
THE PROCEEDINGS OF THE
NEW ZEALAND SOCIETY
OF
ANIMAL PRODUCTION
VOLUME 62 2002

RESIDUAL EFFECTS OF PRENATAL NUTRITION ON THE POSTNATAL PERFORMANCE OF MERINO SHEEP

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SUMMARY

The residual effects of high and low planes of grazing nutrition in early and late pregnancy of merino ewes on the growth, wool follicle development and clean wool production of their lambs has been studied over a period of three years.

An adverse temporary effect of undernutrition in early pregnancy on lamb growth during the first 7 months of postnatal life was recorded. Severe undernourishment of ewes in late pregnancy reduced the birth weights and growth of single lambs throughout the experimental period, and also reduced wool follicle population and clean wool production. The effects of these two periods of undernutrition were cumulative.

Wether lambs were heavier than ewes at all times, the magnitude of sex difference in body-weight being related to pasture productivity and climatic conditions.

The results are discussed in relation to husbandry practices of sheep in a pastoral environment.

IN the Mediterranean-type environment of South Australia, pasture herbage generally sustains animal growth during the autumn-winter-spring rainfall period but is quantitatively and qualitatively deficient during the 5 to 6 months of sumer drought. Typical biphasic animal growth curves result, with troughs and peaks of weight gains associated with pasture productivity (Donald and Allden, 1959; Allden, 1959).

Breeding ewes in southern Australia are most commonly mated in the spring, lambing occurring at the time of autumn rains and renewed pasture productivity. Pregnancy in sheep thus coincides with summer drought and pasture shortage. Undernutrition of ewes, especially in late pregnancy when saved pasture resources are depleted, becomes more the rule than the exception, with consequent high mortality of new-born lambs. Reid (1961) estimated that in Australia some 600,000 ewes die each

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year in late pregnancy; and at least 7 million lambs die in the first few days of life, largely from nutritional causes. A comparable situation of less striking magnitude exists in New Zealand.

Apart from these neonatal losses of lambs born to undernourished ewes, severe maternal undernutrition in early pregnancy can affect embryo implantation (Edey, 1965), distort placental development, retard foetal growth (Everitt, 1964, 1966) and lead to a reduction in the number of lambs born, particularly to maiden ewes (Bennett *et al.*, 1964). Prenatal nutritional history may also influence body and fleece characteristics of those lambs surviving the neonatal rigors (Schinckel, and Short, 1961; Schinckel, 1963; Taplin and Everitt, 1964).

This report deals with the long-term postnatal growth and productivity of merino lambs born to, and reared by, ewes severely undernourished in early and/or late pregnancy. As the lambs in this field study were suckled by their dams, a cumulative effect of pregnancy nutrition and lactational performance on lamb growth is implicated. The isolated effects of pregnancy nutrition *per se* on the postnatal productivity of lambs were reported by Taplin and Everitt (1964); they selected a number of lambs born to ewes in the experiment reported here and artificially reared them on a standardized feeding regime from birth to 12 weeks of age.

MATERIALS AND METHODS

PRENATAL NUTRITION

In November, 1962, 100 three-year-old merino ewes (South Australian strain) were randomized into four equal groups, and each group joined with a merino ram. After mating, the ewes were allocated alternately to one of four nutritional treatments, namely: HH, a high plane throughout; HL, a high plane for the first 90 days followed by a low plane to lambing; LH, a low plane for the first 90 days followed by a high plane until lambing; LL, a low plane throughout.

The experimental objective was a 25% gain (HH, LH) or loss (LL, HL) in gross body-weight achieved by controlled grazing during 140 days of pregnancy, after which a supplementary concentrate feed was offered *ad libitum* to all ewes in order to reduce losses.

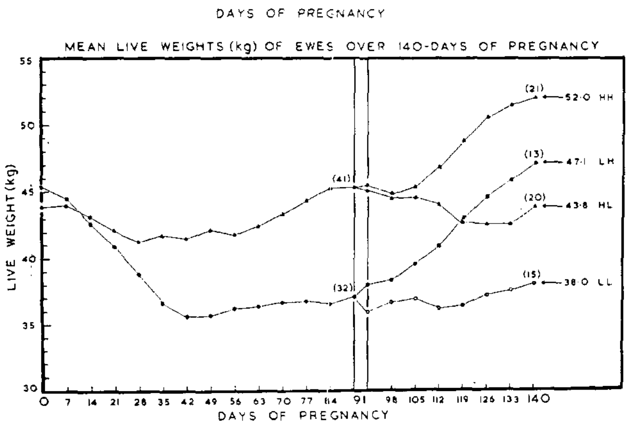

Fig. 1: Mean relative and absolute gross body weights of ewes during 140 days of pregnancy. The numbers of pregnant ewes are shown in parentheses.

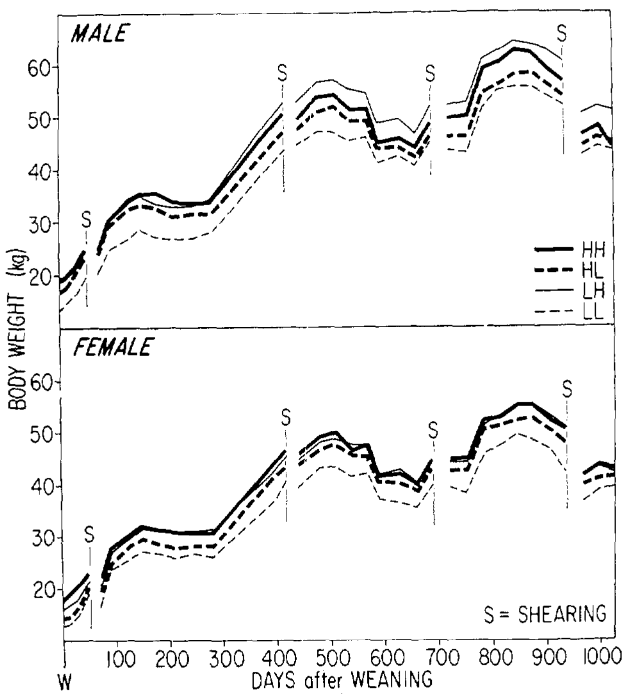

Fig. 2: Mean growth curves of lambs from the time of weaning.

Postnatal Nutrition and Management

All ewes and their lambs grazed together after lambing on pastures consisting predominantly of *Phalaris tuberosa* and subterranean clover (*Trifolium subterraneum*).

Lambs were weaned on to pasture at 12 weeks of age and shorn approximately 2, 16, 24 and 33 months after weaning. Ram lambs were castrated at birth using the rubber ring method.

Measurements

Body-weights of ewes were recorded at weekly intervals during pregnancy. A single subjective "condition" (fatness) score was applied to each ewe at mating, after 90 days of pregnancy, and at lambing by one experienced observer whose repeatability and discriminatory powers had been studied previously (Everitt, 1962). A scoring system of 10 points was used where score 10 represented "very fat" and score 1 "emaciated". The width of the udder (Owen, 1957) of each ewe was recorded at lambing time.

Lambs were weighed within 12 hr of birth and at intervals thereafter until the trial terminated in May, 1966.

Wool follicle development in the lambs was examined in histological sections from biopsy skin samples (Frazer and Short, 1960) 1 cm in diameter, taken from the midside at birth, 12 weeks and 18 months of age.

Total clean wool output of lambs was recorded at shearing times.

Biometrical Analyses

Treatment effects were isolated by analysis of variance with primary comparisons of plane of nutrition before (H/- *v.* L/-) and after (-/H *v.* -/L) 90 days of gestation, of lamb sex, sires, and the interactions.

Ram effects and interactions were neither appreciable nor consistent and have been ignored in the presentation of the results.

RESULTS

Animal Numbers

Figure 1 records the number of ewes in each group unmarked by a harnessed vasectomized ram 90 days and

140 days after mating; the latter also represents the number of ewes lambing.

After 90 days, 82% of well-fed ewes were presumed pregnant but only 64% of low plane ewes. Lambing percentages (lambs born/ewes mated) were 84, 80, 52 and 60 for HH, HL, LH and LL groups, respectively. No twin lambs were born.

Four LH ewes aborted in late pregnancy (118, 124, 129 and 130 days after mating) but no infective causative agents were isolated from the conceptuses. Three of these foetuses were markedly underweight for their age but no observations on placental development were recorded.

The numbers of lambs born and alive at selected stages are shown in Table 1.

TABLE 1: NUMBERS OF LAMBS BORN AND ALIVE AT SELECTED TIMES

Age	Group								Total
	HH		HL		LH		LL		
	♂	♀	♂	♀	♂	♀	♂	♀	
Birth	7	14	11	9	3	10	8	7	69
7 days	7	13	10	9	3	10	6	5	63
12 weeks (weaning)	7	13	10	8	3	10	4	5	60
3 years	7	13	10	8	3	9	4	4	58

Greater losses were suffered by lambs born to undernourished ewes, especially in the first week of life, than prenatally well-nourished lambs.

EWE PERFORMANCE

Mean body-weights of ewes during 140 days of pregnancy are shown in Fig. 1. Body-weight gains and losses were considerable although not as precise as planned owing to the group feeding.

At mating time the mean body-weight of all ewes was 44.5 kg (c.v. 8.5%). After 90 days of pregnancy, well-fed ewes were heavier ($P < 0.001$), by 8.3 kg, than ill-fed ewes. Highly significant differences ($P < 0.001$) in body-weight existed between the four groups after 140 days of pregnancy. Post-partum body weights of HH, HL, LH, LL ewes were 45.1 kg, 38.8 kg, 41.4 kg and 33.6 kg, respectively, indicating the substantial weight loss in pregnancy suffered by LL ewes in particular.

Table 2 records the mean fatness scores applied to the ewes during pregnancy, the length of gestation and width of the udder at lambing time.

At mating time, the ewes were considered to be in moderate condition with a mean score of 4.8. After 90 days of undernutrition some depletion of body fatness had taken place in ill-fed ewes; and by the end of pregnancy significant differences in "condition" were recorded, LL ewes particularly being judged very lean. These alterations in body "condition" follow the changes noted in liveweight (Fig. 1).

Length of gestation was not significantly affected by treatment, the mean duration for all ewes being 150.2 days.

The width of the udder at lambing time was reduced in those ewes subjected to underfeeding in pregnancy, with a marked effect on the udder development of LL ewes.

LAMB PERFORMANCE

Growth

Mean birth weights and weaning weights of the lambs are recorded in Table 3.

Undernutrition of ewes in early as well as late pregnancy reduced birth weight of lambs but the decrement was twice as large in -/L as L/- lambs. The effects of undernutrition in these two periods were cumulative. Males were heavier than females at birth but not significantly so.

By weaning time (12 weeks of age) these nutritional effects on lamb body-weight had increased and wether lambs were significantly heavier than ewes.

Mean growth curves of the lambs from weaning onwards are illustrated in Fig. 2.

The biphasic nature of growth curves of animals in this pastoral environment is clearly seen, and can be related to the pattern of climatic conditions existing during the post-weaning phase of the trial, shown in Fig. 3. Animals showed the characteristic cessation of body-weight increase during the summer drought, pasture

Table 2: Mean Condition Scores of Ewes, Length of Gestation and Udder Width at Lambing Time

Character	Group HH ♂	HH ♀	HL ♂	HL ♀	LH ♂	LH ♀	LL ♂	LL ♀	S.E.	Significance of differences: Sex (♂ — ♀)	Nutrition < 90 days (H/-)-(L/-)	Nutrition > 90 days (-/H)-(-/L)
Fatness Scores												
Mating	5.0	4.7	4.6	4.8	5.0	4.5	5.0	5.1	0.28	—	—	—
After 90 days	4.7	4.9	4.7	4.6	3.0	3.1	3.0	3.7	0.22	N.S.	***	—
After 140 days	4.7	5.1	2.8	3.2	3.0	3.2	2.5	2.7	0.25	N.S.	***	***
Length of gestation (days)	151	149	151	151	150	150	150	150	0.59	N.S.	N.S.	N.S.
Udder width (cm)	13.7	13.4	11.1	9.5	11.6	12.8	8.8	8.2	0.58	N.S.	***	***

***: $P < 0.001$; **: $P < 0.01$; *: $P < 0.05$; N.S.: $P > 0.05$.

Table 3: Birth Weights and Weaning Weights

Character	Group Means HH ♂	HH ♀	HL ♂	HL ♀	LH ♂	LH ♀	LL ♂	LL ♀	S.E.	Significance of differences: Sex (♂ — ♀)	Nutrition < 90 days (H/-)-(L/-)	Nutrition > 90 days (-/H)-(-/L)
Birth wt. (g)	4,243	3,977	3,307	3,169	4,145	3,559	3,291	2,466	200.6	N.S.	***	***
Weaning wt. (kg)	19.1	17.7	17.0	14.4	17.7	16.1	13.3	13.1	0.92	*	**	***

***: $P < 0.001$; **: $P < 0.01$; *: $P < 0.05$; N.S.: $P > 0.05$.

shortage periods. Under the favourable autumn conditions, growth of the sheep accelerated, enabling them to make good the deficit in body-weight. Nevertheless, it is interesting that, over the post-weaning period under study, body-weight gains of these growing animals were quite small.

Mean differences of main effects (nutrition before and after 90 days of pregnancy, and sex) on body-weight, together with a notation of statistical significance, are shown in Fig. 4.

Nutrition of the ewe in early pregnancy affected lamb growth in early postnatal life, but the effect progressively diminished until, 18 weeks after weaning, it was small and not significant. Undernutrition in late pregnancy exerted a much greater influence on lamb growth, persisting throughout the experimental period. Likewise, the sex effect was marked, wethers being heavier than ewes at all times. The cyclical nature of the sex effect and, to a lesser degree, the late pregnancy nutrition effect are noteworthy and can be related to the shape of the growth curves (Fig. 2) and the climatic pattern (Fig. 3). Analysis shows that, in periods of pasture shortage, wethers lost weight more rapidly than ewes, thus decreasing the sex difference. Under abundant feeding, as in the autumn, wethers gained weight more rapidly than ewes, the sex difference increasing.

Wool Follicle Development

Estimates of mature follicle densities and follicle ratios at birth, 12 weeks and 18 months of age are recorded in Table 4.

The total population of mature follicles per animal was estimated from the measured follicle density and surface area; the latter being derived from the formula of Malan and Curson (1936). Schinckel and Short (1961) used this technique and discussed the inadequacies but emphasized its usefulness in illustrating relative differences recorded for different animals at the same time. Population estimates are recorded in Table 5.

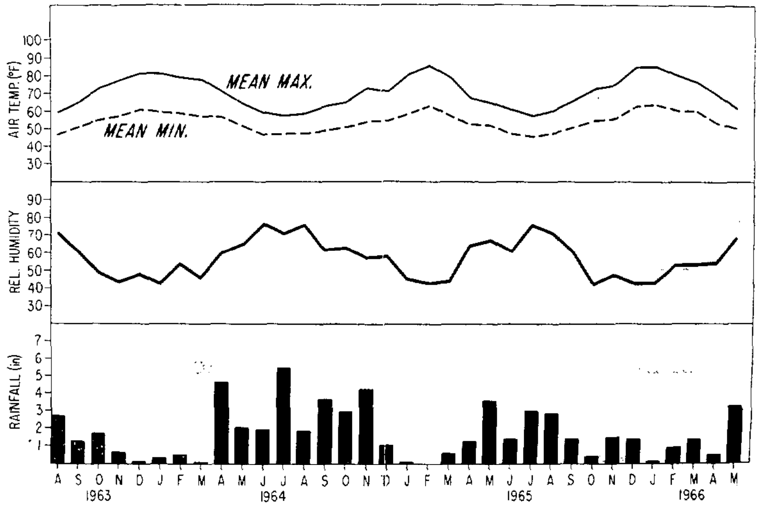

Fig. 3: Meteorological records during the post-weaning phase of the trial.

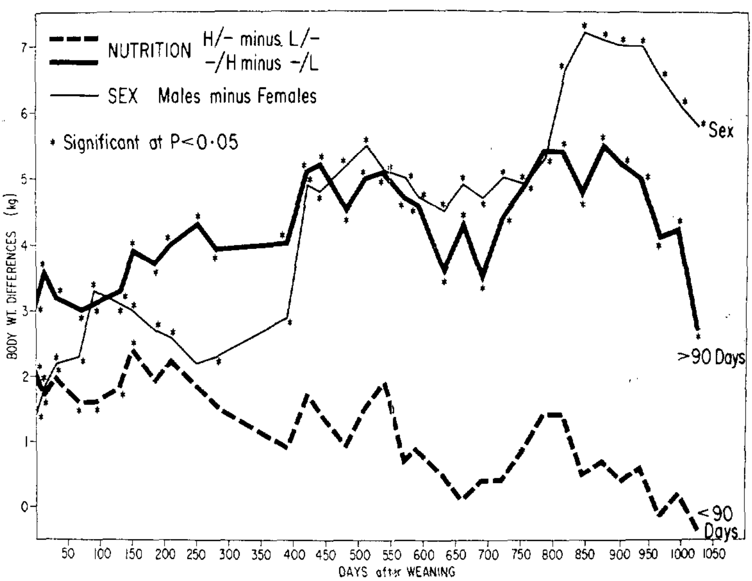

Fig. 4: Mean differences of main effects on lamb body weight. Statistically significant (P<0.01) differences are shown by S.

TABLE 4: DENSITY OF MATURE WOOL FOLLICLES AND FOLLICLE RATIOS AT THREE AGES

Character	Mature Follicles/cm²								S.E.	Significance of differences		
	HH		HL		LH		LL			Sex	Nutrition	
	♂	♀	♂	♀	♂	♀	♂	♀		(♂ — ♀)	< 90 days (H/-)-(L/-)	> 90 days (-/H)-(-/L)
Birth												
Pf	1,777	1,679	1,793	1,652	1,622	1,718	2,316	2,221	114.3	N.S.	***	***
Sf	5,099	6,133	4,119	5,386	4,619	6,045	2,907	4,859	565.4	***	N.S.	***
Pf + Sf	6,876	7,812	5,912	7,038	6,241	7,763	5,223	7,080	579.9	***	N.S.	*
Sf/Pf	2.97	3.66	2.27	3.30	2.83	3.68	1.58	2.30	0.36	**	N.S.	***
12 weeks												
Pf	489	590	589	629	575	544	534	591	40.9	N.S.	N.S.	N.S.
Sf	6,596	7,717	6,563	5,937	5,540	6,658	5,946	6,108	385.5	N.S.	*	N.S.
Pf + Sf	7,084	8,307	7,152	6,554	6,115	7,203	6,480	6,698	380.1	N.S.	*	N.S.
Sf/Pf	14.01	14.01	11.35	9.91	10.80	12.48	10.07	10.54	1.23	N.S.	N.S.	*
18 months												
Pf	240	301	273	292	298	267	267	333	16.6	*	N.S.	N.S.
Sf	4,171	4,193	3,784	4,060	3,813	4,128	3,520	3,290	273.7	N.S.	N.S.	*
Pf + Sf	4,411	4,494	4,057	4,352	4,111	4,396	3,787	3,623	283.0	N.S.	N.S.	N.S.
Sf/Pf	17.73	13.96	14.02	14.09	13.03	15.58	13.20	9.90	0.90	N.S.	**	***

***: $P < 0.001$; **: $P < 0.01$; *: $P < 0.05$; N.S.: $P > 0.05$.

TABLE 5: ESTIMATED POPULATIONS OF MATURE WOOL FOLLICLES

Character	No. of Mature Follicles × 10^6								S.E.	Significance of differences		
	HH		HL		LH		LL			Sex	Nutrition	
	♂	♀	♂	♀	♂	♀	♂	♀		(♂ — ♀)	< 90 days (H/-)-(L/-)	> 90 days (-/H)-(-/L)
Birth												
Pf	3.9	3.5	2.3	2.9	3.7	3.3	3.3	3.3	0.22	N.S.	N.S.	*
Sf	11.4	12.9	7.6	9.6	10.4	11.9	4.3	7.7	1.29	*	N.S.	***
Pf + Sf	15.3	16.4	10.9	12.5	14.1	15.2	7.6	11.0	1.39	N.S.	N.S.	***
12 weeks												
Pf	3.4	3.8	3.8	3.5	3.7	3.3	2.8	3.0	0.19	N.S.	**	*
Sf	46.8	52.1	43.0	34.8	37.1	41.2	32.1	31.5	3.78	N.S.	**	**
Pf + Sf	50.2	55.9	46.8	38.3	40.8	44.5	34.9	34.5	3.79	N.S.	**	**
18 months												
Pf	3.4	4.1	3.9	3.9	4.6	3.6	3.6	4.1	0.23	N.S.	N.S.	N.S.
Sf	60.1	57.6	53.7	54.1	58.7	56.7	48.2	40.7	4.03	N.S.	N.S.	**
Pf + Sf	63.5	61.7	57.6	58.0	63.3	60.3	51.8	44.8	4.16	N.S.	N.S.	**

***: $P < 0.001$; **: $P < 0.01$; *: $P < 0.05$; N.S.: $P > 0.05$.

TABLE 6: CLEAN FLEECE WOOL PRODUCTION

Clean Fleece Wool (g)

Age at Shearing	HH		HL		LH		LL		S.E.	Significance of differences		
										Sex	Nutrition	
	♂	♀	♂	♀	♂	♀	♂	♀		(♂ — ♀)	< 90 days (H/-)-(L/-)	> 90 days (-/H)-(-/L)
20 weeks	816	847	812	843	788	823	568	540	51.2	N.S.	N.S.	***
18 months	3,390	3,321	3,247	3,228	3,072	3,242	2,854	2,746	177.7	N.S.	N.S.	**
23 months	1,134	1,146	1,113	1,121	1,087	1,117	946	910	54.0	N.S.	N.S.	**
33 months[1]	2,370	2,215	2,305	2,238	2,106	2,231	1,847	1.802	82.2	N.S.	N.S.	**
Total	7,710	7,529	7,477	7,430	7,053	7,413	6,215	5,998	332.5	N.S.	N.S.	**

[1]Note: Estimated from greasy fleece weights and previous yield proportions.

***: $P < 0.001$; **: $P < 0.01$; N.S.: $P > 0.05$.

Primary Follicle Density: The number of mature primary wool follicles (Pf) per unit area of skin at birth was significantly greater in lambs born to ewes undernourished in early (L/-) and late (-/L) pregnancy than in lambs born to well-fed ewes. This reflects the smaller size of the prenatally undernourished sheep (Table 4). Differences at later samplings were not significant. Male lambs did not differ significantly from ewes in Pf density at any sampling stage.

Secondary Follicle Density: The density of mature secondary wool follicles (Sf) at birth was reduced by undernutrition in late but not early pregnancy. At later stages lambs which had suffered undernutrition *in utero* had lower densities of Sf than their better-fed mates but these differences were not in all cases significant.

Follicle Ratios: The ratio of Sf to Pf is a measure of the course of Sf development because all Pf are mature at birth with no further postnatal initiation. Table 4 shows a reduced Sf/Pf ratio at all stages for lambs born to undernourished ewes, although these differences attained significance only in certain cases. The Sf/Pf ratio was significantly greater in ewe lambs than males at birth but differences at later samplings were not significant.

Total Mature Follicle Populations: At birth, lambs born to ewes ill-fed in late pregnancy had significantly lower Pf, Sf and Pf + Sf populations. Early pregnancy nutrition did not significantly affect wool follicle populations at birth (Table 5).

Population differences at later samplings continued to favour lambs born to well-fed ewes with a curious significant effect of early pregnancy nutrition at 12 weeks of age which was not significant at 18 months. At the last sampling the Pf + Sf population of lambs well-fed in late pregnancy exceeded that of their ill-fed mates by over 9 million follicles.

Sex differences in follicle populations were relatively small and not significant.

Clean Wool Production

Mean weights of clean wool produced are recorded in Table 6. Greasy wool fleece weights only were, in fact, recorded at the last shearing but yield proportions based on previous shearing data were applied to provide an estimate of clean wool production.

A notably smaller weight of clean wool was produced by the LL lambs at each shearing, the differences between other groups being negligible and not significant. It is interesting, however, that the differences in wool production diminished as time progressed. The lifetime production of wool was considerably reduced in lambs born to ewes undernourished throughout pregnancy.

DISCUSSION

The establishment of an early pregnancy nutritional effect on single lamb birth-weight and on lamb growth for some seven months after birth (Fig. 4) represents a most interesting result of this experiment. In sheep intended for wool production over a period of several years, such a residual effect loses significance. When, however, lambs are slaughtered for meat production at, say, 4 to 5 months of age, this prenatal penalty assumes considerable importance.

Ewe nutrition in late pregnancy exerted a much more powerful, more persistent effect on single lamb birth-weight and growth which was cumulative to the effects of early pregnancy nutrition. A nutritional effect on the birth weight of twin lambs is well-known and documented (reviewed Schinckel, 1963). Single lambs born to ewes severely undernourished throughout pregnancy were about 34% smaller at birth and about 9% smaller at maturity in the study of Schinckel and Short (1961). The present experimental results are in general agreement.

Severe restriction of feed intake during the first few weeks of postnatal life has a marked effect on mature body size, the development of secondary wool follicles, the birthcoat shedding cycle, and wool production (Schinckel and Short, 1961; Doney and Smith, 1964; Wiener and Slee, 1965). The residual effect of pregnancy nutrition on lactational performance of the ewe and thus on lamb growth cannot readily be distinguished in this trial. Despite the evidence on the poor udder development of the LL ewes at lambing time (Table 2), the milking performance of these ewes may not have retarded lamb growth to any great extent. Weaning weights of lambs hand-reared by Taplin and Everitt (1964) were 17.2, 15.5, 16.8 and 12.0 kg for HH, HL, LH and LL lambs, respectively (3 males and 3 females per group). These weights rank in the same order as those for field-reared lambs and also suggest that the hand-rearing was not efficient overall.

The results confirm the suggestion (Taplin and Everitt, 1964) that retardation of foetal growth before 90 days of pregnancy may be partially compensated under an abundant feeding regime from 90 days to lambing. Residual effects of prolonging the underfeeding past 90 days need resolving, for any further shortening in the time available for re-feeding before lambing may impair the efficiency of any compensatory process. Low planes of maternal nutrition up to 4 weeks before lambing had an appreciable adverse effect on the birth weight and body-weight gains of lambs reared to 6 weeks of age in the study of McClymont and Lambourne (1958).

The association between the sex effect on growth with climatic conditions, and thus pasture productivity, helps to explain the divergence of results from growth experiments studying sex effects *per se*. Clearly, the superiority of males over females in growth rate will be apparent only under good feeding conditions; under sub-maintenance feeding, males in fact tend to lose weight more quickly than females.

Development of wool follicles was affected by pregnancy nutrition and the results are in general agreement with those of most workers (Schinckel and Short, 1961; Doney and Smith, 1964; Taplin and Everitt, 1964; Wiener and Slee, 1965), but not others (Ryder, 1955; Wildman, 1958) where nutritional deprivation was less severe. In this present study, early as well as late pregnancy nutrition increased the Pf density at birth, suggesting that Pf maturation can be delayed by severe maternal undernutrition. The higher Pf density of the light lambs born to undernourished ewes was sufficient to compensate for the greater skin area of larger lambs born to well-fed ewes. Thus, these results do not entirely confirm earlier findings (Schinckel and Short, 1961) that small prenatally undernourished lambs actually have a smaller population of primary follicles.

Very little evidence was adduced to show that Sf density was affected by nutrition in early pregnancy. This conforms with the time of first initiation of secondary follicles (reviewed, Schinckel, 1963). The nutritional effects on wool follicles at 12 weeks of age may reflect a lactational effect on the accession to maturity of secondary follicles during early postnatal life, an effect subsequently obscured or compensated by development changes in the period between 12 weeks and 18 months of age.

Malnutrition in late pregnancy severely reduced the density of mature secondary follicles, the Sf population and the Sf/Pf ratio at all stages, although there was some evidence of partial compensation with the passage of time.

Schinckel and Short (1961) found that merino lambs born to ewes undernourished throughout pregnancy (L/-) resulted in smaller animals with fewer fibres (54.8×10^6) than well-fed (H/-) lambs (66.8×10^6). Temporary differences in secondary fibre number were found by Doney and Smith (1964) when comparing twin-born with single-born Scottish Blackface lambs given adequate postnatal nutrition. Undernutrition in late pregnancy reduced the birth coat of lambs reared by Taplin and Everitt (1964) but prenatal influences on clean wool production were substantially overcome by 20 weeks of age. Wiener and Slee (1965) found that differences in maternal environment following egg transfer clearly affected wool follicle density, Sf/Pf ratio, fibre medullation, diameter and length.

Clean wool production, therefore, tends not to be affected to such a great extent by these prenatal treatments, because reduced follicle density is associated with the production of longer, coarser wool fibres (Schinckel and Short, 1961; Doney and Smith, 1964; Wiener and Slee, 1965). Such compensation may not be complete, as in the LL sheep of this study, for the lifetime production of wool from these animals was notably least.

It can be concluded, therefore, that there are marked residual effects of late prenatal undernutrition manifested as a reduction in body size and wool follicle population and the production of a lighter, coarser fleece. To a lesser extent, undernutrition in early pregnancy can also adversely affect lamb growth and the development of productive characteristics.

From the animal production viewpoint, the primary implication of these results is that husbandry methods which do not severely restrict foetal growth are prerequisites for efficient animal productivity. The permissible degree and timing of undernutrition in pregnancy so as not to permanently affect lamb growth needs resolving, for this could be one component in the search for increased production per acre.

ACKNOWLEDGEMENTS

Dr W. G. Allden is thanked for advice at all times and for organizing the continuation of the trial during the absence of the author in the last year of the trial. S. Richardson diligently cared for the experimental animals at all stages. Miss C. Mattson assisted with the clerical work, and D. Messent in statistical matters. Acknowledgement is also made of the skilled technical assistance of R. Brady, Roseworthy Agricultural College, South Australia, in the histological processing of skin samples.

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