Lambing in Relation to the Diet of the Pregnant Ewe

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(*Received* 29 *July* 1948)

Thomson & Fraser (1939) fed three groups of fourteen Greyface ewes on a diet of concentrates, turnips and hay in amounts which induced different weight changes during their pregnancy. The first group (Group I) was allowed just to maintain weight and strength, and gained about 3·6 kg. (8 lb.) while in lamb. The second group was fed *ad lib.* and gained about 22·7 kg. (50 lb.). The third group received the restricted diet until the last month of pregnancy, when *ad lib.* feeding commenced; the average weight gain was 9·1 kg. (20 lb.). The lambs of the second two groups were comparable in birth weight and general vitality, but those delivered by ewes on the restricted diet were more than 1 kg. lighter and 'were also lacking in vitality. Many of the lambs, particularly the twins, in Group I were so weak that they required assistance in suckling their dams or by bottle feeding.... Some of the ewes in this group had very little milk.'

Wallace (1948) conducted somewhat similar, but much more intensive studies, on groups of half-bred or Suffolk ewes. His main findings were that the maternal plane of nutrition had a profound effect on the weight and development of the foetus; ewes on a diet which was restricted during the crucial period carried foetuses which were light and whose organs and tissues weighed less than those of foetuses of similar weights from well-fed mothers. He also showed that the level of the maternal diet determined the degree of udder development and milk yield, which was reflected in the subsequent growth of the lambs. Wallace's paper, which contains a wealth of detail, was unfortunately not available to us while our work was being planned and carried out, so that in certain respects the data now reported have not the advantage of being closely comparable with his in detail.

Our purpose was to confirm and extend the earlier work of Thomson & Fraser (1939), with special reference to the problem of the vitality of lambs, and to consider the degree of individual variability within a fairly large flock of pregnant ewes.

EXPERIMENTAL

Husbandry arrangements. The animals used were eighty-one Sutherlandshire Cheviot gimmers (1½ years of age) mated with three rams of the same breed. Although they formed a reasonably 'even' commercial flock, they varied considerably in size, build and fatness. Their weights ranged from 35 to 52·7 kg. It has been shown (Baird, 1945) that in human beings maternal height and the birth weight of infants are correlated. Since there might be a similar size effect in sheep, the flock was randomly distributed in respect of size between two experimental groups and the three rams. The index of size used for this purpose was $L \times B$, L being the length between the angle of the sternum and the tuberosity of the ischium, and *B* the breadth between the external angles of the ilium.

The ewes were tupped outdoors during October–November 1946, on good grass, in three equal groups, each group running with one of the rams. About the 4th week of pregnancy they were housed indoors in individual or small-group pens. The individual pens were constructed from metal tubes, and animals were isolated only in the physical sense; 'company' seems to be important for the well-being of animals. Individual feeding arrangements were maintained for all animals throughout pregnancy; each animal was offered weighed amounts of the staple foodstuffs, and any uneaten residue was weighed. The diets used are described below. Up to the 10th week of pregnancy the amount of food given was regulated in an attempt to bring each animal to a uniform level of fatness, corresponding to 'fairly good' grading by an experienced shepherd. This attempt to regulate the fatness of the animals was only partly successful, for it was soon noticeable that certain ewes tended to remain thin when eating *ad lib.*, whereas others lost weight only slowly in spite of fairly severe restriction.

After the 10th week of pregnancy the ewes were grouped as thirty-three 'high-plane' animals, receiving a liberal high-protein diet, and forty-eight 'low-plane' animals receiving a restricted low-protein diet. In the event, there were at lambing thirty high-plane and forty-four low-plane ewes; four ewes proved not to be pregnant and three aborted following intravenous inoculation, in connexion with an immunity experiment on four animals, with a vaccine of *Bacterium typhosum* which had a high content of Vi antigen together with H and O antigens. In the high-plane group, sixteen ewes bore single lambs and fourteen bore twins; in the low-plane group twenty-two ewes bore single and twenty-two bore twin lambs. The food given to the high-plane group was regulated to produce a weight increase of about 30%, and that of the low-plane group was restricted so as to cause a fall of about 5%. The mean weight changes actually produced are given in Fig. 1. There was no evidence of appreciable skeletal growth of the ewes during the period of study.

Although the system of randomization successfully matched the mean weights before tupping of the two dietary groups, the mothers of twins started off by being about 5 lb. heavier than those of singles, and this difference was maintained throughout pregnancy. We did not attempt to determine in advance which ewes carried twins and which singles. The difference between the mean weights before mating of the mothers of singles and of twins was tested statistically, and would be unlikely to occur by chance oftener than once in 20–50 trials. The weight difference was accounted for mainly by fatness, although the heavier group was also slightly larger in skeletal size, measured in this case by $\sqrt[3]{(L \times B \times H)}$, where L and B are as defined above (p. 290), and H is height at withers. It is, therefore, likely that twinning tended to occur selectively in better conditioned ewes, presumably through some normal physiological mechanism (Hammond, 1940, p. 63).

It is of interest to compare the weight changes induced in our flock with those observed among pregnant hill ewes. Fraser (1939) states that on Garrochoran, Argyllshire, a poor West Highland grazing, Blackface ewes are in good condition about October and then weigh about 40 kg. (90 lb.). 'Even by the time tupping commences in late November the ewes are falling back in condition. They are, in fact, mated when their weight has fallen to about 80 lbs. (36 kg.). This is one very probable reason of the low fertility observed, since it is known that sheep are most prolific when mated in improving condition. Then, while the ewes are in lamb, between November and April, they are progressively losing weight. Thus a ewe weighing 90 lbs. (40 kg.) in October may weigh 60 lbs. (27 kg.) when ready to lamb. After lambing she may weigh only 50 lbs. (22·5 kg.). That is to say, a ewe on a grazing of this type will lose almost half her

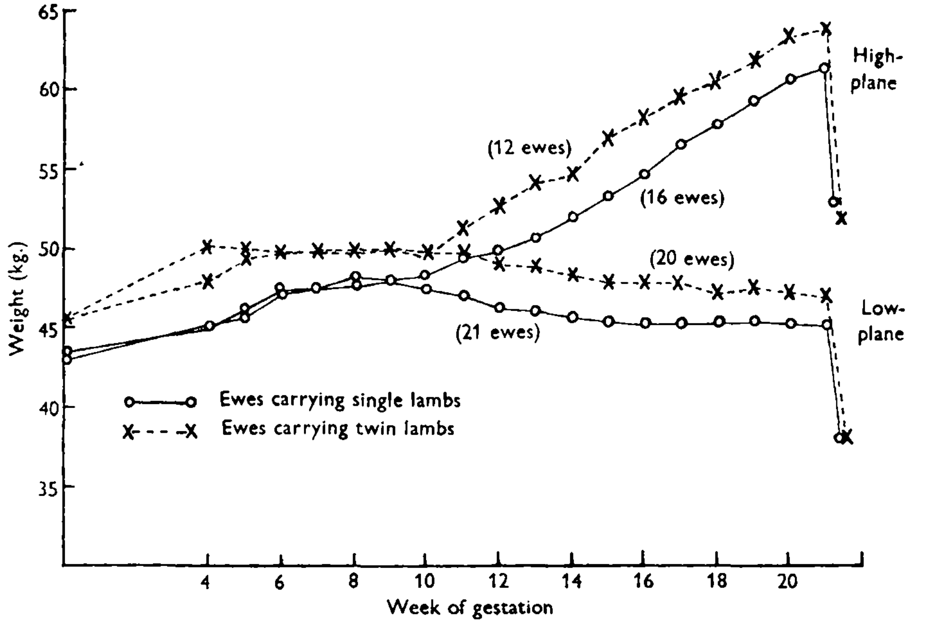

Fig. 1. Average weight changes of ewes. The number of ewes in each group is given in brackets. Four kept in metabolism cages and weighed irregularly and one which aborted following pregnancy toxaemia are excluded.

weight during winter and early spring.' We have extracted from the records of the Rowett Institute the average monthly weights of groups of Blackface ewes maintained on untreated Garrochoran pasture between 1930 and 1935, and the changes in weight during pregnancy are shown in Fig. 2. It appears that these animals lost weight considerably more than our low-plane ewes, but that, except during 1930–1 and 1932–3 the main weight loss took place during the earlier weeks of pregnancy. The mean weight losses were not as severe as that described by Fraser, who was referring to the exceptional ewe or to an exceptional year (such as 1930–1). Although productivity was undoubtedly very low in such bad years, a consideration of the data suggests that Blackface ewes can withstand a much heavier loss of weight during pregnancy without unduly serious consequences than could our hill Cheviot ewes. Breed differences must be taken into account in drawing general conclusions from details of performance.

The diets. The indoor diet up to the 10th week of pregnancy consisted of Timothy hay, swedes and concentrates, in the proportions of 1:3:1 (by crude weight), water *ad lib.*, a salt and a mineral lick, and 5 ml. of cod-liver oil daily. The concentrate mixture consisted of maize 8 parts, oats and bran 2 parts each, linseed-cake meal and fish meal 1 part each. From the 10th week, the high-plane group received hay, swedes and concentrates in the proportions of 1:3:1·5, and the low-plane group the same foodstuffs

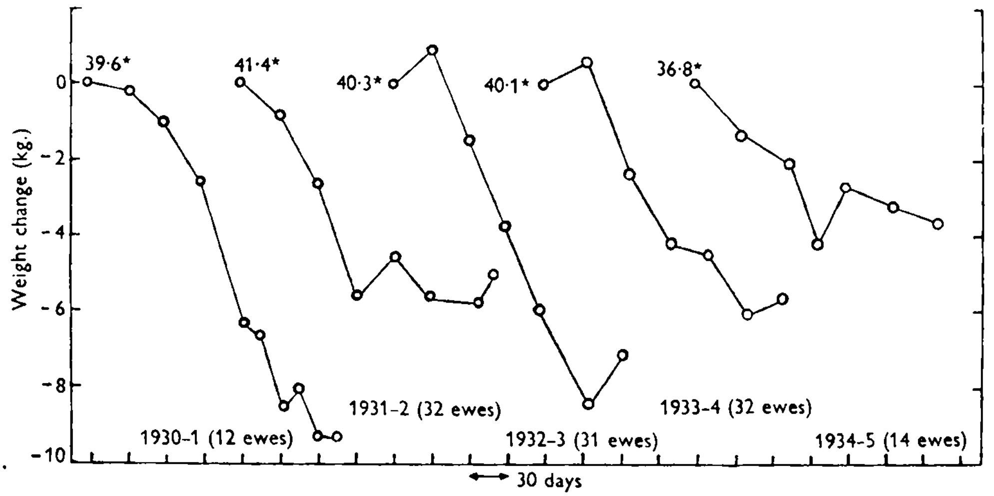

Fig. 2. Average weight changes of Blackface ewes on natural hill grazing. (Garrochoran, Heft 4, 1930–5.) Weighing in each year began in October (about 6 weeks before mating), and ended in April (just before lambing). * Mean initial weight of group (kg.).

Table 1. *Average daily food intakes (g.) of ewes*

	Week of pregnancy	High-plane	Low-plane
Dry matter	5th	622	651
	10th	579	504
	15th	856	336
	20th	860	329
Crude fibre	5th	110	114
	10th	98	91
	15th	134	79
	20th	134	77
Gross digestible energy as starch	5th	450	474
	10th	422	362
	15th	641	221
	20th	642	215
Protein equivalent	5th	54	57
	10th	53	43
	15th	83	21
	20th	83	21

Figures derived from Wood & Woodman (1939).

in the proportions of 1:3:0·25. Water, salt, minerals and cod-liver oil were given as before. The amounts fed were regulated to induce the weight changes desired, as described above.

Fig. 3 shows the average amounts of hay and concentrates fed, the amount of swedes fed being thrice the amount of hay shown. Table 1 gives the average composition of the diet as fed throughout pregnancy, and Fig. 4 expresses the low-plane intake as a percentage of the high-plane intake. Diets for ewes carrying singles and twins respectively are not given separately. Ewes carrying twins actually received slightly less food

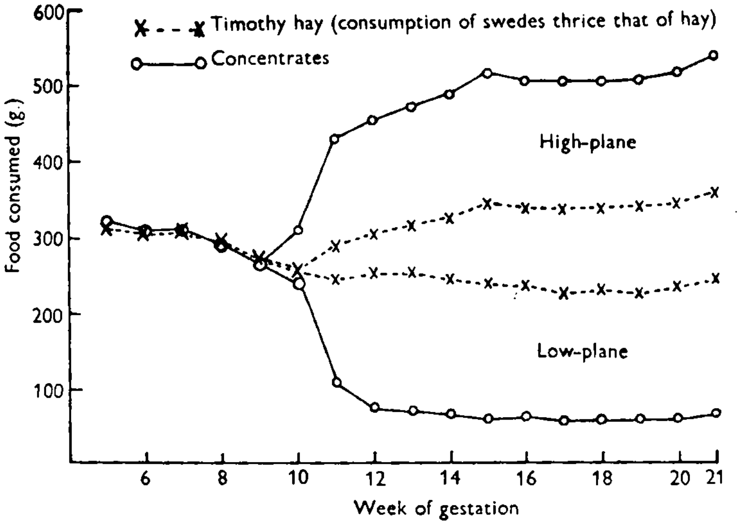

Fig. 3. Average daily consumption of foodstuffs by ewes.

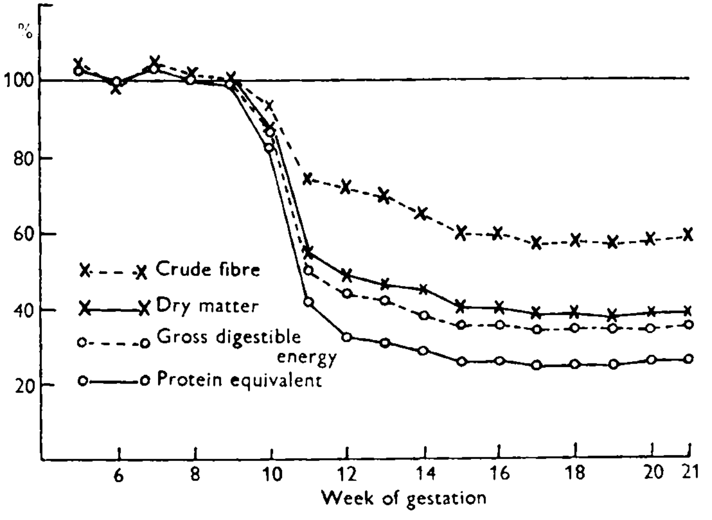

Fig. 4. Average daily food intake of low-plane ewes expressed as percentage of that of high-plane ewes.

than those carrying singles. As we did not know until the end of pregnancy which ewes carried twins and which singles, the former, which tended to gain or to maintain weight better than the latter, were offered less food in the effort to maintain uniformity. It can be seen from Fig. 4 that low-plane ewes received about one-third of the food given to the high-plane ewes, with relatively higher fibre and lower protein contents.

Pregnancy toxaemia. Seven low-plane ewes developed signs of toxaemia late in pregnancy. Six of them proved to be carrying twins. The ewe carrying a single lamb was affected only slightly and recovered completely within 24 hr. on receiving a slight increase of diet. In the first case occurring, the animal was found lying with its head in a feeding box during the 16th week of pregnancy. It acted as though it were blind and dazed and its breath smelt strongly of acetone; ketonuria was present. It would not touch food. Glucose (50 g.) was given intravenously and molasses was fed by bottle. Two days later its condition had improved, but a week after the onset of symptoms macerated twin lambs were born. All other cases were much milder, though with similar symptoms, and it was noted that the exercise associated with the disturbance of examination was usually sufficient to restore normal behaviour. In three cases (including one relapse) 1 ml. of 1:1000 adrenaline hydrochloride (*Liquor adrenalinae hydrochloridi*, B.P.) was injected subcutaneously with minimal disturbance to the animal, and it was found that normal behaviour, including apparent restoration of sight and appetite occurred dramatically within 10 min. Before one of these adrenaline injections a control injection of normal saline had been given, without any observable effect within 20 min.

When these cases began to occur, the food intake of the thinner low-plane ewes was slightly increased, in the hope of preventing termination of pregnancy by toxaemia. The effect on the mean intake of all low-plane ewes was negligible, as is evident from Fig. 4. In the event, no serious case occurred after the first, and all other ewes that developed toxaemia lambed normally about term.

When these cases were occurring, the country was snowbound and many hill sheep were virtually without food for long periods. We were interested to hear that pregnancy toxaemia was then a major problem in local veterinary practice.

Procedure during lambing. During the height of lambing, an observer remained with the animals night and day, so that detailed observations were made on the majority of animals. A form was used to record details of times and behaviour. In general, animals were left to fend for themselves, and no assistance was given to mother or lamb. In a few cases, however, there was some degree of human intervention, usually to save a dying lamb which was required for further investigations.

The observations recorded here include only those made in the first few days after lambing. Details of milk yields and lamb growth will be reported separately.

A film was made to illustrate certain phenomena dealt with in this investigation, the precise nature of which is difficult to describe on paper.

RESULTS

Duration of pregnancy. The difference between the length of gestation in the four groups was not conspicuous, but Table 2 shows that there was more irregularity in the low-plane groups.

Parturition. The first sign of the onset of labour in a ewe is restlessness, and it is not easy to time it precisely. The average times given in Table 3 are therefore derived from individual observations which were necessarily approximate, and conceal a wide range of individual variation. Precipitate and rapid labours were more common in the low-plane group, in which some sheep succeeded in delivering themselves unobserved, though inspected at frequent intervals, but uterine inertia sometimes prolonged labour, especially when the lamb was malpresented. The delay in the birth of the second lamb in low-plane twins appeared to be due to exhaustion of the uterine muscle. In general terms, thin ewes with small lambs often had rapid labours, but twinning or any other complication of delivery caused exhaustion, with consequent delay.

Table 2. *Duration of gestation in the ewes*

	Days					
Group	141–142	143–146	147–150	151–152	153–156	Exclusions
Low-plane (twins)	3	9	7	1	1	One aborted at 16 weeks owing to toxaemia
High-plane (twins)	—	2	9	2	—	One unknown
Low-plane (singles)	1	4	12	2	1	Two unknown
High-plane (singles)	—	—	15	1	—	—

Table 3. *Type and duration of labour in the ewes*

	Single lambs		Twins	
	High-plane	Low-plane	High-plane	Low-plane
No. of labours observed throughout	10	17	9	16
No. malpresented, assisted or otherwise abnormal	1	4	2	4
Average duration of labour (min.)	162	81*	90+61	72+109†

* Excluding two precipitate labours. † Excluding one precipitate labour.

Table 4. *Birth weights and measurements of lambs*

	Single lambs		Twin lambs	
	High-plane	Low-plane	High-plane	Low-plane
Average birth weight (kg.)	4·8 (16)	3·7 (22)	3·5 (28)	2·3 (37)
Average poll-rump length (cm.)	45·1 (16)	41·6 (22)	41·5 (28)	37·2 (37)
Average chest girth (cm.)	37·9 (16)	33·9 (22)	34·5 (28)	28·0 (37)
Average shoulder height (cm.)	37·4 (16)	34·2 (20)	33·8 (23)	29·8 (21)

Figures in brackets indicate the number of animals. A few stillborn and most macerated lambs were not weighed or measured.

Size and condition of lambs at birth. The mean birth weights and measurements of the lambs are given in Table 4. Although, as Wallace (1946) has shown, the skeleton is one of the foetal tissues least affected by maternal undernutrition, it can be seen that our low-plane lambs were appreciably smaller than their high-plane counterparts, i.e. the low weights of the former were not entirely a matter of changes in soft tissue. If the average measurements of poll-rump length, chest girth and shoulder height in each group are multiplied together and the product used as an index of 'bulk', the ratios of these products and the ratios of the mean birth weights between groups are surprisingly similar:

	'Bulk'	Weight	Ratio (weight/'bulk')
Low-plane, twin (taken as unity)	1·00	1·00	1·00
High-plane, twin	1·56	1·55	1·00
Low-plane, single	1·55	1·62	1·05
High-plane, single	2·06	2·14	1·04

Since chest girth is the only one of these measurements likely to be influenced by tissues other than skeleton, it is fair to say that a reduction in weight of lambs was accompanied by an almost proportionate reduction of size.

Table 5. *Birth weight of lambs in relation to weight of placenta*

	Av. weight of placenta per lamb				Av. no. of cotyledons per lamb				No. of ewes			
	Singles		Twins*		Singles		Twins*		Singles		Twins	
Birth wt. of lambs* (g.)	High-plane (g.)	Low-plane (g.)	High-plane (g.)	Low-plane (g.)	High-plane	Low-plane	High-plane	Low-plane	High-plane	Low-plane	High-plane	Low-plane
1000–1999	—	—	—	176	—	—	—	29	—	—	—	3
2000–2999	210	402	437	300	50	64	52	46	1	2	1	11
3000–3999	—	457	452	325	—	82	48	50	—	13	11	1
4000–4999	463	556	—	—	75	82	—	—	10	6	—	—
5000–5999	450	—	—	—	60	—	—	—	4	—	—	—
All	442	480	451	277	69	80	48	43	15	21	12	15

* The mean weight of pairs of twins has been used, and the total weight and number of cotyledons in twin placentas have been halved.

Although, when group averages are considered, there was a marked relationship between the maternal weight change during the second half of pregnancy and the birth weight of the offspring, there was considerable individual variability within each group. Table 6 gives the data for individuals.

McKenzie & Bogart (1934) have shown that there is a correlation between the condition of the placenta and the 'thrift' of the lamb. Table 5 shows the average weight of placenta and number of cotyledons in each experimental group and for each birth-weight category of lamb.

There was, within each experimental group, a tendency for the weight of placenta and number of cotyledons to increase as birth weight rose, but individual variations were large. Relatively to the weight of lamb produced, the weights of the low-plane twin placentas were very small (see also Table 6). We were not able to devise a useful system of describing the 'quality' of each placenta, apart from the two characters used in the table, but notes were made in each case and most placentas were photographed. It was not possible to account satisfactorily for individual differences in birth weight within each experimental group by reference to placental characteristics; in some cases there seemed to be a satisfactory correlation, but there were numerous exceptions.

There was no evident correlation between the birth weight of lambs and the ram used, or the duration of pregnancy.

The 'condition' of lambs was assessed subjectively by an experienced shepherd on the basis of their general physical condition, and yielded the results given in Table 7.

Table 6. *Values for food intake, ewes' weight change, and weight of products of conception of animals for which complete data are available*

Ewe no.	Length of gestation (days)	Total intake of gross digestible energy as starch* from 70th day of gestation until lambing (kg.)	Wt. of ewe: At 70 days (kg.)	Wt. of ewe: At term (kg.)	Wt. of ewe: After lambing (kg.)	Wt. of lamb produced (kg.)	Wt. of placenta (kg.)
			(a) High-plane ewes				
			Single lambs				
136	150	51·7	45·9	58·6	51·3	4·60	0·45
138	150	49·5	44·0	59·5	50·4	5·74	0·33
140	149	47·0	46·8	59·9	50·6	4·88	0·48
141	150	47·1	49·7	65·8	57·9	4·95	0·35
150	149	50·0	50·2	61·3	53·8	5·79	0·53
151	148	50·4	48·8	62·7	53·1	4·61	0·61
155	147	48·2	47·7	54·9	48·8	2·93	0·21
165	152	48·8	43·4	52·9	45·9	4·78	0·40
167	149	50·8	48·6	60·4	52·9	4·59	0·37
170	148	50·0	45·9	61·7	49·3	5·13	0·35
173	148	49·1	53·8	66·7	57·7	4·65	0·70
176	147	49·5	49·7	67·2	56·3	4·93	0·53
185	149	51·5	50·2	66·7	56·3	5·68	0·60
193	150	43·4	50·6	58·3	49·9	4·53	0·47
206	149	46·1	52·7	63·6	54·0	4·14	0·28
Mean	149	48·9	48·5	61·3	52·5	4·79	0·44
			Twin lambs				
123	151	41·9	52·9	71·7	58·1	7·20	0·73
127	150	53·1	49·5	66·5	53·1	7·75	0·79
158	148	45·6	49·0	66·3	55·4	6·22	0·86
161	146	49·7	52·2	62·2	51·3	6·87	0·68
164	149	50·4	44·3	58·1	44·9	6·31	0·90
174	151	49·1	49·7	55·8	45·4	6·73	0·95
179	150	50·6	44·9	59·9	45·8	7·49	1·03
183	148	42·2	47·9	62·7	50·6	6·99	0·93
186	148	49·5	52·9	64·5	53·1	7·82	0·98
196	150	47·1	52·0	70·6	53·8	7·70	1·18
209	148	47·2	49·3	63·1	54·7	5·98	0·88
Mean	149	47·8	49·5	63·8	51·5	7·00	0·90
			(b) Low-plane ewes				
			Single lambs				
182	149	16·9	52·4	49·7	39·0	3·59	0·43
187	142	17·9	45·2	44·9	38·1	4·53	0·35
188	149	22·5	40·6	35·9	30·0	4·09	0·37
194	144	15·1	47·9	45·6	39·7	3·10	0·40
198	149	16·7	50·2	49·0	42·0	3·48	0·36
200	156	15·9	55·2	53·3	44·9	4·75	0·82
201	143	16·7	45·9	43·1	37·7	3·28	0·50
208	147	16·4	49·0	44·7	36·3	3·52	0·65
121	152	18·6	47·0	45·4	38·1	3·60	0·50
131	150	18·1	48·1	44·9	39·0	4·21	0·45
135	148	18·5	45·4	43·4	34·9	3·67	0·44
137	148	16·8	44·3	39·5	33·6	2·95	0·48
145	150	19·1	42·0	40·9	35·4	3·55	0·53
148	150	19·3	50·6	46·8	37·7	4·51	0·73
153	149	18·8	46·8	43·4	36·5	3·20	0·35
157	146	16·5	42·4	41·5	34·5	3·79	0·50
169	151	17·5	49·9	48·4	39·5	4·60	0·63
175	150	17·4	46·5	46·8	33·8	3·89	0·40
156	147	18·8	51·3	44·7	39·3	3·23	0·48
Mean	148·4	17·8	47·4	44·8	37·4	3·76	0·49
			Twin lambs				
126	149	16·6	52·4	49·0	37·7	4·71	0·85
128	142	15·9	49·5	44·0	34·7	5·46	0·24
139	143	16·9	48·4	44·7	37·7	4·60	0·63
143	147	16·6	49·9	49·7	39·7	4·66	0·60
146	146	15·4	52·0	48·8	39·3	4·63	0·37
162	146	17·9	48·8	48·8	39·9	4·53	0·53
171	150	20·2	45·9	44·3	35·6	4·66	0·64
172	145	14·9	52·7	50·2	40·6	4·41	0·55
190	146	15·9	52·2	50·8	39·7	4·57	0·60
191	152	19·0	50·8	48·4	37·7	5·07	1·08
192	144	17·7	46·1	40·6	33·1	3·98	0·47
195	150	18·2	46·8	42·9	34·0	3·76	0·29
202	144	14·5	49·0	48·6	39·5	4·18	0·54
Mean	146·4	16·9	49·6	47·0	37·6	4·55	0·57

* See footnote to Table 1.

Initial activity of live-born lambs. Table 8 shows the time which lambs in each group took to get to their feet after birth. The criterion was that the lamb should stand for the first time on all four feet; naturally it took longer to attain adequate balance and muscular control.

Table 7. *Condition of lambs at birth*

	Single lambs		Twin lambs	
	High-plane	Low-plane	High-plane	Low-plane
No. observed	16	20	22	36
Condition:				
Very good	9	3	3	—
Good	7	13	12	4
Fair	—	4	7	12
Poor	—	—	—	20

Table 8. *Time taken by lambs to get to their feet*

	Singles		Twins	
	High-plane	Low-plane	High-plane	Low-plane
No. of live lambs observed	13	17	22	27
No. standing in				
15 min. or less	10	11	16	9
16–30 min.	3	6	3	7
31 min. or more	—	—	2	5
No. which never stood	—	—	1	6

Thus, apart from a number of extremely weak low-plane twins, most live-born lambs were on their feet within half an hour, and there was little difference between the groups in this respect. If a lamb was not moribund at birth, it was capable of taking the first steps towards the udder.

Mortality among lambs. The number of lambs stillborn or dying from causes present at birth is shown in Table 9. In this table, a category 'presumptive neonatal death' is added to the stillbirth and neonatal death classes. The reason is that certain lambs were required for special purposes and were removed from their mothers shortly after birth. If one of these lambs was undoubtedly starving progressively until hand fed or transferred, and if its mother was unsuccessful as the foster-mother of another lamb, it was classified as a 'presumptive neonatal death' although death might actually be prevented by appropriate treatment. Some illustrative cases are given later. In fact, most of these lambs were actually moribund before resuscitative measures were adopted.

Maternal behaviour. Ewes generally showed no interest at all in stillborn or moribund lambs, but, as was shown in Table 8, many lambs were lively enough at birth, even in the low-plane twin group. Many low-plane ewes were slow to tend their lambs, because of exhaustion caused by labour. Continued interest of the mother was at least partly dependent on the liveliness of her lamb, but frequently low-plane ewes exhibited little or no sustained maternal instinct even with a lively lamb. Even when mothering was adequate, many low-plane ewes had little or no milk for their lambs, which quickly lost vitality through starvation. Table 10 illustrates these points.

We formed the impression that a ewe with a full udder was an attentive mother and

Table 9. *Deaths among lambs*

	Singles		Twins			
	High-plane	Low-plane	High-plane		Low-plane	
Total no. of lambs born	16	22	28		44	
Stillbirths	—	2	3	singles	14	(4 paired, 10 singles)
Neonatal deaths*	—	2	2	singles	17	(8 paired, 9 singles)
Presumptive neonatal deaths†	—	4	—		7	(2 paired, 5 singles)
Survived, with own mothers, during neonatal period	16	14	23	(18 paired, 5 singles)	6	(None paired, 6 singles)
		Causes of death				
Stillbirths	—	1 hydronephrosis	1 asphyxia		2 pregnancy toxaemia	
		1 haemorrhage *in utero*	2 no cause found		1 asphyxia, 11 no cause found	
Neonatal deaths	—	2 starvation	1 hydronephrosis, 1 no cause found		10 starvation, 7 debility—unable to stand	

* Deaths, usually within 48 hr., from causes present at parturition. † See text, p. 299.

Table 10. *Maternal behaviour of ewes*

	Singles		Twins	
	High-plane	Low-plane	High-plane	Low-plane
(a) Time after birth at which ewes began to tend their live lambs				
No. of observations	13	15	20	26
5 min. or less	12	9	19	13
6–10 min.	—	3	—	2
11 min. or more	1*	3	1*	3
Assistance to mother required	—	—	—	5 (maternal weakness)
Never tended lambs	—	—	—	3 (2 moribund at birth, 1 died in 24 hr.)
(b) Maternal attentiveness in cleaning lambs (excluding macerated stillbirths)				
No. of observations	15	17	25	39
Good	15	11	22	19
Perfunctory or casual	—	3	2	4
No interest	—	3 (1 stillbirth, 1 weakling lamb, 1 healthy lamb)	1 (dying lamb)	16 (7 stillbirths, 9 neonatal deaths)
(c) Willingness to allow suckling (lambs able to stand)				
No. of observations	15	18	20	23
Willing	12	10	18	3
Perfunctory or casual	3	3	2	14
Not willing	-	5	—	6

* Accuracy of record doubtful.

vice versa, although exceptionally a few low-plane ewes with small udders and almost no milk looked after their lambs with eagerness.

Table 11 shows the condition and measurements of udders in each group of ewes. Milk yields will be discussed in a later paper. Here it may be said that a typical high-plane mother with a single lamb had a bulging udder from which ample colostrum could be expressed, and the typical low-plane mother, especially with twins, had a small udder, from which a few drops of colostrum might be expressed with difficulty. The difference was reflected in the neonatal mortality rates (Table 9).

Table 11. *Condition and measurements of udders of ewes*

	Singles		Twins	
	High-plane	Low-plane	High-plane	Low-plane
No. of observations	16	22	12	21
Very good udder	7	—	6	—
Good udder	9	4	6	—
Fair udder	—	14	—	7
Poor udder	—	4	—	14
Average width of udders, diameter in line of teats (cm.)	19·2	14·9	18·7	12·4
Average distance between teats, point to point (cm.)	17·0	13·8	17·1	11·5

It was observed that hungry low-plane lambs often wandered out of their cages (there was ample space between the bars) and endeavoured to suck other ewes. As ewes soon knew their own lambs from strangers, these lambs usually received a hostile reception, and in consequence wandered around, visibly shrinking, until death from starvation overtook them, usually within 2 or 3 days, or they were rescued.

Condition of starving lambs. The earlier a starving lamb is aided, the better its chance. By judicious application of heat and bottle feeding, we were able to revive some lambs which were obviously well on the way to death.

A rectal temperature falling towards 100° F. was a danger signal, and once the temperature had started to fall rapidly it was very difficult to prevent death. The following histories of low-plane lambs are illustrative. (Those lambs that recovered under treatment were classified as 'presumptive neonatal deaths'.)

Lamb 348

One of twins born at 7 p.m. on 8 April 1947; weight 2530 g. Mother has very poor udder. 9 *April*. 10.30 a.m. 101·1° F.; 11.30 a.m. 101·0° F.; 12 noon 100·8° F. Given a good suck at a high-plane ewe; sucked strongly. 12.45 p.m. 102·0° F.; 3 p.m. 102·0° F.; 4 p.m. 103·0° F.; midnight 101·6° F. Standing, but listless. Apparently had no milk from mother and cannot be persuaded to suck teats, though it sucks a finger quite strongly.

10 *April*. 4 a.m. 95·4° F. Too weak to suck a high-plane ewe, and very apathetic, though just able to stand and bleat strongly. Given 2 oz. cow's milk by bottle (sucked strongly) and put in incubator room. 7.45 a.m. 102·0° F. Slightly more lively and sucked a high-plane ewe vigorously. Replaced with mother. 10 a.m. 100·0° F.; 10.30 a.m. 99·4° F. Weak and listless, but able to stand. Fed 2 oz. cow's milk, but not very interested. Returned to incubator room. 12.30 p.m. 102·8° F. Condition rather worse. 2.30 p.m. Moribund and unable to stand or suck, though quite warm. Bleat fairly strong, but infrequent. Stomach felt bloated. Lamb killed.

Lambs 345 *and* 346

Twins born at 6.30 p.m. on 7 April 1947, weights 2330 and 2375 g., respectively. Udder development of ewe negligible.

8 *April*. 12 noon. Lamb 345 very collapsed and unable to stand, lying spread-eagled. Temperature 102·8° F. Given 2·5 oz. cow's milk by pipette (unable to suck). After feed was just able to stand and mouth teat. Bleat fairly strong. Temperature after feed 101·1° F. Lamb 346 had definitely had no milk by 12.45 p.m. (Crusts still on teats. One drop of colostrum expressed with difficulty.) Lamb keen but thin and becoming weak. 2.30 p.m.: lamb 345, 94·4° F.; lamb 346, 102·4° F. Lamb 345 is moribund and unable to stand or suck. Bleat feeble. Given 2 oz. cow's milk by pipette. Barely able to swallow. Lamb 346 fairly lively, and sucked 1 oz. cow's milk from bottle. 4 p.m. Lamb 345 died. Lamb 346 still lively.

9 *April*. Lamb 346 moribund; temperature not recorded on clinical thermometer (under 94° F.). Unable to swallow when given milk by pipette, and died at 12.50 a.m.

Lamb 269

Single lamb, weighing 4085 g., born about 5 p.m. on 12 March 1947. Lively and eager to suck.

13 *March*. Looking very empty, with loose, sagging skin. Temperature 99° F. Given 6 oz. cow's milk.

14 *March*. Moribund. Given 50 ml. saline into flank, and several oz. of warm milk by pipette. Rectal temperature 68° F. (by laboratory thermometer). Pulse 40/min. Placed on heated tray in warm room. After 2 hr. could lift head. Pulse rate 80/min. but irregular. Breathing laboured. Belly looked bloated. 1 hr. later could stand. Breathing fast and jerky. Given 2 oz. colostrum from a high-plane ewe and placed in incubator room.

15 *March*. In surprisingly good condition, though breathing fast and jerky. 50,000 units penicillin intramuscularly. Bottle fed.

16 *March*. Better. Tried lamb on mother, which had a little colostrum, but mother would not stand to be sucked. When ewe held, lamb sucked one teat vigorously. Lamb bottle fed.

17 *March*. Lamb given away as a pet. Reported to have died a few days later (cause not known).

Table 12. *Summary of main findings*

	High-plane		Low-plane	
	Singles	Twins	Singles	Twins
No. of ewes*	15	11	19	13
Average weight of food consumed from 70th day of gestation to parturition, in terms of gross digestible energy as starch† (kg.)	48·9	47·8	17·8	16·9
Average maternal weight change from 70th day of gestation to parturition (kg.)	+4·0	+2·0	−10·0	−12·0
Average weight of lamb produced (kg.)	4·79	7·00	3·76	4·55
Average weight of placenta produced (kg.)	0·44	0·90	0·49	0·57
Net production or loss of tissue (kg.)	+9·23	+9·9	−5·75	−6·88
Vitality of lambs at birth (Tables 7–9)	High	Adequate	Adequate	Poor
Survival rate at 4 days of age (Table 9) (%)	100	82	64	14
Maternal vitality after labour (Table 10*a*, *b*)	High	High	Impaired	Poor
Udder development (Table 11)	Good	Good	Poor	Very poor
Maternal instinct (Table 10*c*)	Excellent	Excellent	Impaired	Poor

* Only ewes for which complete data are available have been included in computing the averages in the first part of this table. The individual data from which the averages have been calculated are given in Table 6.

† See footnote to Table 1.

Productivity of groups, and individual variations. The salient points for each group as a whole, brought out by all the data already reported, are summarized in Table 12.

Table 6 gives data for the individual animals used in computing average productivities in Table 12. In an attempt to explain individual variations of birth weight within each experimental group, scatter diagrams were prepared in which birth weight and 'net production or loss of tissue' were plotted against average and total food intake from the 70th day of gestation, average weight change and percentage weight change of ewes. These diagrams, which are not reproduced here, can be reconstructed from the data in Table 6.

Within any given dietary group, there was no indication of any correlation between average or total food consumption of the ewe and the net production or loss of tissue or birth weight of the lamb. With high-plane single lambs there was a suggestion that bigger lambs were born to ewes gaining most weight, but a similar correlation was not evident in other groups. The variation in performance within each group (high-plane or low-plane; twins or singles) may therefore have been mainly an expression of genetic or other inherent metabolic differences. There is, however, no question that such variations within groups were overshadowed by differences between groups imposed by the diets during the second half of pregnancy.

It should be noted that the birth weights of lambs in comparable dietary groups overlapped to a considerable extent, despite a clear division of food intake and of 'net productivity'. In other words, several low-plane ewes succeeded in producing lambs as large as those of certain high-plane ewes, though the food intake of the one group was only about one-third of that of the other group. This confirms the generally accepted idea that the foetus is an efficient 'parasite' and that birth weight is not, in itself, a sensitive indicator of reproductive efficiency of individuals. Some low-plane ewes were capable of producing large and reasonably lively lambs, though the chances of survival of those lambs throughout the dependent early stages of separate existence were small.

DISCUSSION

It is apparent from the data presented that single lambs from mothers on a low plane of nutrition and twin lambs from mothers on a high plane of nutrition exhibited a similar degree of vitality, and that in both instances this vitality was lower than that of high-plane single lambs. Low-plane twin lambs, with their 32% stillbirth rate, high neonatal mortality and frequent constitutional weakness were obviously seriously devitalized as a result of the severe nutritional strain on the mothers. It is probable that, under natural conditions with exposure to the elements, all low-plane twins would have died very quickly.

But the vitality of the lamb is not the whole story. More low-plane singles than high-plane twins died, and the cause appeared to lie in the mother rather than in the lamb. The most important effect of underfeeding of the ewe seemed to be on her udder development and milk supply, which may have been so impaired that even a lively lamb simply starved to death. We shall show in a later paper that, provided a lamb has sufficient stamina to start life on its own, its subsequent performance is conditioned almost entirely by the food it receives, i.e. within certain limits, a poor start need not be a permanent handicap to growth and development. An inadequate milk supply of the ewe was frequently associated with a serious failure of maternal instinct, so that even if the mother had a little milk, the lamb may not have been given an adequate chance of sucking it out. There seemed to be little co-operation by other ewes, who resented the attentions of strange lambs, while they had their own lambs to look after.

Any attempt to apply the conclusions in this paper to human reproduction must be undertaken with due caution. There is little doubt that serious undernutrition of human mothers lowers the birth weight of infants, but mere lowering of the birth weight does not necessarily connote lowered vitality of the infant. Indeed, Smith (1947) claims that during the Dutch famine of 1945, although maternal undernutrition lowered the average birth weight of infants by about 10%, there was no increase of stillbirths and neonatal deaths, nor any obvious effect on lactation. The absence of any important effect on the vitality of the offspring of such a comparatively small decrease of birth-weight is understandable in the light of these data for sheep, as low-plane single lambs, though about 25% lighter than high-plane singlets, were not devitalized to any important extent. The low-plane ewes, however, did have impairment of lactation. Human twinning is so comparatively rare, that it is not at present profitable to compare the fate of our twin lambs with that of human twins, though it is not improbable that twin pregnancies in the Dutch and other famines were proportionately more liable to mishap, as they were in our sheep.

In the sheep, severe impairment of reproductive efficiency was caused by dietary restriction alone, in so far as the material environment and handling of all animals were similar, and individual variations were accounted for by random distribution. It is not unreasonable to suppose that the greater part of the wastage in lambing of hill sheep under natural conditions is due to impaired nutrition of the pregnant ewes. Several workers in the field of human reproduction (cited by Baird, 1945; Burke & Stuart, 1948) have produced direct or indirect evidence that the nutrition of the human mother during pregnancy has similar importance. Nevertheless, as human existence is considerably more complex than that of the sheep, particularly in respect of psychological factors, and since the physiology and pathology of human reproduction differ in certain respects from those of the ruminant, our findings in sheep have only suggestive importance for man.

SUMMARY

1. The effect of a restricted low-protein diet during the second half of pregnancy has been studied on Sutherlandshire Cheviot ewes. The dietary restriction was controlled so as to induce a gross weight loss of about 5% during this part of pregnancy.

2. In ewes carrying single lambs, there was little impairment of the vitality of lambs at birth, despite a considerable reduction of birth weight. The ewes, however, showed evidence of weakness after parturition, had little milk, and some had impaired maternal instinct.

3. When the additional strain of twinning was present, lamb vitality at birth was seriously impaired, maternal vitality was low, milk production was negligible and maternal interest in the lambs were frequently absent.

4. These findings have obvious importance for sheep farming. Caution must be exercised in applying them to the field of human reproduction.

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Permanent Colostomy in the Rat

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(*Received* 5 *August* 1948)

Fistulas at various levels of the alimentary tract of different animals are of great value in nutritional studies. The rat, although frequently employed in nutritional investigations, does not yet appear to have been subjected to studies with the fistula technique although these offer the best, or only, means of solving certain problems. In order to study the microbiology of the caecum it became necessary to devise a technique for making a permanent fistula into the gut of the rat.

EXPERIMENTAL

Site of fistula. The immediate object being a study of the microbiology of the caecal contents, the fistula had to be made either directly into the caecum or into the colon immediately distal to the caecum. The colon immediately distal to the caecum was chosen because greater thickness and muscularity made it more likely to withstand the operative technique.

Type of fistula. Because rats are inquisitive, it was decided not to use any form of cannula since the animal would probably subject the outer end to such abuses that success would be jeopardized. A 'complete' colostomy operation was devised and Fig. 1 *a* indicates that sampling of the intestinal contents or the injection of various substances into the colon or caecum can be easily done with this method.

Operative technique. For a general account of rat surgery reference should be made to the comprehensive book of Griffith & Farris (1942). Fine nylon monofilaments (nos. 1 and 2) were used throughout the present work, even for buried sutures; Haxton's (1945) warm approval of this material is justified.

Young (2–8 months old) rats are suitable. Anaesthesia is induced with a small dose of 'Nembutal' (Abbott Laboratories Ltd.) (0·004 g./100 g. body-weight injected intraperitoneally) and maintained, if necessary, with ether. The fur over the right side of