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The Effects of Heat Stress on the Development of the Foetal Lamb

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Abstract

Environmental heat stress in tropical sheep suppressed lamb birth weight, but the animals which did not experience hyperthermia under natural environmental conditions gave birth to significantly heavier ($P<0\cdot01$) lambs than their less adapted counterparts. Climate chamber studies designed to simulate the rectal temperature patterns of tropical sheep demonstrated that, without nutritional intervention, heat stress during the last month of pregnancy significantly retarded foetal growth (birth weight 2·3 kg *v.* 3·4 kg; $P<0\cdot01$) and maturation of wool follicles ($P<0\cdot01$). By comparison, severe nutritional restrictions during the last 3 months of pregnancy also caused a significant reduction in lamb birth weight (3·2 kg *v.* 3·9 kg; $P<0\cdot01$), but this difference was not so marked.

Introduction

Work on the influence of maternal hyperthermia in suppressing lamb birth weight was pioneered by Yeates (1958) and continued in climate chambers by numerous workers (see Cartwright and Thwaites 1976*a*, 1976*b*). Yeates concluded that some process associated with heat other than undernutrition was involved in the foetal dwarfing syndrome. The subsequent studies of Cartwright and Thwaites ascribed all the reduction in size and weight to nutritional effects. The present study was designed to align these general findings to the practical situation. It is known that where sheep in Australia experience high environmental temperatures and solar radiation loads during pregnancy, there is a high incidence of lambs of low birth weight and high lamb mortalities (Moule 1954; Rose 1972).

In this paper we attempt to provide some practical evidence of the effects of maternal hyperthermia on lamb birth weight, and compare the effects of heat stress with those of poor nutrition as determinants of foetal development. Firstly, the effects of a tropical summer climate on the rectal temperatures of pregnant ewes, and the influence of this heat stress on lamb birth weight and subsequent wool production are described. Next, the effects of heat stress on lamb development are assessed when the natural rectal temperature patterns are simulated in climate chamber conditions and animals are pair-fed to dissociate nutritional factors from the effects of heat stress on lamb development. Finally, pen-feeding studies designed to ascertain further the effects of poor nutrition during the last 3 months of pregnancy on lamb birth weight are described.

Materials and Methods

These experiments were conducted at the 'Toorak' Research Station in tropical north-western Queensland (long. 142°E., lat. 21°S.). Mean monthly temperatures are 35°C or higher for 6 months of the year. The vast plains offer little shade protection from the intense solar radiation loads of summer (4300 $KJ/m^2/h$).

All sheep used in these experiments were adult Peppin Merinos. The stage of pregnancy (accurate to ± 1 day) was determined by using harnessed rams at the time of joining (Radford *et al.* 1960). Lamb weights were measured as soon as the birth coat was dry.

Field Studies

Sixty-four ewes were joined in spring and their lambing performance for the subsequent two years was recorded. These ewes had in previous years been joined in autumn, thus any effects of previous pregnancies were minimized. Rectal temperatures were recorded for 10 days in January after the second year's joining, when the daily maximum temperature ranged from 37° to 43°C. The method of measuring the rectal temperature of sheep under environmental conditions has been described previously (Hopkins *et al.* 1978). The mean monthly maximum temperatures experienced during the last 4 months of gestation varied from 34 to 37°C in the first year and from 33 to 41°C in the second year. The rectal temperatures of a random sample (seven) of the newborn lambs of the second drop were measured during exposure to the environment.

Greasy fleece weights and body weights of the offspring were recorded until maturity. Since greasy fleece weight (GFW) values at $2\frac{1}{2}$ years are closest to life-time means (Brown *et al.* 1968; Rose 1974), GFW at about 26 months was taken as representative of mature values. However, to avoid any confounding effect from lambing, GFW values of female offspring at about 14 months were used for studying relationships with ewe rectal temperature.

Animal House Studies

Twenty-two pregnant sheep were stratified into two groups (heated and control) on the basis of body weight at 115 days' pregnancy. Animals in the heated group were placed in a climate room on day 117 of pregnancy and subjected to heat stress in order to raise the rectal temperature to *c.* 40°C. The elevated rectal temperatures (recorded daily) were maintained for 16–17 h each day during the last month of pregnancy. These diurnal temperature patterns were not markedly different from those exhibited by non-fasted sheep exposed to solar radiation during the summer months in this environment (Hopkins *et al.* 1978). The control animals were maintained at normal winter room temperatures in an animal house. The heat-stressed ewes were offered 1500 g lucerne pellets per head daily, and the average amount eaten was fed to the control ewes the following day. Body weights were recorded at 120, 130 and 140 days' gestation.

A further 12 ewes were studied more intensively. Hysterotomies were performed on these at day 110 of pregnancy to determine foetal foreleg length (olecranon process-distal extremity of hoof) and to collect a midside sample of foetal skin. These animals were then stratified into heated and control groups on the basis of foetal foreleg length, and pair-fed throughout the remainder of pregnancy.

Base-line temperatures and respiratory rates were recorded for all animals for three consecutive days immediately before heating. These measurements were then continued three times a week until lambing. Lamb birth weights and gross anatomical measurements were recorded (foreleg length, thorax girth, crown–rump length). Midside skin samples were collected from lambs in the intensively studied group for assessment of wool follicle development.

Pen Studies

Fifty pregnant sheep were divided at random into two groups, and fed at a high and a low plane of nutrition respectively during the last 78 days before lambing. From 70 to 110 days' pregnancy, these sheep were run in suitably grassed paddocks according to their group's nutrition status. The animals were then held in two large pens and fed on lucerne hay either *ad lib.* or on a restricted basis. The restricted intake group received 500 g daily from 110 to 125 days' pregnancy, and 900 g daily from day 125 through until term. Ewe body weights were recorded fortnightly, and lamb weights were measured at birth. These studies were done during the winter to obviate any influence of heat stress on lamb birth weight.

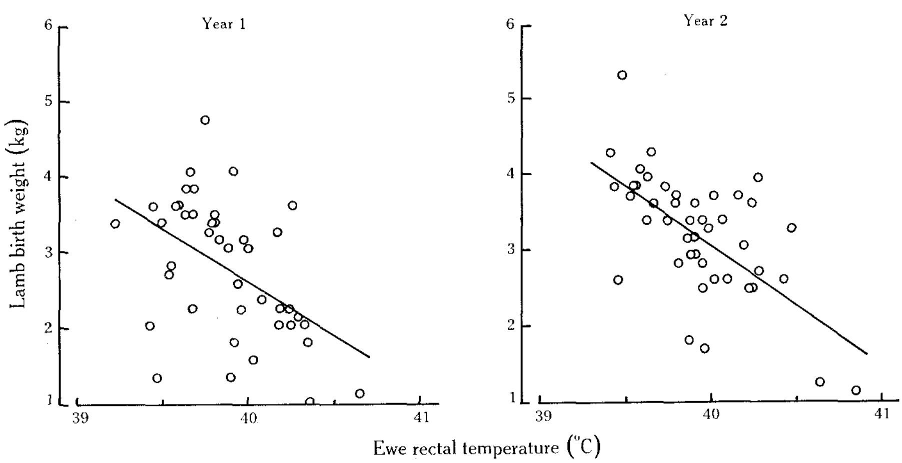

Fig. 1. Significant decrease ($P<0\cdot01$) in lamb birth weight with increasing rectal temperature of the ewe. Observations were made in consecutive years during exposure to the natural summer climate.

Results

Field Studies

There was a significant decline ($P<0\cdot01$) in lamb birth weight with increased ewe rectal temperature in both years ($1\cdot42\pm0\cdot39$ kg/°C; $1\cdot58\pm0\cdot30$ kg/°C, Fig. 1).

The mean rectal temperatures of ewes with various rearing performances are given in Table 1. The mean rectal temperature of ewes which did not rear a lamb (40·1°C) was significantly different from that of ewes which reared two lambs (39·8°, $P<0\cdot01$).

The least-squares mean birth weight of lambs which did not survive to marking (2·31 kg) was significantly different ($P<0\cdot01$) from that of lambs which survived to marking (3·30 kg); SE of difference, 0·18. The least-squares mean birth weights of lambs in the two years were significantly different ($P<0\cdot05$; 2·63 kg, 2·98 kg; SE of difference, 0·16).

Ewe rectal temperature (t, °C) explained 58% of the variance of GFW at 26 months for male offspring of the first drop. The addition of metabolic weight of the offspring to the regression did not significantly explain any more of the variance in GFW.

$$\text{GFW} = 55 \cdot 3 - (1 \cdot 27 \pm 0 \cdot 39)t \qquad (P < 0 \cdot 05).$$

Table 1. Mean rectal temperatures (°C), standard errors, and number of ewes (in parenthesis) in various rearing performance categories

		Year 1	
		Didn't rear a lamb	Reared a lamb
Year 2	Didn't rear a lamb	40·1 (19) ±0·08	39·9 (12) ±0·10
	Reared a lamb	39·9 (16) ±0·08	39·8 (17) ±0·08

Similarly, for the female offspring of the first drop, ewe rectal temperature explained 76% of the variance of the GFW at 14 months, but metabolic weight did not make any significant additional contribution (Fig. 2).

$$\text{GFW} = 59 \cdot 0 - (1 \cdot 39 \pm 0 \cdot 29)t \qquad (P < 0 \cdot 01).$$

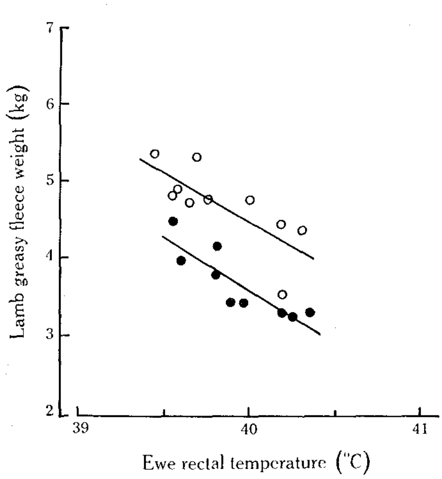

Fig. 2. Significant relationship ($P < 0 \cdot 01$) between ewe rectal temperature and the greasy fleece weight of male (○) and female (●) progeny at 26 and 14 months respectively. All measurements were made during exposure to natural climatic conditions.

For the male offspring of the second drop no significant relationships were established between mature GFW, metabolic weight and ewe rectal temperature. For female offspring 33% of the variance of greasy fleece weight could be explained by metabolic weight (Fig. 3).

$$\text{GFW} = 0 \cdot 20 + (0 \cdot 21 \pm 0 \cdot 08) W_m \qquad (P < 0 \cdot 05),$$

where W_m is the metabolic weight ($kg^{0 \cdot 75}$).

Rectal temperatures of 42°C were recorded in each of three 1-day-old lambs examined while they lay in the shade of a trough when ambient temperatures were

38–39°. Subsequently, four more lambs (3 days old) registered temperatures of 42–43° when ambient temperatures reached 41–43°.

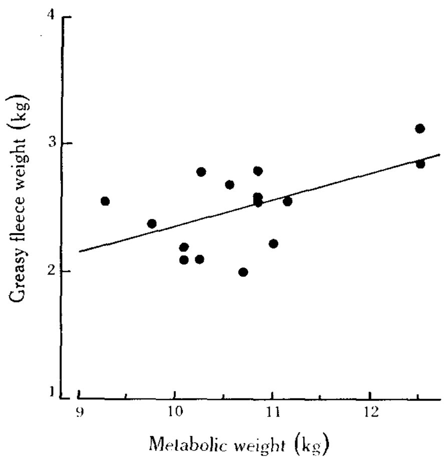

Fig. 3. Significant relationship ($P < 0 \cdot 05$) between the greasy fleece weight of weaner ewes (14 months) and their metabolic weight.

Animal House Studies

The mean (±SE) rectal temperature was 40·0°C (±0·07°) for heat-stressed ewes and 38·7° (±0·03°) for the control animals. Heat-stressed ewes had a mean respiratory rate of 188/min (±4·6), compared with the controls' 32/min (±1·2).

Heat stress did not have a detrimental effect on the well-being of the ewe, as shown by the liveweights and feed intakes listed in Table 2.

Table 2. Mean liveweights and feed intakes of ewes during the last month of pregnancy

	Groups (n = 17)	Stage of pregnancy (days): 115	120	130	140
Mean liveweight (kg)	Heated	37·4	37·8	38·4	39·2
	Control	37·7	37·1	38·2	39·0
SE		±0·4	±0·4	±0·3	±0·5
Mean daily feed intake (g)	Heated	960	985	970	925
	Control	945	980	965	915
SE		±35	±35	±32	±38

The average birth weight of lambs in the heated group was only 2·3 kg, compared with an average of 3·4 kg for the controls. Although the heat treatment caused a pronounced reduction in lamb birth weight, the reduction in skeletal size was less striking ($P < 0 \cdot 01$) (Table 3).

Table 4 demonstrates the extent to which heat stress between 117 days' gestation and term influenced the maturation of wool follicles. Although the treatment had a marked effect on this developmental parameter ($P < 0 \cdot 01$), the potential secondary/primary follicle ratios were not markedly affected by heat stress.

Table 3. Mean anatomical measurements of day-old lambs born to heat-stressed and thermoneutral ewes

Groups (n = 17)	Birth weight[A] (g)	Foreleg length (cm)	Thorax girth (cm)	Crown–rump length (cm)
Heated	2271 (7·73)	23·2	30·4	48·8
Thermoneutral	3387 (8·13)	26·3	35·1	53·8
SE	(±0·04)	±0·3	±0·5	±0·5
$\frac{\text{Heated} \times 100}{\text{Thermoneutral}}$	67%	88%	87%	91%

[A] Log$_e$ of value in parenthesis.

Table 4. Effect of heat stress on the mature secondary/primary (S/P) wool follicle ratio of developing lambs

Six lambs per group were sampled at 110 days' gestation and at birth. An additional 11 lambs from each group were sampled at birth only

Group	S/P wool follicle ratio		
	110 days' gestation	Birth	Birth
Heated	0·44	2·9	3·0
Control	0·23	4·5	5·1
SE	±0·11	±0·5	±0·3

Table 5. Liveweights of ewes fed *ad lib.* or on restricted intakes during the latter half of pregnancy, and birth weights of their lambs

Plane of nutrition of ewes	n	Ewe liveweights (kg) Weeks before lambing commenced[A]: 8	6	4	2	0	n	Lamb birth wts (g)
High	25	37·9	38·4	41·8	43·3	44·5	26	3919
Low	25	37·0	34·5	34·7	32·2	34·4	27	3156
SE		±0·8	±0·8	±0·9	±0·9	±0·9		±104[B]
Significance		NS	**	**	**	**		**

[A] Lambing period extended over 11 days.
[B] Average standard error.
** $P<0·01$; NS, not significant.

Pen Studies

Table 5 shows the liveweights of pen-fed ewes during the last half of pregnancy and the birth weights of their lambs. Ewes on the high plane of nutrition were in forward store condition at the time of parturition; animals receiving the restricted intake were in poor condition. The mean birth weights of lambs born in these groups were 3·9 kg and 3·2 kg respectively ($P<0·01$).

Discussion

Merinos which maintain a low rectal temperature during exposure to high solar radiation loads are more adapted to the semiarid tropical environment than animals which exhibit a high rectal temperature under these conditions (Hopkins *et al.* 1978).

Adapted ewes in the present study produced heavier lambs following a summer gestation than the less-adapted animals of the same flock. Pasture conditions were favourable during the latter half of pregnancy, and all ewes were in forward store condition. The lambs of the second drop were weaned onto poor conditions, and only about half survived to maturity.

Although the physiological mechanisms responsible for inducing decreased lamb birth weight following maternal hyperthermia have been the focus of a good deal of research attention, their nature remains obscure (Alexander 1974). In the present study animals were paired on the basis of foetal size prior to heating, and subsequent differences in the feed intake of the ewes were excluded. If restricted nutrition of the foetus *per se* is important in determining foetal size under these conditions, then the low birth weight syndrome probably arises from abnormalities in placental uptake or alterations in uterine blood flow. In the absence of heat stress the uptake of glucose by the foetus is dependent on the concentration of this nutrient in the uterine artery (Battaglia and Meschia 1973), while foetal amino acid uptake rate is not markedly influenced by maternal blood levels (Hopkins *et al.* 1971).

If the availability of nutrients to the foetus is not the major cause of retardation of foetal development, then metabolic dyscrasias in the foetus may be a consequence of foetal hyperthermia. This possibility is highlighted by the fact that the Merino foetus at 117 days' gestation normally weighs *c.* 1750 g (Cloete 1939), and yet the heat-stressed animals in the present study weighed a mean of only 2300 g at term, a weight comparable to that of a normal 124-day foetus. Since the concurrent indices of longitudinal growth indicate only a 10–15% reduction in these parameters, then it is likely that protein and/or fat tissue was catabolized in the foetus during this period of hyperthermia.

Whether foetal hyperthermia induced an abnormal pattern of hormone secretion as suggested by previous workers is open to conjecture (Macfarlane *et al.* 1959; Ryle and Morris 1961). This treatment has been shown to produce little change in the plasma cortisol concentration, and in the expected decrease in plasma thyroxine levels of the catheterized foetal lamb (Hopkins 1972). However, measurement is yet to be made on the secretion *rate* during heat stress both of these hormones and of the protein hormones of pituitary origin which are known to control growth processes. From the evidence available it seems reasonable to suggest that uterine blood flow, placental insufficiency, or metabolic dyscrasias of the foetus are likely to constitute the major avenues for future research on this topic.

Reports of Cartwright and Thwaites (1976*a*, 1976*b*) suggest that nutrition of the heat-stressed ewe and her foetus is likely to be the major cause of low lamb birth weights and retarded wool follicle development. The data presented in the present experiments indicate that heat stress *per se* was a more likely determinant of these phenomena. Furthermore, they suggest that the legacy of heat stress *in utero* is subsequently reflected as a decrease in greasy wool production of the lambs at 14–26 months. The pen studies described herein demonstrate the extent to which poor nutrition can influence lamb birth weight. Although the nutritional restrictions were maintained in one group for at least half of the gestation period, the degree of foetal dwarfing so induced was markedly less than that induced by heat stress during only the last 30 days of gestation.

Elevated ambient temperatures caused a very marked degree of hyperthermia in young lambs. During exposure to high ambient temperatures, these lambs panted strenuously from 9 a.m. until late afternoon. Respiratory rates were too high to count accurately. In the cool of the evening the lambs fell asleep, apparently exhausted from their thermoregulatory efforts. It is likely that they may fail to suck during this critical period, particularly if their mothers were to take advantage of the cooler conditions to graze. Circumstances of this nature, when coupled with the physiological considerations of lamb survival (Alexander 1964) and the practical observations with sheep in this environment (Rose 1972), afford an explanation for the high neonatal mortality rate which causes a crippling loss to the sheep industry of north-western Queensland.

Both the poor survival of low birth-weight lambs and the depressed wool growth of tropical sheep are production parameters which can be linked with the results of these experiments. Breeding suitably adapted sheep or tempering the impact of the tropical climate by the strategic use of shade may afford a means of improving productivity from the vast semiarid plains of northern Australia.

Acknowledgments

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