelimbs of the lamb required correction. The other two ewes delivered their lambs unaided. All the lambs were healthy and able to suck a short time after birth.

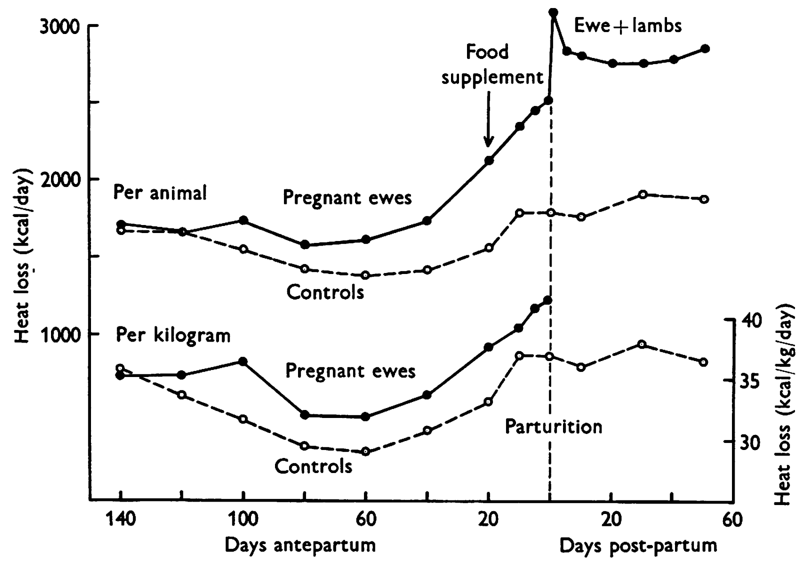

Fig. 2. Mean heat losses during pregnancy and lactation.

Heat output during pregnancy. For the first month after mating the heat outputs of the pregnant and non-pregnant ewes were similar; thereafter the pregnant animals had a higher rate of heat loss than did the non-pregnant ones. In Fig. 2 the mean heat losses of each group are shown on a 'per animal' basis, and on a 'per unit weight' basis. The heat loss from the control animals declined during the first 3 months of the experiment. This decline was not associated with any obvious reduction in activity, and the heat output of the control ewes rose again after the first 3 months; it is noteworthy that this rise began *before* the ration of concentrate mixture was increased. These variations in the heat loss by the control animals are probably due to a seasonal rhythm.

On a 'per animal' basis the pregnant ewes showed a steady rate of heat loss for the first 3 months of gestation, after which it increased steadily until term. When these heat losses are expressed 'per unit body weight' the picture is somewhat altered in the first half of pregnancy when, after an initial constant period, a decline in heat loss occurred between the 6th and 11th week of gestation.

Heat output at parturition. Each ewe was kept in the calorimeter before, during and after parturition for as long a continuous period as was administratively possible. Figure 3 shows the heat losses of the three ewes at parturition. Heat losses in this figure are on a 'per animal' basis and the calorimeter records were integrated over 6-hr periods, except near the time of delivery, when shorter intervals were measured.

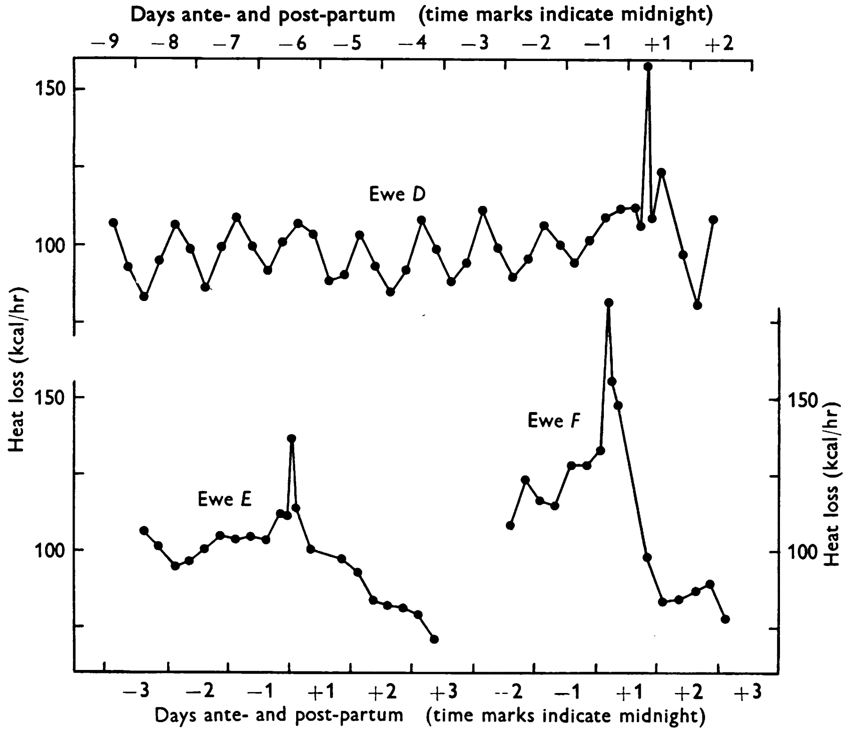

Fig. 3. Heat losses of the ewes at parturition. The estimated heat losses of the lambs after parturition have been subtracted from the measured totals.

The records of heat loss during the actual delivery of the lambs were similar in the two cases where this was accomplished without assistance. The heat loss showed a very steep rise up to a maximum (this phase occupied only 5–10 min) followed by a slower decline which flattened out at about the original level 90 min after the first sudden increase.

Ewe *D* was in the calorimeter for 8 days immediately before lambing. Her heat output showed a well defined diurnal rhythm in this period. This rhythm was abolished about 18 hr before the birth of the lamb, when the rate of heat loss increased and was irregularly maintained at about 110 kcal/hr until parturition occurred. In the 90-min period which included the delivery of the head of the lamb (at about two thirds of the way through this period) the rate of heat loss rose to 158 kcal/hr. This figure is the total heat loss measured. As well as the metabolic rate of the ewe it includes the heat losses in the cooling of amniotic fluids, of the lamb's head and any metabolic heat loss from the delivered head. About half an hour after the birth of the head it was apparent that without assistance the ewe would be unlikely to deliver successfully a live lamb. Consequently the calorimeter was opened and the lamb was delivered by hand. The calorimeter was immediately closed again but about 1 hr's measurement of heat output was lost. Six hours later the calorimeter was opened, the ewe removed and the rate of heat loss of the lamb only was measured for a 2-hr period. The ewe was then returned to the calorimeter and the combined heat losses of ewe and lamb were measured for a further 16 hr, after which another 2-hr measurement of the heat loss of the lamb was made.

Continuous measurements of the heat loss from ewe *E* were made over the 60 hr, and from ewe *F* over the 36 hr, immediately preceding parturition. No distinct diurnal rhythms can be seen in these cases, possibly because of the relatively short period of measurement uncomplicated by the onset of labour. During the final 18 hr of gestation the rate of heat loss from ewes *E* and *F* was 105 kcal/hr and 130 kcal/hr, respectively. In the 90-min periods which included the actual deliveries the heat losses rose to 140 kcal/hr for ewe *E* and 187 kcal/hr for ewe *F*. These maximum rates are for the heat loss due to the metabolism of the ewes and for that due to the cooling of placenta, amniotic fluids and lambs, but do not include the heat loss due to the metabolism of the lambs. This was deducted from the total recorded heat loss by extrapolating back to the time of birth the subsequently measured rate of heat loss of the lambs alone. This extrapolation may not be fully justifiable, because of rapid change in metabolic rate during 6–24 hr after birth (Dawes & Mott, 1959), but the error involved is probably small. In all, three 2-hr measurements of the heat loss of the lambs from each ewe were made in the first 60 hr after the births, the remainder of these periods being devoted to measurements of the combined heat losses of ewe and lamb.

Heat losses from lambs. These are shown in Table 2. Each measurement was made over a 2-hr period. In the case of the twin lambs '*f*', the mean value from a combined measurement of heat loss, is given. There was no obvious explanation for the apparently low values of the first two measurements on lamb '*e*'. The discrepancy might be explicable in terms of the rise in metabolic rate which occurs in the first day after birth (Dawes & Mott, 1959).

It had originally been intended to continue making separate measurements of the heat loss of each lamb until it was weaned, but after the first 2 days the behaviour of both ewes and lambs was noticeably abnormal during separation and the sum of their separately measured heat losses far exceeded the figure found during measurement of their combined losses. Such measurements were therefore discontinued.

TABLE 2. Heat loss of lambs

Time after birth (hr)	Heat loss kcal/lamb/hr			Heat loss kcal/kg/hr		
	d	*e*	*f*	*d*	*e*	*f*
6–12	37·9	23·4	25·6	8·2	5·3	8·4
24–34	32·2	25·9	24·4	7·5	5·3	7·3
51–58	—	34·2	26·3	—	7·0	7·4

TABLE 3. The heat losses in reproduction

	Mean heat loss per ewe (Mcal)* Pregnancy (145 days)	Lactation (50 days)	Total
Pregnant ewes	255·5	136·5	392
Control ewes	216·0	90·0	306
Difference	39·5	46·5	86

* 1 Mcal = 10^6 cal.

Heat losses during lactation. Measurements of heat loss were made on each ewe with her offspring at approximately 10-day intervals throughout the first 2 months of lactation, that is until about the beginning of weaning. The mean heat output of the lactating ewes was about 2800 kcal/day (Fig. 2). During this period the lactating ewes were losing weight while the control animals were gaining weight (Fig. 1) and had a heat loss of 1800 kcal/day.

Increase in heat loss due to reproduction. Integration of the areas beneath the curves for the heat losses of the pregnant and non-pregnant ewes provides figures for the total energy expenditure of each group and for the additional energy expenditure required for reproduction. These figures are given in Table 3.

DISCUSSION

In direct calorimetry heat loss is measured: this is equivalent to heat production, or metabolic rate, after making any necessary corrections for changes in body weight and temperature. Except at the time of delivery these remained virtually constant within the course of each measurement.

The over-all picture of the results presented here is similar to that reported by Ritzman & Benedict (1931) and by Brody (1938) if allowance is made for the differences in the body weights of the animals concerned. When expressed per unit body weight the heat output of the pregnant ewes was constant during the first 6 weeks of gestation. During this period the corresponding heat output of the non-pregnant ewes fell. There was therefore a relative increase in the heat production per unit body weight of the pregnant animals during the first third of pregnancy. Morrison (1956) described a somewhat similar situation in the rat. In the second third of pregnancy the heat output per unit body weight fell to a level which, although low in relation to the heat output at the start of the experiment, was, in fact, above the contemporaneous level of heat output of the non-pregnant control ewes on the same weight basis. Rowe & Boyd (1932) reported that in human beings there is a decline in metabolism in the third and fourth month of pregnancy. More recently Gur'janova (1959) has published figures for the oxygen consumption of pregnant heifers. These figures suggest that the metabolic rate was either constant or rose slowly through the first 9 months of the 9½-month pregnancy.

The area between the curves in Fig. 2, equivalent to 86 Mcal, provides an estimate of the additional energy cost to the ewe of bearing and rearing her offspring. From the point of view of animal feeding this figure represents the additional requirement of metabolizable energy. Brody (1938) made similar calculations: his results suggested that the additional cost of pregnancy in his ewes was 23 Mcal, but he concluded, 'We suspect that our heat increments of gestation in sheep are for some reason too low'. The difference between the 39·5 Mcal suggested here (Table 3) and the 23 Mcal suggested by Brody lies, not in a differing estimate of the heat output of the pregnant ewes, but in the differing base lines from which the ensuing calculations were made. The base line used by Brody was drawn parallel to the abscissa at the level of heat output at the time of mating. Inspection of Fig. 2 shows that if such a procedure had been adopted here the energy cost of pregnancy would have been only about half of that found by integrating the whole area between the curves. The major source of inaccuracy in our estimate lies in the period after parturition, when the control ewes were gaining and the lactating ewes losing weight. Any changes in feeding régime intended to prevent these changes in weight would lead to an increase in the measured additional energy cost of lactation.

The measurements of heat loss during parturition presented here support those published previously (Brockway & Pullar, 1961). The rate of heat loss in the 18-hr period preceding delivery is increased by about 10–15 kcal/hr over earlier levels, that is an additional 200–250 kcal is expended during this period. This increased level of heat output is not wholly accountable in terms of obvious activity, and, although there is undoubtedly some restlessness at this stage, overt signs of labour are not apparent until 1½–3 hr before delivery (Thomson & Thomson, 1949). As it proved to be impossible to carry out accurate weight balances on the ewes at the time of parturition the metabolic component of the heat loss cannot be separated from the purely physical component (due to the cooling of the delivered contents of the uterus) during the 90-min period which included the actual delivery. The mean heat loss in this 90-min period was 238 kcal; the heat loss in a typical 90 min before delivery would be 169 kcal. The actual figures for ewes *E* and *F* from this experiment and for the two Swaledale ewes (nos. 1 and 2) in the previous experiment (Brockway & Pullar, 1961) are shown in Table 4. The excess heat loss at delivery, 69 kcal, includes any additional

TABLE 4. Excess heat loss at delivery

Ewe	Heat loss in 90 min at delivery (kcal)	Heat loss in 90 min before delivery (kcal)	Excess heat loss at delivery (kcal)
E	210	158	52
*F**	273	195	78
1†	210	165	45
2*†	257	158	99
Mean	238	169	69

* Twin lambs. † Brockway & Pullar (1961).

metabolic output from the ewe, the cooling of the placenta and amniotic fluids from the deep body temperature of the ewe to calorimeter temperature (38–10° C) and a component due to a decrease in the mean body temperature of the lamb at delivery. The magnitude of these separate factors is difficult to estimate, but it seems probable that the purely physical factors account for as much as half the total excess heat loss at delivery. Thus it would appear that most of the muscular effort of labour had been accomplished in the preceding period and that even then the effort involved was slight. There is very little information in the literature on the energy expended during labour in other species, and what there is is confined to human subjects. Stähler (1936), Sampson, Rose & Quinn (1945) and Gemzell, Robbe, Stern & Ström (1957) measured oxygen consumption, and found that in the normal labour of multiparae it was indicative of moderate physical work. Pardee & Mendelson (1941), Brown, Sampson, Wheeler, Gundelfinger & Giansiracusa (1947) and Hendricks & Quilligan (1956) came to a similar conclusion from their studies of the circulation during normal labour and parturition.

The rate of heat loss of the lactating ewes could not be measured separately from that of their lambs except on the first 2 days after delivery. During that period the mean heat loss of the lactating ewes was about 42 kcal/kg/day, a figure in close agreement with that given by Ritzman & Benedict (1931). The values given here for the combined heat losses of ewe and lamb are in contradiction to the findings of Carpenter & Murlin (1911) who found that, in human subjects... 'the curve of total energy production of mother and child suffers no deflexion at birth'. The difference here may be in part due to the differing ambient conditions under which the measurements were made, and partly a reflexion of the different states of development of new-born lamb and baby.

As the lamb is solely maintained by the ewe until the time of weaning their combined heat losses are an indication of the ewe's requirement for metabolizable energy during this time. The figure reported here, 136·5 Mcal for 50 days, does not include the energy retained in, nor that excreted by, the growing lamb and is insufficient to maintain the ewe's body weight at its pre-mating level: this is presumably physiologically desirable but may be economically impracticable.

SUMMARY

1. The heat losses during pregnancy, parturition and lactation of three ewes were measured by direct calorimetry and compared with those of three similar but reproductively inactive ewes over the same period of time.

2. During pregnancy the ewes expended 39·5 Mcal more energy than did the non-pregnant animals.

3. The additional energy cost of labour and parturition was about 200–300 kcal.

4. In 50 days the lactating ewes lost 46·5 Mcal more heat than did the non-lactating animals.

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