FACTORS AFFECTING FOETAL GROWTH AND DEVELOPMENT OF MERINO SHEEP WITH PARTICULAR REFERENCE TO MATERNAL NUTRITION

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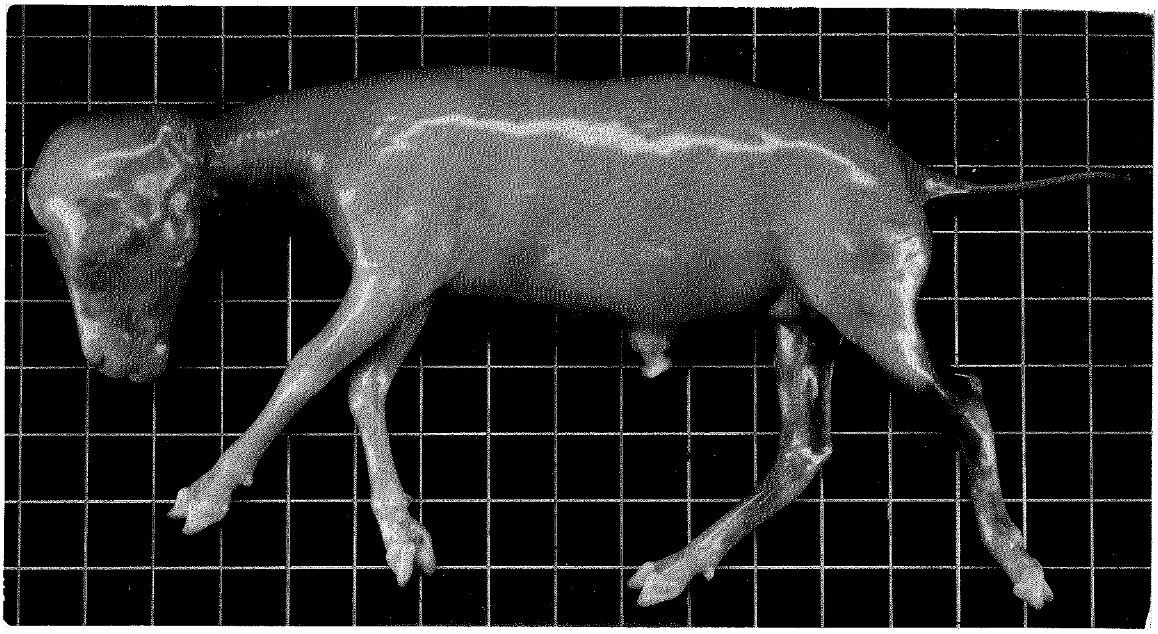

"..... and surely we are all out of the computation of our age, and every man is some months older than he bethinks him. For we live, move, have a being and are subject to the actions of the elements and the malice of diseases in that other world, the truest microcosm, the womb of our mother ....."

(Browne, 1642)

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SUMMARY

1. Prenatal growth and development of sheep was studied in two experiments.

2. Mature Merino ewes, mated to Merino rams, were kept under field conditions during the summer drought periods of 1962-63 and 1963-64 in the Mediterranean-type environment of Adelaide, South Australia.

3. Ewes were fed individually after mating on a controlled quantity of a pelleted ration to achieve desired rates of body weight gain or loss. Representative ewes were slaughtered at mating, and after 90- and 140-days of pregnancy.

4. Strong evidence was adduced that the growth of single foetuses in the first 90-days of gestation is dependent upon the level of maternal nutrition. Undernutrition in late gestation led to a marked reduction in the growth of single foetuses.

5. Male foetuses were heavier than females after 90-days of gestation, while the larger of two sires left heavier progeny after 140-days and at birth.

6. Body tissue reserves of the ewe partially protected the foetus from undernutrition in early gestation. Fat ewes offered feed *ad libitum* throughout pregnancy produced relatively light single foetuses after 140-days; this was associated with a steady decline in feed consumption from early pregnancy onwards.

7. Foetal body conformation, composition and skeletal ossification was very closely related to body weight. Undernutrition retarded foetal development in a general and not differential manner, with no obvious disturbance of allometric growth patterns.

8. Wool follicle and muscle fibre development were retarded by maternal undernutrition, with evidence of differences due to sex and the size of the sire.

9. Foetal weight and placental weight were closely related when the variance due to sex and sire was eliminated. Placental development was greatly affected by undernutrition.

10. Uterine fluids were increased in weight, and other components of the gravid uterus reduced, by undernutrition. Nutritional effects on other components of the ewe empty body were largely proportional to the effects on bodyweight.

11. Less greasy wool of lower yield was produced by undernourished ewes. Clean fleece production declined in late as compared with early pregnancy, lending support to the proposal of an adreno-cortical effect due to stress. Efficiency of wool production tended to decrease curvilinearly as feed intake increased.

12. The nett body weight response of the ewes to feed intake led to higher estimates for maintenance than those given in the literature for housed sheep but less than those for grazing animals. Nutrient requirements for weight gain were less than other estimates.

13. The literature is reviewed and the results discussed in relation to growth and development theories; to the grazing management of breeding ewes; and also to the retarded performance in postnatal life of sheep severely undernourished during their prenatal existence.

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STATEMENT

This thesis contains no material which has been accepted for the award of any other degree or diploma in any University and, to the best of my knowledge and belief, contains no material previously published or written by another person, except when due reference is made in the text of the thesis.

G. C. Everitt

1. GENERAL INTRODUCTION

Animal production, as a science, is basically one of integration relying heavily upon other scientific disciplines for information. The latter, coupled with practical agricultural experience, is collated into a complex programme of animal management. Productive efficiency of domesticated animals is thus governed by the action and interaction of biological, physical and sociological factors.

The study of animal growth is of paramount interest in the biological context, for growth itself is the product of diverse and powerful forces, blending with production on the one hand and reproduction on the other.

Much of the knowledge about mammalian growth originates from studies in postnatal life, for here cause and effect can readily be observed. The antiquity and variety of these investigations is symptomatic of the complex and dynamic nature of growth. The dominating nutritional influence on postnatal growth in relation to other factors receives general recognition.

Prenatal growth, on the other hand, particularly of domesticated animals, has received relatively scant attention. It is important that this should be rectified. An increasing proportion of the life-span of meat-producing animals, for example, is being spent in utero, due to a general policy of reducing slaughter age. Less obvious is the fact that the potential for later production of wool and milk, as well as meat, may be defined during gestation. Cells, tissues, organs and systems are all initiated here in a sequential developmental pattern, events of later life permitting or restricting their productive possibilities. The extent to which the latter may be modified by factors operating during the intra-uterine formative stages appears inadequately appreciated.

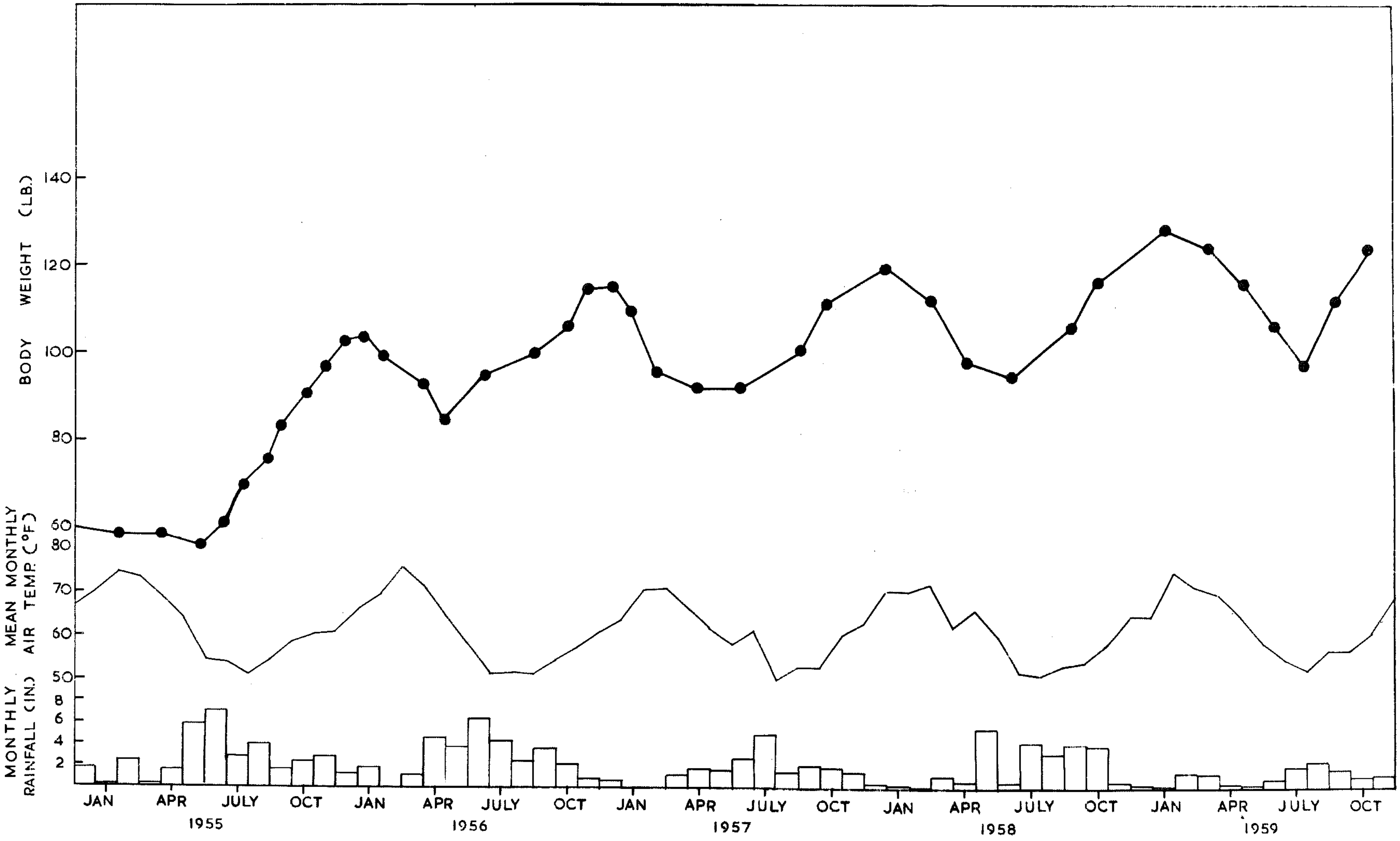
This thesis seeks a better understanding of factors affecting growth and development of the sheep in utero. A genetic component of variation and the effects of foetal sex on the growth of the offspring have been investigated. Maternal nutrition, however, was the principal factor studied. Nutritional influences in prenatal life are mediated through the maternal organism so considerable attention has been directed to the reaction of the mother; to the way in which she strives to protect her developing offspring from the stresses of an unfavourable environment.

Undernutrition bordering upon starvation threatens a large proportion of the world human population and it is upon the reproducing female that the burden rests most heavily. In this connexion, Barcroft (1946), the eminent physiologist, stated, "The prospect of semi-starvation which hangs over much of the world at the present time suggests the possibility of other researches on the effect of maternal malnutrition on foetal development". A modest contribution towards an improved appreciation of this universal problem represents an underlying philosophy of the present research programme.

Much dissension exists at present, however, as to the manner in which nutritional effects on developmental processes are manifested. This conflict of views is of great interest to students of animal growth, but is of particular importance in the production of domesticated animals. The opportunity to examine the effects of undernutrition on the development of the immature (foetus) and mature (ewe) sheep has been accepted in these present studies.

In the agricultural context, critical periods of undernutrition in the life cycle of animals at pasture may be associated with seasonal food shortage of natural origin or with deliberate managerial procedures imposed by man. The greater part of southern Australia, for example, is characterised by a Mediterranean-type environment with mild wet winters and hot dry summers. Nutritional requirements of grazing animals may be satisfied during the influential rainfall period of autumn-winter-spring from the available herbage of sown pasture. The dry mature herbage offering during the 4-6 months of summer drought, however, is deficient in both energy and protein and is frequently unable to support even maintenance requirements of grazing stock. Moreover, a delay in the onset of the autumn rainfall season may result in a quantitative deficit of pasture,

Fig. 1:1.- Seasonal changes in the growth of Merino wethers maintained on sown pasture in the Mediterranean - type environment of Adelaide, South Australia (from Donald & Allden - unpublished data; reproduced by permission of the authors).


BODY WEIGHT (LB.)
140
120
100
80
60
MEAN MONTHLY AIR TEMP. (°F.)
80
70
60
50
MONTHLY RAINFALL (IN.)
8
6
4
2
JAN
APR
JULY
OCT
JAN
APR
JULY
OCT
JAN
APR
JULY
OCT
JAN
APR
JULY
OCT
JAN
APR
JULY
OCT
1955
1956
1957
1958
1959

so that it is not unusual for the grazing animal to be subjected to prolonged periods of undernutrition.

Without the intervention of man the grazing animal thus suffers spasmodic food deprivation of varying severity. The animal strives to maintain itself, catabolising body tissue reserves accumulated during periods of plenty. Triumph over this environmental hazard leads the grazing animal subsequently to face relative feed abundance. By these means the growth curve of the pastoral animal assumes a biphasic form, with troughs and peaks associated with pasture productivity; an example is shown in Fig. 1:1. From the nutritional point of view the summer drought period is equivalent to the temperate winter; the undernutrition problem is common in principle if not in detail.

Man attempts to buffer these environmental rigours through herding his flocks and herds; by adopting methods of food conservation during times of plenty; and by offering the conserved fodder in times of natural shortage. However, man demands more of his beasts than mere survival. Domesticated animals are the converters of forage into milk, meat and fibre of use to man, and economic production is essential to the continuation of the animal industries.

Reproduction is particularly sensitive to environmental influences. This is unfortunate for breeding animals form a keystone in any animal production enterprise. A compromise between their nutritional and physiological demands with other managerial requirements peculiar to the local environment is frequently necessary. The time selected for mating breeding ewes is a good case in point.

In seeking yet further improvement of animal production from pasture man loads additional, perhaps unrecognised, stresses upon his animals. Production per unit area of land replaces production per animal as the criterion of economic success. Heavier stocking rates, within limits, increase output per acre but there may also be a concomitant increase of seasonal deficiencies, of drought risks, of vulnerability to disease and parasites, and of increased stress on animals and plants. Increasing the stocking rate generally necessitates restricting the feed intake of the grazing animal to a level below that of appetite leading, in turn, to improved utilization of available fodder.

In the strategical planning of breeding ewe management, early pregnancy has come to be regarded as a period of feed conservation with either maintenance or loss of maternal body weight. The degree to which weight loss may be enforced after mating without risk of damage to the maternal organism or her developing in utero offspring is not known. Nor is it known if the foetus possesses recuperative or compensatory powers of growth and development following a period of restriction, such as that commonly observed in postnatal life. These points receive attention in this thesis.

Success of the animal enterprise comes therefore to depend more and more on the extent to which man can exert effective control over the environment. Axiomatically, he must possess a comprehensive appreciation of the physiological limitations of his grazing animals. These studies attempt to define some of these limitations in the Merino breeding ewe.

The literature review commences by placing the experiments, and their underlying hypotheses, into the context of the environment with collation of general information about reproduction and the grazing management of breeding ewes. Notes on the definition, measurement and analysis of growth phenomena follow with an appraisal of normal prenatal growth and development of ovines. In order to place the role of maternal nutrition in proper perspective it is necessary to appreciate, in the broadest possible terms, all the factors known to affect ovine foetal growth, and a discussion along these lines is presented.

An account of the programme of investigation expressing the philosophy of the work undertaken follows the literature review. The programme involved two experiments and the report of each of these has been divided into sections dealing with the methods, results and their discussion; followed by a general discussion and conclusions. A bibliography and appendices conclude the thesis.

2. LITERATURE REVIEW

A. THE ENVIRONMENT

I. A Brief Outline of the Australian Environment and the National Sheep Flock

Australia, a land mass of approximately 3 million square miles, lies between 10° and 43° south of the equator. A hot dry continent, it corresponds in latitude with Greece, southern Spain and Mexico of the northern hemisphere. The wide variations in physical geography, soils, climate and vegetation have been described in detail by several authorities (C.S.I.R.O. 1949). Land resources of Australia are summarised in Table 2:1, taken from Carter (1962), and in Fig. 2:1, after Trumble (1946). Less than one-third of the total area receives an adequate precipitation. In general terms, the high rainfall coastal areas receive an average of 20 in./year, the fringe wheat-sheep zone 10-20 in./year, and the vast inland pastoral zone 5-20 in./year. Seasonal and annual rainfall varies markedly however, and drought, potentially of catastrophic proportions, represents a constant problem throughout most of Australia (Franklin 1962).

The total sheep population of Australia numbers approximately 153 millions, with 30 per cent. in the high rainfall areas, 40 per cent. in the wheat-sheep zone and 30 per cent. confined to the inland arid pastoral country (Comm. Bur. Census Stats. 1963). Three-

TABLE 2:1 LAND RESOURCES OF AUSTRALIA (after Carter 1962)

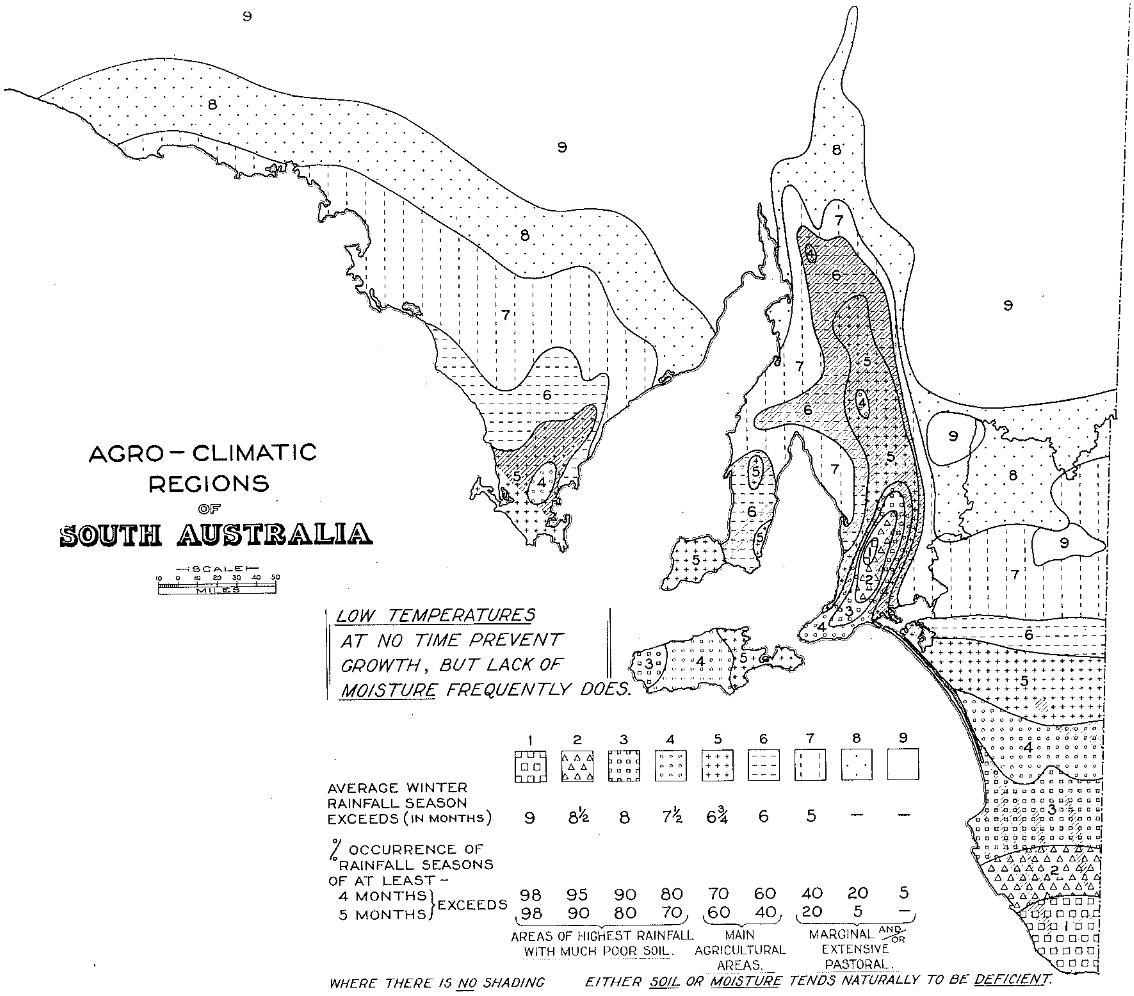
State or Territory (Area and Percentage)	Regions of Satisfactory Rainfall		Existing and Potential Land use			
	Area m.acres	Proportion of Total %	All crops, fallow, resting* m.acres	Forest m.acres	Improved Pasture m.acres	Residual available for development** m.acres
South Australia (380,070 sq.mls.; 12.79%)	26.59	10.9	6.50	0.76	4.60	8.08
New South Wales (309,433 sq.mls.; 10.42%)	112.23	56.7	9.80	7.86	9.53	56.98
Victoria (87,884 sq.mls.; 2.96%)	52.06	92.6	8.00	5.74	10.77	14.53
Queensland (667,000 sq.mls.; 22.45%)	225.82	52.9	3.80	9.02	2.26	154.29
Western Australia (975,920 sq.mls.; 32.85%)	87.34+	14.0	9.00	6.88	7.69	41.94
Tasmania (26,215 sq.mls.; 0.88%)	16.78	100.0	0.40	3.04	1.39	7.76
Northern Territory (523,620 sq.mls.; 17.62%)	57.98	17.3	0.01	0.36	-	43.11
Aust. Cap. Territory (939 sq.mls.; 0.03%)	0.60	100.0	0.01	0.13	0.07	0.24
Australia (2,971,081 sq.mls.; 100.00%)	579.40	30.5	37.52	33.79	36.31	326.93

* Resting includes volunteer leys

** Based on 75% utilization of well watered area.

\+ Includes 17.19 m.acres in northern tropical area.

Fig. 2:1.- Agro-climatic regions of South Australia
(after Trumble 1946).



AGRO-CLIMATIC
REGIONS
OF
SOUTH AUSTRALIA

LOW TEMPERATURES AT NO TIME PREVENT GROWTH, BUT LACK OF MOISTURE FREQUENTLY DOES.

	1	2	3	4	5	6	7	8	9
	▣	△	▫	▫	+	┄	¦	·	☐
AVERAGE WINTER RAINFALL SEASON EXCEEDS (IN MONTHS)	9	8½	8	7½	6¾	6	5	—	—
% OCCURRENCE OF RAINFALL SEASONS OF AT LEAST – 4 MONTHS EXCEEDS	98	95	90	80	70	60	40	20	5
5 MONTHS EXCEEDS	98	90	80	70	60	40	20	5	—
	AREAS OF HIGHEST RAINFALL WITH MUCH POOR SOIL.				MAIN AGRICULTURAL AREAS.		MARGINAL AND/OR EXTENSIVE PASTORAL.		

WHERE THERE IS NO SHADING EITHER SOIL OR MOISTURE TENDS NATURALLY TO BE DEFICIENT.

quarters of the national flock are Merinos, 15 per cent. crossbreds or comebacks, 8 per cent. Polwarths and Corriedales and 2 per cent. British breeds. Merinos predominate in all States except Victoria and Tasmania.

Reproductive rates of the national flock are notably poor (Schinckel 1963), annual lamb markings percentages seldom exceeding 70 per cent. Watson (1962) stresses that in the world survey of sheep reproductive performance conducted by Thomson & Aitken (1959), marking percentages of between 20 and 30 for Merino sheep in the Australian inland pastoral zones were the lowest of any recorded. In a wider context, Moule (1962a) comments that, "The main essentials for high reproduction rates are a genetic predisposition towards high fertility, a high proportion of successful matings followed by a normal gestation, and a high rate of survival of new born lambs." and later acknowledges that frequently none of these requirements is fulfilled in Australia. Losses occur at all the three main stages considered by Robinson (1951, 1957) of importance in the reproductive process; (1) in the number of ova shed, (2) in the number of these ova that become fertilised; and (3) in the number of fertilised ova that develop normally by the time of birth. Adverse climate, nutrition and disease all exert their toll, apart from influences of breed, strain and age of the animal (Thomson & Aitken 1959; Watson 1957, 1962, 1964; Schinckel 1963). Reproductive failure is, in fact, a major problem of the Australian sheep industry. Provision of sufficient sheep to increase the national flock for the higher stocking intensities demanded by pasture improvement will probably represent a major problem of the future.

II. An Outline of the Environment of southern and South Australia with particular reference to the Waite Agricultural Research Institute, Adelaide

The State of South Australia, with a land area of approximately 380 thousand square miles (Table 2:1), represents 13 per cent. of the Australian continent. Only 11 per cent. of the State territory receives a satisfactory rainfall.

Soils of the State are varied (C.S.I.R.O. 1949) but 'red-brown earths' with a loam-textured topsoil, clay subsoil and calcareous deep subsoil are represented at the Waite Institute (Litchfield 1951).

A grazing stock population of some 15 million sheep and 300 thousand beef cattle is supported. Merinos account for nearly 13 millions, and "wool-type" (Merino, Corriedale, Polwarth) animals nearly nine-tenths, of the total sheep population (Comm. Bur. Census Stats. 1963).

The Waite Agricultural Research Institute, Adelaide, is located in an area with a climate representative of a large part of southern Australia. This Mediterranean-type environment has been

been described in general terms by several authorities (collated by Best 1958); in relation to agricultural production by Trumble (1937); and in the context of animal production by Donald & Allden (1959) and Willoughby (1959).

Mild wet winters and hot dry summers characterise the climate. At the Institute the mean annual rainfall is approximately 25 in. Winter rains of high reliability commence in the March-June period concluding in September - October. The cool rainfall period, of 6-7 months, is followed by a summer drought period of 5-6 months. For 3 months of the influential rainfall period the mean monthly temperature lies between 50-55°C. Pasture growth, although retarded by the lower winter temperatures, is not inhibited, some growth occurring during every month of the seven to eight months of influential rainfall.

Pastures of southern Australia have been described by Christian & Donald (1949) and those of South Australia by Donald (1958). The latter authority notes that South Australia, "... has little grassland; most of the area receiving over 10 in. annual rainfall carries a climax vegetation of sclerophyll forest, mallee or heath of negligible value for grazing purposes." Cleared, uncultivated ground will carry a sparse stand of perennial grasses of such genera as <u>Danthonia</u>, <u>Stipa</u>, <u>Eragrostis</u>, <u>Chloris</u> and <u>Aristida</u>. Mediterranean annuals commonly comprise sown pasture; Wimmera ryegrass (<u>Lolium</u>

rigidum Gaud.), *Phalaris tuberosa* L., barrel medic (*Medicago truncatula* Gaertn.) and subterranean clover (*Trifolium subterraneum* L.) being the principal sown species. The last species, Donald (1960) states, has been sown on 25-30 million acres in southern Australia, for it is remarkably successful as a fodder plant and in raising the fertility of vast areas of poor soils. The main effect of pasture improvement has been to increase forage production and conservation in the spring, with little contribution to "filling-in" the troughs between autumn and spring peaks (Moule 1962*b*). Each additional acre of improved pasture laid down is regarded by Kinsman & McLennan (1961) as responsible for an additional 1.3 sheep or equivalent in beef cattle.

Pasture improvement, resulting from the use of legumes and phosphatic fertiliser, has led to noteworthy increases in the number, and alterations in the structure, of the State stock population (Kinsman & McLennan 1961; Everitt 1962*a*). Fertilised pasture in South Australia increased in area from approximately 1.6 million acres in the 3-year period 1947-50 to 3.7 million acres in 1957-60. The State sheep flock increased over this time from 10 to 15 millions. Breeding ewes mated to "meat-type" rams (Longwools + Shortwools) have also increased markedly in the past decade (Comm. Bur. Census Stats. 1963), indicating the trend towards meat production in an improved environment (Everitt 1962*a*).

III. Animal Production from Pasture in southern Australia and the Nutrition of the Breeding Ewe

Climatic factors determining the rate of pasture production are such that the amount of material presented to the grazing animal in southern Australia varies profoundly both seasonally and annually. Sown pastures are more variable than the less productive native pastures.

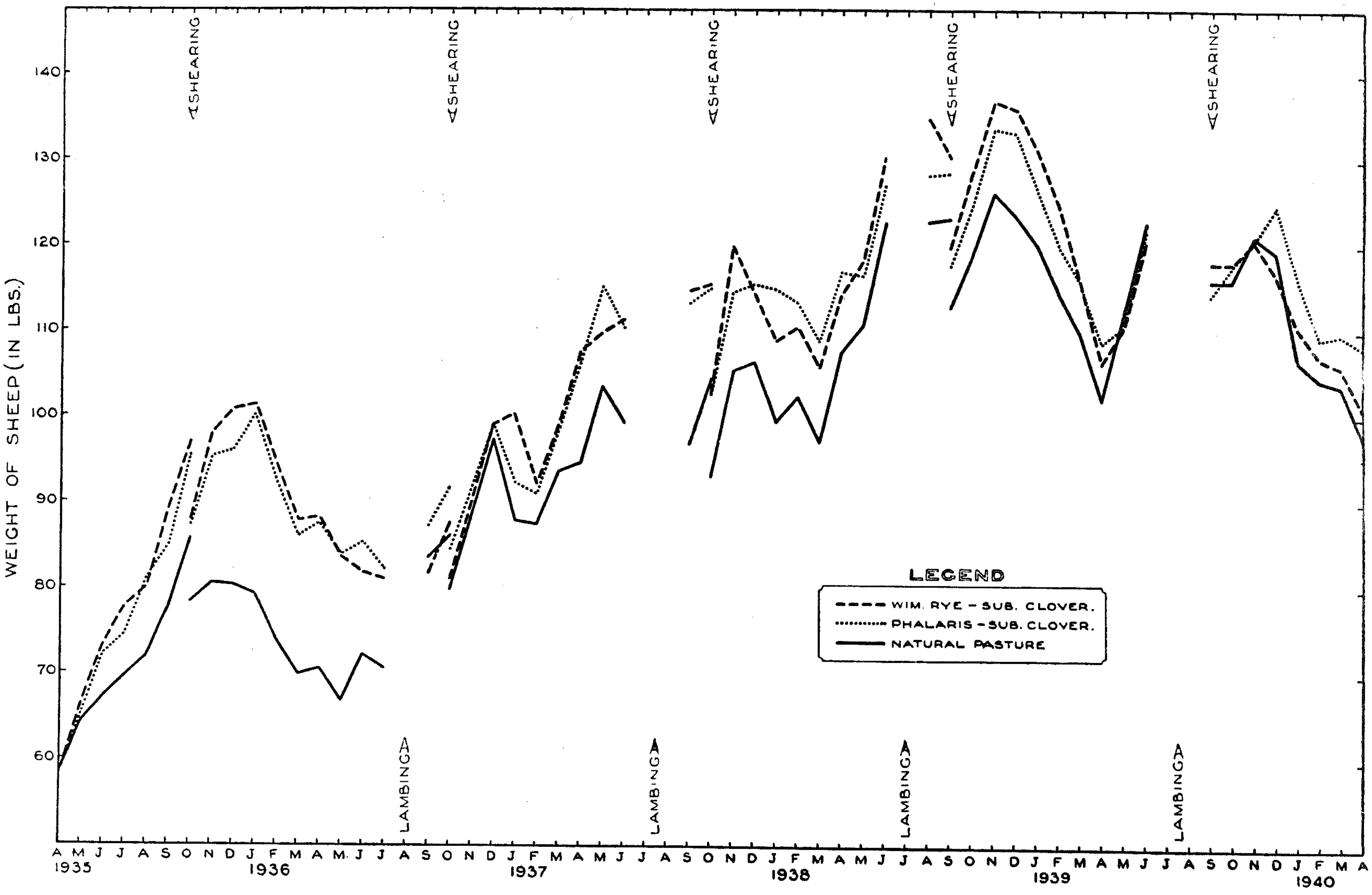
Excess pasture growth carried over from the spring flush into the summer rapidly dries and matures, becoming inadequate in terms of energy and protein supplies (Donald & Allden 1959). The herbage quantitatively dwindles as the summer drought continues until effective autumn rains reinitiate plant growth. If early and sustained rains occur pasture growth may exceed current demands of the animals. Any excess green feed is carried over into the winter, but rarely in sufficient quantity to satisfy livestock demands throughout this period of slow or even negligible pasture growth. The later the occurrence of regenerating rains in autumn and winter, the less likely is the pasture to grow rapidly enough to meet the immediate demands of the animals. The pasture is subjected to continued defoliation to low levels from growth initiation onwards and the livestock experience a prolonged dietary deficit. The rapid pasture growth in spring normally exceeds animal requirements, permitting some fodder conservation. With the approach of summer the species mature, dry out and digestibility falls to low levels (Willoughby 1959).

Despite recognised advantages derived from winter and spring lambing in southern Australia (Lang, Tulloh & Fennessy 1952; Allden 1956; Watson 1958, 1964; Dun, Ahmed & Morrant 1960; McGarry & Stott 1960; Lloyd Davies 1962) breeding ewes are commonly mated at the start of the summer period. This practice attempts to coincide lambing with the onset of autumn rains and renewed pasture growth, as well as ensuring that the offspring are well-grown by the time of the succeeding summer drought period (Weatherly 1958). Weaner ill-thrift during their first summer is a major problem of animal production in the environment (reviewed by Donald & Allden 1959). The superior ovulation rate of Merino ewes mated in autumn (Watson 1958, 1964), with improved lambing percentages (Allden 1956; Dun *et al*. 1960; McGarry & Stott 1960) is thus compromised by the ability of their offspring to survive the rigours of summer drought.

Breeding ewes mated in the spring are therefore pregnant throughout the hot drought season under gradually deteriorating pasture conditions. Increased nutritional demands of the ewes due to pregnancy can seldom be satisfied from pasture alone and undernutrition of varying severity, particularly in late pregnancy, becomes more the rule than the exception. Examples of these seasonal effects on the bodyweight of ewes, and of annual differences, may be seen in Fig. 2:2, taken from Neal Smith (1942).

Vital statistics of the Australian flock (Comm. Bur. Census Stats. 1963) indicate that about 55 million ewes are mated annually

Fig. 2:2.- Mean live weights of Leicester x Merino comeback cross ewes maintained on natural and improved sown pastures in the South-East of South Australia : from Neal Smith (1942). The marked fluctuations in body weight within seasons, especially in the latter part of pregnancy, and also from year to year, are associated with variation in pasture productivity.



SHEARING
SHEARING
SHEARING
SHEARING
SHEARING
LAMBING
LAMBING
LAMBING
LAMBING
WEIGHT OF SHEEP (IN LBS.)
140
130
120
110
100
90
80
70
60
LEGEND
WIM. RYE – SUB. CLOVER.
PHALARIS – SUB. CLOVER.
NATURAL PASTURE
A M J J A S O N D J F M A M J J A S O N D J F M A M J J A S O N D J F M A M J J A S O N D J F M A M J J A S O N D J F M A
1935
1936
1937
1938
1939
1940

but approximately 16 million ewes fail to produce a viable lamb surviving to independence. When commenting upon the Australian problem of undernutrition of ewes in late pregnancy, Reid (1961) states, "In a good season, some 600,000 ewes die each year in late pregnancy; at least 7 million lambs die in the first few days of life. We believe that the causes of these losses are largely nutritional."

B. THE DEFINITION, MEASUREMENT AND ANALYSIS OF GROWTH

I. General

(a) Definition

Growth is a complicated and highly integrated process. It is hardly surprising to find a near numerical equality of definitions with studies made of the subject; a state of affairs which Richards (1955) justifiably laments. For the purposes of formulating this present thesis, two definitions appear adequate.

In their classical treatise on human embryology Hamilton, Boyd & Mossman (1945) define growth as: "... increase in spatial dimensions and in weight, (and) is the resultant of three different processes:

(a) Multiplicative, increase in the number of cells;
(b) Auxetic, increase in the size of the cells; and,
(c) Accretionary, increase in the amount of non-living intercellular material."

Hammond (1940), in specific relation to farm animals, states lucidly:

"As an animal grows up two things happen: (1) It increases in weight until mature size is reached; this we shall call Growth, and (2) it changes in its body conformation and its various functions and faculties come into full being; this we shall call Development".

(b) Measurement and Analysis

The variety of techniques used in the measurement of animal growth has been reviewed on several occasions (Hammond 1940; Brody 1945; Zuckerman 1950; Palsson 1955; Pomeroy 1955; Brozek 1963). In brief, the animal growth curve is commonly expressed as either the actual weight of the animal over a specified time, or the weight gained per unit of time, or increments of weight expressed as percentages of previous weights. Each method has a number of advantages and disadvantages and, as Palsson (1955) comments, "The method used depends mainly on the point of view from which growth has been studied".

Developmental changes present greater difficulties of appraisal because of their spatial nature. Body and carcass linear measurements, together with carcass dissection (Butterfield 1963a), are frequently employed but photogrammetry and in vivo physio-chemical techniques (reviewed by Brozek 1963; Panaretto 1963; Kirton 1963,

1964) are now receiving great attention. The classical Hammond or Cambridge school evaluated developmental changes by, for example, expressing a measurement recorded at one age as a percentage of the same measurement at another age. When reviewing these established methods, Tulloh (1963) criticised their value and concluded, ".... it appears best to base calculations on the original data rather than to transform them into ratios or percentages,"; and advocated greater use of Huxley's (1924) allometric equation ($y = bx^k$). Richards (1955) too, states, "... when the allometric equation is adequate it should be used."

More complex mathematical representations of linear body measurements have been forwarded from time to time (e.g. Medawar 1945; Brody 1945). Taylor (1958), for instance, attempted an integrated description of the emergence and permanence of size differences. His proposed model of the linear growth process was:

$$Yt = pYt - 1 + M\ (1 - p) + Et,$$

where, Yt = size at age t; M = mature size; p = a constant growth potential; Et = growth error (the deviation from expected growth due to illness, malnutrition). The impracticability of this model supports Pomeroy's (1955) statement that, "The chief purpose of applying mathematical formulation to growth data is to facilitate the handling and interpretation of what is usually an unwieldy mass of observations. Consequently elaboration of mathematical treatment is only justifiable if it simplifies the interpretation of the observations, and any tendency towards mathematical elaboration without a corresponding gain in biological significance is best avoided."

Berrill (1955) agrees, believing that the mathematical sophistication and formidable terminology " ... have done much to obscure the issue".

II. THE SIGNIFICANCE OF THE ALLOMETRIC EQUATION IN GROWTH STUDIES

Huxley (1924) first demonstrated the simple but significant relation between the magnitude (weight or linear measurement) of a differentially growing organ or part (y) and the magnitude of an animal (x). He showed that:

$$y = bx^k$$

where b and k are constants. The constant b (fractional coefficient), Huxley (1932) stresses, has no particular biological significance since it merely denotes the value of y when x equals unity i.e., the fraction of x which y occupies when x equals 1; it is, in fact, as Hersh (1955) points out, the intercept value.

The constant k, on the other hand, assumes great importance for it implies that the ratio of the specific or relative growth rate of the organ to the relative growth rate of the body remains constant, the ratio itself being denoted by the value of k. Relative growth rate in this context is the <u>rate of growth per unit weight</u> i.e., the actual absolute growth rate at any instant divided by the actual size at that instant.

Huxley's (1932) exposition on allometry, or heterogony as he then termed it, is of special significance in anthropometry (Hersh 1955) and particularly in the interpretation of the experimental results presented in this thesis and it is worth dwelling further upon some of Huxley's proposals. He points out, for example, that in biological problems frequently little is known of the actual <u>rates</u> of growth but, since the organ and body have both existed for the same length of time when measured, the time factor cancels out. The actual rates will alter continuously but the <u>ratio</u> of the relative growth rates will remain constant.

Huxley termed k as the Constant Differential Growth Ratio or the Growth Coefficient of an organ. An organ may thus show positive or negative allometry if it is growing faster or slower respectively than the body as a whole; if it is growing at the same rate it is isometric. Large results stem from comparatively small deviations in k, provided that growth continues over a considerable range in size.

Another valuable aspect of the allometric equation is that the expression $y = bx^k$ can be transformed into:

$$\log y = \log b + k \log x,$$

to give, generally, a straight line from the slope of which k can be ascertained. Logarithmic plotting emphasises, too, the multiplicative nature of the growth process, equal spaces on the graphed logarithmic scale denoting equal amounts of multiplication. On the ordinary absolute scale equal spaces denote equal additions. Criticism of Huxley's attempt to derive a theoretical basis for his allometric equation have been forwarded (Medawar 1945; Richards & Kavanagh 1945; Needham 1950). The general consensus appears to be that it is a useful empirical formula for studying growth gradients.

III. GROWTH GRADIENTS

Differential development of body parts has been known for centuries. Xenophon (400 B.C.), for instance, knew that, "The colt that is largest in the shanks at the time he is foaled makes the biggest horse. For in all quadrupeds the shanks increase but little in size as time goes on, whereas the rest of the body grows to them, so as to be in the right proportion." (Marchant 1925).

Thompson (1917) showed that by employing Cartesian coordinates the shape of one species could be derived from the shape of a closely related species by controlled distortions of the grid. This geometrical transformation of an organism or organ provided evidence of the existence of orderly growth changes within the body. These changes in form were considered to result from alterations in the relative growth gradients of the parts of the body during the growth phase.

Subsequently, Huxley (1932) examined growth gradients in a wide variety of species through application of the allometric equation. Stephenson (1962a) comments that the equation can only relate the growth of a single part of the body or organ to the whole in any individual comparison, although it is possible to fit the curve to several measurements taken on different parts of the body and compare the results. Huxley (1932) recognised, and Stephenson (1962a) re-affirmed, that the validity of application of the equation depended upon, firstly, growth being multiplicative in nature and, secondly, the part and the whole commencing growth at the same age with constant growth relationships thereafter. The former of these two premises was reviewed by Stephenson (1962b) while Huxley (1932) himself devotes much discussion to the implications of the latter. Schmalhausen (cited by Huxley 1932) developed an equation to correct for differences in the commencement of development of the part and the whole. As the time at which organs start development is not accurately known this correction factor is ignored, meaning that the values of k in some cases may be slightly incorrect. As Stephenson (1959) points out, "The foetal life in sheep is relatively long, however, and provided the development of the parts that were measured occurs relatively early in foetal life, the error in ignoring this complication should not be great". At this present time there appears insufficient factual evidence to do more than recognise these possible limitations.

The studies of Scammon & Calkins (1929) on the prenatal growth of humans provided the first major contribution to the description of foetal growth gradients. Their existence in the prenatal life of a wide variety of mammals has since been demonstrated. In the sheep, major contributions are those of Hammond (1932), Wallace (1948), Palsson & Verges (1952), Joubert (1956a), Stephenson & Lambourne (1960) and Stephenson (1959, 1962a, 1964). These studies reveal gradients proceeding antero-posteriorly along the main axis and centripetally along the limb axes, with similar gradients for internal organ systems (vertebral column, gut; for example) as well as for the external form. A few exceptions have been noted (the sacral region of the vertebral column, for example), apparently concerned with special adaptive growth of particular organs or parts.

At birth the head, limbs and fore-quarters of the lamb are relatively well-developed, the skeleton relatively better developed than the skeletal musculature. "Waves of growth" (Hammond 1940) begin at the head and extremities of the limbs and spread down the trunk and up the limbs. The cranium of the axial skeleton is the earliest developing bone, waves of increasing growth intensity passing posteriorly towards the lumbar region and downwards to the nose and lower jaw. Growth in length of the long bones takes place earlier than growth in thickness. Little is known of the relative order of maturity of individual skeletal muscles in prenatal life but, in postnatal life, the abdominal muscles develop latest (Butterfield 1963b) and not the loin muscles as defined by the Cambridge school (Palsson 1955). Fat is accumulated in the various fat depots at different rates in the order of : mesenteric fat, perirenal fat, intermuscular and subcutaneous fat. A similar pattern occurs in the major tissues and organs which attain their maximum rate of growth in a definite order with age; broadly, nervous tissue, bone, muscle and fat. Allometric growth of individual organs appears primarily functional; brain, eyes, kidneys and heart, for example, being early maturing organs. Those organs of most physiological significance to the animal are relatively well developed at birth, as distinct from those organs which have an unimportant function until some time after birth (rumen, gonads; for example), when the young begin to eat fibrous food and reproduce.

Studies of the postnatal growth and development of farm animals (reviewed by Palsson 1955), in particular, have clearly shown not only the continuation of these gradients but how they wax and wane in the different regions of the body as time progresses.

Hammond (1921) first theorised that one of the chief advances made by man in creating improved breeds of sheep, and other meat animals, has been simply to steepen and extend growth gradients which already operate during the life of ancestral forms. His explanation implies that at the start of the growth period the dimensions of the parts and the whole are similar in both improved and unimproved types, but that as subsequent growth rates of the parts differ, differences in conformation soon appear. Thus, the body proportions of the adult Mouflon sheep develop only to about the same extent as exists in the improved Suffolk breed at approximately 3 months old.

Many of the concepts developed by the Cambridge school under Hammond, and since strongly advocated (Hammond 1940, 1961; Palsson 1955), rest upon this proposed ability of man to exert genetical and nutritional control over the growth gradients. Wallace (1948), however, from his studies of nutritional influences on prenatal and postnatal growth and development of sheep, opposed the view presented by his colleagues Hammond (1932, 1940) and Palsson & Verges (1952) working with sheep, and of McMeekan (1940-41) and Pomeroy (1941) with pigs. Even severe nutritional stress, Wallace (1948) contended, did not alter in great degree the allometric relationships of different parts of a tissue or body part. This suggested either that the effect of such stress was a general one on the part concerned and not differential in nature, or that a control mechanism within the individual maintained the normal allometric relationships under such stress conditions. Controversy impinged upon the validity of including fatty tissue in the comparisons.

Wilson (1958) concluded from work on goats that nutritional treatment effects should be examined on a fat-free basis, and challenged many of the significant results claimed by McMeekan (1940-41). Recent re-analyses of the original Cambridge data on sheep and pigs (Tulloh 1963; Elsley, McDonald & Fowler 1964) support Wallace's (1948) contention that striking nutritional effects on the growth gradients were recorded in the first place because differences in body weight, and especially body fatness, had been neglected in the comparisons. Body conformation differences in beef production assume no great importance when considered on a fat-free basis (Butterfield 1963b; Everitt 1963a). Profound differences in the anatomical and chemical composition of entire and castrated rams, entire and ovariectomised ewes become negligible when considered on a fat-free weight basis (Everitt & Jury 1965 a,b).

Gunn (1964a,b) disregarded body weight differences in his recent examination of the effect of levels of first winter feeding on performance of Cheviot hill ewes; he found quite large differential effects on live animal measurements, which were ascribed to nutritional and seasonal treatments. Taplin & Everitt (1964), on the other hand, could find little evidence of a differential nutritional effect on the linear dimensions of Merino lambs at birth, or later ages, after differences in body weight had been taken into account. For these animals differences in body fatness would be negligible in such a comparison, and the authors concluded that prenatal undernutrition manifested itself as an overall reduction in body mass - a conclusion in line with the allometric concept.

Scientific opinion is therefore sharply divided into two schools about the influence of nutrition on growth gradients. On the one hand, the Hammond school suggests that a period of restricted nutrition during prenatal and postnatal life differentially affects the various tissues or parts of the body depending on the stage of development at the time of restriction. On the other hand, exponents of Huxley's (1932) allometric concept propose that the form of an animal depends almost solely on its absolute size and restricted nutrition causes a more or less uniform retardation of development, except insofar as fatty tissue is concerned. Palsson (1955) highlights the contention by stating, "... since the plane of nutrition affects the various parts and tissues of the body as well as different parts of the same tissue differentially, the theory of a constant specific growth ratio between the growth of any two parts of the animal, formulated by Huxley (1924, 1932) in his heterogonic or allometric equation $y = bx^k$ and widely used by students of growth, cannot safely be applied to growth in animals of determinate growth

(Palsson & Verges 1952)".

Application of allometry to the effects of undernutrition in foetal life may nevertheless have to take cognizance of the difference between size and physiological maturity. To a large extent the size of an animal at birth determines its functional maturity and ability to survive (Alexander 1964c). Although a high plane of nutrition may promote rapid growth and development, and a small animal of the same age is always less mature than a bigger one, if one animal attains a given size more slowly than another it will in some respects be more mature by the time it does so. Appleton (1929), for example, showed how this applied in skeletal development of the rabbit foetus. Pomeroy (1960) found that the largest foetus within a litter of pigs was more advanced in ossification than the smallest but the appearance of ossification centres was not delayed in the latter. Wallace (1948) found that foetuses from ill-fed ewes were in a less advanced state of ossification than foetuses of the same age from well-fed ewes. A newborn animal of small birth weight after a normal gestation period will be more mature than one of the same weight born prematurely. In other words, a distinction between size, developmental and physiological maturity with age may need to be made.

Opposition to Hammond's (1921) proposal that man exerts control over evolutionary genetical growth gradients has also recently been forwarded by Stephenson (1962a). He compared prenatal growth and development of the Australian Merino and Romney x Southdown cross sheep foetuses at several ages. Breed differences in several dimensions were clearly shown, for which two explanations were offered. Firstly, that the allometric growth gradients differed between the two breed groups in those measurements showing most variation. The gradients, Stephenson contends, were altered only for certain specific types of measurements and the altered rate must take effect for almost the whole growth period. Secondly, morphogenesis may produce different dimensions of the parts at the start of the growth period, with similar subsequent growth rates leading to the conformation differences characteristic of the two types.

The second of these two premises appears *a priori* the most plausible. Castle & Gregory (1929) found a marked positive relationship between blastocyst diameter and racial size of parents. Breed differences in the size of the rabbit foetus are distinguishable as early as 41 hrs. after conception by differences in the number of blastomeres formed (Gregory & Castle 1931). These size differences may result from different amounts of glutathione (Gregory & Goss 1933*a*,*b*,*c*)- a coenzyme important in cell division, endocrine and metabolic activity (Crook 1958). The results of Beatty (1958) would also indicate genetical control over blastocyst size but variation in the latter may be due to differences between eggs in the time of ovulation, or the time of fertilisation, or maternal effects, as well as genetical factors (Hafez & Rajakoski 1964). In this connexion

Berrill (1955) states that, "Final size in these animals is accordingly a reflexion of early or even initial conditions". On the other hand, sheep and cattle embryos develop at the same rate during the first week after fertilisation (Green & Winters 1945), but with subsequent divergence in the rate of development. Clark (1934) found that ova from the same ewe corresponded more closely in their measurements than those from other individuals of the same breed. It is not yet known whether ovum size bears any relation to the subsequent growth of the foetus.

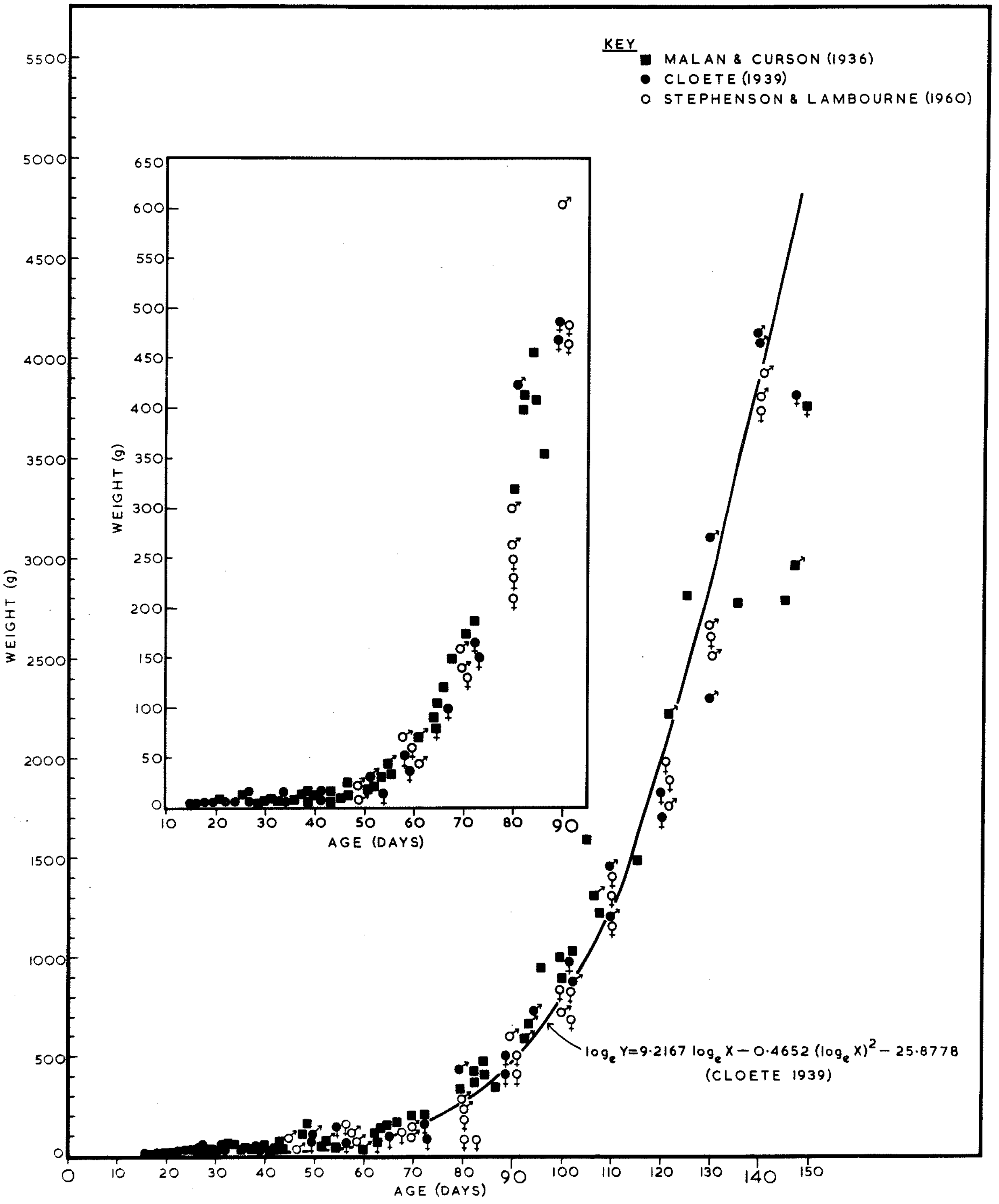
The finding of Tulloh & Romberg (1963) of a marked gravity effect on the shape of the long bones in sheep, overwhelming nutritional effects, also negates the plausability of Hammond's (1940, 1961) views on genetical and nutritional control of growth gradients.

C. NORMAL PRENATAL GROWTH AND DEVELOPMENT OF THE OVINE

Prenatal growth and development of the ovine has been thoroughly investigated by few workers. The studies of Green & Winters (1945) with the Shropshire, of Wallace (1948) with crosses between Border Leicester, Cheviot and Suffolk breeds, of Joubert (1956a) with unspecified breeds, and of Stephenson & Lambourne (1960) and Stephenson (1959, 1962a, 1964) with the Australian Merino represent significant contributions. Age changes in foetal body weight, and of a very limited number of external body measurements (mainly crown-rump length) have been recorded by others (Winters & Feuffel 1936;

Fig. 2:3.- Prenatal growth of Merino sheep. Constructed from the data of Malan & Curson (1936a), Cloete (1939) and Stephenson & Lambourne (1960). Males and females are shown where the sexes were recorded in the original data. The curve relates only to the data of Cloete (1939).

PRENATAL GROWTH OF MERINO SHEEP



Barcroft 1946; Eaton 1952; El-Sheikh, Hulet, Pope & Casida 1955; Alexander 1964b). Galpin (1935) gave ill-defined crown-rump measurements, but not weights, for New Zealand Romney foetuses. Foetal weight and crown-rump measurements for the Australian Merino were recorded by Dun (1955) and for the South African Merino by Curson & Malan (1935) and Malan & Curson (1936a). For the latter strain of the Merino, Cloete (1939) made a fairly comprehensive analysis of the weight and length changes of different parts of the body. The crown-rump age curves constructed by Cloete (1939) and Dun (1955) are sometimes used in determining the age of foetuses. Such estimates may be misleading (Alexander 1964b) due to retardation of foetal growth in weight but not in linear dimensions.

Available data about the weight-age relationship in Merino foetuses have been assembled in Fig. 2:3. The lamb makes about 70 per cent. of its growth in weight during the last 30 per cent. of gestation, increasing by approximately 200 g./day just prior to parturition (Wallace 1948).

The ovine embryo grows from a single cell of about 140 microns in diameter (Clark 1934) to a full-term foetus composed of many millions of cells of different types over a period of approximately 150 days (Asdell 1946). A convenient division of the prenatal existence, employed by several workers (Hammond 1940; Green & Winters 1945; Hamilton *et al*. 1945; Barcroft 1946; Palsson 1955; Robinson 1951, 1957) is into ovum, embryonic and foetal phases.

General principles of cleavage, early development and implantation of the egg are dealt with in detail by Boyd & Hamilton (1952) and Harvey (1959). In the sheep, the ovum phase is of 10-11 days duration (Winters & Feuffel 1936) and is one of cell cleavage, cell size decreasing progressively with little change from an approximately spherical shape. Nutritional requirements are drawn from the deutoplasm of the ovum while the many celled blastocyst absorbs fluids and metabolites from the uterine luminal fluid - the "uterine milk" - a time of substantial embryonic mortality (Hammond 1959).

During the tenth to the thirty-fourth day of gestation, the embryonic phase, growth proceeds by increase in cell number with comparatively little change in cell size or body weight (Joubert 1956a) but with differentiation of tissues, organs and their major systems and establishment of the main features of the external body. Histotrophic nutrition of this phase is aided by the vitelline circulation in the yolk sac (a transitory and minor route in the sheep), and the phagocytic trophoblast cells, the latter ingesting both cellular and fluid elements. Hammond (1959) compares the action of the phagocytic cells with cancer cells, with their uncontrollable metabolism. The first attack upon the uterine mucosa occurs between the seventeenth and eighteenth day after conception in the sheep; "... at this time there is a very loose attachment of membrane to caruncle, the former being held in position by the accumulation of fluid in the central portion ..." (Amorso 1952). The syndesmochorial-type placentation of the sheep continues to increase in size and weight until approximately 90 days of gestation; regressing slowly thereafter to term (Cloete 1939; Barcroft 1946; Wallace 1948).

From approximately 35 days to term (the foetal phase) absorption of nutrients takes place by the allantoic circulation of the placenta. The nature of the blood-borne nutrients consists of amino-acids, glucose, a limited amount of protein but apparently no fat (Popjak 1954). Fat may be taken up by the placenta but if so it is then broken down to smaller molecules which pass on to the foetal soma for synthesis in the appropriate way. Amino-acids and many minerals appear to reach the foetal blood stream by active transport across the placenta (Huggett & Hammond 1952; McCance & Widdowson 1961) but it is not yet known how the foetus acquires essential fatty acids.

The various foetal organs grow at markedly different rates (Wallace 1948) with great increase of cell size but not number (Joubert 1956a; for skeletal muscular tissue), and with change in external body form (Cloete 1939; Joubert 1956a; Stephenson & Lambourne 1960; Stephenson 1959, 1962a) resulting in continuous changes in conformation. Late gestation, especially from 90-days onwards in the sheep, is a stage of "... rapid absolute increment rather than of striking differentiation, and the changes in external body form take place quite slowly through differences in the relative growth rates of the various segments and parts of the body". (Scammon & Calkins 1929).

Skin and skeletal muscle are two tissues of direct interest in animal production; the former primarily because of its close association with wool production, the latter not only for its obvious importance in meat production but also because of associations with body size, metabolism, locomotion and general efficiency of production.

Prenatal development of sheep skin with its constituent wool follicles has been the subject of much research effort. The mass of literature is reviewed by Fraser & Short (1960) and Schinckel (1963). For the present purpose it is sufficient to note certain salient features. Primary and secondary follicles are the morphological units from which wool fibres are produced. Primary follicles are all initiated prior to 90-days of foetal age; secondary follicles are initiated from then until the time of birth. In the Merino only a small proportion of the total secondary follicle population is actually producing fibre at birth (Short 1955). Follicle density is estimated from biopsy samples. The formula of Malan & Curson (1936b):

$$\text{Surface area} = 3.543 \text{ Foetal body weight}^{0.771}$$

is frequently used to estimate total follicle population, despite recognised limitations (Schinckel & Short 1961).

Morphological and histological studies of the prenatal development of skeletal muscle are sadly lacking. Wallace (1948) observed the development of the musculature as a whole, but the present state of knowledge is largely based on the studies of Joubart (1956a).

He inferred that the number of skeletal muscle cells is a genetic characteristic determined by 90-days of foetal age in the sheep. Subsequent growth of muscular tissue occurs by increase in the diameter and length of this constant number of fibres (Joubert 1956b).

Literature on the relationship between cell number, cell size and ultimate body size has been reviewed (Joubert 1956c; Everitt 1963b). Berrill (1955), when reviewing the determination of size, states that, "... body size is primarily a reflexion of cell number rather than cell size". A positive association between the number of nuclei in striated muscle and growth rate in beef cattle (Herold & Nelms 1964) and the pig (Staun 1963) has been reported.

The neonatal lamb thus results from a series of orderly processes that transform the single-celled ovum into a vastly complex organism typical of the species. At birth the lamb is born with a relatively large head and long well-developed legs and neck, while the trunk is short, shallow and narrow. In a metrical sense the potential for later production of wool and meat is largely determined by the time of birth.

Maximum growth takes place after the formation of the extra-embryonic membranes, differentiation of tissues and organogenesis. Absolute prenatal growth continues throughout gestation but relative growth (percentage increment change) declines from about mid-gestation

(Cloete 1939; Barcroft 1946; Brody 1945; Wallace 1948; Joubert 1956a). Time operates in all pregnancies however. The foetus can spend only a limited period in utero and foetal growth, even of singletons, may falter toward the end of its normal time there (McKeown & Record 1952), the postmature foetus showing signs of undernutrition and actually losing weight (McCance & Widdowson 1961), probably because of placental dysfunction (Gershon & Strauss 1961).

D. FACTORS AFFECTING OVINE FOETAL GROWTH AND DEVELOPMENT

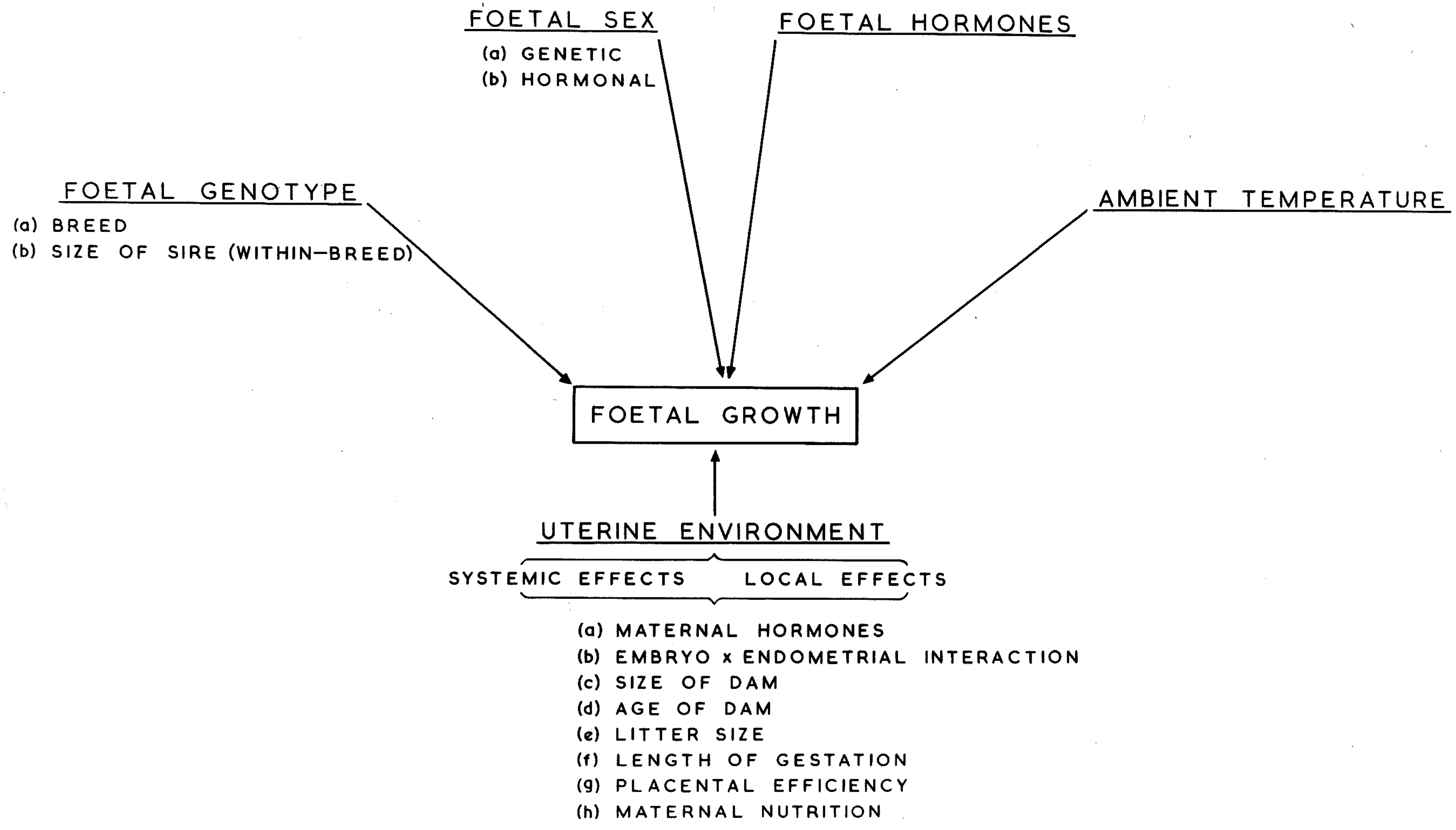
Postnatal growth of animals is directly affected by environmental influences, apart from genotype. For the animal in utero these same factors may operate directly or, together with others, indirectly, mediated through the maternal organism (Millis 1953).

Several reviews of factors affecting the birth weight of lambs have been published (Wallace 1948; Ali 1953; Guyer & Dyer 1954; Palsson 1955; Hunter 1956; Robinson 1957; Starke, Smith & Joubert 1958; Schinckel 1963). As Schinckel (1963) points out, birth weight per se may have little intrinsic value; its practical importance rests upon its relationship to lamb survival, to postnatal growth and to adult performance. Birth weight is also, however, an easily measured parameter of the intense physiological activity expended in utero during the preceeding 5 months in the case of lambs.

Major factors known to influence ovine prenatal growth are summarised in Fig. 2:4. Although not shown in detail, several of the

Fig. 2:4.- A summary of factors affecting foetal growth and development.

A SUMMARY OF FACTORS AFFECTING FOETAL GROWTH AND DEVELOPMENT



factors are inter-related in their effects, with circuitous routes of influence on foetal growth. Available literature about each of the factors is now reviewed.

I. Foetal Genotype

(a) Breed

Breed differences in lamb birth weight are well established (reviewed by Starke et al. 1958). Genotypic variation may account for 25-30 per cent. of the variation in birth weight within a flock (Chapman & Lush 1932).

Differences in linear dimensions of lambs due to the breed of sire were found by Jamison et al.(1961) to be highly correlated with birth weight. This proportionality of dimensions with body weight may well apply to other studies reporting striking breed differences in the conformation of offspring.

Bonsma (1939) found no significant difference in birth weight between first-cross lambs out of Merino ewes by Dorset Horn, Romney Marsh and Border Leicester sires; in contrast to earlier work of Colebatch & Scott (1931). Both Bonsma (1939) and Starke et al. (1958) concluded that the Ryeland is inherently larger at birth than most other breeds but this was due, in part, to a longer gestation period. This characteristic is transmitted to its offspring by the Ryeland sire whether mated to ewes of its own breed or crossed.

Columbia ewes provided a better maternal environment for foetal growth than Hampshire ewes in the study of Foote, Pope, Chapman & Casida (1959); the former breed was skeletally larger as judged by the length of the shin bone and the carcass. Bellows, Pope, Chapman & Casida (1963), however, reported the converse situation for these two breeds.

Metacarpus length, an early maturing character (Hammond 1932; Palsson & Verges 1952) was found by McLean (1948) to be highly heritable. Breed of the ram significantly affected birth weights of lambs, and metacarpal length, in the reciprocal crossing experiments of Hunter (1956) working with the large Border Leicester and small Welsh Mountain breeds. In the cross-breeding experiment of Foote et al. (1959) there was evidence that the additive genetic contribution of the Hampshire parents produced larger foetuses than that of the Columbia.

Starke et al. (1958) studied birth weights of lambs out of Merino, Blackhead Persian and various first and second cross ewes by sires of several breeds. They concluded, "... the sire exerts a decided influence on the prenatal growth of the foetus and its weight at full term".

The New Zealand Romney foetus grows at a faster rate than the South African Merino (Stephenson 1959). Breed affected growth in foetal body length in the study of Stephenson & Lambourne (1960), but at the same age and body length the Romney x Southdown cross produced a heavier foetus than the Australian Merino. A genetic effect (either primary or through maternal influences) on muscle size and weight, bone thickness and perhaps visceral weight, but not on increase in skeletal length, was suggested.

The Romney x Southdown cross foetus has a shorter neck of greater circumference and width than the Merino from an early age (Stephenson 1962a), with a wider head, longer nose and relatively longer and deeper trunk. Foetuses of this cross also differ from the Merino in the rate of increase with age of components in the growth of bone and muscular tissue, and in the conformation of the body at any particular weight (Stephenson 1964). Non-additive gene action was found by Bellows et al. (1963) in Columbia x Hampshire cross foetuses. The genetic contribution of the Columbia breed appeared dominant to the Hampshire in its effect on shin bone length in single foetuses.

Genetic differences between two breeds of one species depend, in the main, presumably on the accumulation of small genetic differences similar to those that lead to the formation of two separate species. If these small differences of genotype are to be usefully employed in improvement programmes then much more will need to be known about the extent, if any, that the growth and development of one tissue or part exerts an influence on another. Stephenson (1964) comments in this connexion, "If it is possible to define these growth gradients accurately then one could alter certain determinants and predict the effect of such alterations on the shape and composition of the body at any particular age .....".

(b) Size of Sire (Within-Breed)

Few workers have shown within-breed variations in birth weight to be due to the effects of different rams. Mumford (1901) and Humphrey & Kleinheinz (1907) concluded that the size of ram has little influence on the size of the lamb. Hammond (1932), however, found that mean birth weight of lambs differed between rams. Limited evidence of a size of sire (within-breed) effect was presented by Starke et al. (1958) but they recognised that their rams were immature and "... lacked sufficient variation in terms of size for a more critical analysis".

In view of the established importance of an inherited capacity for rapid growth rate in beef production, it is surprising that so little work has been undertaken to determine, in the first place, the influence of the size of the sire on the size, and especially growth rate, of the offspring in sheep. Evidence is available (Dun & Hayward 1962; Tallis, Turner & Brown 1964) indicating that wool production is not antagonistic in requirements to meat production, rapid growth rate with large ultimate body size being a desirable feature of both. When discussing the relationship between live weight and the efficiency of sheep production, Coop (1964) found that for every 4.54 kg. increase in live weight the feed requirement increased by approximately 7 per cent., at about the same rate as did fleece weight and twinning percentage. This means that in terms of efficiency of feed conversion or production per acre the large 68 kg. sheep is as efficient as the small 45 kg. sheep.

II. Foetal Sex

Sex has a twofold effect on live weight growth (Pomeroy 1955); a direct effect due to genetic differences between males and females and an indirect endocrinological influence. Stephenson (1962a), in commenting upon the chromosome balance of XX and XY within cells, cites a supporting example from *Drosophilla melanogaster*. Sex effects on postnatal growth and body composition of sheep have recently been reviewed (Everitt & Jury 1965a,b).

Ram lambs are generally heavier at birth, by 200-500g., than ewe lambs (reviewed by Starke *et al*. 1958; Donald 1962), although Hammond (1932), working with small numbers, reported the converse. Bonsma (1939) found that ram lambs were heavier than ewes at birth by 6.7 *per cent*., compared with estimates of 5.1 *per cent*. by Phillips & Dawson (1937) and Starke *et al*. (1958). Male pig foetuses were heavier than females at all the stages of gestation studied by Pomeroy (1960).

No sex differences in the birth weight of either Merino or Romney x Southdown cross sheep were recorded by Stephenson &

Lambourne (1960). They did find, however, that cross-bred males were heavier than females between 50-80 days of foetal age which they ascribed to a chance effect. Stephenson (1962a) reversed his opinion in further analysis of the same data; he concluded that ram foetuses of both breed groups were larger than females in the size of the head and neck, but only in early (50-80 days) foetal life. Disappearance of the sex effect with age was attributed to increased variation of the linear surface measurements in larger foetuses arising from nutritional and other environmental influences.

Sex effects on postnatal live weight growth are dependent for their expression on adequate nutrition (Palsson & Verges 1952). McKeown & Record (1953) reached a similar conclusion in relation to sex effects on human foetal growth. Starke *et al*. (1958) found that a dam of small body size inhibited full expression of the growth potentialities of the male lamb.

Placental development is related to foetal sex and thus to foetal growth rate (McKeown & Record 1953). At equal placental weight (cotyledons only), Alexander (1964a,b) found that ram foetuses were heavier than ewes.

Keller (1920) and Beer (1925) demonstrated somatic sex differences in the bovine foetus as early as the second month of prenatal life. The male was plumper and better muscled than the female in the cervical and shoulder regions - a result substantiated by more recent work with sheep in the studies of Stephenson

(1962a), using linear body measurements, and from carcass dissection (Hammond 1932; Palsson & Verges 1952). When reviewing sex differentiation in prenatal life, Amoroso (1956) concluded that castration of males has greater effects on growth than ovariectomy of females.

Further definition of sex effects on growth is clearly desirable from both academic and practical points of view. Sex effects a powerful influence on postnatal growth, feed conversion efficiency and body composition in postnatal life (Turton 1963; Prescott & Lamming 1964; Everitt & Jury 1965a,b) but little is known of the underlying physiological mechanisms, or of periods when growth is most sensitive to the sex influence.

III. Foetal Hormones

Sex effects on growth are, as mentioned earlier, intimately concerned with the endocrine system as a whole. The endocrine environment of the foetus has been reviewed in detail by Amoroso (1956) and Raynaud (1963) and, to a lesser extent by Macfarlane (1961) and Holm (1964). It is clear that this is a field of active endeavour with laboratory, but not farm, animals.

The free-martin condition, well-known in cattle but recently reported in sheep (Alexander & Williams 1964), indicates the existence of circulating sex hormones of foetal origin.

Stephenson (1962a), citing his own unpublished work with sheep, found no evidence of histological function of the foetal pituitary and thyroid glands prior to 80-days of age. He points out, however, that early differentiation of the gonads may lead to production of some male and female sex hormone without functional establishment of the hypophysis. Annison & Lewis (1959) found that the foetal thyroid of lambs was functional only in the last third of gestation.

Stress caused by restriction of the umbilical blood flow in the foetal lambs elicited a response of the denervated heart in the study of Reynolds (1953) which, he concluded, "... could only be due to epinephrine or a related substance." Holland (1958) found that the adrenals of the foetal rat were reduced in weight when their mothers were stressed by low atmospheric pressure. He suggested that increased concentrations of maternal cortical hormone circulating on both sides of the placenta inhibit foetal adreno-corticotrophic hormone and hence normal development of the foetal cortex.

With regard to hypophyseal and thyroid functions in the foetus, Macfarlane (1961) states that, "The foetus appears to have sufficient impetus from genetic and embryological processes to grow without a pituitary gland ..." and later, "On the other hand thyroid deficiency leads, even in the newborn, to stunting and defective metabolism."

IV. Ambient Temperature

Temperature effects upon postnatal performance and reproduction have been studied for some time. Clegg & Ganong (1959) and Winchester (1964) provide reviews of the topic with emphasis on temperate regions, while the reviews of Macfarlane, Pennycuik, Yeates & Thrift (1959), Macfarlane (1961) and Yeates & Parer (1962) devote greater attention to arid areas. It is, however, only in comparatively recent times that effects of ambient temperature on foetal growth *per se* have come to be appreciated.

Calves born after a hot summer gestation were observed by Bonsma (1949), in South Africa, to be smaller than those developing *in utero* in cooler seasons. Merino lambs born in tropical Australia were reported by Morley (1954) and Moule (1954) to also suffer retardation of birth weight.

In a controlled experiment with a small number of pregnant Romney ewes fed on lucerne hay, Yeates (1953) exposed the animals to temperatures of 40.5°C. Heat-stressed ewes attained a daily rectal temperature of 41°C compared with 39.5°C for unheated control ewes. Under hot conditions lamb mortalities *in utero* were recorded while the lambs born were retarded in size. Higher ambient temperatures (44.5°C for 7 hours each day over 3-4 months of late pregnancy) were needed to reduce birth weights, by 20 *per cent.*, of single Merino lambs in a later study by Yeates (1956). Heat stress and maternal undernutrition during pregnancy may exert an additive effect on lamb birth weight (Yeates 1958).

Shelton (1964) found that yearling ewes were affected by heat stress more adversely than mature ewes, as judged by lamb birth weights. This could, in fact, be a further demonstration of an additive effect of heat and poor nutrition, for the maternal tissues in young growing ewes may compete severely for a limited supply of nutrients (Hammond 1944).

It is claimed (Yeates 1953, 1956, 1958; Yeates & Parer 1962) that lambs born to heat stressed ewes differ in conformation from lambs born after maternal undernutrition. These workers suggest that the former are well-proportioned miniatures of normal lambs. The proposal rests upon the belief that undernourishment in prenatal life causes a differential effect on developing tissues and parts of the body; and conforms with the Hammond school in this connexion. Contrary evidence has recently been forwarded (Taplin & Everitt 1964) suggesting that prenatal undernutrition causes an overall reduction in body mass and that, <u>at the same body weight</u>, ill-fed lambs have much the same conformation as well-fed lambs.

Studies on the tissues of lambs dwarfed by high temperatures (Ryle & Morris 1961) nevertheless suggest effects of heat. Anterior pituitary and adrenal gland weights, corrected for differences in body weight, were greater in dwarf than control lambs. Dwarf lambs had a reduced cell size in the pituitary gland, with less cortex and smaller cells in the adrenal cortex, and a reduction in the number and size of cells in the urinary bladder. No effects on the foetal thyroid were observed. It would be of interest to examine these parameters in undernourished lambs of comparable body weight.

Macfarlane _et al_. (1959) suggest that foetal dwarfing may be due to, "... placental defect, reduced blood supply, pituitary insufficiency or adrenal steroid excess... " Macfarlane (1961) later inclines to the view that the foetal pituitary is in some way inhibited by the effect of heat _per se_ on the mother for, he points out, lambs dwarfed at birth can grow to normal size on good food. He concluded that the output of most of the endocrine glands appears to be reduced by ambient temperatures above 27°C. Neither cortisone nor corticotrophin given to the ewe influences foetal growth (Robinson & Morris 1960).

More recently, Shelton (1964) has concluded that the effect of heat in pregnancy is specific for the developing embryo as no significant effects were observed on the weight or body condition of the ewe. He proposes four possible physiological bases for the adverse effects. Firstly, that the high ambient temperature reduces thyroxine output and thus basal metabolic rate - a view in line with general observations (Macfarlane 1961). Secondly, a direct effect of body temperature on the rate of foetal cell division - a possibility receiving some support from the studies of Ryle & Morris (1961). Thirdly, that the developing embryo suffers a nutritional deficiency from reduced uterine blood supply; this might occur due to increased peripheral circulation as a means of dissipating increased heat load. Lastly, Shelton (1964) proposed a reduction in maternal feed intake through reduced foraging ability under field conditions, and/or voluntary reduction of intake in an attempt to reduce basal heat production. Graham (1964a) has found that the heat production of pregnant Merino ewes increases two-fold at subcritical temperatures (below 28-35°C) and is also elevated at high temperatures.

With the exception of Shelton's (1964) studies, most of the experiments conducted so far have involved small numbers of animals, with disproportionate sub-class numbers and confounding effects of sex on lamb birth weights. Evidence of a concomitant reduction in feed intake of heat-stressed ewes remains equivocal. Macfarlane (1961) states in this connexion, "It is not easy to distinguish the effects of nutrition and heat, however. Probably there are multiple interactions ... between food supply, thyroid, adrenal and pituitary functions." There is need for experiments, using large numbers of animals, with strict control of intake, and valid comparisons of characteristics of both heat-stressed and undernourished lambs in prenatal, neonatal and postnatal life.

V. Uterine Environment

Several factors contribute to the uterine environment; these are summarised in Fig. 2:4 and the evidence relating to each is examined in following sections of this review. Quite clearly, however, the partition of the uterine microcosm into components must be to some extent artificial for the action of one factor is generally dependent upon, and perhaps mediated through, others. Some physiological aspects of pregnancy has recently been reviewed by Holm (1964).

A. GENERAL CONSIDERATIONS

Studies of a maternal effect on foetal and postnatal growth, exerted through the uterine environment, with mice (Bateman 1954; Cox, Legates & Cockerham 1959; Brumby 1960), rabbits (Venge 1950; Adams 1953), pigs (King & Young 1956; Joubert 1962), sheep (Lopyrin, Loginova & Karpov 1950; Hunter 1956; Foote *et al.* 1959; Dickinson, Hancock, Hovell, Taylor & Weiner 1962; Bellows *et al.* 1963), cattle (King & Donald 1955; Joubert & Hammond 1958; Dickinson 1960), horses (Walton & Hammond 1938; Flade 1957) and man (reviewed by Drillien 1964) all provide evidence that the maternal contribution to variability of birth weight is greater than the paternal contribution. Large maternal size appears positively correlated with faster prenatal growth.

The classical experiment, described by Brody (1945) as a, "... dramatic illustration of spatial effect on growth ...", was that of Walton & Hammond (1938). They made reciprocal crosses between the large Shire horse and the small Shetland pony. Crossbred offspring were compared with foals of both pure breeds. At birth the crossbred foal from the Shire mare approximated three times the size of the crossbred foal from the Shetland mare. As postnatal life proceeded the size difference between the reciprocal crosses diminished, but was still marked at four years of age, at which time the weight of the foal from the Shire mare was still nearly twice that of the foal from the Shetland mare.

In cattle (Joubert & Hammond 1958; Dickinson 1960) the maternal effect on size at birth and subsequent ages is less striking than in the horse but exceeds that in sheep (Hunter 1956; Dickinson *et al*. 1962) while the latter is greater than in swine (Joubert 1962), rabbits (Venge 1950; Adams 1953) or mice (Bateman 1954; Brumby 1960). Bateman (1954) found that the prenatal influence accounted for 41 *per cent*. of the total variance in body weight of mice at 12-days of age; the postnatal influence accounted for less, 32 *per cent*.

The magnitude of the maternal effect appears proportional to the length of gestation or the time in which the uterine environmental factors can operate. When maternal tissues compete with the foetus for available nutrients over a longer period there is a greater effect upon ultimate foetal size.

For sheep, Hunter (1956) made reciprocal crosses between the large Border Leicester and the small Welsh Mountain. Comparison of the crossbred and purbred lambs out of the large and small mothers, respectively, showed that the small ram had less influence on the size of the lamb from the large dam than the large ram had on the lamb from the small dam. A small ewe may depress the weight of a relatively large foetus more than a large ewe would increase it, if the genetic difference in size is large enough (Donald, Russell & Taylor 1962). Lopyrin et al. (1950) also found that birth weights of both "transferred" and normally-born lambs depended chiefly upon the breed and body weight of the ewe in which they develop.

Further studies of maternal and genetic factors on the size of lambs at birth employing ovum transfer techniques were carried out by Dickinson et al. (1962). Reciprocal crosses were made between ewes of the large Lincoln breed and the small Welsh Mountain. Lamb genotype was the most important factor influencing body weight (considered as a late maturing character) and cannon bone length (early maturing). Although maternal x foetal interactions were recorded, the results largely agreed with those of Hunter (1956). As the maternal environment became smaller, and thus poorer in a general sense, genotype differences decreased in magnitude but nevertheless remained distinct. It was concluded that a ewe was able to respond to progressively greater demands by the lamb or lambs of progressively larger (combined) potential size - but in accordance with the law of diminishing returns.

Evidence of an "enhancement effect" on foetal growth in rabbits was offered by Beatty (1958). When genetically large and genetically small offspring are born in the same litter after heterospermic insemination, the average difference in birth weight between them was greater than when they were conceived in different litters after homospermic insemination. This accentuation of the difference in birth weight has been noted in twins of humans (Beatty 1956) and ovines (Donald & Purser 1956).

Three possible mechanisms whereby the maternal organism may be able to influence the rate of foetal growth and the size attained by the young at birth were suggested by Walton & Hammond (1938). These were:

(1) maternal regulation of foetal nutrition;

(2) maternal hormonal control; and

(3) cytoplasmic influences.

The evidence for each of these factors was reviewed by Hunter (1956) and there can be no doubt that the first, foetal nutrition, predominates in importance. Both Venge (1950) and Hunter (1956) concluded that a cytoplasmic influence on birth weight was negligible; this factor receives no further mention in this review.

Control of foetal growth was proposed by Hammond (1944) to be solely a systemic or general effect. He envisaged a limited pool of nutrients in the maternal blood for which the foetuses compete. As each draws its ration, so much the less remains for the others. Following on from the observations of Child (1920) of gradients of metabolic activity in the tissues and organs of the body, Hammond (1944) forwarded his "Theory of the Partition of Nutrients According to Metabolic Rate". The basis of his proposal is shown in Fig. 2:5, while Fig. 2:6 shows a diagram, published by Barcroft (1946), lending some support from a physiological point

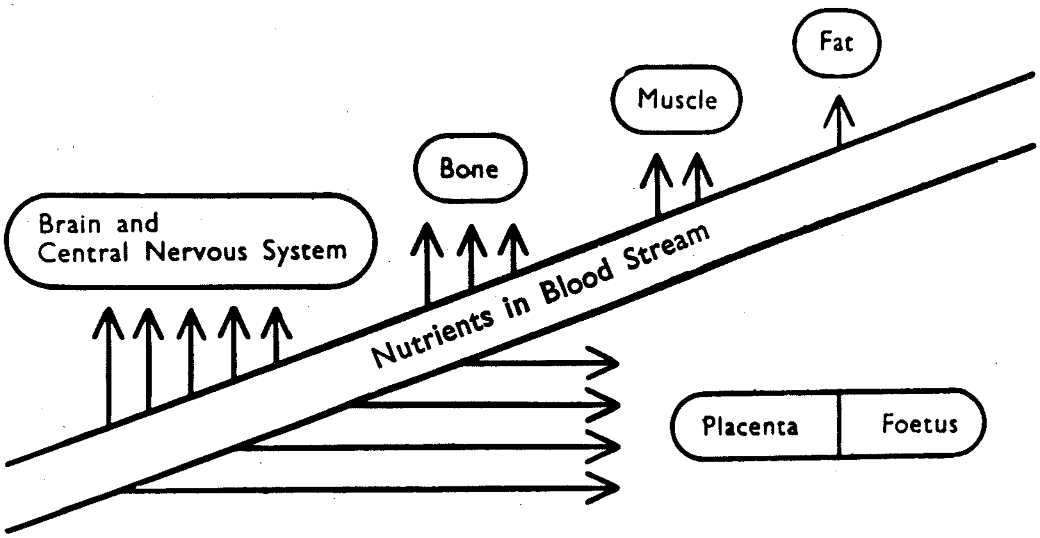
Fig. 2:5.- Diagram to illustrate "The Theory of Partition of Nutrients According to Metabolic Rate", proposed by Hammond (1944).

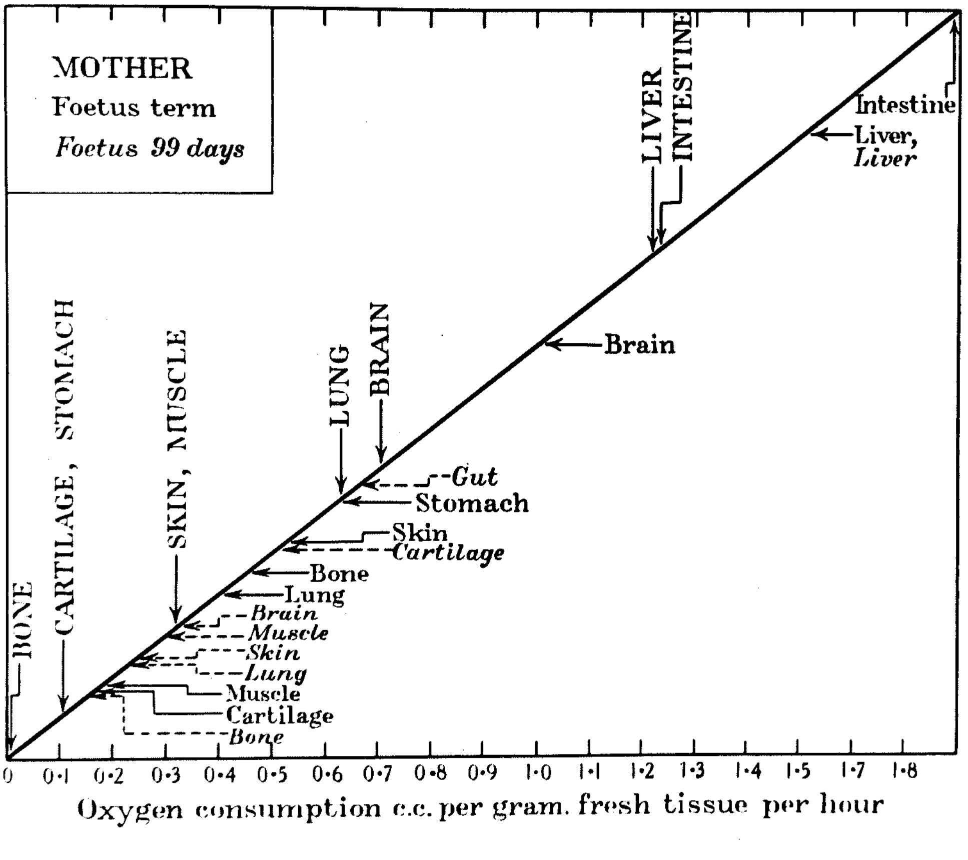
The number of arrows denotes the metabolic rate of the tissues, placenta and foetus.

When the nutritive supply is plentiful all tissues receive sufficient nutrients for normal growth as well as maintenance. Reduction of nutrients in the blood stream results in the deduction of one arrow from each tissue; deposition of fat stops, while growth of other earlier maturing tissues is retarded. Further reduction in nutritive supply reverses the arrow for fat, with deduction of a further arrow from other tissues. At a very low level of nutrition growth of bone ceases; fat and muscle are catabolised to provide for maintenance, the growth of the foetus and functioning of the central nervous system. Further reduction of nutrient supply results in foetal death and finally the animal itself.

Fig. 2:6 The metabolic rate of foetal and maternal tissues; from Barcroft (1946).

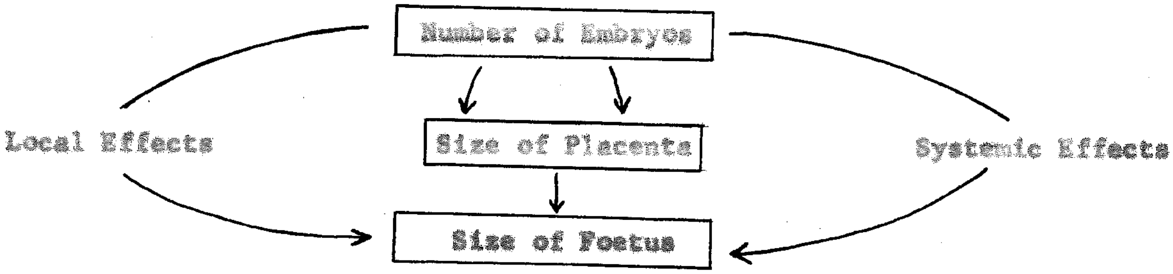
In most cases foetal tissues have a higher metabolic rate than their maternal counter-parts, with the exceptions of muscle and lung. Between 99-days and term all foetal tissues, except cartilage and muscle, show an increase in metabolic rate.


Fat
Muscle
Bone
Brain and Central Nervous System
Nutrients in Blood Stream
Placenta
Foetus


MOTHER
Foetus term
Foetus 99 days
BONE
CARTILAGE, STOMACH
SKIN, MUSCLE
LUNG
BRAIN
LIVER
INTESTINE
Intestine
Liver,
Liver
Brain
Gut
Stomach
Skin
Cartilage
Bone
Lung
Brain
Muscle
Skin
Lung
Muscle
Cartilage
Bone
0
0·1
0·2
0·3
0·4
0·5
0·6
0·7
0·8
0·9
1·0
1·1
1·2
1·3
1·4
1·5
1·7
1·8
Oxygen consumption c.c. per gram. fresh tissue per hour

of view. Palsson (1955) and Robinson (1957) have reviewed the evidence relating to the theory. It is, in fact, this proposal which forms a basis of the Hammond or Cambridge school of thought on the control of growth and development in domesticated animals.

Evidence suggesting the need for modification of the sole action of general effects on foetal growth has recently been forwarded. Eckstein, McKeown & Record (1955) studied pregnancy in the guinea-pig and found that the number of embryos in the same uterine horn was more important than the number in the opposite horn in determining both placental and foetal weights. They proposed that in addition to general effects there were important local effects operating, especially in multiple litters. The principle underlying the local effect is one of hydrodynamics of blood flow to the placentae. Their proposal is summarised below in the diagram taken from McLaren & Michie (1960):-



Eckstein *et al*. (1955) pointed out that, since resistance to blood flow through the placenta is low, the pressure at which blood is supplied to each placenta may be inversely related to the number of placentae

Fig. 2:7.- Control of prenatal growth, after McLaren & Michie (1960). The diagram shows the retardation of growth caused by:-

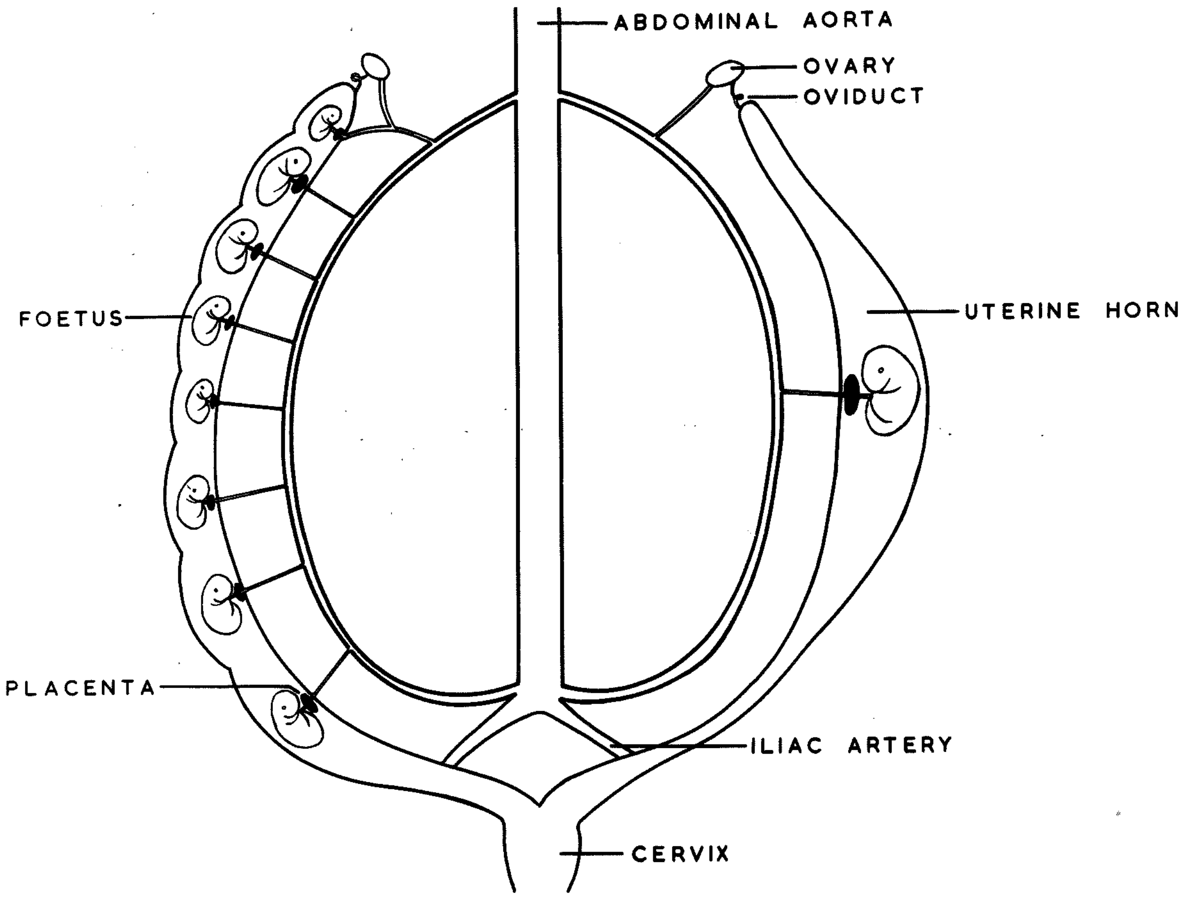
(a) more foetuses in the uterine horn;

(b) position of the top foetus in the horn; and

(c) increasing distance from the ends of the horn.

The correlation between placental and foetal sizes is also indicated.

CONTROL OF FOETAL GROWTH



after: McLAREN and MICHIE (1960)

supplied by the uterine artery on the same side. Blood supply, with its dissolved nutrients, may condition the rate of foetal growth, both directly, and also indirectly by determining placental size in early pregnancy. To accommodate residual, systemic effects Eckstein *et al*.(1955) postulated that changes of blood pressure on one side may be transmitted to some extent to the contralateral uterine artery.

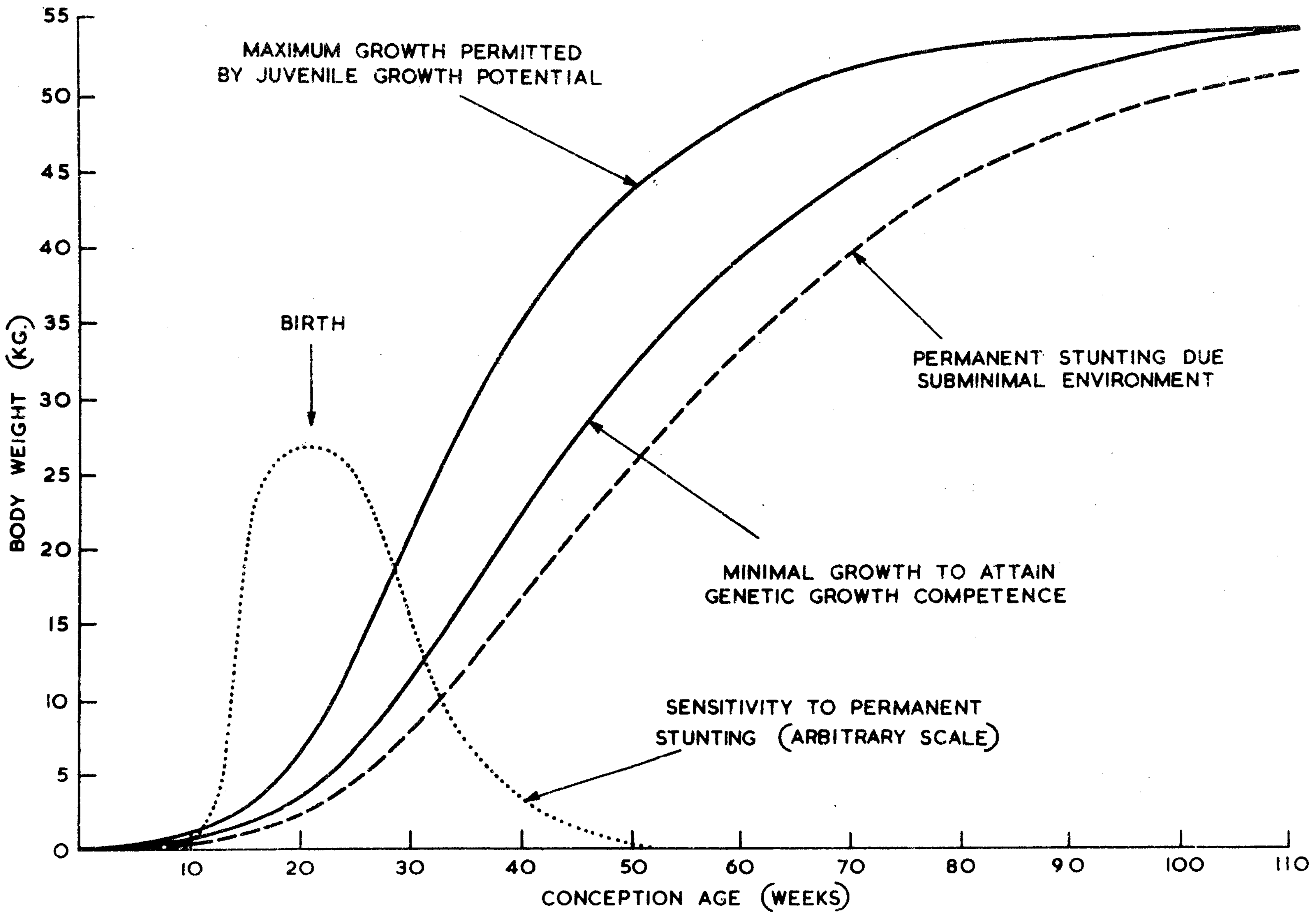
McLaren & Michie (1960) developed this haemodynamic theme of control of prenatal growth from experimental work with mice. Their summary of the various factors controlling foetal growth is shown in Fig. 2:7. The last sentence of their report is of interest; they state, "It remains to be seen whether such differences in weight at birth as that between the Shire-Shetlands and Shetland-Shires of Hammond and Walton can be accounted for in terms of vascular architecture and the mechanics of fluid flow."

Finally, the attractive hypothesis of Dickinson (1960) relating to maternal effects on mammalian growth may be noted. A model is proposed, illustrated in Fig. 2:8, which attempts to integrate nutritional and genetical control of growth. Two basic terms are suggested: (1) Juvenile Growth Potential, and (2) Genetic Growth Competence. The latter, in relation to an animal, tissue, organ or body dimension controls the level of nutritional requirements needed for maintenance and growth. When nutrients are in short supply the genetic growth competence represents the competitive status of

Fig. 2:8. The mammalian growth model proposed by Dickinson (1960), adapted by Schinckel (1963).

The relationship is between body weight and conception age for a hypothetical sheep maturing at about 110 weeks (conception age) and at 55 kg. body weight.

Schinckel (1963) added the parameter of "sensitivity to permanent stunting (arbitrary scale)" as an approximation from results in the literature.


MAXIMUM GROWTH PERMITTED
BY JUVENILE GROWTH POTENTIAL
BIRTH
PERMANENT STUNTING DUE
SUBMINIMAL ENVIRONMENT
MINIMAL GROWTH TO ATTAIN
GENETIC GROWTH COMPETENCE
SENSITIVITY TO PERMANENT
STUNTING (ARBITRARY SCALE)
BODY WEIGHT (KG.)
55
50
45
40
35
30
25
20
15
10
5
0
10
20
30
40
50
60
70
80
90
100
110
CONCEPTION AGE (WEEKS)

of the character under review. Furthermore, growth competence, Dickinson proposes, controls mature size, since growth of a character will cease when the metabolic potential of the character is only adequate to maintain the mass of tissue already formed. On the other hand, juvenile growth potential represents the ability of the young animal to grow when nutritional and general environmental conditions are favourable.

The model, "... envisages a family of 'normal' growth curves bounded by two extreme growth paths - a maximum path determined by the 'juvenile growth potential' and a minimum path conforming to the 'genetic growth competence'" (Schinckel 1963). Certainly this growth model is helpful in unifying the biological concepts of maternal effects, permanent stunting, compensatory growth and genotype.

B. SPECIFIC FACTORS OF THE UTERINE ENVIRONMENT

I. Maternal Hormones

Walton & Hammond (1938) suggested that growth hormone from the maternal pituitary gland may be a mechanism of co-ordination of foetal and maternal size. Preparations of anterior pituitary extract (Snyder 1934; Watts 1935) and purified growth hormone (Barnes & Sayer 1952; Coles 1954) injected during pregnancy increase the weight of the young at birth. Massive doses of progesterone fail to prolong pregnancy in the ewe (Bengtsson & Schofield 1963).

Hammond (1944) suggested that an internal secretion, or production of a metabolic substance by the mother, may limit foetal growth since the supply of unlimited food to a doe carrying a large litter does not increase the weight of individual young to the extent that they approach the weight of young in small litters.

Gregory & Goss (1933a,b,c) proposed that the amount of glutathione in the embryo may be a cause of breed differences in rabbit foetuses. Hammond & Marshall (1952) suggested that the amount of glutathione or its precursors supplied by the mother may be a limiting factor retarding growth of the young.

Thyroxine may also be a limiting factor (Ryle 1963) for the developing egg may require an increased oxygen supply (reviewed, Holm 1964).

II. Embryo x Endometrial Interaction

The end-product of the complex phenomenon of reproduction, offspring, represents the culmination of an integrated sequential pattern of physiological processes. The timing of one process in relation to another may be almost as important to final success as the process itself. Little is known about the importance of this integration in the prenatal growth of farm animals, but it is interesting that the stage of development of the embryo in relation to that of the endometrium can affect foetal growth and development in the rat (Noyes, Doyle & Bentley 1961). Fertilised ova were transferred into the uterine horns of recipient rats in different stages of pseudopregnancy. One additional day of development before implantation gave ova a selective advantage over normally developed controls in terms of foetal weight at term. Working with the rabbit, Hafez (1962) found that foetal growth may be retarded if the rate of embryonic development was asynchronous with that of endometrical progestation.

These results have considerable bearing upon the technique of ovum transplantation in the sheep (Moore, Rowson & Short 1960), where synchronisation of physiological states of donor and recipient plays an important role in success (Moore & Shelton 1964).

III. Size of Dam

The maternal contribution to the variability of birth weight is undoubtedly greater than the paternal contribution, especially in multiparous species. Venge (1950), for example, estimated that 50-75 per cent. of the variability in foetal size of rabbits could be accounted for by maternal factors, especially dam size.

Donald & McLean (1935) found an increase of 0.5 kg. in lamb birth weight for every 4.5-6.8 kg. increase in body weight of Merino dams. The weight of the ewe accounted for 24 per cent. of the variation in birth weight in Bonsma's (1939) studies; he estimated, too, an increase of 73 g. in birth weight for each 1.0 kg. increase in body weight of Merino ewes. Irrespective of breed, Hamada (1954) estimated birth weight to increase by roughly 100 g.

for an increase of 1.0 kg. in ewe body weight. Starke et al. (1958) recorded an approximate increase of 87 g. in birth weight for every 1.0 kg. increase in body weight of Merino ewes but less, 49 g. and 26 g. for Blackhead Persian first-crosses and second crosses out of half-bred ewes respectively. This positive relationship between ewe body weight and lamb birth weight has been appreciated for some time (Mumford 1901; Humphrey & Kleinheinz 1907; Hammond 1932). On the other hand, Hunter (1956) could find no significant within-group association in his reciprocal crossing experiments; probably because of small numbers of sheep. Ewes with longer carcasses produced heavier foetuses at 140-days of age, while ewes with fatter carcasses produced smaller foetuses, in the study of Foote et al. (1959)

IV. Age of Dam

The effect of the age of the dam on foetal growth and birth weight of sheep is difficult to dissociate from the effect of concomitant increase in maternal size.

Young dams that have not attained adult size continue to grow during their first pregnancy. Maternal tissues may therefore compete severely with the foetus for available nutrients (Hammond 1944).

Hammond (1932) referred to the inability of young ewes to produce lambs of equal birth weight to offspring from mature ewes. The influence of the age of the ewe on birth weight is sufficiently powerful to obscure the effect of foetal sex (Donald & McLean 1935). At equal ewe body weights, Bonsma (1939) found that lamb birth weights increased with successive pregnancies, which he attributed to the additional nutritional requirements of the young ewe for growth. Kincaid (1943) obtained an increase of approximately 286 g. in birth weight of lambs with each successive pregnancy from two-six years, while Starke _et al_., (1958) found a comparable annual increase of 227 g. up to the third pregnancy. In the reciprocal cross experiments of Hunter (1956) mature ewes gave birth to heavier lambs than young ewes.

Starke _et al_. (1958) cite research indicating that the larger size of mature ewes is independent of previous breeding; virgin ewes of mature age produced lambs of equal birth weight to those from ewes of similar age which had been previously bred. The effect of age of ewe is also related to an increase of gestation length; Terrill & Hazel (1947) estimated this at 0.27 days/year.

Breed and weight of ewe have been used to specify the maternal environment and magnitude of genetic demand. Such criteria are probably inadequate. Dickinson _et al_. (1962), for example, showed that Scotch Blackface ewes at their first parturition, although heavier than Welsh Mountain ewes in their fourth pregnancy, yielded somewhat smaller lambs.

V. Litter Size

An increase of litter size in polytocous species reduces the rate of prenatal growth because of competition between individual foetuses *in utero*. Venge (1950) concluded that the size of the litter in multiparous animals had the greatest influence of all non-genetic factors on birth weight. Foetal size tends to be inversely proportional to the number in a litter of rabbits (Wishart & Hammond 1933; Venge 1950) and pigs (Pomeroy 1960). This relationship appears determined, for the rabbit at least, by variation in placental functions and in the duration of pregnancy. Retardation of foetal weight in large litters becomes much more marked as pregnancy proceeds.

Among uniparous species multiple births occur to a greater extent in sheep and goats than in other members of the class; and this has an important bearing on the economy of sheep production. Starke *et al*. (1958) found that, at equal body weight of ewes, individual members of a twin lamb pair were 16 *per cent*. lighter at birth than singles but the pair was heavier, by 67 *per cent*., than the singles. This result agrees with most others. Singleton lambs may be some 120 *per cent*., and triplets 90 *per cent*., of the weight of twins at birth (Hammond 1932). Moreover, the nutrition of the dam during the latter stages of pregnancy affects the growth of individual members of a multiple litter more than that of singles (reviewed by Schinckel 1963).

Evidence on the mechanism of retardation of prenatal growth in large litters is conflicting. Hammond (1934) found the birth weight of rabbits to vary from 44 g. in litters of 13 to 98 g. in litters of 1. Smaller litters usually have the longer pregnancy but the decrease of birth weight is about 2 g. per individual for each additional young in the litter, independent of decreases due to the shortened pregnancy in large litters (Wishart & Hammond 1933). That such inhibition in foetal growth was not due to the large number present in the uterine horn, but to limitation of some nutritional substance in the maternal blood stream was postulated by Hammond (1944).

The latter belief has been modified recently by McLaren & Michie (1960), following on from the work of Eckstein _et_ _al_. (1955). These workers postulate that the influence of litter size on foetal size is manifested as the _local effect_ in addition to the _general_ _systemic_ _effect_ (Fig. 2:7) subscribed to by Hammond & Marshall (1952). An increase in the number of foetuses within the _same_ horn could have both local _and_ general effects on foetal growth; whereas an increase in the number located in the _other_ uterine horn could have only a general effect.

The ratio of local to general effects varies with the species. In the ox and sheep, with small litters, only a general effect is manifested. When the litter becomes numerically large, as in the rat, rabbit or pig, a local effect on contiguity of foetuses within the same horn becomes manifest. Casida (1956) and

Waldorf, Foote, Self, Chapman & Casida (1957) cite substantial evidence to show the existence of general and local effects affecting foetal growth in the pig. They conclude that general factors are less important in swine than in the guinea-pig (Eckstein & McKeown 1955), probably because of a "spacing" phenomenon operating in pigs, distributing embryos somewhat more equally in the two horns. No effect of position in the uterine horn was apparent with 4-5 piglets or less within a horn, but with 6 or more piglets those in the centre of the horn tended to be lighter than those at the cervical or ovarian ends. The finding that the foetal membranes were also lightest in the middle of the uterine horn, and were more affected than the foetal weight, agrees with the observations of McLaren & Michie (1960) on the mouse - see Fig. 2:7. In the sheep, El-Sheikh et al. (1955) found that the chorion at 40 days of gestation weighed less for twins than singles, and less in ill-fed than well-fed ewes, although in neither case were foetal weights reduced.

Placental development is thus affected by factors of the maternal environment (litter size, nutrition) before an effect on foetal growth is recorded.

VI. Length of Gestation

Asdell (1946) collated estimates of the length of gestation of different breeds of sheep. On the average, gestation in sheep lasts 150 days, but is influenced by many factors - reviewed by Hammond & Marshall (1952), Clegg (1959) and Holm (1964); while

McKeown & MacMahon (1955) present a detailed discussion of sex effects on the length of gestation in mammals.

In some animals, notably the guinea-pig and man, length of gestation is progressively reduced by an increase in litter size (McKeown & Record 1952; Eckstein & McKeown 1955) and this further limits the weight which multiple foetuses can attain *in utero*. A small reduction in the total time spent *in utero* can make a large difference to birth weight, and the extent of the functional development of the young, because the gain in weight is very rapid shortly before term. In the sheep, for example, foetal weight increases at a rate of approximately 200 g./day (Wallace 1948). Twin lambs are frequently carried *in utero* for a shorter time than singles (Asdell 1946), by 0.6 days (Clegg 1959). Kelley (1943), on the other hand, in Australia, found no difference between the length of pregnancy preceding single or multiple births after elimination of the effects of foetal sex and sire.

Gestation length in sheep has a heritability of 30-40 *per cent*. (Clegg 1959), and earlier-maturing mutton breeds (e.g. Dorset Horn) have a shorter gestation (144-148 days) than fine-wool breeds (147-152 days), such as the Merino (Terrill & Hazel 1947).

Although Clegg (1959) proposes that the gestation length of males exceeds that of females, Asdell (1946) concluded that sex of lamb has no detectable effect, in agreement with the work of Bonsma (1939) and Starke *et al*. (1958).

Poor nutrition in late pregnancy may reduce the time that the foetus spends in utero. Thomson & Thomson (1949) showed that maternal undernutrition during the second half of pregnancy reduces the length of gestation for twin sheep foetuses. Alexander (1956) reduced the gestation length of Merino ewes by applying a severe nutritional stress late in pregnancy; the reduction was greater the heavier the conceptus at the time of imposition of the stress.

In humans, Bishop (1964) established a correlation between maternal heart volume and prematurity. He proposed that patients with a small heart had a reduced cardiac output with decreased uterine blood flow; the latter resulting in a relative uterine hypoxia or other physiological change leading to myometrial irritability. No similar observations on domesticated animals have been made.

The recent studies of Alexander (1964a,b) on the sheep placenta strongly suggest that this organ plays an important part in the determination of gestation length. Biggers, Curnow, Finn & McLaren (1963) found that gestation length in mice was inversely related to litter size. This was believed to be a systemic effect and not due to local crowding in the uterine horn. They suggested that oestrogen, known to irritate the uterus (Reynolds 1949), secreted by the placentae might sensitize the uterus to the action of oxytocin. The total mass of the litter appears more important than the number of young (McLaren & Michie 1963).

Uterine distension may dictate, in part, the duration of pregnancy, for uterine "tolerance" to distension falls towards term and is less in first than second human pregnancies (McKeown & Record 1952). Guinea-pigs behave like humans in this respect (reviewed by Eckstein *et al*. 1955).

The time of parturition is therefore determined by the interplay of a large number of diverse factors (Holm 1964), and a question invariably raised in discussion is that of cause and effect; does the size of the foetus determine the length of gestation or is the latter determined by the former? Hunter (1956) reviews the evidence and his own observations provide probably the best compromise explanation of the phenomenon. He recorded longer gestation periods of Border Leicester ewes carrying "transferred" Welsh Mountain lambs than Border Leicester ewes carrying either pure-bred Border Leicester or cross-bred lambs. From this result Hunter suggested that a foetus considerably smaller than is normal for the breed is carried longer *in utero*. He also found that larger lambs were born after longer gestation periods. He postulated the operation of two mechanisms. On the one hand, foetal size may modify gestation length and, on the other, the length of gestation may modify the size of the lamb at birth. Probably both mechanisms operate simultaneously but the first is more effective when foetal size is extreme. Within a narrower range of foetal size length of gestation is the more influential factor.

VII. Placental Efficiency

The anatomical and physiological complexity of the several classifications of mammalian placenta (Amoroso 1952) is revealed by the extensive literature on the subject (Barcroft 1946; Amoroso 1952; Huggett & Hammond 1952; Villee 1960; for reviews).

Anatomically, the syndesmochorial-type placenta of the sheep serves as an arterio-venous shunt in the maternal circulation (Barcroft 1946) with close juxtaposition of maternal-foetal blood in the cotyledons (Wimsatt 1950; Crawford 1956; Tsutsumi 1962). Growth of the maternal placenta is considered by Huggett & Hammond (1952) to be in the nature of a scar tissue reaction attempting to repair damage done by the encroachment of the trophoblast.

Physiologically, the placenta plays an active role in foetal nutrition (Huggett & Hammond 1952; Popjak 1954; Robinson 1957; Dancis 1960; Hagerman & Villee 1960; Widdas 1961; for detailed reviews). Moreover, it has an important endocrinological part to play in pregnancy (Amoroso 1952, 1955, 1960; Holm 1964) with its ability to secrete oestrogen (Harkness, McLaren & Roy 1964) and progesterone, release of gonadotrophins and, possibly, adrenocortical-like steroids. These latter functions are strikingly illustrated by the ability of the intact placenta to preserve pregnancy phenomena in the absence of the foetus (Amoroso 1955; Lehr, Krukowski & Colon 1964).

It follows, therefore, that the amount of food reaching the foetus depends on the quantities of available nutrients in the maternal blood flowing through the placenta, together with the size, age and other parameters of the organ (Villee 1960) which formulate its efficiency. A quantitative assessment of overall placental efficiency cannot yet be made (Holm 1964). However, further progress with an artificial placenta (Lawn & McCance 1962) should elucidate principles of foetal nutrition. Most studies to date have concentrated upon components of the placenta especially, in the sheep, on the cotyledons.

The period of maximum embryonic growth is preceded by a period when placental growth is at its peak. The placenta, in fact, grows more rapidly than the foetus in early pregnancy (Huggett & Hammond 1952) exceeding the weight of the foetal body up to about 90-days of gestation in the sheep (Cloete 1939; Wallace 1948). Barcroft (1946) suggests that restricted placental size at this time may retard subsequent foetal growth through limitation of nutrient diffusion, particularly oxygen, while Moustgaard (1959) states, "... the factor limiting the nutrition of the foetus will be mainly the size of the maternal and foetal placental contact." In late pregnancy the sheep placenta loses its priority for growth and merely maintains or slowly loses weight towards term (Cloete 1939; Wallace 1948).

Senility of the placenta leads to autolysis with marked macroscopic and microscopic structural changes (Amoroso 1952; Gershon & Strauss 1961) in preparation for parturition (Hammond & Marshall 1952).

Not surprisingly, the association between placental weight (either entire or of its components) and foetal weight has received considerable attention in a number of species (reviewed by Huggett & Hammond 1952; Eckstein, et al. 1955; Robinson 1957). The valuable recent studies of Alexander (1964a,b) have done much to clarify the role of the cotyledonary component of the sheep placenta in determining foetal weight at, or near, term.

Alexander (1964a) found positive relationships between birth weight of the lamb and the weight of intact cotyledons and of foetal cotyledons. At equal cotyledon weight, single foetuses were heavier than twins, males heavier than females and foetuses of older ewes tended to be heavier than those of younger ones. Near the time of parturition increases in foetal weight were associated with increasingly large increments in cotyledon weight, i.e. a curvilinear relationship. In the sheep, as in man (Warkany, Monroe & Sutherland 1961) a number of very small foetuses with very small placentae reached full term. At constant placental weight, foetal weight was reduced by maternal undernutrition in the study of Alexander (1964a). Thomson & Thomson (1949) found that undernutrition of the ewe in late pregnancy reduced placental weight in twin bearing ewes but not in ewes carrying a single lamb. Undernutrition in early pregnancy appeared to elevate cotyledon weight in the work of Foote et al. (1959); Alexander (1964a) suggests there may have been a reduction of foetal weight at constant placental weight in this work.

Foetal weight and the number of cotyledons are only slightly correlated (Alexander 1964a) because of a compensatory increase in the weight of individual cotyledons when they are few in number. The compensation involves both foetal and maternal component tissues of the cotyledon. The number of cotyledons per foetus varies with breed and strain of sheep, with litter size, age (or parity) of ewe, sex of lamb and with environmental conditions and the number of caruncles (rudimentary cotyledons - Amoroso 1952) in the uterus.

The finding that fine and medium wool Merinos possess fewer cotyledons than any other breed for which data have been recorded is of special interest. This suggests that the Merino foetus may be at a relative disadvantage in terms of intrauterine nutrition.

Birth weight can be markedly reduced through surgical removal of caruncles in the non-pregnant ewe, but is more closely associated with the weight of functional cotyledons than with their number (Alexander 1964b). It is interesting that individual cotyledons increase in size, especially the foetal component tissues, after reduction in the number of caruncles. This implies a degree of foetal control under adverse circumstances.

Alexander (1964b) reached the important conclusion that,

"... while very little placental tissue is necessary to allow gestation to reach the 100th day, when foetal weight begins to increase rapidly, subsequent foetal growth is limited by the size of the placenta" supporting the proposal that, "... a factor limiting the size of the foetus is the size of the placenta, and more particularly of its vascular bed." (Barcroft 1946). In the last connexion the studies of Hoversland, Watling & Van Horn (1954) on the placentae of Rambouillet, Targhee and Columbia ewes are of interest. They counted the cotyledons and measured the diameter of at least 10 _per cent_. of them; from which the total cotyledonary area was calculated. Single lambs with a mean number of 77 and a total area of 330 sq. cm. compared with twins having a mean number of 87 and an area of 462 sq. cm. More cotyledons, with a greater area, were found in the pregnant than vacant uterine horn. Large oblong cotyledons in the area of the body of the uterus were noted with great variation in the size of others. A valuable extension of this work would be to estimate the area of the chorionic villi as a component of the placental exchange surface during pregnancy (Wilkin & Bursztejn 1957).

The recent research of Alexander (1964 _a_,_b_) has been cited in some detail here because many of his results, derived from large numbers of sheep placentae, place in proper perspective the more tentative conclusions of other workers, based on much smaller numbers (McKenzie & Bogart 1934; Cloete 1939; Barcroft 1946; Wallace 1948; Thomson & Thomson 1949; El Sheikh _et al_. 1955; Foote _et al_. 1959;

Bellows et al. 1963).

Several points of interest derived from studies of other species are relevant to this general discussion. Placental size is inversely related to the number of individuals in the litter (Eckstein et al. 1955). Nutrition and growth of individual foetuses in a litter of mice depend upon the location of their placentae both in the uterus and with reference to their neighbours (McLaren & Michie 1960 : Fig. 2:7). As in mice, swine foetuses and membranes located at the extremes of a uterine horn are larger than those toward the centre (Waldorf, et al. 1957). In mice, if two embryos implant too close together, the two adjacent placentae fuse to a greater or lesser degree (McLaren & Michie 1960). If one member of a fused pair dies, the survivor grows as well as the other (non-fused) embryos in the horn. But if both members of the fused pair survive, their average weight is significantly reduced. Blood flow in the uterine artery may, therefore, be lower if there are several placentae in one uterine horn than if there were only one. A reduction in blood flow would limit the oxygen supply to at least the more distally placed placentae.

Lehr et al. (1964) have recently reported a technique which should prove useful for studying maternal-foetal interrelations and the placental barrier. They ligated the umbilical cord of rat foetuses on the 19th day of gestation. After foetal exclusion the uteri exhibited the shape, colour and configuration of normal uteri. The foetus died and although the placenta was normal in size and configuration it was lower in weight.

These observations are, of course, intimately concerned with hypotheses of local and general effects on foetal growth, but they also emphasise the importance of nutritional competition _in utero_. They indicate, too, the relevance and complexity of the concept of placental efficiency in its relationship to prenatal growth. Holm (1964) states, "... an effective placenta is one which sustains pregnancy and foetal life and measurement is made retrospectively in this unsatisfactory manner." Clearly, no one simple proposal can explain the term and greater attention needs to be paid to such possibilities as those suggested by Moustgaard (1959). He proposes that foetal nutrition depends on: (1) the content of nutrients in the maternal blood; (2) the irrigation coefficient of the uterus; (3) the velocity constant of transplacental passage of nutrients and metabolic products; and (4) the exchange area of the placental barrier.

Although the sheep is essentially a uniparous animal, the quest for increased productivity will demand an increasing degree of multiparity. Observations on multiparous small animals may then assume great significance. Finally, it may be noted that studies of the sheep placenta may contribute to a better understanding of one of the most serious problems currently facing the Australian sheep industry - cystic glandular hyperplasia of the endometrium, more commonly known as "clover disease" (reviewed Moule, Braden & Lamond 1963; Lloyd Davies & Nairn 1964). Characterised by a progressive decline in fertility, attaining catastrophic proportions, the condition is permanent and irremedial and appears closely associated with placentation.

VIII. Maternal Nutrition

Abundant evidence exists on the effects of undernutrition in postnatal life; the extensive literature has been surveyed from time to time (Jackson 1925; Keys, Brožek, Henschell, Michelsen & Taylor 1950; Wilson & Osbourn 1960; McCance & Widdowson 1962; Schinckel 1963). Blaxter (1957) and Reid (1960) provide reviews of the effects of defective nutrition during pregnancy in farm livestock, while Giroud (1959) deals with embryonic nutrition in broader terms.

Developmental sequelae of foetal undernutrition, especially in ovines, have received little attention. Although numerous studies on the nutrition of the pregnant ewe have been undertaken (reviewed Thomson & Aitken 1959; Schinckel 1963; Reid 1958, 1963) there remains the singular contribution of Wallace (1948) as a classical analysis of nutritional effects on ewe and foetus.

Lamb birth weight, as a comprehensive index of nutritional stress in gestation, has understandably received greatest attention. It is clear that poor feeding of the ewe in late pregnancy can markedly reduce this parameter, especially where more than a single foetus is carried *in utero* (reviewed by Thomson & Aitken (1959) and Schinckel

(1963).

The relatively immense increase of ovine foetal mass late in gestation makes striking contrast to the small increment in weight up to about 90-days of prenatal life (see Fig. 2:3). Schinckel (1963) points out that the effects of poor maternal nutrition will become progressively more exacting as foetal demands for nutrients increase and as the time for birth approaches. The degree of nutritional stress required to reduce the birth weight of single lambs is substantially greater than that required for twins; this is clearly shown by comparing the results of Schinckel & Short (1961) with those of Wallace (1948). In fact, many of the reports of undernutrition effects on lamb birth weights, collated by Schinckel (1963), fail to show an appreciable reduction for single lambs, especially where the trial has been conducted under field grazing or feed-lot conditions.

Studies of the nutrition of pregnant ewes fall into two broad categories. Firstly, there are those experiments conducted in pens, permitting strict control of feed intake and management of individuals, but suffering the defects of small numbers of animals held in an artificial environment (Wallace 1948; Schinckel & Short 1961; for example). On the other hand, there are those studies in a field grazing situation involving larger numbers of experimental animals, subjected to environmental rigours, but lacking information on the food eaten with less attention paid to the individual than the flock

(Coop 1950; Papadoulos & Robinson 1957; for example). Neither system of experimentation is entirely satisfactory and extrapolation of results from one set of conditions to the other rather hazardous.

Nutrient requirements, for example, of grazing sheep appear substantially greater for maintenance, but less for body weight gain, than those for pen-fed animals. Coop (1961) reviewed the work undertaken in this field and presented additional information from his New Zealand studies. Later, Coop (1962<u>a</u>) collated estimates in the literature of maintenance requirements (expressed as T.D.N./lb./day) for sheep weighing 100 lb. Table 2:2 records the same estimates in terms of D.O.M./g./day for sheep weighing 45.4 kg.; more recent estimates are also included.

Lambourne (1961) found that the maintenance requirements of grazing sheep were greater than those of pen-fed sheep of similar body weight. The increase was 10-30 <u>per cent</u>. for heavy (fat) sheep grazing good pasture, rising to 50-100 <u>per cent</u>. for medium and low weight sheep on poor pasture. The apparent increase in maintenance requirements could be associated with the climatic environment of temperature, wind and rain; walking; hormonal or metabolic factors; and harvesting the grass (Coop 1961, 1962<u>a</u>; Coop & Hill 1962; Coop & Drew 1963; Lambourne 1961; Lambourne & Reardon 1963). More recent studies have indicated the relative importance of these factors. Graham (1964<u>b</u>) found that muscular work, mainly standing and eating, accounted for nearly 40 <u>per cent</u>. of the daily energy expenditure of

TABLE 2:2 ESTIMATES OF NUTRIENT REQUIREMENTS (D.O.M./g./day)
FOR MAINTENANCE OF SHEEP WEIGHING 45.4 kg.

Specification	Estimate	Authority
Basal metabolism	265	* 70 $W^{0.75}$ Cal.
Energy equilibrium	334	* Marston (1948)
	365	* Armsby
	378	* Blaxter & Graham (1955)
	356-425	* Henneber, Kellner
Pen-fed	359)	Langlands, Corbett,
	372)	McDonald and Pullar (1963)
	418	Phillipson (1958)
	418	Coop (1961, 1962a)
	459	Coop & Drew (1963):1961 trial, indoors.
	460	* Garrett, Meyer & Lofgreen (1959)
	464	* Watson, Scott, Skilbeck & Ellis (1937)
	473	* Wallace (1948)
	499	Coop & Drew (1963):1961 trial, outdoors.
Yard-fed	404	* Franklin (1952)
	434	* Coop (unpublished data)
Pasture-fed	463	Langlands, Corbett, McDonald & Reid (1963)
	617)	Coop (1961)
	672)	Coop & Hill (1962)
	740)	
	731	Allden (personal communication)
	781	Lambourne (1955)
	825	* Greenall (1959)
	894	Coop & Drew (1963):1962 trial, shorn sheep on short grass for a long time.
Recommendations	621	N.R.C. (1959)
	642	* Woodman (1948)
	716	* Morrison (includes some gain)

Note: * Taken from Coop (1962a), based on the assumption that 454g. T.D.N. is equivalent to 434g. D.O.M.

sheep at maintenance grazing a poor but level pasture, with drinking water available, and only 10 per cent. of that for a caged animal. The same authority (Graham 1964b) found that the energy cost of standing (0.34 ± 0.02 kcal./hr./kg. body weight) was greater than that of rumination (0.24 ± 0.03 kcal./hr./kg.); the energy cost of grazing was 0.54 ± 0.05 kcal./hr./kg. body weight irrespective of the type of sward and associated grazing behaviour. Shearing increased the maintenance feed requirement by approximately 40 per cent. in pen-fed sheep, and 20 per cent. in low maintenance grazing sheep, in the studies of Coop & Drew (1963).

When reviewing the experimental evidence for the influence of prenatal nutrition on lamb birth weight, Thomson & Aitken (1959) deplore that most workers have presented nutritional response of ewe body weight in absolute gains or losses and not relative to ewe body weight at the commencement of the feeding period. Schinckel (1963), too, after collating the evidence of nutritional effects on lamb birth weights comments, "Direct comparison of the different results can be made only in the broadest terms because of the variety of techniques, breeds, and levels of nutrition involved." Response of lamb birth weight appears, nevertheless, to vary with the magnitude of the difference in ewe body weight between the relatively high and low planes of nutrition but depends, too, on how inadequate the low plane may have been. Thomson & Aitken (1959) point out that in some experiments "low plane" ewes show, in fact, an increase in body weight over a critical period (Coop 1950), while high plane ewes may exhibit slight or substantial gains, or even weight loss.

Few studies of pregnancy nutrition in sheep have incorporated a serial slaughter programme so that maternal tissue changes have received inadequate attention. The work of Wallace (1948) is a notable exception in this regard. As far as prenatal growth of Merino sheep is concerned only two studies of normal foetal growth (Malan & Curson 1936a; Cloete 1939), and a series on genetic aspects (Stephenson & Lambourne 1960; Stephenson 1959, 1962a, 1964), have been reported. In those experiments involving a slaughter procedure, the degree of nutritional stress imposed on the ewe has not been great, with examination of few foetuses at any one stage. The Low Plane ewe in the study of Wallace (1948), for example, lost approximately 14 per cent. of gross body weight during the first 90-days of gestation; one pair of twin foetuses was compared with foetuses derived from one Maintenance ewe and one High Plane ewe. Furthermore, in field grazing trials death claims those ewes and/or their lambs subjected to the greatest degree of stress. Schinckel (1963) recognised the possibility of this bias when comparing the pen-feeding experiment of Schinckel & Short (1961) with the unpublished results of a field trial (Schinckel & Lambourne).

Apart from ewe and lamb mortalities arising from impaired maternal metabolism (reviewed Reid 1958, 1961, 1963), the reduced weight and associated neonatal incompetence of lambs at birth (reviewed Alexander 1964c), coupled with restrained maternal behaviour, are held responsible for a large proportion of the massive neonatal mortalities inflicted upon the Australian sheep industry.

Restricted postnatal performance of offspring born to ewes undernourished in the pregnancy is of equal concern, but less obvious, than reduction of birth weight (McClymont & Lambourne 1958; Schinckel & Short 1961; Taplin & Everitt, 1964). Thomson & McDonald (1956) found that, on average, any deviation below the mean in lamb birth weight is magnified 3-4 fold by weaning time. In the pen experiment of Schinckel & Short (1961), for example, differences in nutritional treatment of Merino sheep prior to 4 months of age resulted in a difference of nearly 20 per cent. in mature body weight. Prenatal and postnatal nutritional treatments contributed equally and additively to this substantial effect. Sheep poorly reared from conception to 16 weeks of postnatal life produced about 20 per cent. less wool at maturity than well-fed mates. The effects of pre- and postnatal nutrition were likewise additive. As adults, offspring from ewes ill-fed throughout the whole of pregnancy were about 9 per cent. smaller, produced about 8.5 per cent. less wool and had about 15 per cent. fewer wool follicles per sheep. The primary effect of restricted feed intake during prenatal life was through a reduction in total follicle number, largely secondaries, associated with a concomitant reduction in body size and skin area. Corrobative evidence for some of these effects was offered by Taplin & Everitt (1964). Turner (1961) has shown that wool production of twins, and of singles born to immature ewes, may suffer from a maternal handicap; a finding supported by the work of Dun & Grewal (1963). Prenatal limitation (twin pregnancy) reduced the number of secondary wool fibres present at birth in the study of Doney & Smith (1964) but, providing postnatal nutrition was adequate, this difference had disappeared by 6 weeks of age. No permanent effects on fibre number, wool production or fleece structure were observed.

No information is yet available, however, on the reproductive performance of offspring derived from ewes ill-fed during pregnancy. An effect of this nature may prove, in fact, of greater practical importance than a restriction of lifetime wool productivity. Retarded early postnatal growth may delay the onset of first oestrus in maiden ewes (reviewed by Joubert 1963), extending the generation interval with economic repercusions. Ovulation rate and lambing percentage are also positively related to the body weight of the ewe when she is mated (Wallace 1961; Coop 1962_b_, 1964). Moreover, a small maiden ewe may exert a maternal effect on foetal growth, producing a small lamb at birth with concomitant temporary and permanent disadvantages.

Coop (1962_b_, 1964) with data derived from several thousands of sheep (mostly Corriedale but also some Romney) in New Zealand over a period of 15 years, has established a critical live weight of the ewe at mating time of 40.9 kg. Above this weight the proportion of barren ewes decreased only slightly from about 9 per cent. to 5 per cent. at 72.6 kg.; below 40.9 kg., however, the percentage increased markedly from 9 per cent. at 40.9 kg. to 50 per cent. at 29.5 kg. Moreover twinning rate increased at a consistent rate of about 6 per cent. per 4.5 kg. increase in ewe body weight at mating time. Survival and growth of the lambs was also higher the larger the ewe at mating time. It was found, too, that the reproductive performance of maiden two-tooth ewes equalled that of older cast-for-age ewes providing that the maiden ewes attained 54.5 kg. at mating time. Coop (1964) comments later, "Not only does failure to produce well grown two-tooth ewes cause an immediate loss in production from the low performance of these sheep but this loss is probably carried on for their whole lifetime" and " ... once a young ewe enters the breeding flock it has very little chance of growing unless it happens to be barren" and "So the live weight attained by the two-tooth ewe (at first mating) sets the limit to its lifetime size and production". Bradford, Weir & Torrell (1960), on the other hand, found ewes restricted in growth from 6-15 months of age to be equal in their reproductive performance under range conditions to well-fed ewes.

In contrast to the many studies of the effects of undernutrition in late pregnancy, the importance of the level of maternal feeding in early pregnancy has received little attention. From the point of view of foetal growth this is, in part, understandable. Although evidence for the ovine is very limited, the additional requirements for nutrients even in late pregnancy in the cow are small (10 kcal./kg. body weight$^{0.73}$ energy retained) as compared with lactation (Blaxter 1962: review).

Table 2:3 shows the nutritional requirements of ewes in early and late pregnancy as estimated by the N.R.C. (1959). Gardner & Hogue (1963) found that T.D.N. levels recommended by the N.R.C. (see Table 2:3) for late pregnancy were adequate for ewes with single lambs but increased levels (125 per cent.) for twin-bearing ewes were needed. Graham (1964c) found the heat increment of pregnancy in Merino ewes increased to 90 kcal./24 hr./kg. foetal tissue at term; urinary nitrogen loss decreased as pregnancy advanced and pregnancy did not affect the digestibility of food eaten.

Retarded early foetal growth and development in the sheep due to inadequate maternal nutrition has not been clearly demonstrated. Hammond (1944) postulated that foetal metabolic rate was highest in early pregnancy, and only slightly less than that of the maternal central nervous system (see Fig. 2:5). He drew support for the foetal component of his "Theory of the Partition of Nutrients According to Metabolic Rate" from the research of Wallace (1948) who was unable to demonstrate any significant effect of maternal nutrition on the weight of twin sheep foetuses at 91-days of gestation. The inadequacies of this premise, recognised by Wallace (1948), have been

TABLE 2:3. NUTRIENT REQUIREMENTS OF PREGNANT SHEEP : data adapted from Tables I and II of N.R.C. (1959)

Ewe Body Wt. (kg)	Body Wt. Gain or Loss/day (g)	Feed		Daily Nutrients per Animal (1)									
		per animal (g)	% of body wt.	Protein (g)	D.P. (2) (g)	T.D.N. (3) (g)	D.E. (4) (therms)	Ca (g)	P (g)	Salt (g)	Carotene (mg)	Vit. A. (I.U.)	Vit. D. (I.U.)
First 15 weeks of pregnancy													
45.4	32	1180	2.6	90.8	49.9	590.2	2.6	3.2	2.5	9.0	1.7	965	250
Last 6 weeks of pregnancy													
45.4	168	1725	3.8	140.7	77.2	908.0	4.0	4.2	3.1	10.0	5.8	2316	250
				Percentage of ration or amount per unit wt. of feed									
				(%)	(%)	(%)	(therms)	(%)	(%)	(%)	(mg/100g)	(I.U./100g)	(I.U./10
First 15 weeks of pregnancy													
45.4	32	1180	2.6	7.6	4.2	50	1.0	0.27	0.21	0.8	0.15	82	21
Last 6 weeks of pregnancy													
45.4	168	1725	3.8	8.0	4.5	53	1.1	0.24	0.18	0.6	0.33	134	15

Note : (1) Based on air-dry feed containing 90% dry matter.
(2) D.P. = digestible protein.
(3) T.D.N. = total digestible nutrients.
(4) D.E. = digestible energy, calculated on the assumption that 1 g of T.D.N. has 4.45 kcal. D.E. Metabolizable energy represents 82% of D.E.

mentioned earlier. El-Sheikh et al. (1955) found no significant differences in ovine foetal development at 40-days of gestation attributable to different levels of maternal feeding. Likewise, no appreciable effect on foetal weight at 25-, 40- or 140-days of gestation was found by Foote et al. (1959) who imposed high and low planes of nutrition on pregnant ewes of two breeds, with marked differences in body size of the ewes due to the nutritional regimes. However, Schinckel (1963) makes brief reference to unpublished work where he found a significant difference in foetal weight at 90-days of age between single and multiple Merino foetuses; the mean weight of 129 single foetuses was 520g., and of 39 twin and triplet foetuses 490 g. As Schinckel (1963) states, "This might well imply that nutrient supply to the foetuses can be a limiting factor before 90-days".

Unlike the animal in postnatal life, the foetus has little opportunity to accumulate nutrient reserves and, if retarded, is limited by time in making up lost ground before birth. These interactions of food, growth and time in foetal life place a different emphasis on the phenomenon of compensatory growth. This biological mechanism, inherent in the growth of all animals (Tanner 1963), is especially important in the growth and production of domesticated species (Wilson & Osbourn 1960; Schinckel 1963).

It is quite clear that, in postnatal life, the duration, severity and particularly the age of the animal at the time of restriction play important roles, with marked differences between species in their reaction. Work with laboratory animals (reviewed by McCance & Widdowson 1962; Widdowson & McCance 1963), poultry (Wilson 1954), pigs (Robinson 1964), goats (Wilson 1958), and cattle (Crichton, Aitken & Boyne 1960; Dickinson 1960), as well as sheep (Hammond 1932; Coop & Clark 1955; Donald & Allden 1959; Bradford *et al*. 1960; Schinckel & Short 1961; Gunn 1964*a,b*; Purser & Roberts 1964) all points to the fact that the earlier in developmental life that the stress is applied, the greater and more lasting will be the effect.

In the rat, Widdowson & McCance (1963) have shown very clearly how in a species born in a relatively immature state, ultimate size and development is permanently restricted when growth is retarded immediately after birth, with diminishing effects as life proceeds. Species born in a relatively more mature state - such as cattle - are capable of overcoming a retardation of growth applied immediately after birth. Crichton *et al*. (1960), for example, reported the effects of different methods of rearing from birth to first calving on mature body weight of dairy cattle. No significant depression of weight at 6 years was detected even in animals reared on low intake to two-years of age, when only 62 *per cent*. of mature weight had been attained.

The sheep approximates the ox more closely than the rat in respect of developmental maturity at birth. In this species the effects of nutritional stress after birth on ultimate size are not so marked as in rats but more so than in cattle. Coop & Clark (1955), in a field trial with Corriedale ewes in New Zealand, found that a substantial body weight difference at 12 months of age, originating from both pre- and post-weaning treatment, was eliminated by 32 months of age after all animals had been realimentated. Retardation of growth after 7-9 months of age failed to reduce the lifetime productivity or mature body weight of Merino wethers in the study of Donald & Allden (1959). A nutritional stress from 4-18 months of age gave a small difference, approximately 4 per cent., at five-years of age in ewes (Coop & Clark 1955). Prenatal and early postnatal nutritional treatments contributed equally and additively to the substantial reduction (20 per cent.) of adult size of sheep in the study of Schinckel & Short (1961). Evidence of marked effects of early environment on the productive performance of South Australian and Peppin Merinos has recently been forwarded by Dun, Alexander & Smith (1964).

These differences between species in their ability to compensate for growth restriction appear related to differences in physiological age (Brody 1945). Completion of organogenesis, in a metrical sense, may mark the period of life when a temporary retardation of growth ceases to exert a permanent effect on ultimate size, development and production. Prior to this time is a period of increasing sensitivity to stress; and after it a period of diminishing sensitivity. In this context, the rat may cease organogenesis at, say, 6 weeks after birth compared with the sheep which appears most sensitive in late prenatal-neonatal life. These suggestions are embodied in Dickinson's (1960) hypothesis for the control of mammalian growth, to which Schinckel (1963) has added an additional component of sensitivity to stress in relation to physiological age (see Fig. 2:8).

The evidence of King (1915, 1916) also suggests that nutrition cannot be held to account for all the effects; she found that even if the "runts" in litters of rats were given special attention and unlimited food they did not attain the weight of their normal littermates even at maturity. Growth hormone boosted growth rate of undernourished rats on ad libitum feeding in the study of Hruza, Fabry, Chrapil & Holeckova (1962); they suggested either a relative pituitary insufficiency during re-feeding, when demands on proteosynthesis are large, or to increased endogenous sensitivity of tissues to the action of the hormone. In the sheep, there is some evidence that cell number of tissues is completed by approximately 90-days of gestation (Joubert 1956a). As there is a limit to the size that individual cells may grow, tissue expansion may be restricted if cell number is retarded early in life. Muscular tissue forms approximately one-third of the live weight of a beef animal, irrespective of fatness (Callow 1944).

Finally, it may be noted that the animal in utero may not have the opportunity for ad libitum food intake to permit compensatory growth. The food supply of the foetus is mediated through the placenta.

If the efficiency of the latter is restricted through maternal undernutrition in early pregnancy, there may be a restriction of food supply to the foetus in late pregnancy, even though the mother is herself feeding ad libitum. There is, in fact, considerable evidence (Alexander 1964a,b) to show that foetal and placental size in late pregnancy of the sheep is closely correlated.

It is, therefore, quite clear that foetal growth in the sheep, and other mammals, can be profoundly affected by maternal nutrition with important residual effects on postnatal performance. It is equally clear that the association is by no means a simple one, but represents the action and interaction of a large number of diverse factors.

E. CONCLUSIONS

This review reveals the prime necessity for integration in the science of animal production, in growth studies and, particularly, in investigations of the prenatal existence.

Losses of substantial magnitude in the animal industries impinge upon the breeding unit, and this is nowhere more true than in the Australian environment. Axiomatically, it is to problems of the reproducing animal that considerable research resources need devoting, for the rewards are potentially enormous.

It is, however, clearly necessary to establish, in the first instance, the most appropriate and valuable techniques, for this is more likely to lead to correct interpretation of the information; albeit that there is no such thing as a "final explanation". The review showed the many difficulties of measuring animal performance, and the controversies inherent in different interpretations.

Classification of the manifold factors affecting growth and development of the animal <u>in utero</u> revealed the pre-eminence of nutrition. Any contribution, therefore, leading towards a better understanding of nutritional demands is worth support; and this factor forms the major variable selected for study in the experimental work of this thesis.

But, it was obvious, too, from the review that nutritional control of foetal growth was substantially more complex than in the animal after birth. The latter, in effect, is influenced directly, the foetus indirectly through circuitous pathways. These studies attempt recognition of these pathways.

3. THE PROGRAMME OF INVESTIGATION

An account of the philosophy underlying the experimental work reported in the thesis is offered in this section.

A. GENERAL MANAGERIAL CONSIDERATIONS

Two procedures may be adopted in assessing the efficacy of grazing management tactics. Firstly, an encompassing experimental management programme can be tested under field conditions, recording deficiencies of the ecosystem as they may occur; alternatively, individual components may first be isolated, examined in detail, and subsequently integrated into a revised grazing management programme. The two approaches have a common objective and are to this extent complementary; the first, however, demands more extensive land resources than the second, especially for breeding animals. Moreover, the interaction and confounding of component factors when grouped together may either escape observation or defy biological interpretation unless the detail of each component is fully appreciated.

Lack of pasture growth during the 5-6 months of summer drought in this Mediterranean-type environment, coupled with the association of pregnancy in sheep over this period, permitted a compromise between the disadvantages of pen-feeding experiments and those of field grazing studies.

Experimental animals were held in an exposed two-acre paddock, bared completely of pasture feed at the start of the summer. Individual feeding on a pelleted diet, quantitatively rationed, ensured that gross body weight during pregnancy proceeded along a predetermined curve. The degrees of weight loss, in particular, imposed on the ewes represented extremes to facilitate interpretation of effects on relatively small numbers of animals. Nevertheless, the selection bore relationship to conditions recorded in farming practice - see, for example, Fig. 2:2 -, especially under prolonged drought, and to other experimental work (e.g. Schinckel & Short 1961).

B. PHYSIOLOGICAL CONSIDERATIONS

Postnatal performance of sheep can be greatly influenced by their prenatal nutritional history. For example, retarded postnatal growth and development of lambs born to Merino ewes severely underfed throughout the whole of pregnancy was recorded by Schinckel & Short (1961) - L/- ewes - and Taplin & Everitt (1964) - LL ewes. The earliest stage of gestation at which maternal undernutrition restricts postnatal performance of the progeny requires careful definition, for this bears directly both upon the strategy of management of breeding ewes and the overall economy of the animal enterprise.

In order to assist appreciation of the physiological reasons for these residual effects, a detailed definition of the influence of prenatal undernutrition on several parameters of foetal growth and development is attempted in this study.

The foetus, however, does not lead an independent existence and cannot reasonably be dissociated from the effects of undernutrition on the maternal organism. Observations on the response of the ewe, and particularly the placenta, to the nutritional treatments have therefore also been recorded.

C. EXPERIMENTAL DESIGNS

I. Experiment A

The Influence of Severe Maternal Undernutrition during Pregnancy, and of the Size of the Sire, on Foetal Growth and Development.

This experiment was designed to provide general information about the effects of maternal undernutrition on the performance of the ewe and her foetus. More specifically, the hypothesis was tested that foetal growth in early pregnancy is independent of the level of nutrition supplied to the ewe. The degree and rate of body weight loss imposed on the underfed ewes approximated those recorded by Schinckel & Short (1961) and Taplin & Everitt (1964).

The effect of the size of the sire on foetal growth and development was included as a second variable for study. Apart from interest in genetic, as opposed to nutritional, control of foetal growth, it was considered initially that difficulties might be encountered in placing all ewes in lamb to one ram. Two Merino rams of markedly different body size were selected for use.

The experiment, therefore, was of 2 x 2 factorial design, involving High v. Low planes of maternal nutrition throughout pregnancy;

and Large v. Small size of ram.

II. Experiment B

The Influence of Ewe Body Weight at Mating, and of Severe Maternal Undernutrition for the first 90-days of Pregnancy, on Foetal Growth and Development

This experiment tested two hypotheses arising from Experiment A. Firstly, that the body weight and condition (fatness) of the ewe at mating buffered the foetus from severe undernutrition in early pregnancy. Secondly, the ability of the foetus for compensatory growth and development in late pregnancy, following a period of poor maternal feeding, was examined.

The design, therefore, was likewise a 2 x 2 factorial; involving ewes which were either Heavy or Light in body weight at mating time, with either High or Low plane of maternal nutrition during the first 90-days of pregnancy.

D. SELECTION OF FOETAL AGES FOR EXAMINATION

Foetuses of two ages (90-days and 140-days) were selected for detailed examination in both experiments. The first, 90-days of age, permitted comparison with the data of other workers (e.g. Wallace 1948; Stephenson & Lambourne 1960; Stephenson 1962a), besides representing a time of marked change in foetal weight (see Fig. 2:3) and development (e.g. Joubert 1956a - for skeletal muscle tissue; Fraser & Short 1960 - for wool follicles).

Although a number of ewes were permitted to lamb, and observations on their offspring recorded at birth, the complication of differences in the length of gestation was overcome by making detailed examinations of foetuses at 140-days of age, a short time before birth. Undernutrition tends to abbreviate the length of gestation (Alexander 1956); in a pilot study (Everitt : unpublished data), two ewes severely underfed throughout pregnancy lambed after 142 days. It was feared that delay in the time of examination nearer to birth (based on 150 days of gestation) might involve loss of foetal material through parturition.

E. EFFECTS OF FOETAL SEX

Foetal sex represented an uncontrollable variable affecting growth and development. Disproportionate sub-class numbers of male and female foetuses resulted, necessitating application of special statistical methods for the study of sex effects.

F. EFFECTS OF MULTIPARITY

Observations of treatment effects on single foetuses were desired and, fortunately, no multiple sets were recorded.

G. EFFECTS OF AMBIENT TEMPERATURE

The ewes were subjected to the normal seasonal levels of ambient temperature operating under the field environment of the experiments. No control could, of course, be exercised in this connexion. However, climatological records at the Waite Agricultural Research Institute over the periods of field activity are presented for information.

H. CONCLUSIONS

In these experiments, the animals were held in a simulated "grazing" situation, subjected to the operation of environmental factors, but with strict control of selected variables either by managerial (e.g. breed, age of dam, feed intake, body weight gain/loss, foetal ages) or statistical (e.g. foetal sex) procedures.

4. EXPERIMENT A

THE INFLUENCE OF SEVERE MATERNAL UNDERNUTRITION DURING PREGNANCY, AND OF THE SIZE OF THE SIRE, ON FOETAL GROWTH AND DEVELOPMENT

A. INTRODUCTION

The objectives of this experiment were three-fold:

(a) to provide general information on the effects of undernutrition during pregnancy on the performance of Merino ewes and their foetuses;

(b) to test the specific hypothesis that foetal growth in early pregnancy is independent of the nutrition supplied to the ewe; and,

(c) to examine the effect of the size of the sire on foetal growth and development.

B. MATERIALS AND METHODS

I. Experimental Design

A 2 x 2 factorial design was employed with two relative levels of maternal nutrition during pregnancy - High Plane (HP) and Low Plane (LP) - and two sires (Ram L and Ram S).

Ewes were randomised into two sire groups at the time of joining in October 1962. After mating ewes were allocated alternately to the two nutritional regimes so that the gross body weight of each individual either increased (HP) or decreased (LP) by 25 *per cent*.

over 140-days of pregnancy.

Six randomly selected ewes were slaughtered at joining time; and after both 90- and 140-days of pregnancy a further 8 HP and 8 LP ewes were killed.

Remaining ewes continued on to lambing.

II. Experimental Animals

(a) Ewes

Table 4:1 summarizes the classifications of the ewes.

Seventy 3-year-old South Australian Merino ewes were selected for the experiment from 95 animals available after weaning their lambs in September 1962. Each selected ewe had successfully reared a single lamb in the 1962 season. The remaining 25 unselected ewes were eliminated for obvious physical faults or because of exceptional leanness. Selected ewes, nevertheless, varied considerably in body weight and fatness at weaning time.

(b) Rams

Two South Australian Merino rams of markedly different frame size were used - see Plate 4:1. The larger sire, Ram L, weighed 92.6 kg. at 27 months of age compared with the smaller one, Ram S, which, on the same occasion, weighed 64.5 kg. at 56 months of age.

Linear body measurements of the rams recorded in October 1962 were : body length (withers to pins), depth of chest, width at shoulders, ribs and hips, and hips to pins, as defined by Turner,

TABLE 4:1. SUMMARY OF CLASSIFICATION OF EWES

Classification	Number of ewes						Total	Remarks
	Group							
	HP/Ram L	HP/Ram S	Total	LP/Ram L	LP/Ram S	Total		
Weaning	-	-	-	-	-	-	70	
Served by teaser ram	-	-	-	-	-	-	64	
No display of oestrus	-	-	-	-	-	-	6	
Mated to entire ram:								
No. of services required for conception:								
1.	10	9	19	7	8	15	34	
2.	5	7	12	7	6	13	25	
3.	1	-	1	3	1	4	5	
Total	16	16	32	17	15	32	64	
Recurrent oestrus after third mating to entire ram	2	-	2	-	1	1	3	
Absence of oestrus after mating to entire ram, followed by later return to teaser ram	-	-	-	1	1	2	2	(1 LP/Ram S ewe returned after 38 days (1 LP/Ram L ewe returned after 42 days
Slaughtered (all with single foetuses):								
Mating	-	-	-	-	-	-	6	
After 90-days of pregnancy	4	4	8	4	4	8	16	1 LP/Ram S ewe not pregnant
After 140-days of pregnancy	4	4	8	4	4	8	16	
Total	8	8	16	8	8	16	32	
Deaths	-	-	-	4	1	5	5	See text for details
Lambing	6	8	14	3	4	7	21	All single lambs
Failure to lamb despite non-return to teaser ram after mating with entire ram	-	-	-	1	-	1	1	

Hayman, Riches, Roberts & Wilson (1953); and fore-cannon length (Hunter 1956).

Biopsy samples, 2 cm. in diameter, were taken from the right Biceps femoris muscle of each ram in August 1962. The number of muscle fibres in each of 10 primary fasciculi, selected at random, was counted, and the diameter of 50 individual muscle fibres measured to the nearest 2μ, from each sample. The procedure has been described in detail elsewhere (Everitt 1963a).

Wool follicle development was examined in histological sections from 1 cm. diameter biopsy skin samples taken from the midside in August 1962. Procedures were based on those described by Clarke (1960) in the review of Fraser & Short (1960). Sections, cut at the level of the sebaceous glands, were stained with Masson's Trichromic stain (without acid fixative).

A 10 x 10 cm. midside skin patch was tattooed on each ram in May 1962. They grazed together, on predominately Phalaris tuberosa L. - subterranean clover swards, for the following 98 days when the wool grown on the midside patch was harvested. Wool samples were scoured, oven-dried and the yield of clean dry wool determined.

III. Management

(a) General

Sheep were accommodated in a 2-acre holding paddock offering no shade and negligible herbage at the start of the trial. A contiguous 2-acre paddock for hand-mating the ewes was used. The

Plate 4:1.- Side and rear views of the two rams (10 x 10 cm. grid).

SIRE S

AGE (mths) 56

WT. (kg) 64·5

SIRE L

AGE (mths) 27

WT. (kg) 92·6

field situation is illustrated in Fig. 4:1 and Plates 4:2 and 4:3.

All ewes were drenched with 1 million I.U. Vitamin A and 250,000 I.U. Vitamin D_3 in October 1962, and again in February 1963. Ewes were also drenched with phenothiazine in October 1962, and with thiabendazole in February 1963, for internal parasite control.

(b) Mating

A vasectomised ram carrying a SIROSINE (Radford 1958) raddle harness and crayon - see Plate 4:4 - ran continuously with the ewes throughout the experiment. After mating with the vasectomised ram, ewes in oestrus were withdrawn to their appropriate fertile raddled ram. Ewes returned to the holding paddock on day 1 of pregnancy. This was accepted as the day following the last observed service of the fertile ram. A similar procedure was adopted for a maximum of three consecutive oestrous cycles in the case of those ewes returning to the vasectomised ram.

(c) Feeding

Ewes were fed once daily in individual stalls located adjacent to the area - see Fig. 4:1. Feeding operations are illustrated in Plates 4:5, 4:6 and 4:7.

The composition of the pelleted diet used throughout the experiment is recorded in Table 4:2. Apparent digestibility coefficients were derived from a digestibility trial with three 2-year-old Merino wethers. This trial lasted for a total of 21 days, the total faecal output being collected in the final 10 days. Faeces were oven-

Fig. 4:1.- Diagram of the experimental area located at the Waite Agricultural Research Institute, Adelaide, South Australia.

DIAGRAM OF THE EXPERIMENTAL AREA

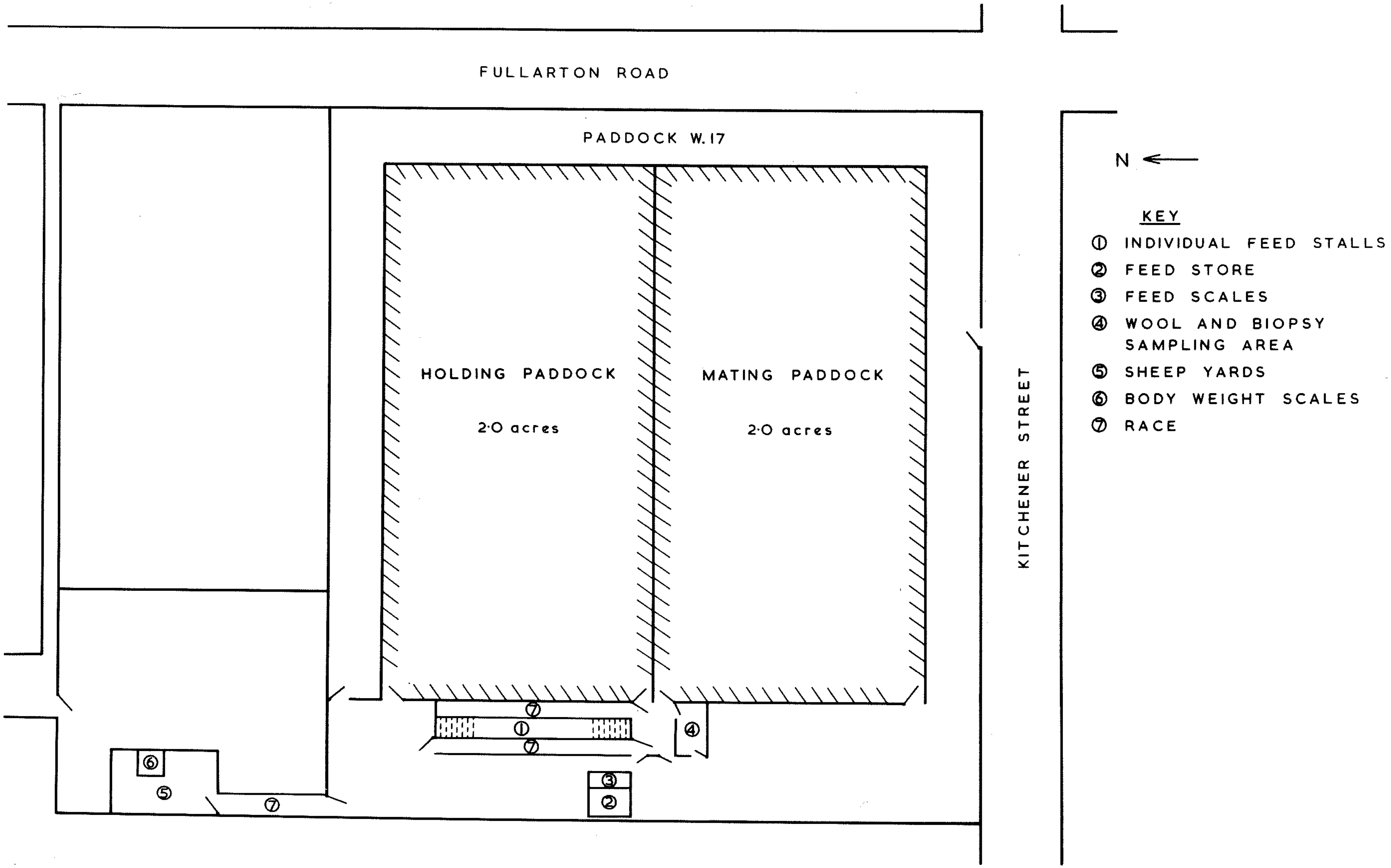
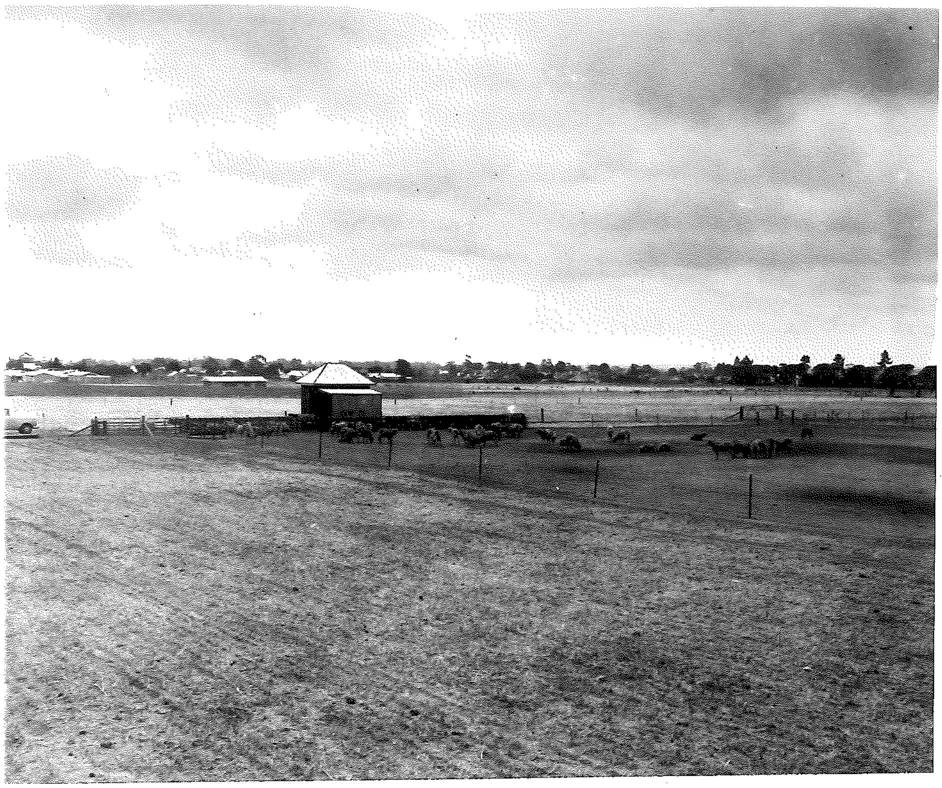


Plate 4:2.- General view of the experimental area. The mating paddock lies in the foreground, with ewes in the holding paddock. The feed store and scales are immediately behind the individual feeding pens.

Plate 4:3.- The inconsequential amount of paddock feed available to the ewes in the holding paddock at the commencement of the trial in November 1962.



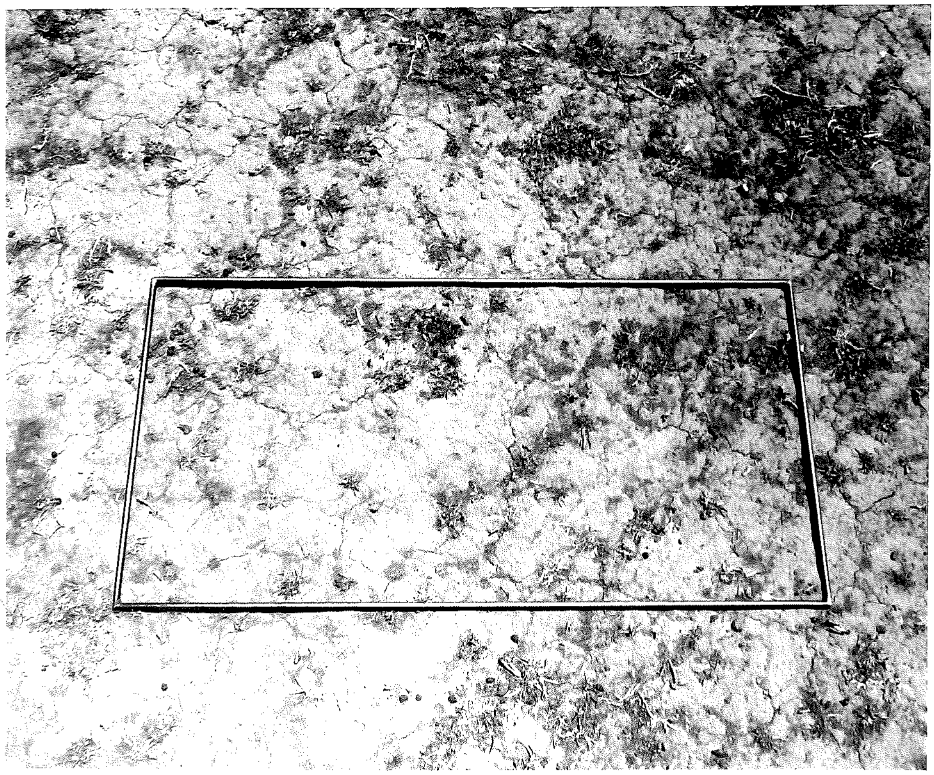


Plate 4:4.- Ram fitted with SIROSINE raddle harness and crayon. Each ram used in the experiment had been tested earlier for wool production - hence the midside wool patch.

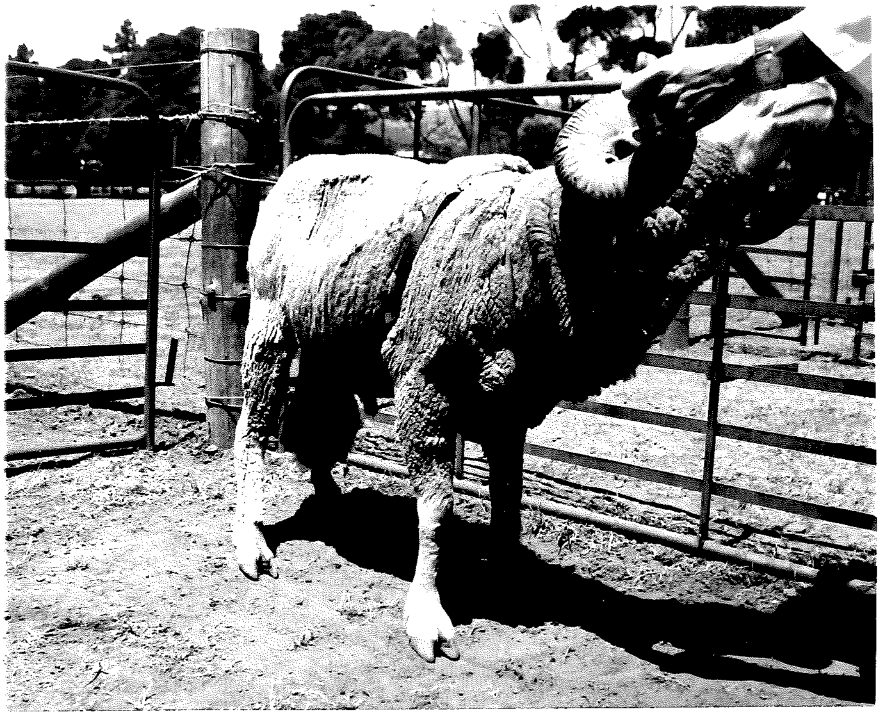


Plate 4:5.- The design and operation of the pens used for individual feeding at the start of the 1962-63 experimental period. Sheep entering pens from the paddock before feeding. The feeding basins were later changed to more enclosed containers to prevent robbery by the ill-fed ewes.

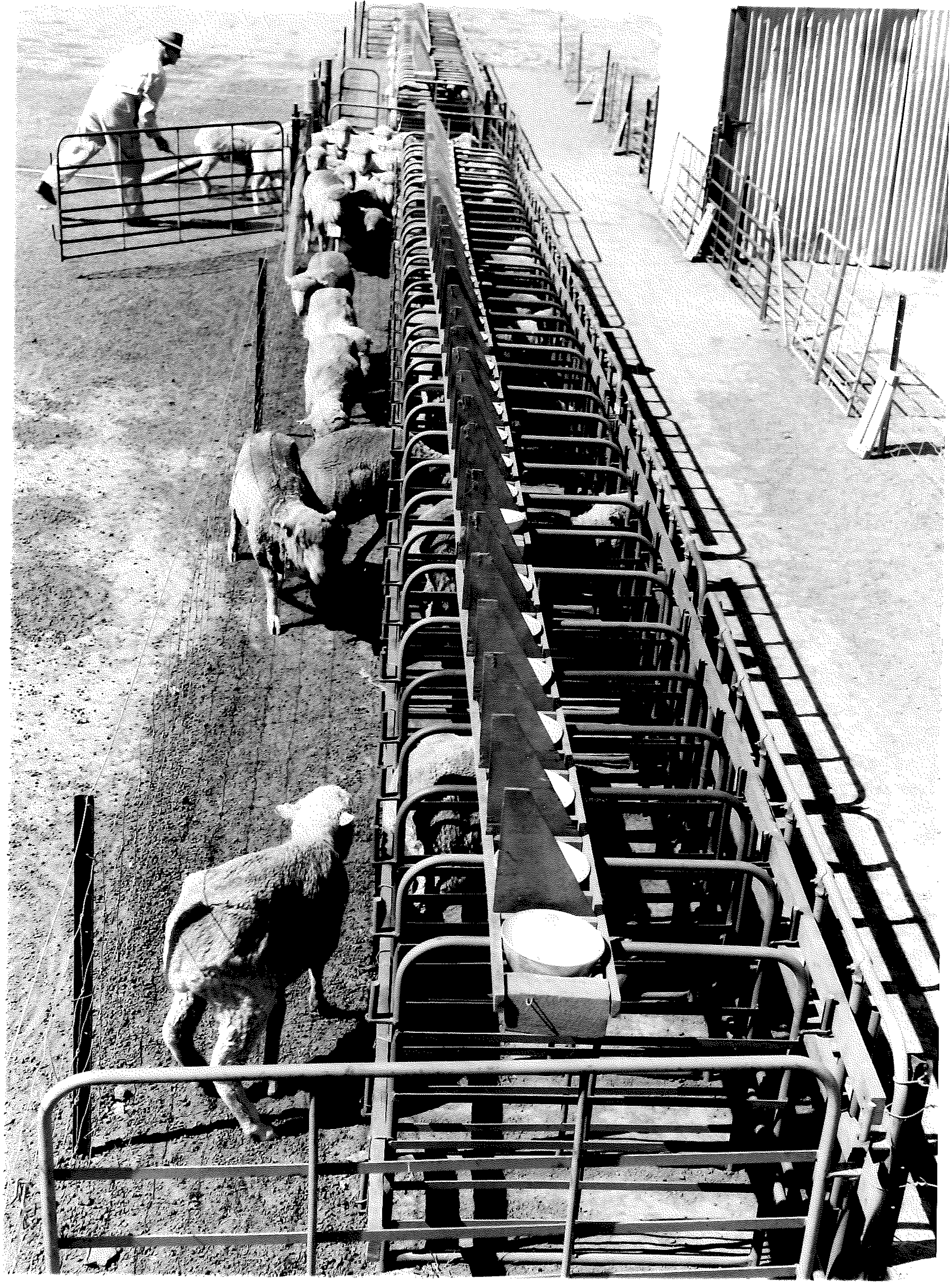


Plate 4:6.- Ewes receiving rations.

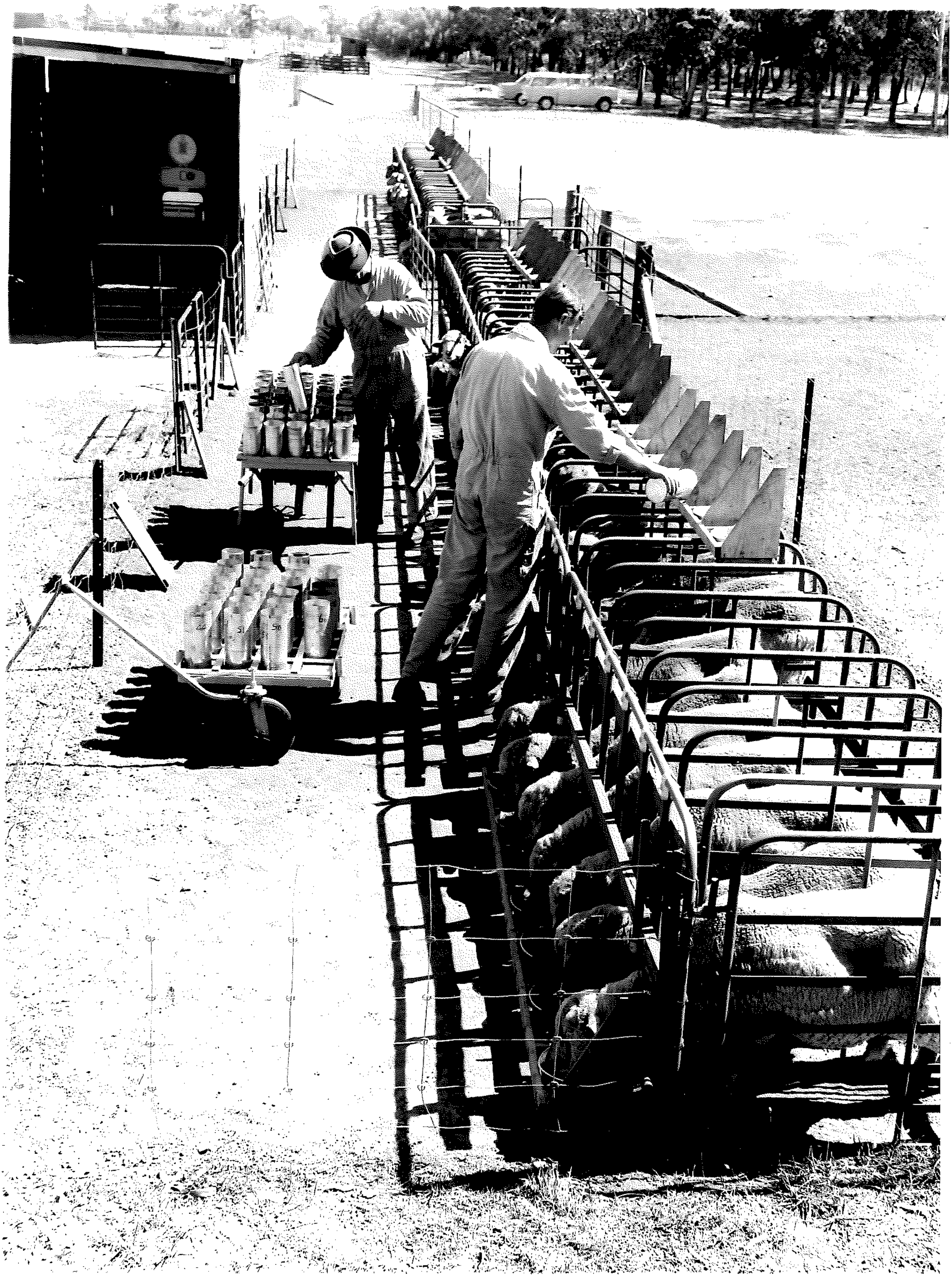

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Plate 4:7.- Ewes leaving pens after feeding

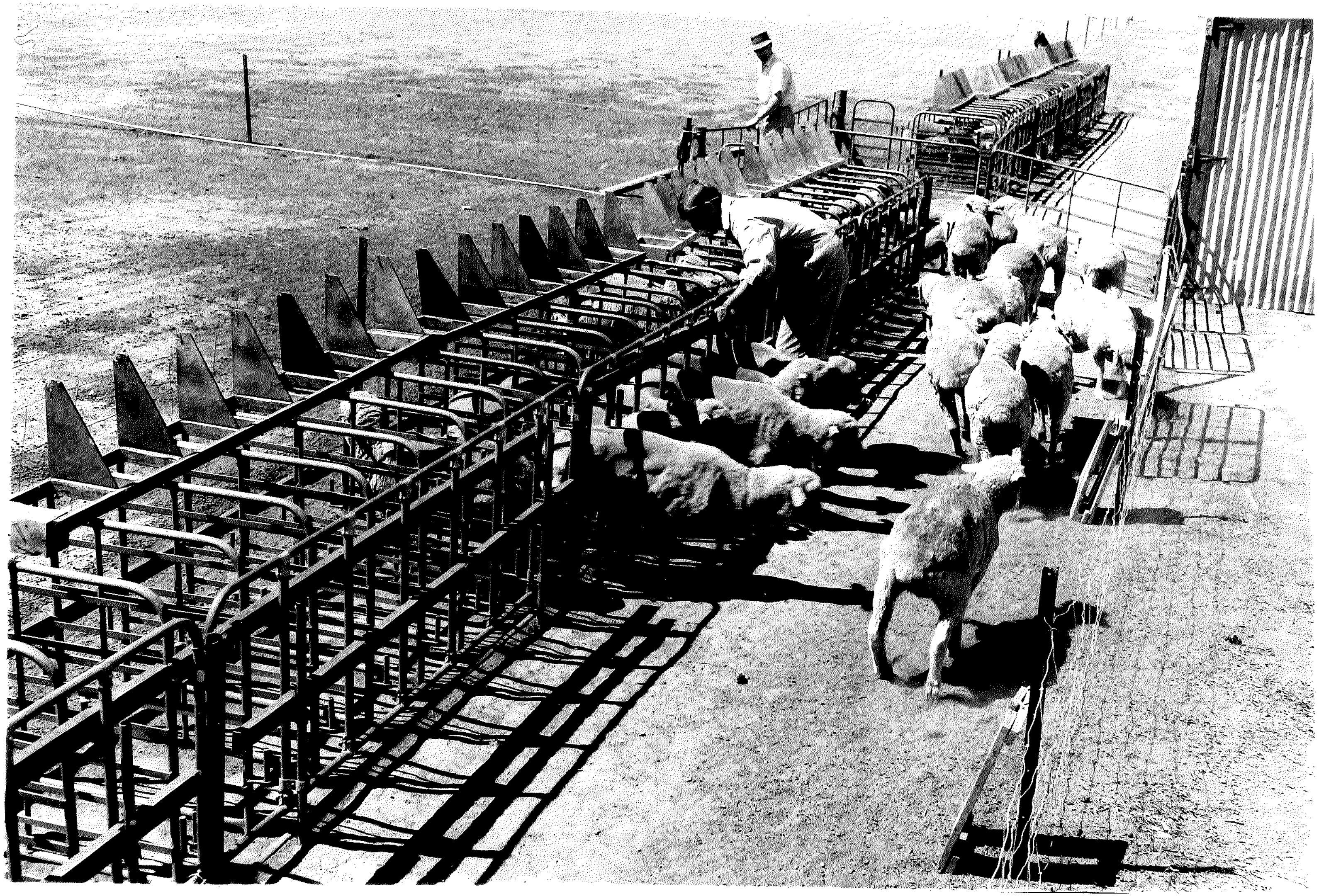


TABLE 4:2. SUMMARY OF THE PRINCIPAL DIETARY CONSTITUENTS

Constituent	Proportion(2)
Pelleted feed (1)	
Lucerne %	45
Barley %	50
Common salt %	2
Limestone (finely-ground) %	3
Dry matter %	95.6 (79)
Composition (% dry matter)	
Ash	8.8
Organic matter	91.2
Ether extractives	4.4 (84)
Crude fibre	12.6 (75)
Crude protein (N x 6.25)	18.1 (85)
Nitrogen-free extractives	58.4 (81)
Ca	0.95
P	0.34
Ca/P ratio	2.79
Na	0.75
Cl	0.80
Digestible organic matter (%)	76
Digestible energy (Cals/g)(3)	3.492

Note: (1) Pellets approximately 1cm long and 0.4 cm diameter

(2) Apparent digestibility coefficients, derived from feeding trials with three wethers, are shown in parentheses.

(3) Derived from the regression equation of Moir (1961):

$$y = 0.0462\ x - 0.158$$

where,

y = Digestible energy in Cals/g

x = Dry matter digestibility %

dried each day and the apparent dry matter digestibility of the diet estimated. A subsample of the dried material was taken for chemical analyses using standard analytical methods (A.O.A.C. 1960).

Ewes were weighed once weekly and the feed offered in the following week adjusted quantitatively to bring the gross body weight of each ewe into line with the desired curve of weight gain or loss.

Drinking water was available at all times.

IV. Wool Production of Ewes

An area approximately 100 sq. cm. was tattooed on the midside of each ewe immediately after shearing in October 1962. For those ewes subsequently slaughtered the wool grown on the midside patch was harvested (Oster clippers, size 40) at mating, and after 90- and 140-days of pregnancy; for those ewes which lambed harvests were taken at mating, after 90-days of pregnancy and again after lambing.

Ewes were carefully shorn by conventional means either immediately before slaughter or after lambing.

Greasy midside and fleece wool samples were scoured, oven-dried and the yield of clean wool determined.

Total clean wool production of each sheep in specified periods was estimated using the ratio method described by Allden (1959), viz:

$$W_e = W_t \times \frac{Pe}{Pt} ,$$

where,

W_e = total clean dry wool (g) grown by each sheep during the experimental period;

W_t = total clean dry wool (g) produced in the shearing interval;

P_t = total clean dry wool (g) produced in the midside patch in the shearing interval;

and,

P_e = total clean dry wool (g) produced in the tattooed midside patch in the experimental period.

V. Body Condition of Ewes

Body condition (fatness) of each ewe was subjectively assessed at weaning, mating and on all subsequent weighing occasions. Scores were applied throughout the experiment by one experienced observer, whose repeatability and discrimination had been studied in an earlier pilot trial (Everitt 1962; Judge C in Paper 1; Appendix 1).

A scoring system of 10 points was used where score 10 equalled very fat and score 1 an emaciated condition.

Four separate scores were applied to each sheep on each occasion. The loin, flank, and tail positions were scored separately and an additional score applied to the whole animal.

VI. Slaughter Procedure

Ewes selected for slaughter were weighed in the paddock (final live weight), shorn, weighed (wool-free final live weight), fasted for 24 hrs., photographed, and then killed by exsanguination at the throat.

The following components of the body were weighed; skull, fore- and hind-feet, skin, blood, brain,eyes, tongue; the gastro-intestinal tract (full and empty) partitioned into oesophagus, stomachs (rumen, reticulum, omasum and abomasum), small intestine, large intestine and rectum; gastro-intestinal contents; heart, lungs and trachea, diaphragm; liver, gall bladder (empty), spleen, kidneys, urinary bladder (empty); adrenals; heart (peri-cardial) fat, caul and mesenteric fat; udder; the hot carcass; and the genital tract which included the vulva, vagina and cervix, ovaries, Fallopian tubes, and the uterus (plus contents, where applicable).

Empty body weight represented starved live weight minus the weight of the gastro-intestinal contents. Corrected empty body weight represented empty body weight minus the weight of the conceptus.

After chilling the carcass was photographed, wrapped in polythene and stockinette bags and deep frozen (-15°C). All other body components were bulked for each animal and also deep frozen.

VII. Dissection of the Gravid Uterus

The dissection of the gravid uterus followed, in principle, the procedures detailed by Wallace (1948).

The following components of the gravid uterus were weighed; functional cotyledons, membranes (amnion plus allantochorion), amniotic fluid, allantoic fluid, necrotic tissue at the tips of the uterine horns, the uterus, and the foetus. Functional cotyledons and the membranes together represented the placenta. Definitions of placental components followed those used by Cloete (1939), Wallace (1948), and, more recently, Alexander (1964a,b).

Functional cotyledons were weighed individually, distinguishing between those from the pregnant and vacant uterine horns. Division of functional cotyledons into maternal and foetal components was attempted initially, but discontinued for reasons discussed later. Representative cotyledons from each animal were preserved in 10 per cent. neutral saline formalin.

The foetus, after ligaturing the umbilical cord, was removed from the uterus, weighed, dried thoroughly with towels, re-weighed (foetal body weight), wrapped in damp towels and refrigerated (5°C) to await further examination. Loss in foetal weight on drying was credited to the weight of amniotic fluid.

VIII. Foetal Body Measurements

A total of 21 external body measurements were recorded from the left side of each foetus. Fig. 4:2 illustrates the position of 16 of the measurements, points of reference following those detailed by Stephenson (1959, 1962a).

Definitions applicable to the other body measurements were:

9. Metacarpus depth - the anterior-posterior distance measured at the mid-point.
10. Metacarpus width - the lateral distance measured at the mid-point.
14. Pelvis width - the distance between the *tuber coxae*.
15. Pelvis length - the distance between the *tuber coxae* and the *tuber ischii*.
22. Tail length - the difference between curved crown-rump length and curved crown-tail length, i.e. measurement 2. *minus* measurement 1.

Measurements numbered 1-7 inclusive, 16 and 17 were recorded with a linen tape, remaining measurements with micrometer calipers.

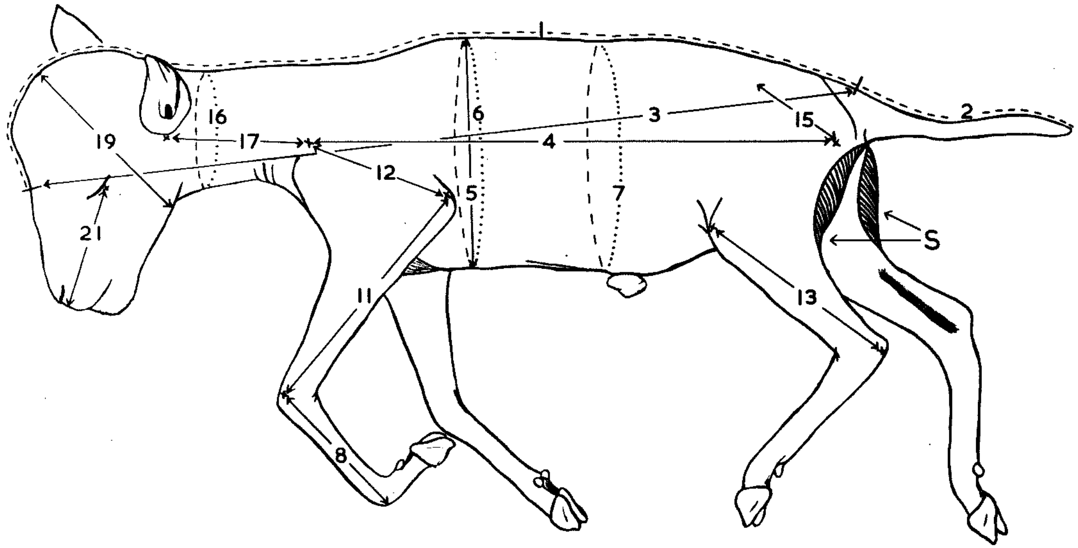
The mean value of duplicate readings of all measurements was used.

IX. Anatomical Dissection of the Foetus

Each foetus was dissected into 32 components, including gastro-intestinal "fill" and the foetal carcass. The procedures adopted followed those described in detail by Wallace (1948) for the ovine foetus and Pomeroy (1960) for the porcine foetus, and, in essence, was very similar to that used in the anatomical dissection of the adult ewes. The skin, however, was not removed until towards

Fig. 4:2.- Position of the foetal body measurements and of the *Semitendinosus* muscle. The length of the tail equalled measurement 2. *minus* measurement 1.

FOETAL BODY MEASUREMENTS AND POSITION OF m.SEMITENDINOSUS



1. CURVED CROWN–RUMP
2. CURVED CROWN–TAIL
3. STRAIGHT CROWN–RUMP
4. TRUNK LENGTH
5. CHEST DEPTH
6. HEART GIRTH
7. NAVEL GIRTH
8. METACARPUS LENGTH
9. METACARPUS DEPTH (NOT SHOWN)
10. METACARPUS WIDTH (NOT SHOWN)
11. RADIUS/ULNA LENGTH
12. HUMERUS LENGTH
13. TIBIA/FIBULA LENGTH
14. PELVIS WIDTH (NOT SHOWN)
15. PELVIS LENGTH
16. NECK GIRTH
17. NECK LENGTH
18. HEAD WIDTH (NOT SHOWN)
19. HEAD DEPTH
20. FACE WIDTH (NOT SHOWN)
21. FACE LENGTH

S. m. SEMITENDINOSUS

the end of the dissection in an attempt to reduce dissection loss due to evaporation.

X. Wool Follicle Development of the Foetus

Biopsy skin samples, 1 cm. diameter, were taken from the midside of all foetuses and wool follicle development examined in histological sections. Procedures were based on those described by Clarke (1960) in the review of Fraser & Short (1960).

XI. Muscle Fibre Development of the Foetus

The right Semitendinosus muscle (see Fig. 4:2 for position) of each foetus was dissected out, weighed, covered in neutral saline for 20 mins. and preserved in 10 per cent. neutral saline formalin. Cross-sections, 8μ thickness, were cut from the centre of the muscle and stained with haemotoxylin and eosin.

Estimation of fibre numbers per fasciculus proved impossible due to poor definition of fasciculi in nearly all sections. The number of muscle fibres per sq. mm. was estimated from counts taken from five separate areas of each section, and a mean value calculated. The latter, multiplied by the cross-sectional area of the total muscle (measured with a planimeter), estimated the total number of fibres in cross-section. This tends to be an over-estimate, for it takes no account of inter-fascicular space, nor of distortion from histological processing. However, the estimates have a relative value and serve for study of treatment effects.

XII. Biometrical Methods

(a) General

Standard analyses of variance and covariance appropriate to a 2 x 2 factorial design, and of regression analysis, were used (Snedecor 1956). Variation due to maternal nutrition and to the rams (each with a single degree of freedom) was isolated, together with the interaction, also with a single degree of freedom. Tables of mean values have been presented, together with the coefficient of variation of the overall or grand mean, the standard error of treatment means, and mean differences of main treatment effects. The generally accepted abbreviations to denote levels of statistical significance have been used throughout, i.e. (*) $P < 0.10$, *$P < 0.05$, ** $P < 0.01$, and *** $P < 0.001$.

It may be noted that the standard error shown in tables of adjusted mean values, derived from covariance analyses, represents the largest of the four standard errors associated with the four adjusted means. Use of the standard error presented to determine, for example, least significant difference leads, therefore, to an approximate test of significance only; with a tendency to reveal fewer significant differences than may actually exist. Adoption of this method of presentation greatly reduces the amount of tabulated statistical information without greatly affecting the biological interpretation.

Examples of analyses described in this section are provided in Appendix II.

(b) Ewe Performance

Analyses of most of the information relating specifically to the performance of the ewes, as, for example, components of body weight and wool production, revealed, not surprisingly, only a small and not significant ($P < 0.05$) proportion of the total variance attributable to the rams. Neither did the interaction attain significance in these comparisons. In order to simplify presentation of the mass of data, without loss of meaningful information, mean values of only HP and LP groups have been offered, together with the mean difference of the nutritional effect (HP - LP). For those few parameters recording a significant sire effect, mean values and the mean difference (Ram L - Ram S) have been included in the presentation.

(c) Foetal Performance

Analyses of foetal data, and associated uterine structures (the placenta, for example), at each of the two foetal ages were complicated by disproportionate subclass numbers of male and female foetuses. For a few cases of special interest (foetal body weights, for example) this non-orthogonality was overcome by "fitting constants" (Kempthorne 1952), using least squares procedures. It was possible in this way to isolate the variance due to foetal sex and obtain a direct estimate of the magnitude of the sex effect from the mean difference (males - females).

An alternative estimate of the sex effect was adopted, however, in the majority of cases. Covariance analysis, employing foetal sex as a discontinuous concomitant variable, with arbitrary values of female equal to zero and male equal to one, was used. The derived regression coefficients indicated the trend of the sex effect; a positive coefficient indicated that male foetuses exceeded females in the measured parameter and the converse with a negative coefficient. The regression coefficient (b) thus estimated the sex effect, while the adjusted mean values derived from the covariance analysis detected real differences between groups.

The growth of foetal body parts (linear measurements or body component weights) relative to the growth of the whole was investigated by plotting a natural logarithmic transformation of a measurement against a natural logarithmic transformation of the whole at each of the two ages. Covariance analysis of logarithmic transformed data using two covariates, foetal sex and foetal body weight or crown-rump length, was undertaken. The first regression coefficient for foetal sex (b_1 : discontinuous independent variable; female = 0, male = 1) estimated the sex effect, independent of foetal body weight. The second regression coefficient for foetal body weight or crown-rump length (b_2 : continuous independent variable) represents, in effect, the value of k in the logarithmic form of the allometric equation ($\log y = \log b + k \log x$), independent of the effects of foetal sex. In other words, b_2 represents the differential growth ratio or growth coefficient of the measured part - the ratio of the specific growth rates of the part and the whole - after adjustment for differences between male and female foetuses. Variance ratios of the transformed data relating to a particular variable, and the adjusted mean values, detected real differences between groups in the stage of development at a specified age when considered at the same foetal body weight (or crown-rump length) with all foetuses of the same (statistical) sex.

It may be noted that a double logarithmic transformation of data gives an approximation to a linear regression. Stephenson (1957) discussed the sources of error inherent in the method and considered it justifiable to fit a regression line by the method of least squares where the dependent and independent variables are highly correlated. This was found to be the case in these studies.

C. RESULTS

I. GENERAL PROGRESS OF THE EXPERIMENT

(a) Climatic Conditions

Meteorological records covering the period of field activity are illustrated in Fig. 4:3.

Ambient temperatures increased from a monthly average of 57.5°F (14.2°C) in September 1962, to 71.6°F (22.0°C) in January and 71.7°F (22.1°C) in February 1963, and then declined to 57.6°F (14.2°C) in May 1963. The maximum daily air temperature exceeded 90°F (32.2°C) on 6 days in November and 4 days in December 1962, and on 9, 4 and 2 days in January, February and March 1963 respectively. There were 2 days in November 1962 and 1 day in February 1963 when the maximum daily air temperature exceeded 100°F (37.8°C).

Little rain fell between October 1962 and the end of April 1963, except for 3.30 in. during the second week of January 1963. The latter precipitation produced some germination of annual species in the experimental area but the amount of green fodder available to the animals was inconsequential at the high stocking rate employed.

Field activities of the experiment were completed by the time of onset of autumn rains in early May, 1963.

(b) General Performance of the Experimental Animals

Table 4:1 shows that 64 ewes, out of the 70 available, were mated to fertile rams; 6 ewes failed to display oestrus. Recurrent oestrus in 3 ewes, return to the ram after a time representing two oestrous cycles (2), and failure to lamb despite presumed pregnancy (1) accounted for further losses.

A smaller proportion of LP ewes (47 *per cent.*) settled to first service than did HP ewes (59 *per cent.*). This may be associated with the drastic reduction of feed offered to LP ewes immediately after mating.

One LP ewe in lamb to Ram S proved non-pregnant when slaughtered after 90-days of pregnancy. Each of the remaining 31 ewes slaughtered during pregnancy carried a single foetus.

No ewe deaths occurred under HP feeding, but, out of 32 LP ewes successfully mated to the entire rams, 5 (16 _per cent._) died between 121 and 137 days of pregnancy. Death ensued in all cases after progressive weakness, prostration and complete inappetence. Post mortem examinations revealed characteristic symptoms of starvation; lack of body fat and oedema of the thoracic and abdominal cavities, with adrenal enlargement. Gravid uteri, in particular, were grossly enlarged with fluid, and a decomposing foetus was found in one ewe. Gross body weight loss of these ewes approximated 25-31 _per cent._ of their weight at mating.

Single lambs were born to 21 ewes. All 14 HP lambs were reared successfully by their dams. LP ewes lacked maternal interest in their young and lactation was never initiated. Plate 4 : 8 illustrates the emaciated state reached after 140-days of undernutrition, and the absence of udder development in LP ewes. Despite constant attention and attempts at artificial rearing, 4 out of 7 LP lambs died within 2 days of birth, 1 within 3 days; two LP lambs were successfully reared by artificial means.

Table 4:1 emphasises the need for generous estimation of the number of animals required at the start of experiments of this nature.

II. MEASUREMENTS OF RAMS

Measurements of the two rams are recorded in Table 4:3. At mating time, Ram S, compared with Ram L, was lighter in body weight, smaller in all skeletal dimensions, with fewer muscle fibres/fasciculus and fibres of smaller diameter. The larger size (surface area) of Ram L failed to compensate for the lower density of wool follicles, the estimated total follicle population being greater for the smaller ram. Estimated clean fleece production, however, favoured Ram L.

III. PERFORMANCE OF EWES

(a) Body Weights and Condition Scores

Table 4:4 records mean body condition scores; differences between positions at each stage were not significant.

A loss in mean body weight of all ewes between weaning and mating was recorded (45.5 kg. ± S.D. 5.2 compared with 41.9 kg. ± S.D. 6.9 respectively), with a concomitant reduction of condition score (whole animal) from 7.0 to 5.5 (Table 4:4).

Ewes were very variable in body weight and fatness at weaning and at mating, as shown by the standard deviations of mean body weights, the coefficients of variation in Table 4:4, and Plate 4:9 which illustrates the carcasses of sample slaughter ewes killed at mating.

Mean gross body weights throughout pregnancy are depicted in Fig. 4:4 for those ewes slaughtered during the trial, and in Fig. 4:5 for those ewes continuing on to lambing. Body weights recorded

Fig. 4:3.- Climatological records for the Waite Agricultural Research Institute during the 1962-63 experimental period.

METEOROLOGICAL RECORDS FOR THE 1962-63 EXPERIMENTAL PERIOD

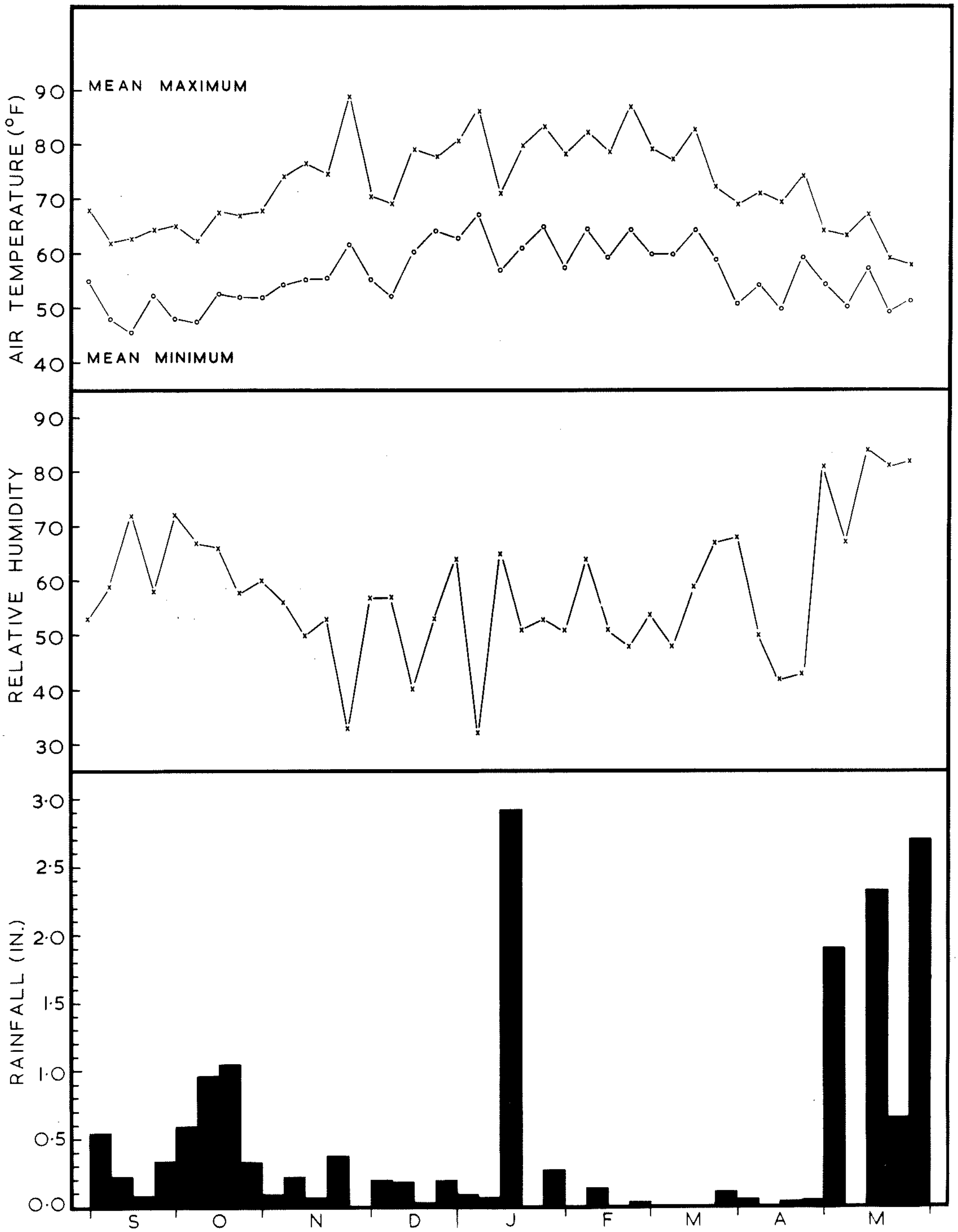


TABLE 4:3. SUMMARY OF MEASUREMENTS OF RAMS

Character	Ram L	Ram S
Age (months)	27	56
Body weight (kg.)	92.6	64.5
Body measurements (cm.)		
Body length	86.5	76.0
Depth of chest	39.5	33.5
Width at shoulders	25.5	22.5
Width at ribs	30.0	26.0
Width at hips	22.5	20.0
Hips to pins	29.0	25.0
Elbow-coronet	45.5	39.0
Fore-cannon length	18.7	16.9
Biceps femoris muscle		
Mean no. muscle fibres/fasciculus	189	107
(C.V. %)	(2.6)	(5.6)
Mean diameter of muscle fibres (μ)	54	44
(C.V. %)	(4.6)	(9.4)
Wool follicles		
Pf/cm^2	206	328
Sf/cm^2	3240	5200
$Pf + Sf/cm^2$	3446	5528
Sf/Pf ratio	15.7	15.9
Estimated total follicle population (1) (millions)	59.8	77.5
Wool production		
Midside clean wool (g)/10 cm^2/100 days	1.029	1.141
Estimated clean fleece (g)/100 days (1)	1786	1600

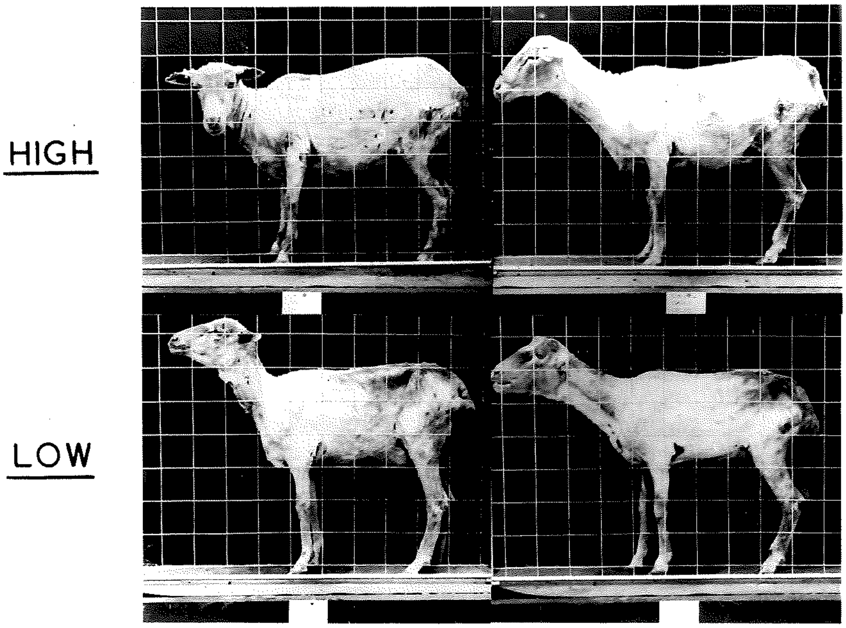
Note:

(1) Estimated from the formula of Lines & Pierce (1931) where :-

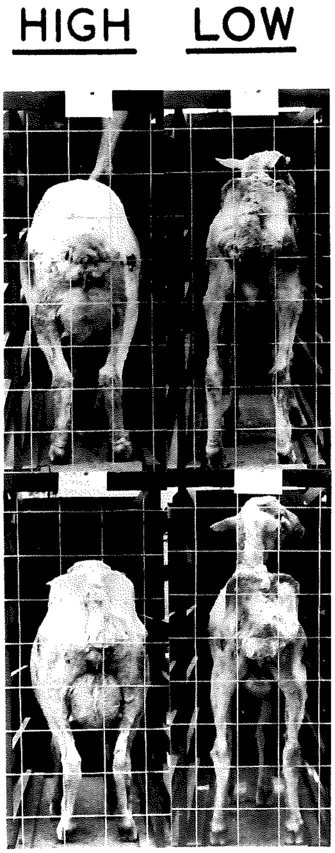
$$\text{Area} = 0.121 \text{ body weight}^{0.59}$$

Plate 4:8.- Side and rear views of representative HP and LP ewes immediately prior to slaughter after 140-days of pregnancy. Note the lack of udder development in the LP ewe (10 x 10 cm. grid).

140 days of pregnancy



140 days of pregnancy



after 90- and 140-days of pregnancy, expressed as percentages of weights recorded at mating, are also shown. The desired degree and rate of gross body weight gain or loss was satisfactorily achieved for both the slaughtered ewes and those lambing, with better accuracy in the former than the latter.

Table 4:4 shows that condition scores changed from 5.5 at mating to 5.6 (HP) and 3.7 (LP) after 90-days of pregnancy, and to 6.2 (HP) and 1.7 (LP) after 140-days. HP ewes never achieved a very fat condition but LP ewes were emaciated by the end of pregnancy.

(b) Food Intake

Mean weekly amounts of dry matter (D.M.) offered, rejected and consumed by the slaughtered ewes are shown in Fig. 4:6.

HP ewes were fed, in effect, ad libitum for most of pregnancy. The very small quantities of feed offered to LP ewes in late pregnancy were necessary to compensate for body weight increase originating from conceptus growth.

Feed consumption of LP ewes increased over the first few weeks of pregnancy. This reflects the initial reduction of gut-fill, necessitating a subsequent increase in rations to bring the recorded body weights into line with the desired curves (see Figs. 4:4 and 4:5). Fig. 4:7 also shows this effect where the mean daily intake of D.M. by slaughtered ewes is expressed as a percentage of mean wool-free body weight. The D.M. intake of HP ewes, as a proportion of

TABLE 4:4. MEAN BODY CONDITION SCORES OF EWES

Time and position	Group means		Overall mean	C.V. %	S.E.	Mean difference (HP-LP)
	HP	LP				
At weaning						
Flank	-	-	6.7	30.2	0.61	-
Loin	-	-	6.0	33.9	0.80	-
Tail	-	-	7.2	40.7	0.73	-
Whole animal	-	-	7.0	37.2	0.71	-
At mating						
Flank	-	-	5.0	28.3	0.58	-
Loin	-	-	5.0	47.3	0.97	-
Tail	-	-	5.8	47.8	1.14	-
Whole animal	-	-	5.5	45.6	1.02	-
Ewes slaughered after 90-days of pregnancy						
Flank	5.5	3.7	4.6	26.8	0.64	1.8*
Loin	5.6	3.9	4.7	26.0	0.63	1.7*
Tail	5.8	4.3	5.0	24.8	0.64	1.5*
Whole animal	5.6	3.7	4.6	27.9	0.66	1.9*
Ewes slaughtered after 140-days of pregnancy						
Flank	6.4	1.7	4.0	23.4	0.47	4.7***
Loin	6.1	1.2	3.6	23.3	0.41	4.9***
Tail	6.2	1.7	3.9	23.0	0.44	4.5***
Whole animal	6.2	1.7	3.9	20.4	0.40	4.5***

Note: Score 10 = very fat; Score 1 = emaciated.

Plate 4:9.- Carcasses of ewes slaughtered at mating; the variation in weight and fatness may be noted (5 x 5 cm. grid).

INITIAL SAMPLE SLAUGHTER EWE CARCASSES

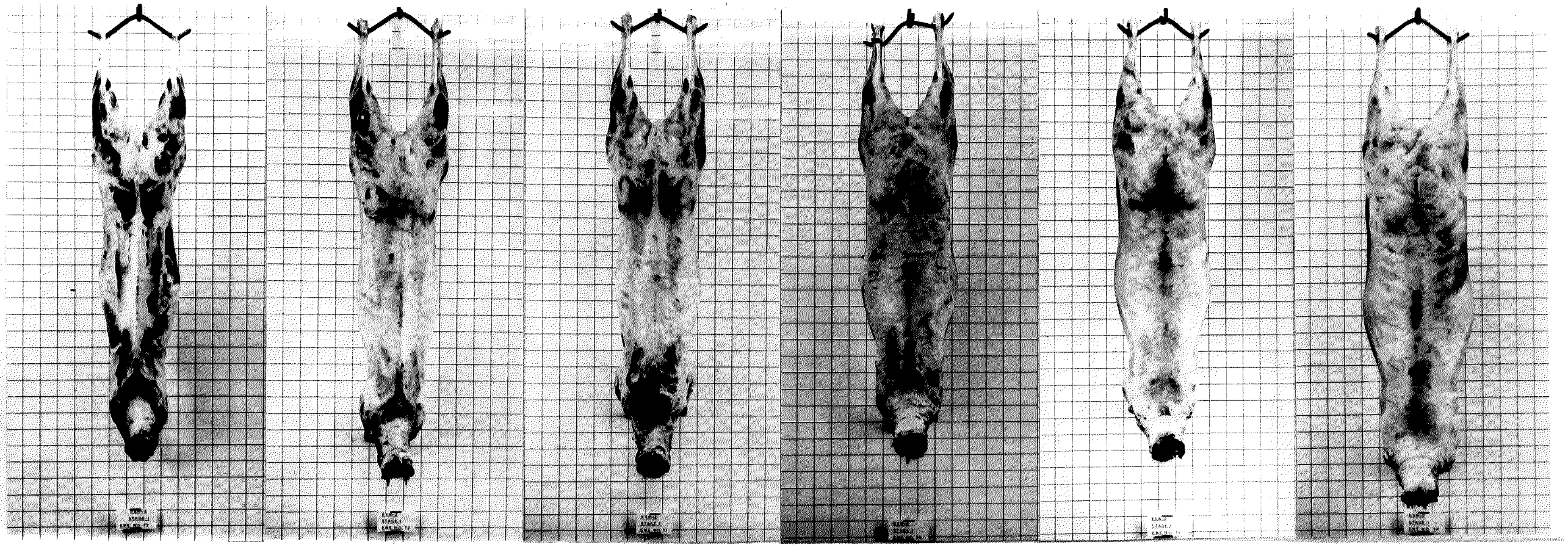


Fig. 4:4.- Mean gross body weights during pregnancy of ewes which were slaughtered and carried a single foetus. The desired mean weight gain or loss over 140 days (± 25 *per cent*. of the weight recorded at mating) is shown by the solid lines; broken lines represent recorded mean body weights.

MEAN LIVE WEIGHTS (kg) OF EWES IN PREGNANCY

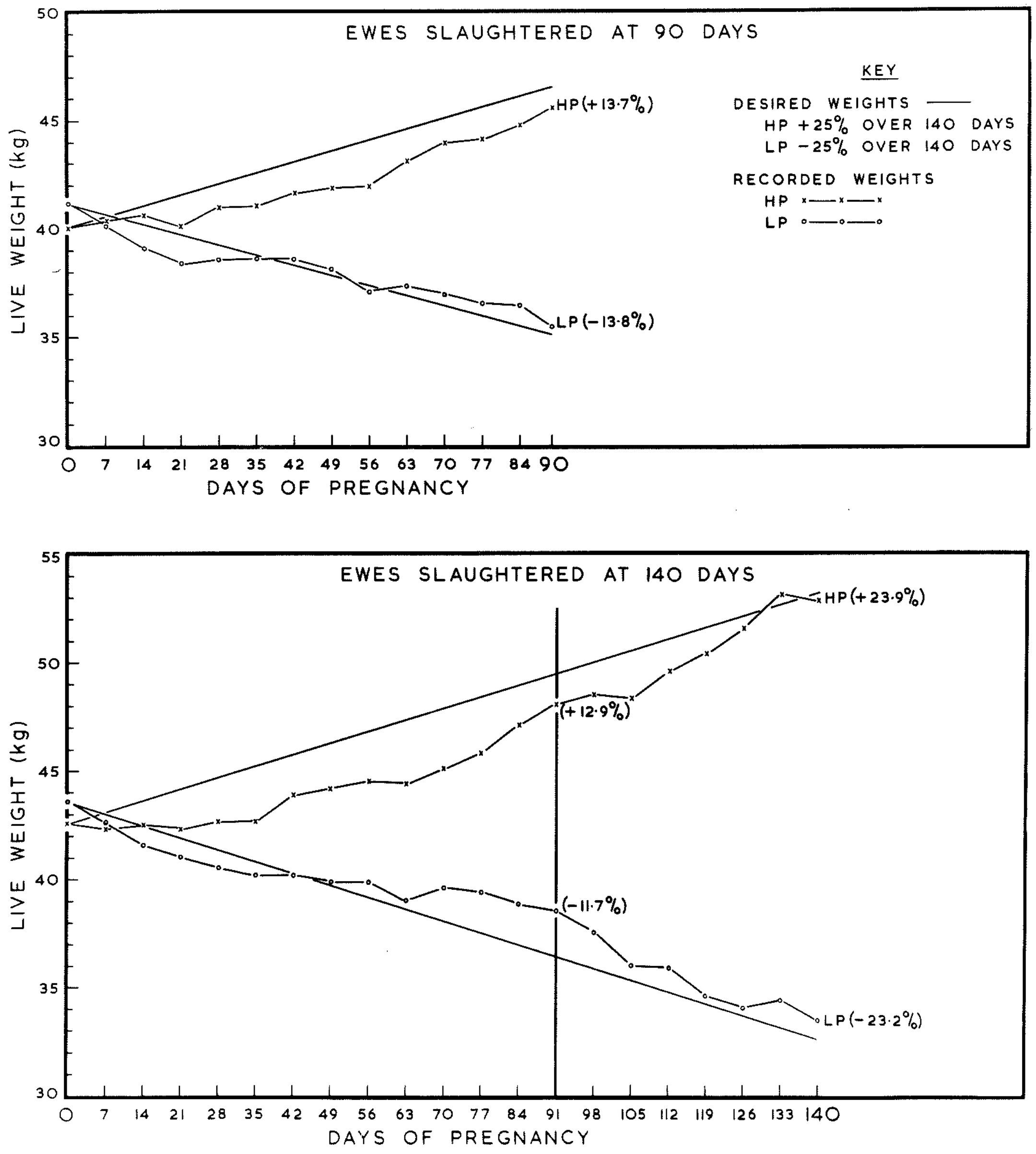


Fig. 4:5.- Mean gross body weights during 140-days of pregnancy of ewes which subsequently lambed. The desired mean weight gain or loss over 140 days (± 25 *per cent*. of the weight recorded at mating) is shown by the solid lines; broken lines represent recorded mean body weights.

MEAN LIVE WEIGHTS (kg) OF EWES OVER 140 DAYS OF PREGNANCY

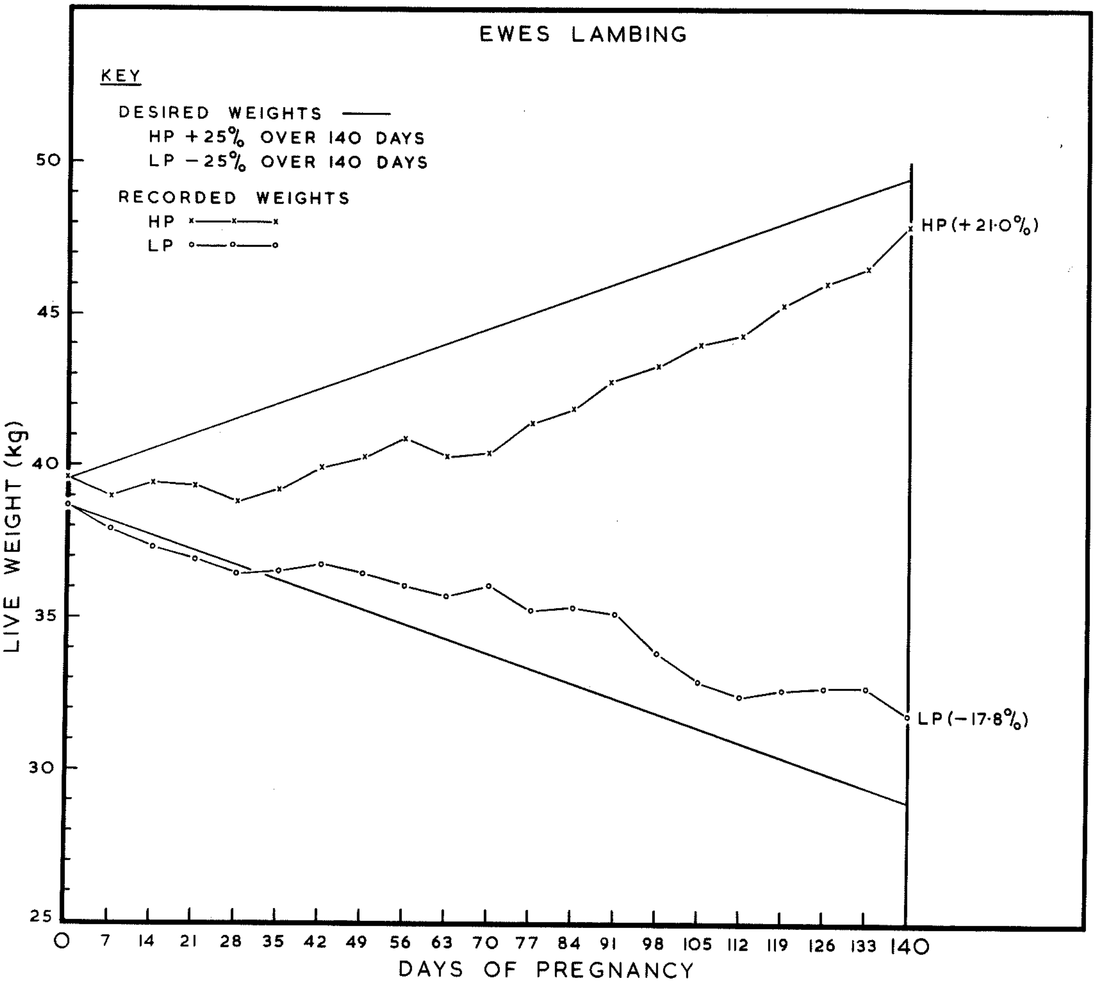
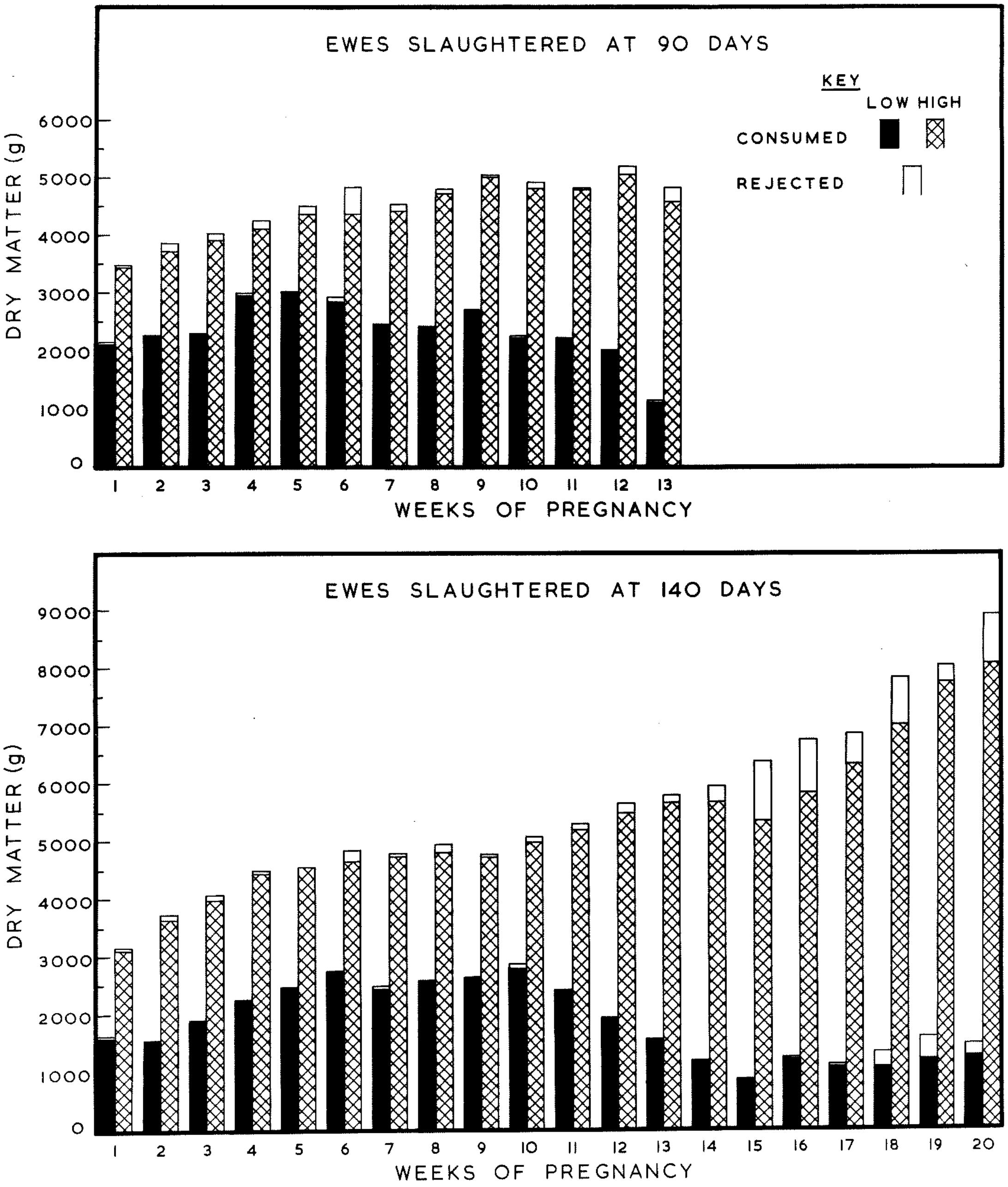


Fig. 4:6.- Mean weekly amounts of dry matter offered, rejected and consumed by the ewes during pregnancy.

MEAN FOOD CONSUMPTION


EWES SLAUGHTERED AT 90 DAYS

EWES SLAUGHTERED AT 140 DAYS

Fig. 4:7.- Mean daily intake of dry matter during pregnancy as a percentage of the mean wool-free body weight. The curves for the first 13 weeks of pregnancy are based on 16 HP ewes and 15 LP ewes; and for the last 7 weeks on 8 HP ewes and 8 LP ewes.

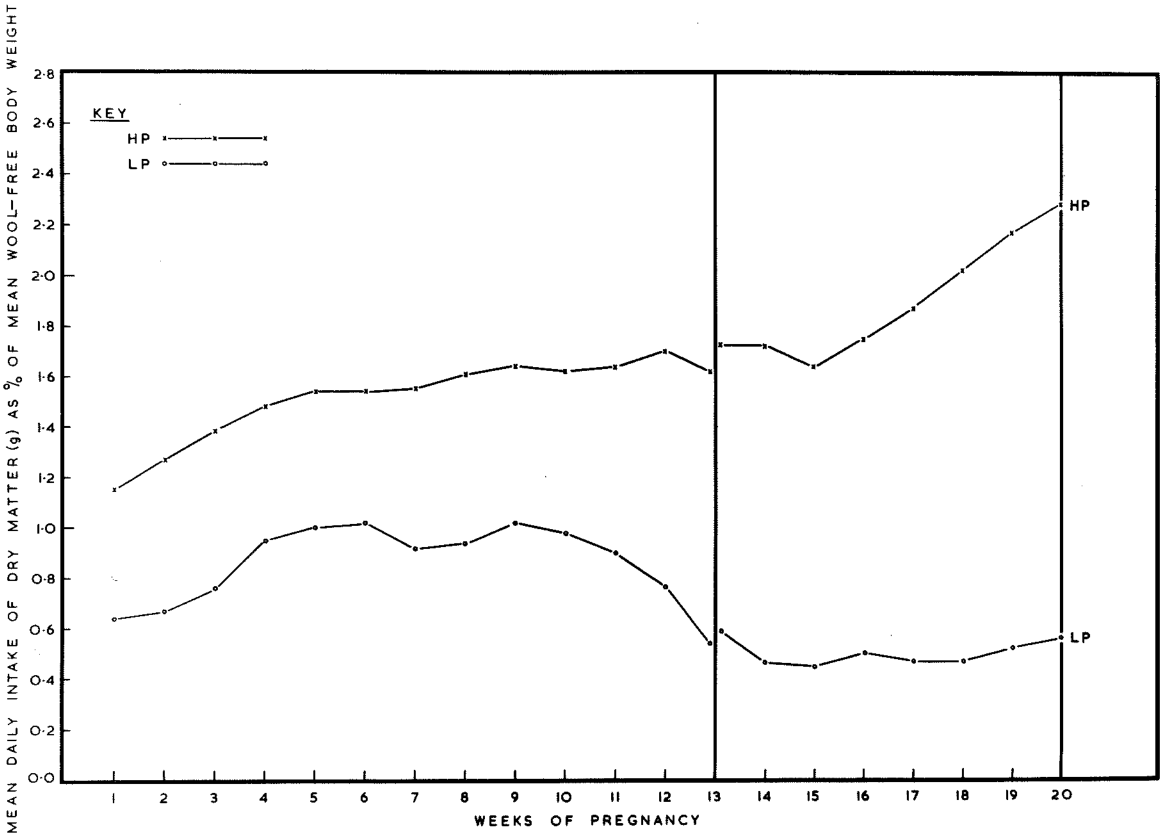

MEAN DAILY INTAKE OF DRY MATTER (g) AS % OF MEAN WOOL-FREE BODY WEIGHT
2·8
2·6
2·4
2·2
2·0
1·8
1·6
1·4
1·2
1·0
0·8
0·6
0·4
0·2
0·0
KEY
HP
LP
HP
LP
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
WEEKS OF PREGNANCY

TABLE 4:5. MEAN DAILY INTAKE (g) OF DIGESTIBLE ORGANIC MATTER

Period	Group means				Overall mean	C.V. %	S.E.	Mean differences	
	HP/Ram L	HP/Ram S	LP/Ram L	LP/Ram S				Plane of nutrition (HP - LP)	Rams (Ram L - Ram S)
<u>Ewes slaughtered after 90 days</u>									
0-90 days	489.3	483.5	250.0	273.7	380.8	19.1	37.5	224.6***	9.0
<u>Ewes slaughtered after 140-days</u>									
0-90 days	523.8	485.3	250.8	234.3	373.5	7.8	14.6	262.0***	27.5
91-140 days	734.3	662.0	128.5	115.8	410.1	8.3	17.0	576.0***	42.5 *
0-140 days	599.0	548.0	207.0	192.0	386.5	6.7	13.0	374.0***	33.0 *
<u>Ewes lambing</u>									
0-90 days	449.8	447.9	223.0	229.0	374.6	11.5	18.8	222.9***	-2.1
91-150 days	512.5	665.8	131.7	146.0	446.7	24.8	48.3	450.3***	-83.8
0-150 days	475.0	535.3	186.7	195.8	403.6	16.4	28.9	313.9***	-34.7

body weight, did not attain the levels suggested by the N.R.C. (1959); recommended intakes of air-dry feed (90 *per cent*. D.M.) for a sheep of 45.4 kg. are 2.6 *per cent*. in the first 15 weeks of pregnancy and 3.5 *per cent*. in the last 6 weeks (Table 2:3). LP ewes rejected some of their meagre ration in weeks 17-20 of pregnancy.

The mean daily intake of digestible organic matter (D.O.M.) is recorded for slaughtered ewes, and for those ewes which lambed, in Table 4:5. Intake of D.O.M. of LP ewes approximated half that of HP ewes in the first 90-days of pregnancy, and one-sixth in the last 50 days. LP ewes consumed less D.O.M./day, and HP ewes more, in the last 7 weeks of pregnancy than the first 13 weeks. Ewes in lamb to Ram L slaughtered after 140-days consumed more D.O.M./day than those in lamb to Ram S, although the difference did not attain significance in early pregnancy. For those ewes lambing, differences of intake associated with sires were in the opposite direction and not significant.

(c) Wool Production and Efficiency of Wool Growth

(i) Production

Mean wool production data of slaughtered ewes are summarised in Table 4:6 and for those ewes lambing in Table 4:7.

More greasy wool was produced by HP than LP ewes, the difference attaining significance in those ewes slaughtered after

TABLE 4:6. MEAN WOOL PRODUCTION (g) OF EWES KILLED AFTER 90- AND 140-DAYS OF PREGNANCY

Character	Group means		Overall	C.V.	S.E.	Mean difference
	HP	LP	mean	%		(HP-LP)
<u>Ewes killed after 90-days</u>						
Midside clean wool/10 cm^2/90 days	9.308	8.180	8.791	18.5	0.840	1.228
Greasy fleece/90 days	1884	1777	1835	11.3	107.5	107
Yield %	51.8	41.7	47.1	18.5	4.5	10.1 *
Clean fleece/day	11.0	8.2	9.7	26.3	1.31	2.8 (*)
<u>Ewes killed after 140-days</u>						
Midside clean wool/10 cm^2						
0-90 days	10.980	6.578	8.779	23.7	1.042	4.402 ***
91-140 days	3.781	1.718	2.749	39.9	0.548	2.063 **
0-140 days	14.761	8.296	11.528	25.8	1.485	6.465 ***
Greasy fleece/140 days	2404	1946	2176	18.8	204.1	458 *
Yield %	55.4	45.1	50.2	5.7	1.4	10.3 ***
Clean fleece/day						
0-90 days	11.0	7.7	9.4	16.8	0.8	3.3 **
91-140 days	6.8	3.6	5.1	34.3	0.8	3.2 **
0-140 days	9.5	6.3	7.9	18.4	0.7	3.2 ***

TABLE 4:7. EWES LAMBING : MEAN WOOL PRODUCTION (g) ADJUSTED TO A GESTATION LENGTH OF 150-DAYS

Character	Group means		Overall	C.V.	S.E.	Mean difference
	HP	LP	mean	%		(HP-LP)
Midside clean wool/10 cm^2						
0-90 days	10.287	6.638	9.637	33.4	1.404	4.189 **
91-150 days	2.992	1.441	2.515	26.2	0.287	1.551 ***
0-150 days	13.819	8.078	12.152	30.8	1.636	5.741 **
Greasy fleece/150 days	2392	1897	2250	12.9	127.0	495 **
Yield %	55.6	44.0	51.7	5.1	1.15	11.6 ***
Clean fleece/day						
0-90 days	11.6	7.7	10.4	18.7	0.85	3.9 ***
91-150 days	4.9	2.5	4.1	18.1	0.32	2.4 ***
0-150 days	8.9	5.6	7.9	18.4	1.16	3.3 ***

TABLE 4:8. MEAN EFFICIENCY OF WOOL GROWTH(1)

Period	Group means		Overall mean	C.V. %	S.E.	Mean difference (HP-LP)
	HP	LP				
Ewes slaughtered after 90-days						
0-90 days	2.25	3.15	2.68	15.4	0.213	-0.90 **
Ewes slaughtered after 140-days						
0-90 days	2.19	3.20	2.69	15.2	0.205	-1.01 ***
91-140 days	0.96	3.00	1.98	34.0	0.336	-2.04 ***
0-140 days	1.65	3.15	2.40	13.2	0.158	-1.50 ***
Ewes lambing						
0-90 days	2.62	3.64	2.90	21.3	0.270	-1.02 **
91-150 days	0.90	1.75	1.67	29.8	0.152	-0.85 ***
0-150 days	1.81	2.92	2.18	20.8	0.198	-1.11 ***

Note: (1) Efficiency = $\frac{\text{Clean dry wool/g/day} \times 100}{\text{Intake D.O.M./g/day}}$

140-days and in ewes lambing. A marked reduction (10-12 _per cent_.) in yield due to poor feeding increased the difference in clean wool production.

The decline of wool growth in late pregnancy as compared with the first 90-days is of particular interest. Under HP, as well as LP, feeding clean fleece production/day was reduced by approximately half in slaughtered ewes, and more than half in ewes lambing.

(ii) _Efficiency_

Table 4:8 records estimates of mean efficiency of wool growth. Wool was more efficiently produced under LP than HP feeding. Efficiency fell in late pregnancy especially under HP feeding; less wool was produced in late pregnancy (Tables 4:6 and 4:7), although feed intake of HP ewes increased both absolutely (Table 4:5) and relative to body weight (Fig. 4:7). This is seen more clearly in Figs. 4:8 and 4:9, in which efficiency of wool production is related to feed intake (on a per unit body weight basis) for ewes slaughtered and ewes lambing respectively. Although considerable within-group variation is apparent, it is clear that as intake fell so efficiency of wool production increased. There is an indication of a curvilinear relation in the latter part of pregnancy for ewes lambing (Fig. 4:9), increasing intake eliciting little response in the already low level of efficiency.

(d) Nutrient Requirements for Maintenance and Body Weight Gain of Ewes

Mean daily intake of D.O.M./g. has been related in multiple regression to mean wool-free conceptus-free body weight$^{0.75}$ (B.W.) in kg., and to mean wool-free conceptus-free body weight gain/g./day (W.G.)

The relationship (based on 12 d.f.) for ewes slaughtered after 90-days of pregnancy is shown in equation (1):-

$$\begin{array}{llll} (1) & \text{D.O.M.} = 42.1 + & 28.8\ \text{B.W.} + & 1.582\ \text{W.G.} \\ & (\text{s.e.}) & (\pm 6.96) & (\pm 0.2447) \\ & & ** & *** \end{array}$$

Maintenance requirement of a ewe weighing 45.4 kg. was therefore 514 g. D.O.M./day, and the requirement for 1 g. of weight gain (between 27.0 - 52.6 kg. body weight) was 1.58 g. D.O.M./day.

Equation (2) shows the relationship (based on 13 d.f.) for ewes slaughtered after 140-days of pregnancy:-

$$\begin{array}{llll} (2) & \text{D.O.M.} = 42.1 + & 29.5\ \text{B.W.} + & 1.1166\ \text{W.G.} \\ & (\text{s.e.}) & (\pm 10.07) & (\pm 0.2575) \\ & & ** & *** \end{array}$$

Over 140-days, therefore, the maintenance requirement of a 45.4 kg. ewe was estimated at 526 g. D.O.M./day, with 1.12 g. D.O.M./day being required for 1 g. of gain (ewes weighing 35.1 - 49.1 kg.)

Fig. 4:8.- Efficiency of wool growth related to feed intake (data relating to ewes slaughtered).

EFFICIENCY OF WOOL GROWTH RELATED TO FEED INTAKE

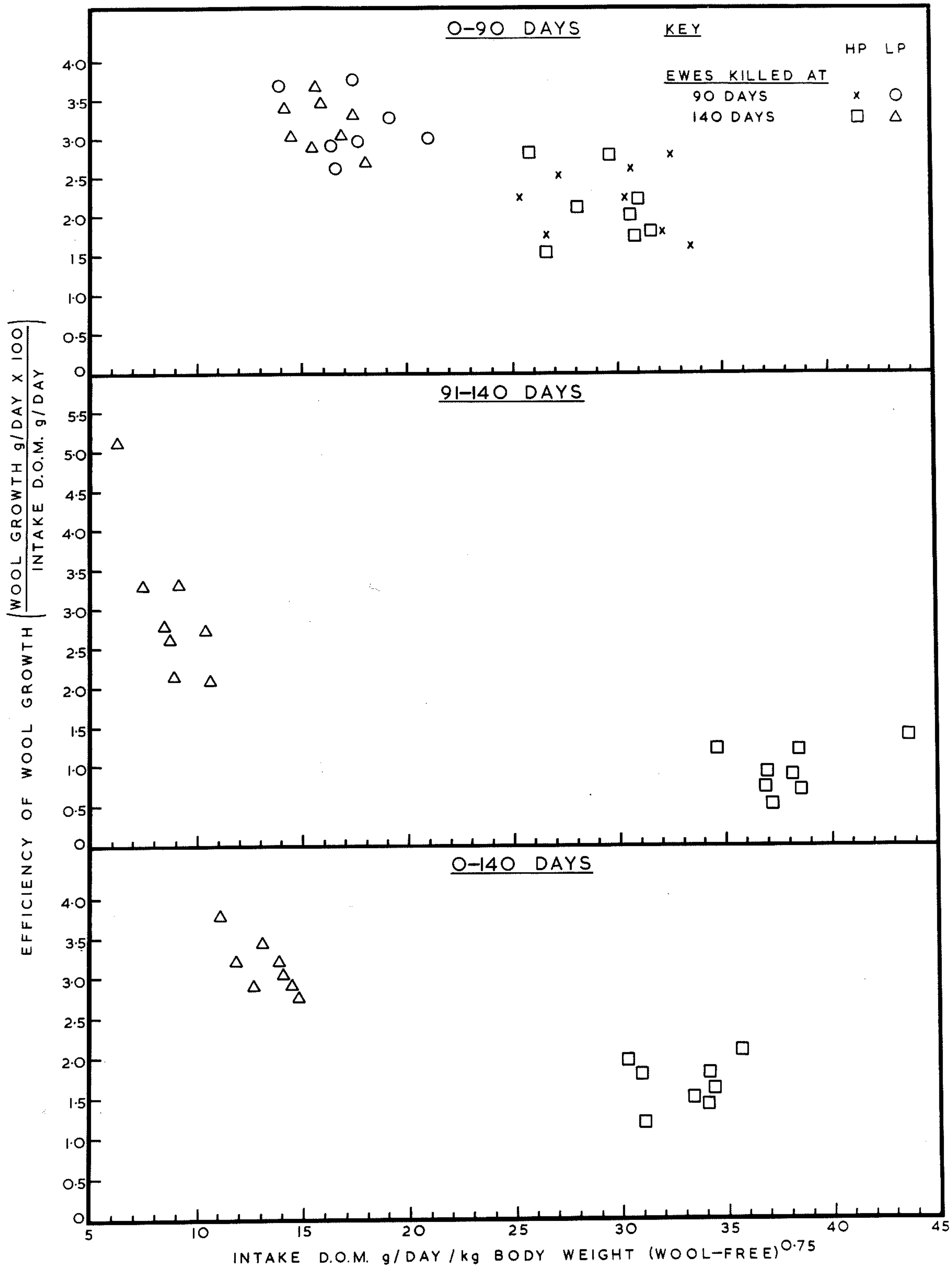
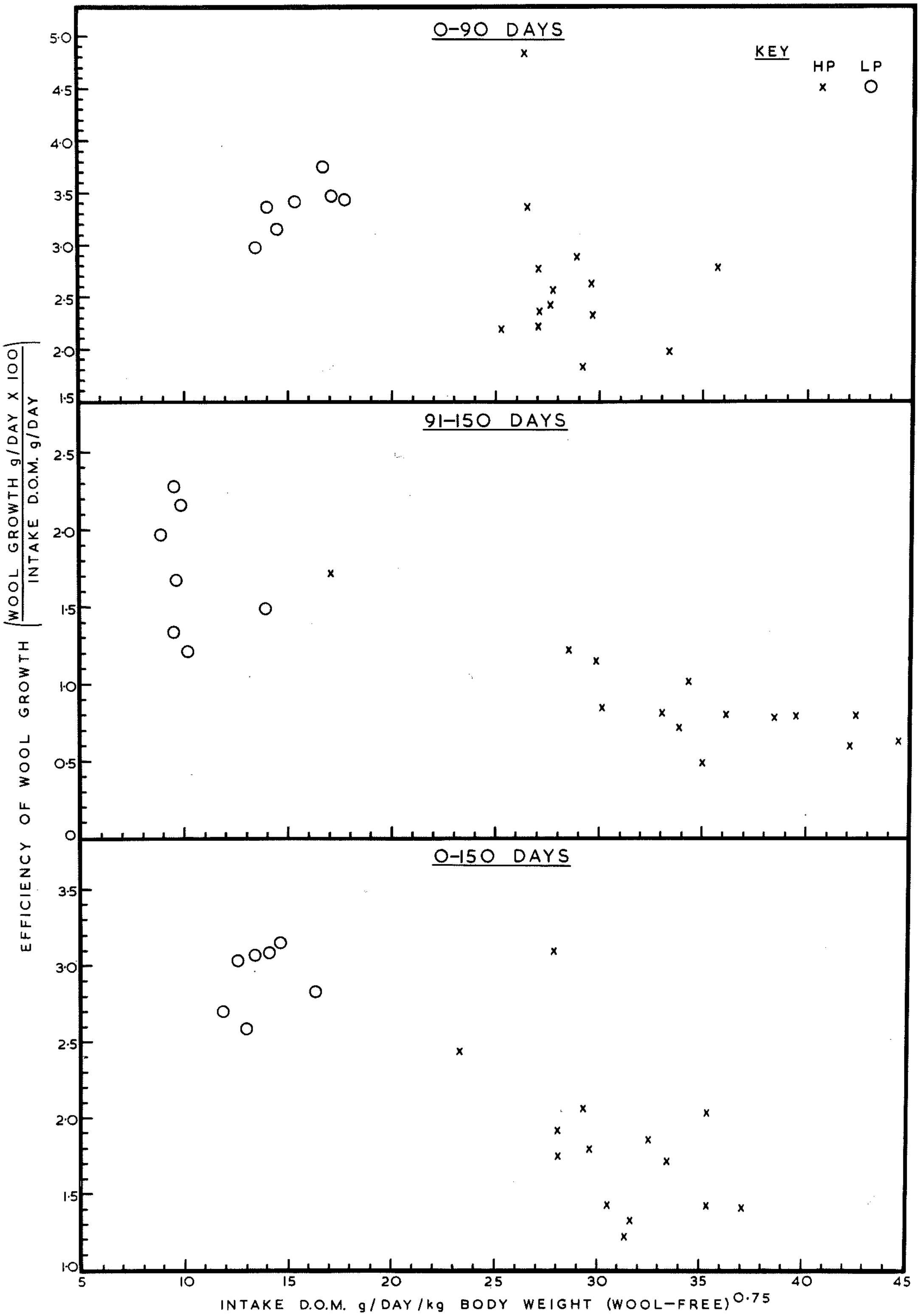


Fig. 4:9.- Efficiency of wool growth related to feed intake (data relating to ewes lambing).

EFFICIENCY OF WOOL GROWTH RELATED TO FEED INTAKE



Maintenance and gain requirements derived from those ewes lambing (17 d.f.) are indicated in equation (3):-

$$\begin{array}{lllll}(3) & \text{D.O.M.} = 322.7 + & 31.9\ \text{B.W.} & + & 1.376\ \text{W.G.} \\ & (\text{s.e.}) & (\pm\ 8.53) & & (\pm\ 0.3438) \\ & & ** & & ***\end{array}$$

For these animals, maintenance requirement of a 45.4 kg. ewe over the whole of pregnancy was estimated at 569 g. D.O.M./day. The requirement for 1 g. of weight gain was 1.38 g. D.O.M./day (ewes weighing 30.1 - 49.2 kg.)

(e) Lamb Birth Weights and Length of Gestation

Mean birth weights and length of gestation for the 21 lambs are recorded in Table 4:9.

Differences between males and females in the length of gestation were not significant; nor did the sire significantly affect length of time *in utero*.

LP feeding, however, abbreviated gestation, by 2.5 days. Birth weight and length of gestation were not significantly associated in covariance analysis. Disregarding sexes, the birth weight of *single* lambs born under LP feeding (2403 g : weighted mean) represented 61 *per cent*. of the mean birth weight of HP lambs (3947 g.).

Lambs sired by the larger ram (L) were heavier at birth than those sired by Ram S; this genetic effect appeared greater for males than females. The number of male and female lambs within sire and nutritional subclasses is insufficient to permit firm conclusions about a possible masking effect of poor feeding on sex and genetic differences in foetal growth. Ignoring sexes, the sire effect under HP feeding (4119 g. - 3818 g.), of 301 g., was less than the effect under LP feeding (2687 g. - 2190 g.), of 497 g.

IV. SLAUGHTER RECORDS

(a) Body Weights and Weight Gains

(i) Body weights

Mean body weights of ewes killed at mating, after 90-days of pregnancy and after 140-days are recorded in Table 4:10. The relation between empty body weight (or corrected empty body weight, where applicable) and wool-free final live weight for all slaughtered ewes is shown in Fig. 4:10. A regression, pooled over all groups, could be fitted to this relationship and the equation used to estimate mean initial empty body weights shown in Table 4:10.

After 90-days of pregnancy (Table 4:10) LP ewes were lighter than HP ewes, the differences in all parameters approaching significance ($P < 0.10$). Representative HP and LP ewes immediately prior to slaughter are shown in Plate 4:10, while the carcasses of all ewes are illustrated in Plate 4:11. The latter clearly indicates the degree of depletion of body tissues in LP animals. Ewes mated to the smaller of the two rams were heavier than those in lamb to Ram L, although the differences attained significance for wool-free final weight only.

TABLE 4:9. LAMBS BORN : MEAN BIRTH WEIGHTS (g) AND LENGTH OF GESTATION (days)

Character	Group means				Overall mean	S.D. (1)	Mean differences	
	HP/Ram L	HP/Ram S	LP/Ram L	LP/Ram S			Plane of nutrition (HP - LP)	Rams (Ram L - (Ram S
Birth weights								
Males	4117 (5)	3763 (2)	2758 (2)	2128 (3)	3334 (12)	309	1497 ***	492 **
Females	4130 (1)	3836 (6)	2545 (1)	2375 (1)	3563 (9)	312	1523 ***	232 **
Total	4119 (6)	3818 (8)	2687 (3)	2190 (4)	3432 (21)	305	1530 ***	399 **
Length of gestation (2)	149.7 (6)	149.8 (8)	146.0 (3)	148.5 (4)	149.0 (21)	2.6	2.5 *	- 1.1

Note:

(1) S.D. = standard deviation.

(2) The difference between males and females in length of gestation was not significant.

Number of observations for each category is shown in parentheses.

After 140-days of pregnancy (Table 4:10) poor nutrition had markedly reduced all the weight parameters. Profound differences in the physical appearance of live animals (Plate 4:8), their body condition (Table 4:4), as well as their carcasses (Plate 4:12) were clearly apparent at this stage. Ewes mated to Ram L were, on average, heavier than those in lamb to Ram S, the difference in final and wool-free final weights approaching significance ($P < 0.10$). This possible sire effect may, in fact, be related to the greater food intake of ewes mated to Ram L (see Table 4:5), and loses significance after elimination of gut-fill.

(ii) Gastro-intestinal contents

Gastro-intestinal contents averaged 6.3 kg. (16.8 per cent. of wool-free body weight) for ewes killed at mating. After 90-days of pregnancy gut contents were significantly ($P < 0.01$) heavier, both absolutely and relatively, in HP than LP ewes; contents of HP ewes averaged 8.9 kg. (20.3 per cent.), those of LP ewes 5.4 kg. (15.4 per cent.). After 140-days gut contents averaged 7.1 kg. (14.1 per cent.) in HP ewes and 4.5 kg. (14.0 per cent.) in LP ewes, the difference in absolute value being significant ($P < 0.01$).

(iii) Weight Gains

Large proportions of gross body weight can be accounted for by the weights of wool, the gastro-intestinal contents and the conceptus. Elimination of these components casts a different light on the weight gains or losses. Differences between

TABLE 4:10. MEAN BODY WEIGHTS (kg.) OF EWES KILLED AT MATING, AND AFTER 90- AND 140-DAYS OF PREGNANCY

Weight	Group means				Overall mean	C.V. %	S.E.	Mean differences	
	HP/Ram L	HP/Ram S	LP/Ram L	LP/Ram S				Plane of nutrition (HP-LP)	Rams (Ram L - Ram S)
<u>Ewes killed at mating</u>									
Wool-free live wt. at slaughter	-	-	-	-	37.4	30.0	4.6	-	-
Empty body wt.	-	-	-	-	31.1	31.1	4.0	-	-
Hot carcass wt.	-	-	-	-	19.1	29.5	2.3	-	-
<u>Ewes killed after 90-days</u>									
Wool-free live wt. at mating	37.8	42.5	38.7	44.5	40.6	19.2	4.0	-	-
Estimated initial empty body wt.(1)	28.3	31.8	29.0	33.2	31.1	-	-	-	-
Wool-free final live wt. at slaughter	40.5	46.7	31.3	37.9	39.2	17.2	3.5	9.0*	-6.4*
Final empty body wt.	32.1	37.4	26.7	30.9	31.8	18.6	3.1	6.0$^{(*)}$	-4.8
Final corrected empty body wt.	30.0	35.2	24.6	29.6	29.9	19.1	2.9	5.5$^{(*)}$	-5.1
Hot carcass wt.	17.1	20.1	13.5	15.8	16.7	24.5	2.1	4.0$^{(*)}$	-2.7
<u>Ewes killed after 140-days</u>									
Wool-free live wt. at mating	43.8	41.3	44.4	42.8	43.1	6.0	1.3	-	-
Estimated initial empty body wt.(1)	32.7	30.9	32.8	32.0	32.2	-	-	-	-
Wool-free live wt. after 90-days	49.2	46.9	39.2	37.9	43.3	6.5	1.4	9.5***	1.8
Estimated corrected empty body wt. after 90-days(1)	36.7	34.7	29.0	28.4	32.4	-	-	-	-
Wool-free final live wt. at slaughter	53.0	47.9	31.7	31.4	41.0	7.2	1.5	18.9***	2.7$^{(*)}$
Final empty body wt.	45.4	41.3	27.3	27.0	35.2	8.2	1.4	16.2***	2.2
Final corrected empty body wt.	37.6	34.2	21.9	22.4	29.0	10.5	1.5	13.8***	1.5
Hot carcass wt.	20.0	18.5	11.7	11.2	15.3	9.1	0.7	7.8***	1.0

Note: Empty body wt. = Wool-free live wt. <u>minus</u> gastro-intestinal contents

Corrected empty body wt. = Empty body wt. <u>minus</u> conceptus

(1) Estimated by regression - see Fig. 4:10 and text.

Fig. 4:10. The relationship between corrected empty body weight (empty body weight minus conceptus) and wool-free final live weight in ewes killed at mating, and after 90- and 140-days of pregnancy.

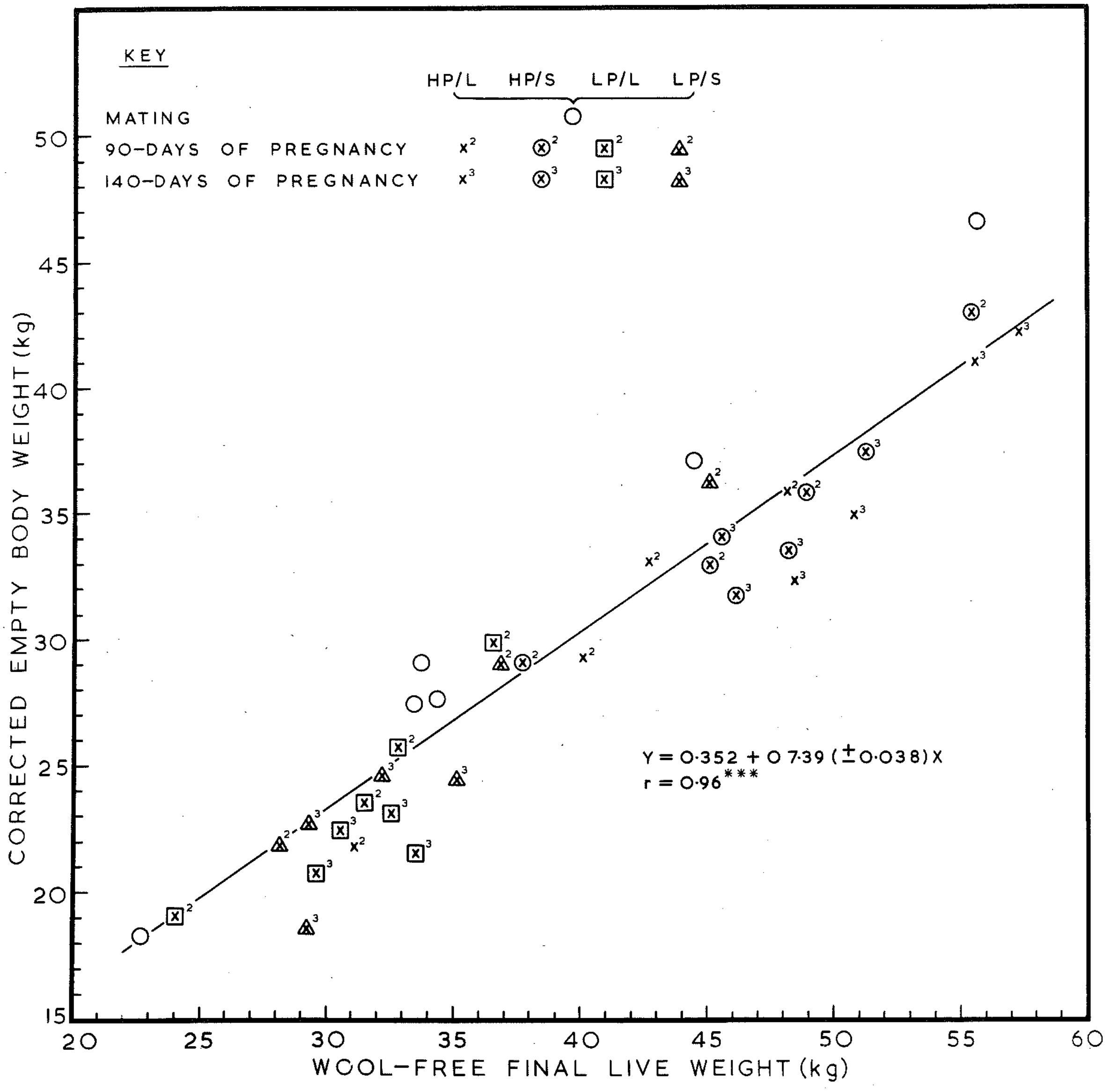

KEY
HP/L
HP/S
LP/L
LP/S
MATING
90-DAYS OF PREGNANCY
140-DAYS OF PREGNANCY
Y = 0·352 + 0 7·39 (±0·038) X
r = 0·96***
CORRECTED EMPTY BODY WEIGHT (kg)
WOOL-FREE FINAL LIVE WEIGHT (kg)
15
20
25
30
35
40
45
50
55
60

Plate 4:10. Representative HP and LP ewes immediately prior to slaughter after 90-days of pregnancy (5 x 5 cm. grid).

90 days of pregnancy

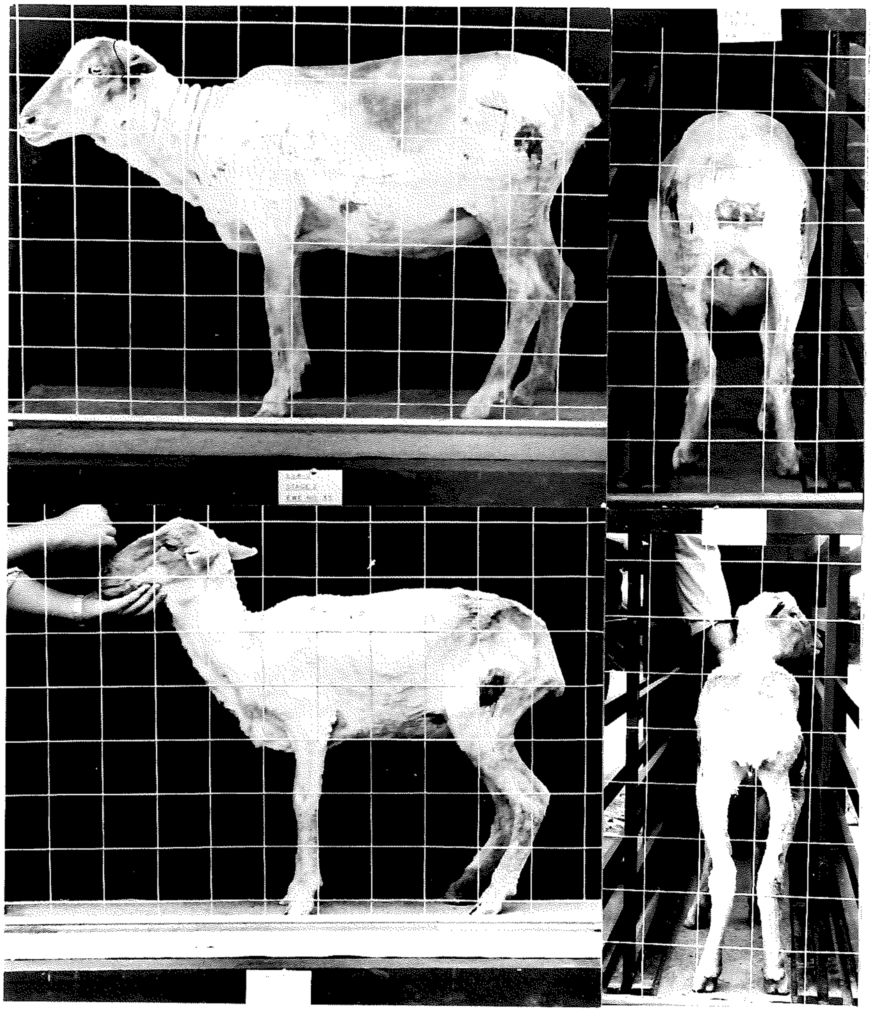


Plate 4:11. Carcasses of ewes slaughtered after 90-days of pregnancy (5 x 5 cm. grid).

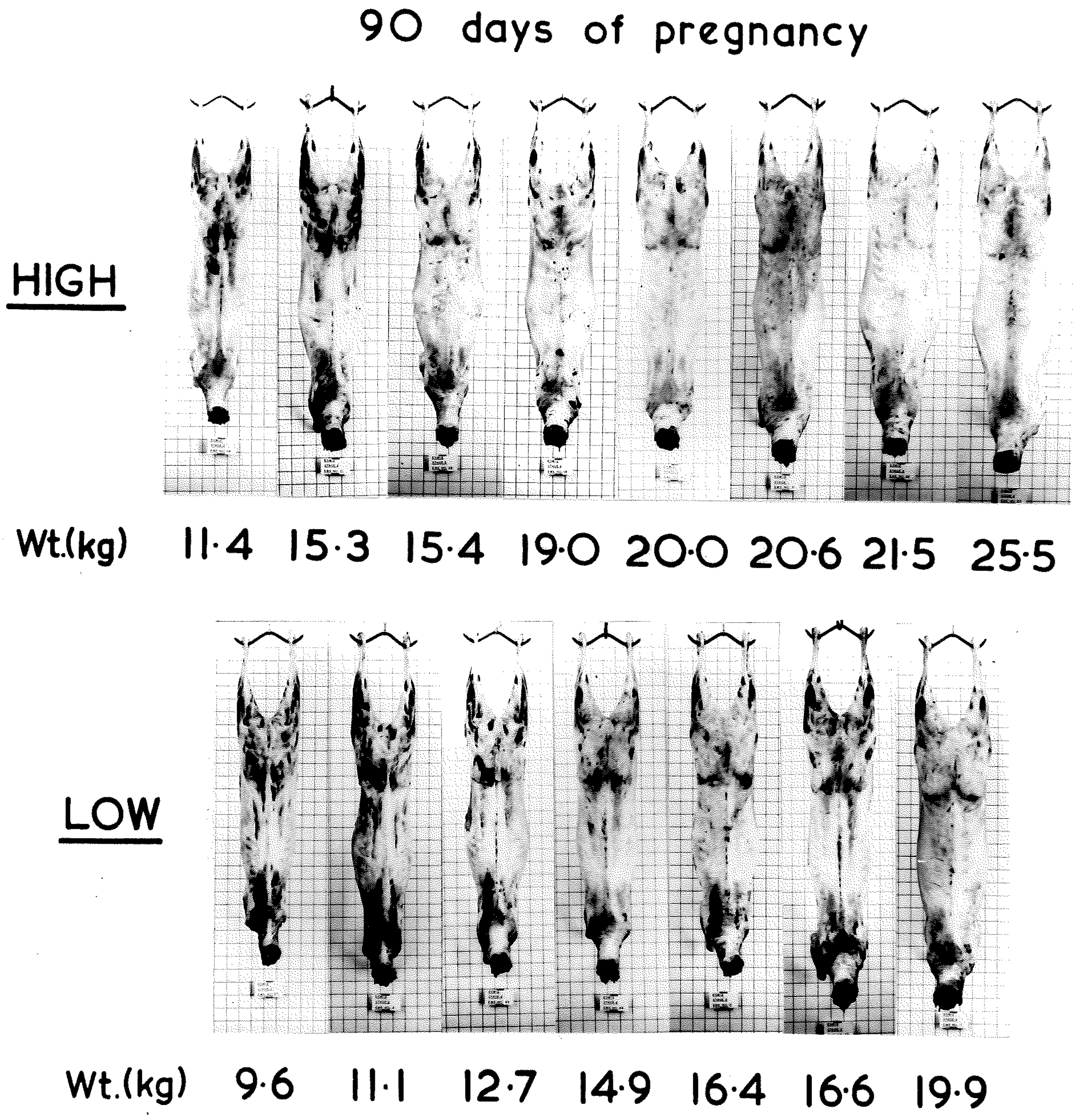
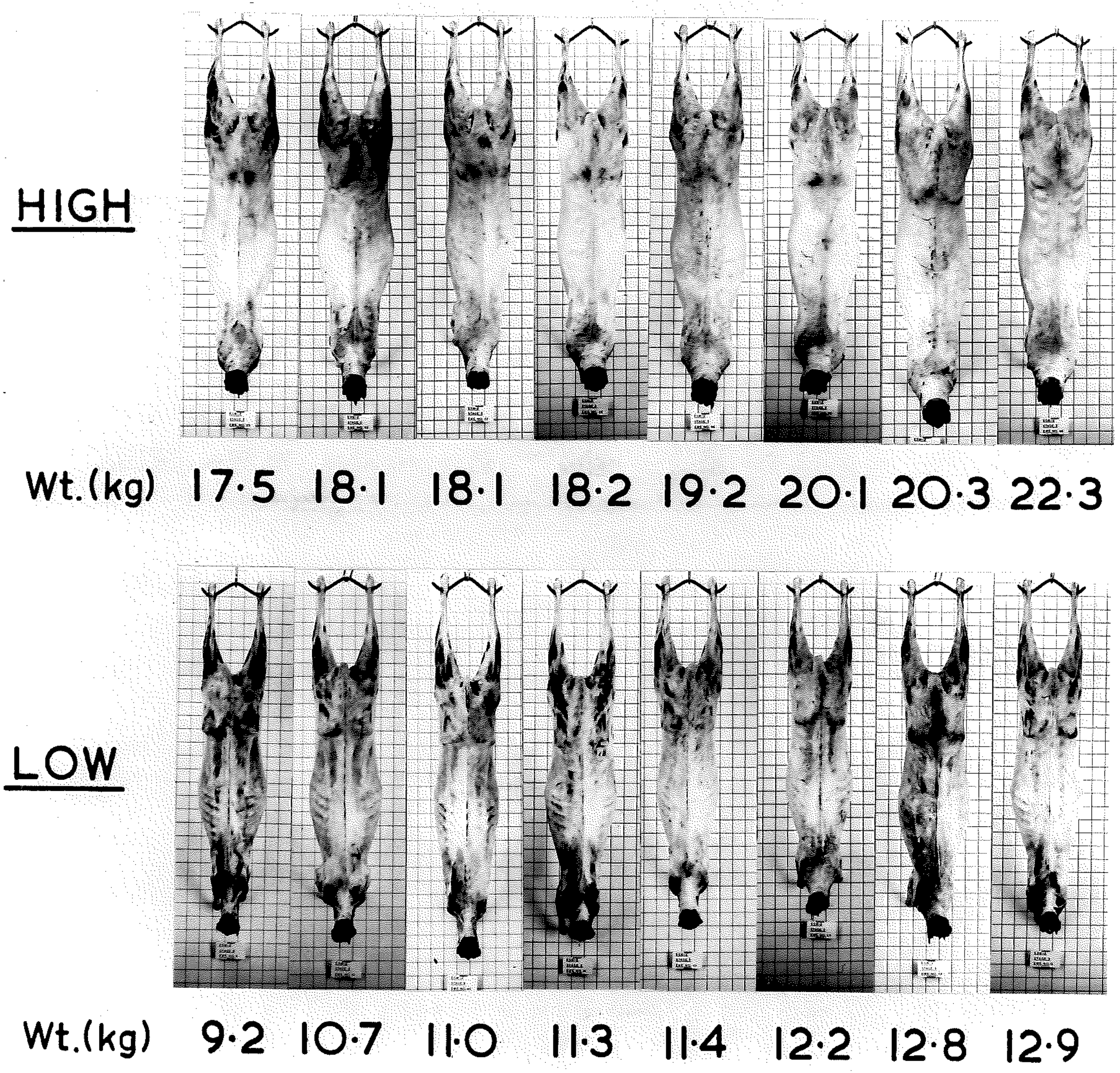

90 days of pregnancy
HIGH
Wt.(kg) 11·4 15·3 15·4 19·0 20·0 20·6 21·5 25·5
LOW
Wt.(kg) 9·6 11·1 12·7 14·9 16·4 16·6 19·9

Plate 4:12. Carcasses of ewes slaughtered after 140-days of pregnancy (5 x 5 cm. grid).

140 days of pregnancy



the mean weights recorded in Table 4:10 have been assembled in Table 4:11, where the weight gains or losses are also expressed as percentages of appropriate initial weights. For example, the difference between the estimated weight of the empty body at mating and the weight of the empty body recorded at slaughter is expressed as a percentage of the former weight.

On the one hand, HP ewes gained as much in gross body weight as LP ewes lost, according to the experimental design (see Fig. 4:4). On the other hand, after elimination of the components of wool, gastro-intestinal contents and the conceptus (Table 4:11 : final corrected empty body _minus_ estimated initial empty body) HP ewes gained 8.4 _per cent_. after 90-days of pregnancy while LP ewes lost 13.0 _per cent_. of body tissues. After 140-days of pregnancy, HP ewes had gained 23.9 _per cent_., and LP ewes had lost 23.2 _per cent_., gross body weight (Fig. 4:4); the _nett_ body weight gain of HP ewes, however, of 12.9 _per cent_. compares with a _nett_ weight loss of 31.6 _per cent_. for LP ewes. Table 4:11 also shows that HP ewes barely maintained nett body weight between 90- and 140-days of pregnancy, while LP ewes lost over 6 kg. of body tissues.

(b) Components of Empty Body Weight

(i) Actual Weights

Mean weights of ewe empty body components recorded at the three slaughter stages are shown in Fig. 4:12, together with the significance of differences due to nutritional regimes.

Differences in component weights due to pregnancy *per se*, but especially undernutrition, can be seen. These effects became more marked as pregnancy proceeded and undernutrition continued.

Some components were exceptionally variable in weight. For example, *caul fat* had coefficients of variation of 85, 73 and 67 *per cent.* associated with the overall mean weights recorded at mating, 90-days and 140-days respectively; LP ewes had 251 g. and 362 g. less fat than HP ewes in this depot after 90-days and 140-days of pregnancy respectively, but these differences did not attain significance.

The *gastro-intestinal tract* (especially the *stomachs*), the *lungs and trachea*, but particularly *blood*, increased in weight during pregnancy under HP feeding. The *udder* increased in weight from 102 g. at mating to 104 g. (HP) and 143 g. (LP) after 90-days, and to 1081 g. (HP) after 140-days; in LP ewes the *udder* at the end of pregnancy weighed (129 g.) little more than at mating (see Plate 4:8).

(ii) Weights after adjustment for differences in Corrected Empty Body Weight

Weights of components recorded after 90- and 140-days of pregnancy were adjusted, in covariance analyses, for differences in the weight of the ewe empty body *minus* the conceptus (corrected empty body weight). Adjusted mean weights, and mean differences, of those components showing significant nutritional treatment effects are recorded in Table 4:12.

TABLE 4:11. MEAN BODY WEIGHT GAINS (kg.) OF EWES KILLED AFTER 90- AND 140-DAYS OF PREGNANCY

Weights	Mean differences				Mean difference as percentage of initial value			
	HP/Ram L	HP/Ram L	LP/Ram L	LP/Ram S	HP/Ram L	HP/Ram S	LP/Ram L	LP/Ram S
<u>Ewes killed after 90-days</u>								
Final <u>minus</u> wool-free live wt. at mating	4.6	6.0	-5.6	-6.0	12.2	14.1	-14.5	-13.5
Wool-free final <u>minus</u> wool-free live wt. at mating	2.7	4.2	-7.4	-6.6	7.1	9.9	-19.1	-14.8
Final empty body <u>minus</u> initial empty body$^{(1)}$	3.8	5.6	-2.3	-2.3	13.4	17.6	- 7.9	- 6.9
Final corrected empty body <u>minus</u> initial empty body$^{(1)}$	1.7	3.4	-4.4	-3.6	6.0	10.7	-15.2	-10.8
<u>Ewes killed after 140-days</u>								
Final <u>minus</u> wool-free live wt. at mating	11.6	9.0	-10.8	-9.4	26.5	21.8	-24.3	-22.0
Wool-free final <u>minus</u> wool-free live wt. at mating	9.2	6.6	-12.7	-11.4	21.0	16.0	-28.6	-26.6
Final empty body <u>minus</u> initial empty body$^{(1)}$	12.7	10.4	- 5.5	- 5.0	38.8	33.7	-16.8	-15.6
Final corrected empty body <u>minus</u> initial empty body$^{(1)}$	4.9	3.3	-10.9	- 9.6	15.0	16.7	-33.2	-30.0
Final corrected empty body <u>minus</u> corrected empty body after 90-days of pregnancy$^{(1)}$	0.9	-0.5	- 7.1	- 6.0	2.5	-1.4	-24.5	-21.1

Note:

Empty body wt. = Wool-free final live wt. <u>minus</u> gastro-intestinal contents
Corrected empty body wt. = Empty body wt. <u>minus</u> conceptus

(1) Estimated by regression - see Fig. 4:10 and text.

Fig. 4:11. Mean weights (kg.) of components of the empty body of ewes killed at mating, and after 90- and 140-days of pregnancy. The significance of the nutritional effect on each component is also indicated.

MEAN WEIGHTS (kg) OF COMPONENTS OF THE EMPTY BODY

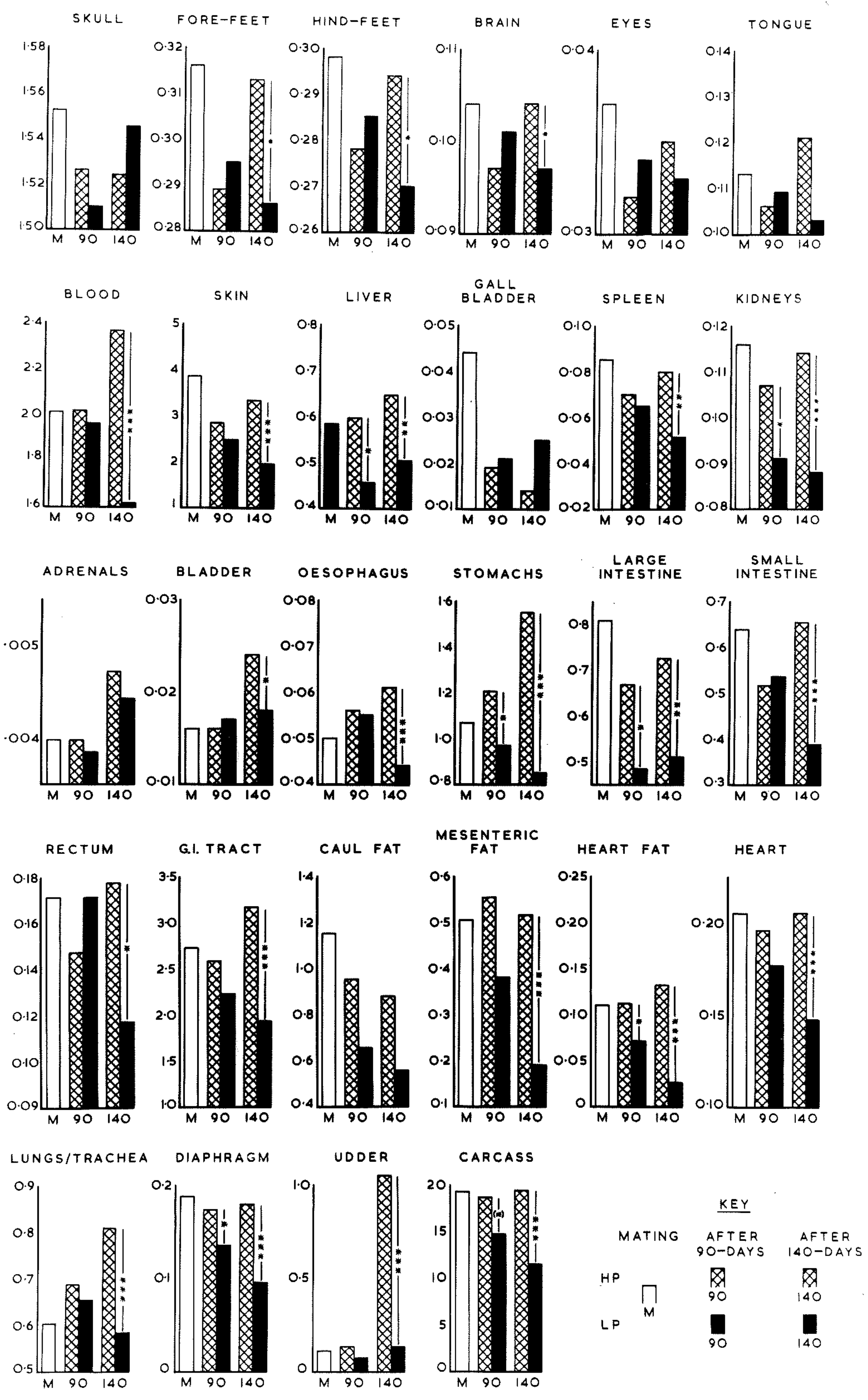


TABLE 4:12. ADJUSTED$^{(1)}$ MEAN WEIGHTS (g) OF EMPTY BODY COMPONENTS OF EWES KILLED AFTER 90- AND 140-DAYS OF PREGNANCY : COMPONENTS SHOWING SIGNIFICANT TREATMENT EFFECTS AFTER ADJUSTMENT

Component	Adjusted means		S.E.	Adjusted mean difference (HP-LP)	
	HP	LP			
<u>Ewes killed after 90-days</u>					
Stomachs	1141	1028	50.2	113	*
Rectum	190	128	22.3	62	*
Adrenals	3.87	4.05	0.09	- 0.18	*
<u>Ewes killed after 140-days</u>					
Skin	3314	1954	171.9	1360	***
Stomachs	1423	968	148.0	465	*
Small intestine	739	302	78.9	437	**
Rectum	212	82	40.8	130	*
Gastro-intestinal tract	2980	2241	260.2	739	*
Kidneys	112	89	7.3	23	*
Adrenals	3.65	5.47	0.42	- 1.82	*
Carcass (kg)	16.8	14.0	0.84	2.8	*

Note:

(1) Adjusted, by covariance, for differences in empty body weight <u>minus</u> conceptus.

(2) Ram effects and interactions were not significant and adjusted means and mean differences are therefore not presented.

After 90-days of pregnancy, significant nutritional effects on only 3 components were shown, as compared with 8 (out of 27 recorded) before adjustment for differences in body weight. Stomachs and rectum were reduced, but adrenals increased, in weight under LP nutrition.

After 140-days of pregnancy, significant nutritional effects on 8 components were recorded after adjustment for body weight differences, as compared with 21 components before adjustment. Adrenals were again heavier in poorly-fed ewes, the adjusted weight at 140-days under LP feeding exceeding that recorded at 90-days. The gastro-intestinal tract as a whole, and stomachs, small intestine and rectum as parts of it, suffered weight loss out of proportion to body weight under LP feeding. Rumen papillae were noticeably reduced in size in LP ewes. The skin, kidneys and the carcass were also reduced in weight by undernutrition.

V. The Genital Tract

(a) Weights of Components

Mean weights of the genital tract, and components, after 90- and 140-days of pregnancy are recorded in Tables 4:13 and 4:14 respectively.

(i) After 90-days : The cotyledons and membranes, and the placenta as a whole, together with the foetus and uterus, were significantly lighter under LP than HP feeding. On the other hand, the weight of amniotic fluid was noticeably increased by undernutrition,

TABLE 4:13. MEAN WEIGHTS (g) OF COMPONENTS OF THE GENITAL TRACT AFTER 90-DAYS OF GESTATION

Component	Group means				Overall mean	C.V. %	S.E.	Mean differences	
	HP/Ram L	HP/Ram S	LP/Ram L	LP/Ram S				Plane of nutrition (HP-LP)	Rams (Ram L - Ram S)
Fluids									
Allantoic	218.3	198.3	195.0	193.3	201.7	9.9	10.4	14.2	10.9
Amniotic	434.8	582.3	690.5	631.0	581.5	35.0	105.2	-152.2	-44.0
TOTAL	653.1	780.6	885.5	824.3	783.3	25.3	102.4	-138.0	-33.1
Placenta									
Cotyledons	521.4	458.1	359.6	292.1	415.5	21.4	45.9	163.9**	65.4
Membranes	136.0	140.0	115.0	119.3	128.1	11.5	7.6	20.9*	- 4.2
TOTAL	657.4	598.1	474.6	411.4	543.6	18.2	51.0	184.8**	61.2
Foetus	538.5	557.1	481.3	478.5	516.2	9.7	26.0	67.9*	- 7.9
Uterus	201.5	212.3	183.3	182.0	195.6	9.0	9.1	24.3*	- 4.8
Necrotic tissue and dissection loss	60.0	46.0	48.5	58.7	52.9	32.3	8.8	- 0.6	1.9
Uterus and contents	2110.5	2169.0	2073.3	1955.0	2085.1	13.6	146.0	125.6	29.9
Vulva/Vagina/Cervix	34.3	36.5	36.8	37.0	36.1	11.4	2.1	- 1.5	- 1.2
Ovaries	2.180	2.079	2.041	2.147	2.109	6.1	0.067	0.036	- 0.003
Fallopian tubes	1.013	1.043	1.029	1.001	1.023	10.1	0.054	0.013	- 0.001
TOTAL (Complete Genital Tract)	2148	2234	2113	1995	2131	13.4	146.9	137	16

TABLE 4:14. MEAN WEIGHTS (g) OF COMPONENTS OF THE GENITAL TRACT AFTER 140-DAYS OF GESTATION

Component	Group means				Overall mean	C.V %	S.E.	Mean differences	
	HP/Ram L	HP/Ram S	LP/Ram L	LP/Ram S				Plane of nutrition (HP-LP)	Rams (Ram L-Ram S)
Fluids									
Allantoic	1486.0	1416.3	615.5	1026.3	1136.0	24.0	136.5	630.3***	-170.6
Amniotic	730.8	690.3	1540.0	678.5	909.9	52.9	240.6	-398.7	451.0 (*)
TOTAL	2216.8	2106.6	2155.5	1704.8	2045.9	28.2	288.2	241.6	280.4
Placenta									
Cotyledons	546.9	432.9	316.4	251.5	386.9	18.0	34.8	206.0***	89.5*
Membranes	256.0	215.0	189.5	158.5	204.8	17.5	17.9	61.5**	36.0 (*)
TOTAL	802.9	647.9	505.9	410.0	591.7	16.1	47.6	267.5***	125.5*
Foetus	4287.0	3783.0	2295.0	2031.0	3099.0	9.5	146.9	1872.0***	384.0*
Uterus	517.5	529.5	360.5	345.0	438.1	13.1	28.8	170.8***	1.8
Necrotic tissue and dissection loss	26.0	14.5	28.0	25.0	23.4	59.3	6.9	- 6.3	7.3
Uterus and contents	7850.0	7081.5	5345.0	4517.3	6198.4	13.1	406.3	2534.6***	798.1 (*)
Vulva/Vagina/Cervix	37.5	43.8	37.8	37.0	39.0	12.4	2.4	3.3	- 2.8
Ovaries	2.845	2.874	2.917	2.604	2.810	11.1	0.156	0.099	0.142
Fallopian tubes	0.889	0.993	0.961	0.850	0.923	10.9	0.050	0.036	0.004
TOTAL (Complete Genital Tract)	7891	7129	5387	4558	6241	13.0	406.9	2538***	796 (*)

but not significantly so, reflecting the large variation of this component. Differences due to the size of the sire were not significant.

(ii) After 140-days : The genital tract and all components (except amniotic fluid, and necrotic tissue/dissection loss) were reduced in weight by undernutrition, although some of these differences did not attain significance. Amniotic fluid was heavier, but allantoic fluid lighter, in LP than in HP ewes.

The genital tract, and most components, were heavier after 140-days of pregnancy in ewes mated to the larger of the two rams. Differences in the weight of the foetus and placenta (cotyledons) attained significance ($P < 0.05$), with an indication ($P < 0.10$) of significant differences in the weight of the uterus and contents, placental membranes and amniotic fluid. Allantoic fluid and the vulva/vagina/cervix were lighter in ewes mated to Ram L than those mated to Ram S, but not significantly so.

(b) Proportionate Composition of the Gravid Uterus

The mean weight of each component of the gravid uterus, expressed as a percentage of the total weight, at both 90- and 140-days of pregnancy is illustrated in Fig. 4:13. Sire effects on the proportionate composition were neither obvious nor significant, and have been ignored.

The foetus comprised 25 *per cent*. of the gravid uterus at 90-days with no significant difference due to ewe nutrition. At 140-days the foetus, as a proportion had increased to 54 *per cent*. under good feeding and 45 *per cent*. under poor nutrition, the difference due to nutrition being significant ($P < 0.01$).

After 90-days the proportion occupied by the total fluids was greater ($P < 0.05$) in LP ewes (42 *per cent*.) than HP ewes (33.0 *per cent*.). This nutritional effect originated largely from the difference ($P < 0.05$) in the proportion of amniotic fluid (33 *per cent*. in LP ewes as compared with 23 *per cent*. in HP ewes). After 140-days the proportion of total fluid had fallen to 34 *per cent*. Undernutrition increased ($P < 0.01$) amniotic fluid, as a percentage, from 10 *per cent*. in HP ewes to 21 *per cent*. in LP ewes.

The placenta, after 90-days, comprised 29 *per cent*. of the gravid uterus in HP ewes but less ($P < 0.01$), 22 *per cent*., in LP ewes. Cotyledons contributed most to this difference; as a percentage of the gravid uterus they represented 23 *per cent*. in HP ewes as compared with 16 *per cent*. in LP ewes ($P < 0.01$). After 140-days the placenta and the cotyledons, as percentages, had fallen to 9 *per cent*. and 6 *per cent*. respectively, with no significant effect of nutrition in either case.

VI. Foetal Weights, and Cotyledon Weights and Numbers

Mean single foetus weights, together with mean weights and numbers of functional cotyledons, after 90-days of pregnancy are recorded in Table 4:15, and after 140-days in Table 4:16.

Fig. 4:12. Proportionate composition by weight of the gravid uterus after 90- and 140-days of pregnancy.

PROPORTIONATE COMPOSITION OF THE GRAVID UTERUS

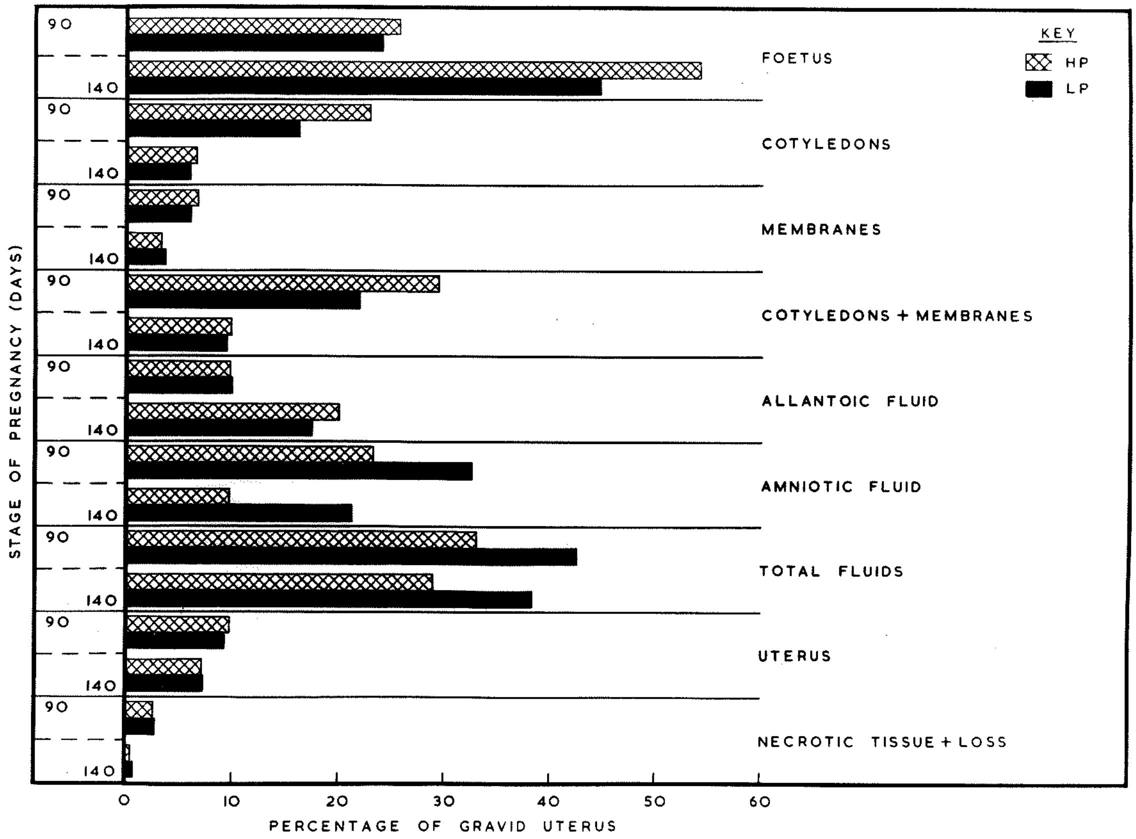


TABLE 4:15. MEAN SINGLE FOETUS WEIGHTS (g), TOGETHER WITH MEAN WEIGHTS (g) AND NUMBERS OF FUNCTIONAL COTYLEDONS, AFTER 90-DAYS OF GESTATION

Character	Group means						Overall mean	C.V %	S.E.	Mean differences		
	Plane of nutrition		Rams		Foetal sex					Plane of nutrition	Rams	Foetal sex
	HP	LP	L	S	Male	Female				(HP-LP)	(Ram L-Ram S)	(Male-Female)
Foetal weight	547.8	490.2	510.4	523.3	559.9	478.2	516 2	9.7	24.0	57.6**	-12.9	81.7***
Cotyledons												
Total weight												
Pregnant horn	320.4	220.8	281.7	260.0	316.3	232.5	271.6	27.7	38.9	99.6*	21.7	83 8*
Vacant horn	169.3	119.9	158.8	126.9	154.3	127.3	143.9	23.5	17.4	49.4**	31.9(*)	27.0
Combined horns	489.7	340.7	440.5	386.9	470.6	359.8	415.5	21.4	45.9	149.0**	53.6	110.8*
Numbers												
Pregnant horn	45.9	43.3	46.7	42.4	46.7	42.9	44.7	16.1	3.7	2.6	4.3	3.8
Vacant horn	30.2	25.4	30.9	24.[illegible]	25.6	30.0	27.9	22.3	3.2	4.8	6.3(*)	-4.4
Combined horns	76.1	68.7	77.6	67.0	72.3	72.9	72.6	10.1	3.8	7.4(*)	10.6 *	-0.6
Average weights												
Pregnant horn	6.99	5.10	6.08	6.00	6.77	5.42	6.05	24.5	0.77	1.89*	0.08	1.35
Vacant horn	5.74	4.72	5.51	5.13	6.03	4.24	5.33	39.4	1.09	1.02	0.38	1.97
Combined horns	6.67	4.96	5.96	5.66	6.51	4.94	5.81	23.2	0.70	1.71*	0.30	1.57
Number of observations	8	7	8	7	7	8	15	-	-	-	-	-

TABLE 4:16. **MEAN SINGLE FOETUS WEIGHTS (g), TOGETHER WITH MEAN WEIGHTS (g) AND NUMBERS OF FUNCTIONAL COTYLEDONS, AFTER 140-DAYS OF GESTATION**

Character	Group means						Overall mean	C.V. %	S.E.	Mean differences		
	Plane of nutrition		Rams		Foetal sex					Plane of nutrition (HP-LP)	Rams (Ram L - Ram S)	Foetal sex (Male-Female)
	HP	LP	L	S	Male	Female						
Foetal weight	4035.7	2163.3	3291.8	2907.1	3024.0	3157.2	3099.2	9.5	146.9	1872.4***	384.7*	-133.2
Cotyledons												
<u>Total weight</u>												
Pregnant horn	315.2	172.3	279.3	208.2	239.7	246.9	243.7	26.8	32.6	142.9***	71.1*	- 7.2
Vacant horn	174.8	111.7	152.4	134.1	144.7	142.0	143.2	22.7	16.3	63.1**	18.3	2.7
Combined horns	489.9	284.0	431.7	342.2	384.4	388.9	386.9	18.0	34.8	205.9***	89.5*	- 4.5
<u>Numbers</u>												
Pregnant horn	49.2	45.8	49.8	45.2	44.9	49.4	47.4	13.7	3.2	3.4	4.6	- 4.5
Vacant horn	24.9	27.2	25.7	26.4	28.3	24.2	26.0	24.6	3.2	- 2.3	- 0.7	4.1
Combined horns	74.0	72.9	75.4	71.5	73.1	73.7	73.4	5.6	2.1	1.1	3.9	- 0.6
<u>Average weights</u>												
Pregnant horn	6.39	3.86	5.71	4.55	5.34	5.00	5.13	24.1	0.62	2.53**	1.16	0.34
Vacant horn	7.36	4.27	6.37	5.26	5.11	5.87	5.81	27.0	0.78	3.09**	1.11	- 0.76
Combined horns	6.62	3.90	5.76	4.75	5.26	5.28	5.25	18.3	0.48	2.72***	1.01	- 0.02
Number of observations	8	8	8	8	7	9	16	-	-	-	-	-

(a) Foetal Weights

(i) After 90-days : LP foetuses, on average, were 12 per cent. lighter than HP foetuses (Table 4:15). Males were heavier, by 17 per cent., than females. Sire and interaction effects were not significant.

Plate 4:13 shows selected HP and LP female foetuses (and their carcasses) after 90-days of gestation. Subcutaneous haemorrhaging, especially of the head, neck and thigh regions, was observed in several LP foetuses; this is shown as darker areas on the LP foetus in Plate 4:13. The effect is seen more vividly in the coloured frontispiece plate which shows a foetus of 90-days of age, derived from an undernourished ewe. It appeared that the haemorrhaging occurred most in those regions of greatest handling of the foetus; the poorly-developed, more fragile tissues of lighter LP foetuses sustaining greater damage from the necessary handling, than HP foetuses.

(ii) After 140-days : The mean weight of LP single foetuses represented 34 per cent. of the mean foetal weight of HP foetuses. The larger of the two sires (Ram L) left heavier progeny than Ram S. Whereas male foetuses were heavier than females at 90-days, females were slightly, but not significantly, heavier at 140-days. Plate 4:14 summarises these treatment effects. (It is of passing interest to observe the black pigmented skin patches of lambs sired by Ram L; pigmented patches, of varying size and colour on

Plate 4:13. Selected HP and LP female foetuses and their carcasses after 90-days of gestation. The darker (haemorrhaged) head and neck of the LP foetus may be noted (2 x 2 cm. grid).

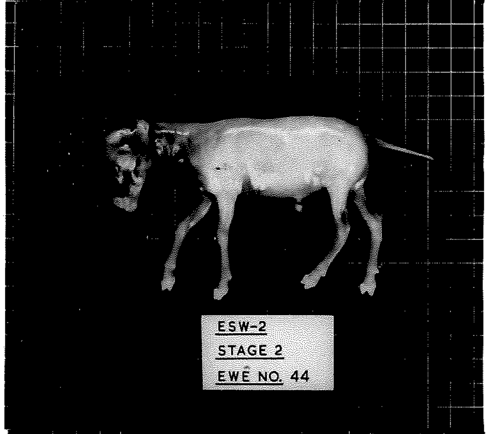
90 days of pregnancy

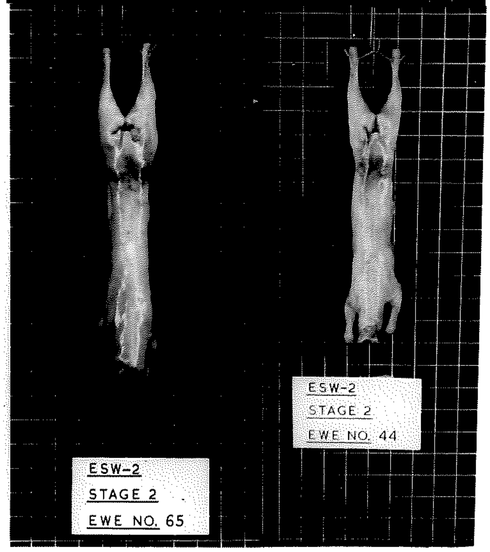
HIGH

524·1(g)

LOW

415·0(g)



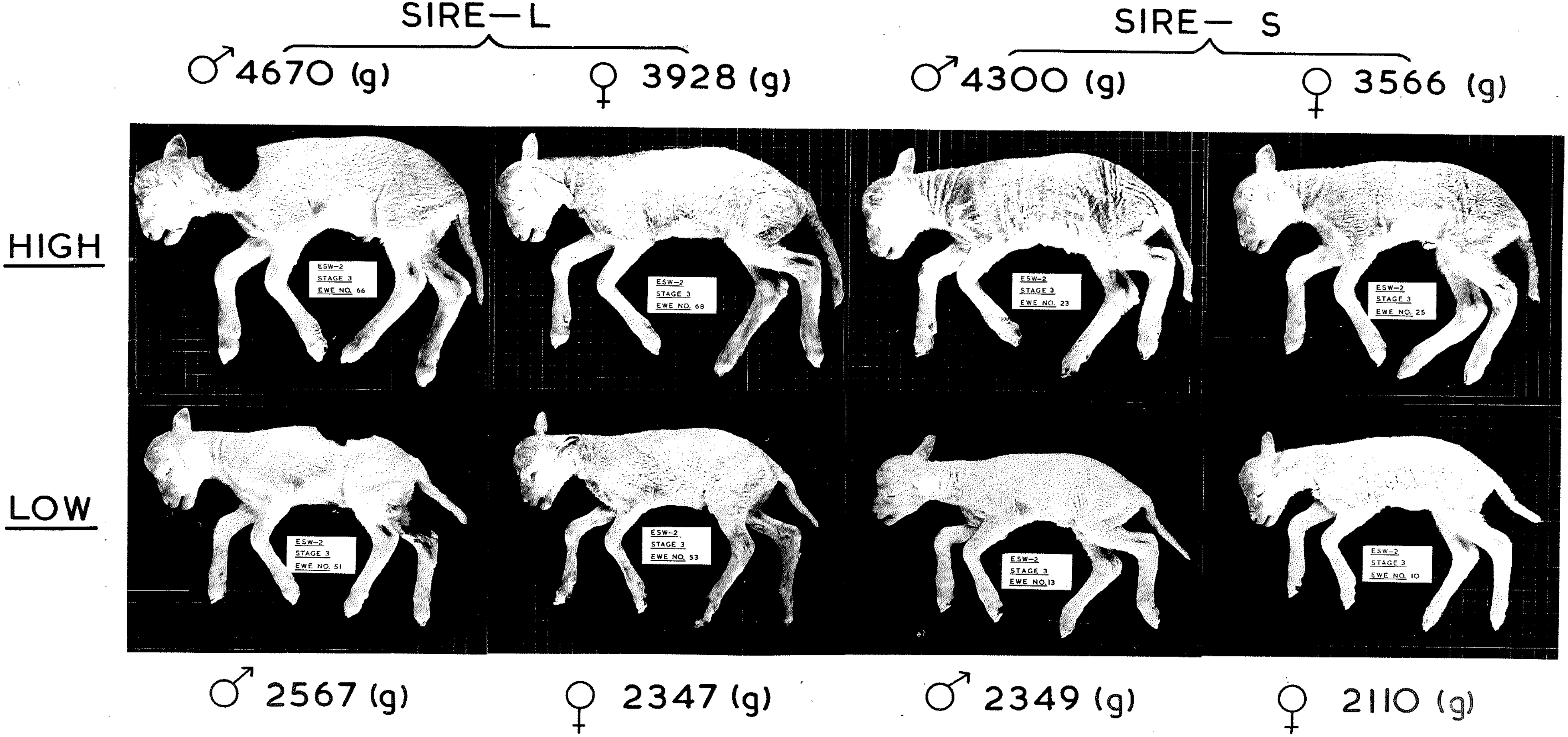


HIGH LOW

218·0(g) 176·2(g)

Plate 4:14. Selected foetuses after 140-days of gestation to show nutritional, sire and sex effects. Skin wrinkle development is more noticeable under HP than LP feeding. The black pigmented patch on the neck of the HP foetus and the loin of the LP foetus can also be seen (2 x 2 cm. grid).

140 days of pregnancy



several lambs sired by Ram L were observed. The presence of the pigment in inbred Peppin Merinos was suggested by Hayman & Cooper (1964) to be due to a recessive gene _w_; Brooker & Dolling (1965) have recently provided further information on this inherited characteristic in medium-wool Merinos).

(b) Cotyledons

(i) Total Weights of Cotyledons

1. _After 90-days_ : Table 4:15 shows that poor nutrition of the ewe reduced the total weight of functional cotyledons. The total weight of cotyledons in the pregnant horn from LP ewes represented 69 _per cent_. of the comparable total weight from HP ewes; and 71 _per cent_. in the vacant horn. Under both HP and LP feeding the total weight of cotyledons in the pregnant horn represented 65 _per cent_. of the weight for the respective combined horns. These results indicate that undernutrition exerted an almost equal effect on the weight of cotyledons in each uterine horn.

Male foetuses were associated with a greater total weight of cotyledons, particularly in the pregnant horn, than females. Foetuses sired by Ram L had more cotyledonary material than those sired by Ram S, but the differences were not significant.

The distribution of cotyledon weights after 90-days of pregnancy is illustrated in Fig. 4:13. Cotyledons varied substantially in weight (C.V. 21.4 _per cent_. for combined horns - Table 4:15). Poor feeding of ewes in early pregnancy prevented individual cotyledons attaining the largest sizes. Some of the heaviest cotyledons appeared to result from fusion of at least two single cotyledons.

2. After 140-days : The total weight of cotyledons in the combined uterine horns was significantly heavier in HP than LP ewes (Table 4:16). Under LP feeding, the weight of cotyledons, as a percentage of the weight in HP ewes, was 55 per cent. for the pregnant horn and 64 per cent. for the vacant horn; suggesting a greater effect of poor nutrition in the former than the latter. The total weight of cotyledons in the pregnant horn under HP feeding represented 64 per cent. of the weight for the combined horns, compared with 61 per cent. under LP nutrition.

Ewes in lamb to the larger of the two rams (L) had a greater total weight of cotyledons than ewes mated to Ram S, although the difference in the vacant horn was not significant. Sex effects on the total weight of cotyledons were neither large nor significant.

Fig. 4:14 shows the distribution of cotyledon weights after 140-days of pregnancy. Marked differences in the histograms can be seen with substantial variation in the size of individual cotyledons. Comparison of Figs. 4:13 and 4:14 suggests that cotyledons regressed in weight between 90- and 140-days of pregnancy. The overall mean weight at 140-days (Table 4:16), of 386.9 g., was less than the comparable weight, of 415.5 g., at 90-days (Table 4:15).

(ii) Numbers of Cotyledons

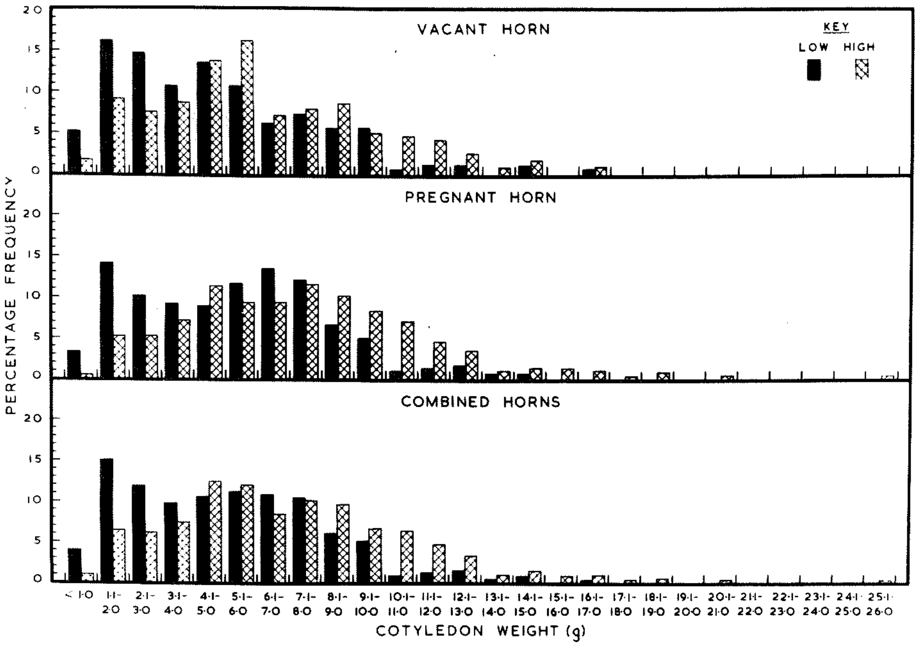
1. After 90-days : The total number of functional cotyledons (Table 4:15) was greater in HP than LP ewes, and greater in

Fig. 4:13.- Mean distributions of functional cotyledon weights after 90-days of pregnancy.

Fig. 4:14.- Mean distributions of functional cotyledon weights after 140-days of pregnancy.

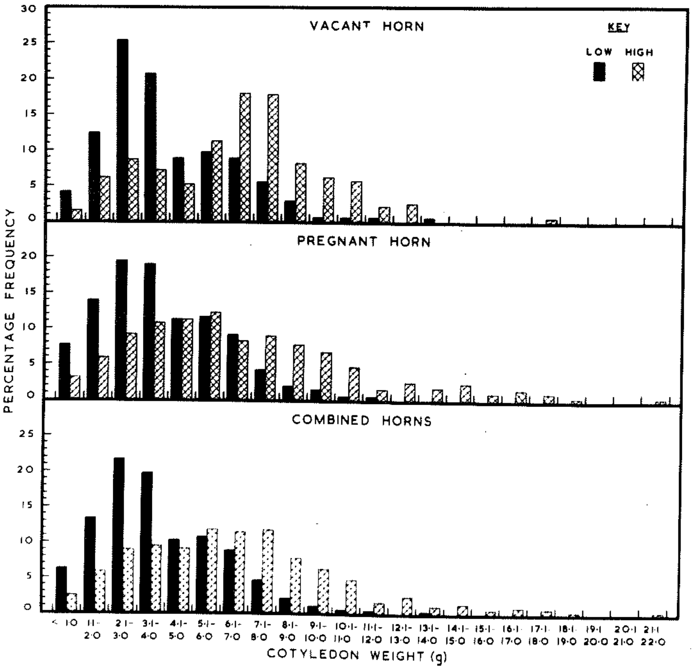
DISTRIBUTION OF COTYLEDON WEIGHTS

90 DAYS OF PREGNANCY



DISTRIBUTION OF COTYLEDON WEIGHTS

140 DAYS OF PREGNANCY



ewes mated to Ram L than Ram S. The sex difference was small and not significant. Nutritional effects on the number of cotyledons impinged more upon the vacant than pregnant horn.

2. After 140-days : Differences in the number of cotyledons (Table 4:16) were not significant, the overall mean number for combined horns (73) equalling the comparable number after 90-days (Table 4:15).

(iii) Average Weights of Cotyledons

1. After 90-days : The average weight of individual cotyledons in the HP ewes was heavier than in LP ewes, significantly so in the pregnant horn (Table 4:15). Male foetuses had cotyledons of greater average weight than females, but the differences did not attain significance. Sire effects were small and not significant.

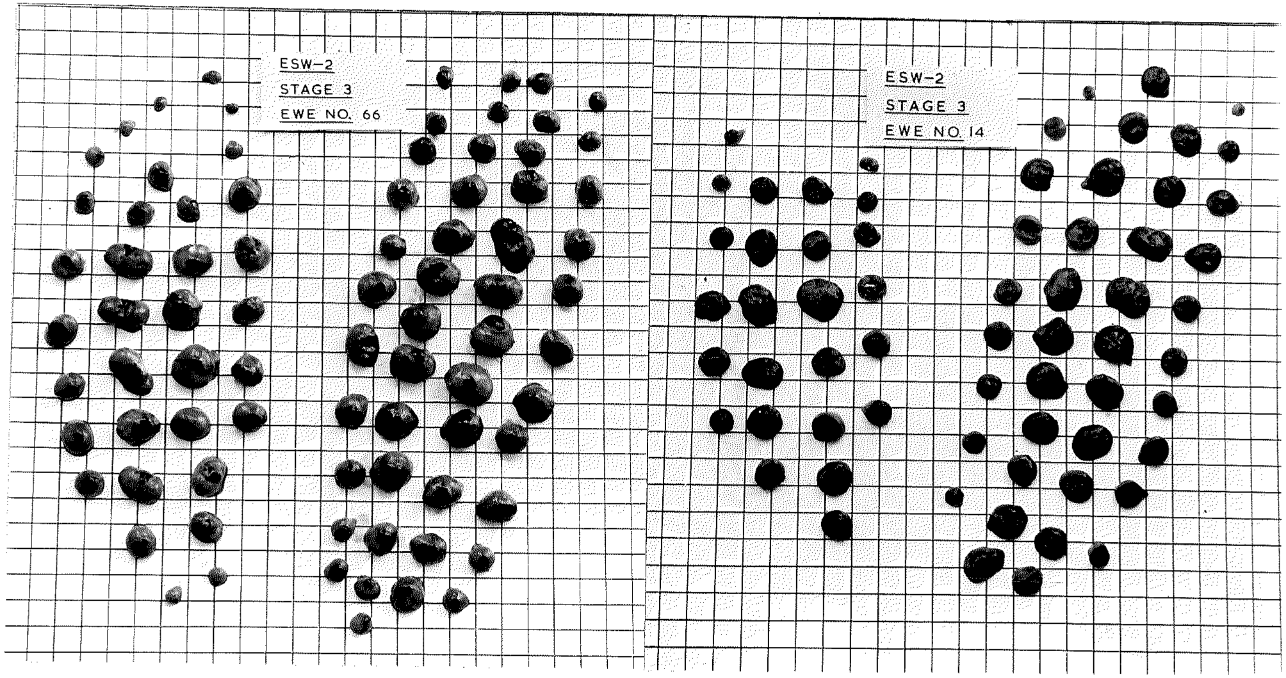
2. After 140-days : HP ewes had cotyledons of significantly greater average weight than LP ewes (Table 4:16). The average weight of cotyledons from ewes mated to large Ram L was greater than from ewes mated to Ram S, but not significantly so.

(iv) Morphology of Cotyledons

Plate 4:15 is a semi-schematic representation of the functional cotyledon array after 140-days of pregnancy from selected HP and LP ewes. The profound effect of poor nutrition of the ewe on the morphological appearance of the cotyledons can be seen. Cotyledons from the HP ewe appear firm, with a convex or cup-shaped body, the peripheral lip of the maternal component curling

Plate 4:15.- Semi-schematic representation of the functional cotyledon array after 140-days of pregnancy from selected HP and LP ewes. The firm, spherical appearance of cotyledons from the HP ewe may be compared with the relaxed flat, atrophied appearance of those from the LP ewe (2 x 2 cm. grid).

140 days of pregnancy



	HIGH		LOW	
	VACANT	PREGNANT	VACANT	PREGNANT
NO.	34	47	25	40
Wt.(g)	178·6	402·9	79·0	103·4

Continued from p. 177

inwards to contain the foetal component. Under LP feeding the cotyledons display senility : a relaxed flat appearance in surface view; an everted foetal component from which the allanto-chorion could be easily detached; and a marked extravasation of darkly pigmented blood. The largest cotyledons located in the central area of the pregnant horn appeared to suffer most in this connexion.

Accurate separation of the distorted cotyledons into maternal and foetal components proved impossible and the attempt was abandoned.

(c) Relationships between Foetal Weight and Placental Components

(i) Foetal weight and the number of cotyledons

Foetal weights at 90-days and 140-days of age were not significantly correlated with the number of functional cotyledons.

(ii) Foetal weight and the weights of placental components

The positive relationships between foetal weight and the weight of the placenta (cotyledons + membranes) after 90- and 140-days of pregnancy are shown in Fig. 4:15.

The relationship after 90-days can be described by the following equation:-

$$\begin{array}{lllll} \text{F.W.} = 237.8 & + \ 36.6\ \text{F.S.} & - \ 16.4\ \text{R} & + \ 1.17\ \text{C.W.} & + \ 4.56\ \text{M.W.} \\ \quad (\text{s.e.}) & (\pm 5.78) & (\pm 5.73) & (\pm 0.34) & (\pm 2.52) \\ & *** & * & ** & (*) \end{array}$$

where,

F.W. = Foetal weight (g.) after 90-days.

F.S. = Foetal sex (discontinuous variable : female = 0; male = 1).

R. = Ram (discontinuous variable : Ram S = 0; Ram L = 1).

C.W. = Total weight (g.) of cotyledons.

M.W. = Total weight (g.) of membranes.

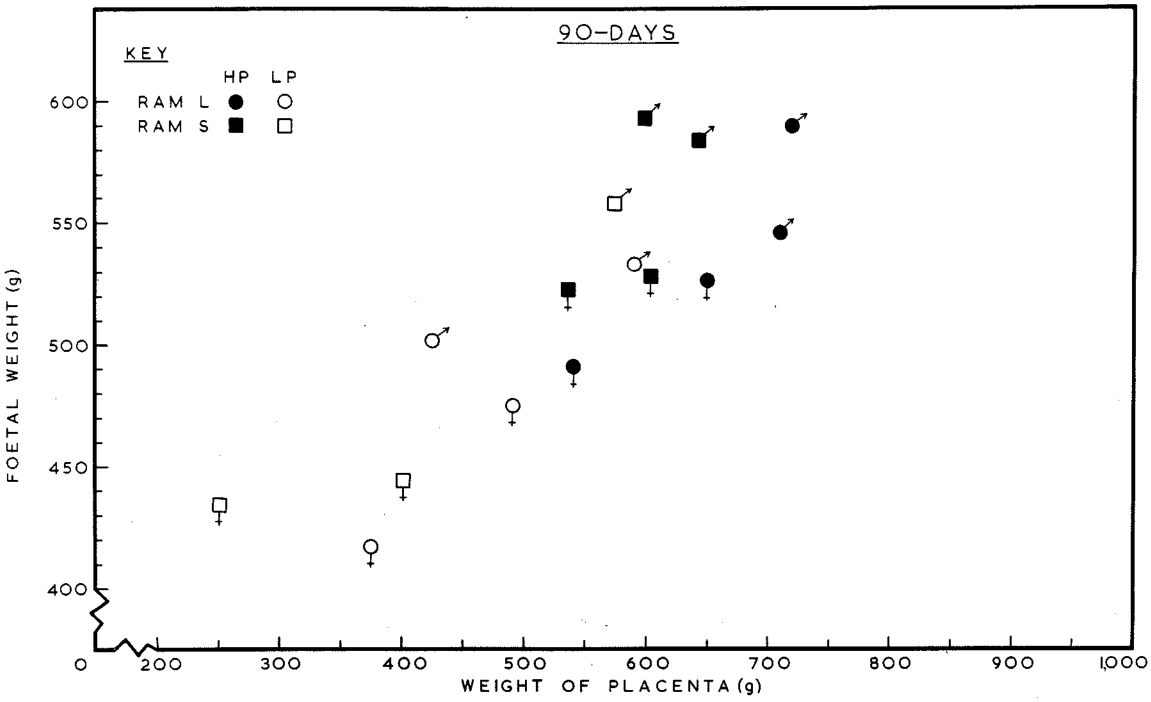
This equation, based on 10 degrees of freedom, has a residual coefficient of variation of 1.8 *per cent*. and accounts for 98 *per cent*. of the variation in foetal weight (R = 0.99). When the variance due to foetal sex and sire is eliminated, each g. of cotyledons supported 1.17 g. of foetus, and each g. of membranes supported 4.56 g. of foetus. On extrapolation the regression line intercepts the foetal weight axis above the origin, at about 0.2 kg.

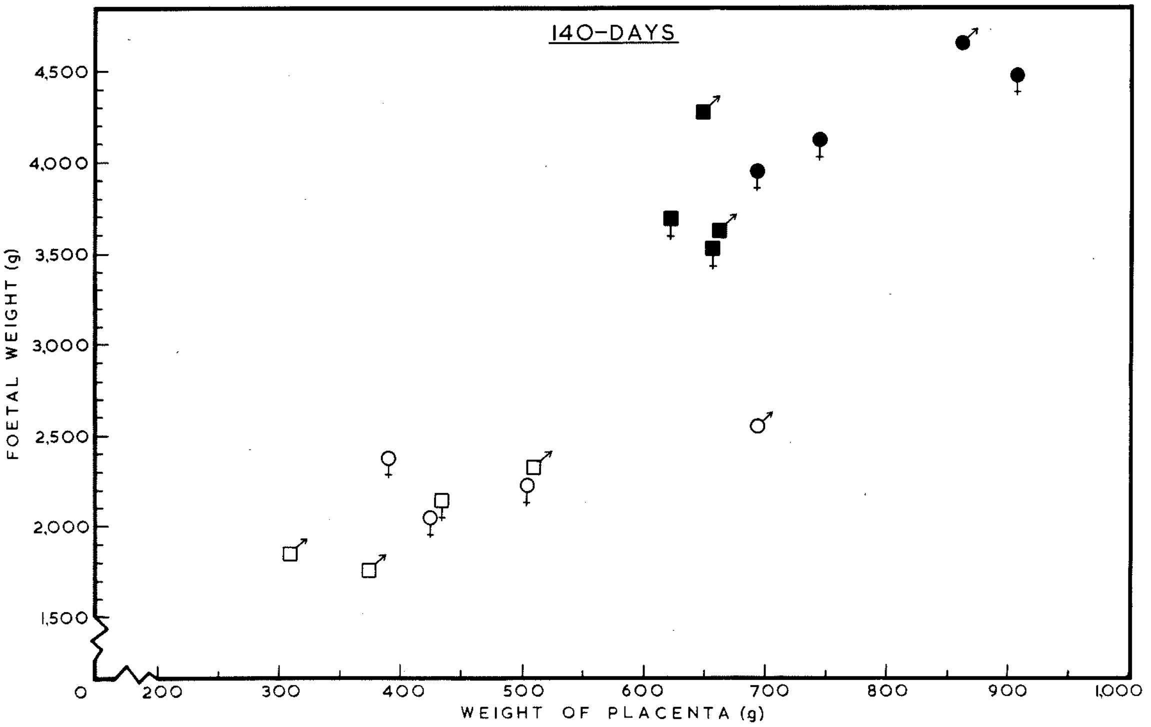
After 140-days the derived equation was :-

$$\begin{array}{lccccc} \text{F.W.} = 262.1 & - \; 59.0\ \text{F.S.} & + \; 268.5\ \text{R} & + \; 6.84\ \text{C.W.} & + \; 16.54\ \text{M.W.} \\ \text{(s.e.)} & (\pm 56.2) & (\pm 26.9) & (\pm 1.80) & (\pm 4.88) \\ & \text{n.s.} & *** & ** & ** \end{array}$$

with a residual coefficient of variation of 15.5 *per cent*. (based on 11 d.f.). The multiple correlation coefficient (R) of 0.91 indicates that 84 *per cent*. of the variation was accounted for by regression on these variables. After 140-days, 6.84 g. of foetus were associated with 1 g. of cotyledons, and 16.54 g. of foetus with 1 g.

Fig. 4:15. The relationship between foetal weight and the weight of the placenta (cotyledons + membranes) after 90- and 140-days of pregnancy.


90-DAYS
KEY
HP LP
RAM L ● ○
RAM S ■ □
FOETAL WEIGHT (g)
600
550
500
450
400
0
200
300
400
500
600
700
800
900
1,000
WEIGHT OF PLACENTA (g)
♂
♀


140-DAYS
FOETAL WEIGHT (g)
4,500
4,000
3,500
3,000
2,500
2,000
1,500
0
200
300
400
500
600
700
800
900
1,000
WEIGHT OF PLACENTA (g)
♂
♀

of membranes. The intercept on the foetal weight axis was again of the order of 0.2 kg.

VII. Foetal Body Measurements

(a) Actual Measurements

Mean foetal body measurements recorded after 90- and 140-days of gestation are recorded in Tables 4:17 and 4:18 respectively. These measurements have been adjusted, by covariance, for the effects of foetal sex but not for differences in foetal body weight.

(i) After 90-days : A negligible sire effect on body dimensions was recorded - in line with the lack of a significant sire effect on foetal weight at this age (Table 4:15). Significant nutritional effects were, however, recorded for all but 5 of the measurements; HP foetuses were larger than LP foetuses in all dimensions, except neck length.

(ii) After 140-days : HP foetuses were larger than LP foetuses in all recorded dimensions, the differences attaining significance except for head width (Table 4:16). Ram L left progeny of generally larger physical dimensions.

Ratios between dimensions recorded at this age - and disregarding differences in foetal weight - portray that lambs born to undernourished ewes are relatively long in the legs. For example, the ratio between trunk length : fore-leg length (radius/ulna + metacarpus) was 1.49 for HP foetuses compared with 1.39 for LP foetuses; while the ratio between trunk length : hind-leg length

TABLE 4:17. MEAN FOETAL BODY MEASUREMENTS (cm) AT 90-DAYS OF GESTATION AFTER ADJUSTMENT FOR DIFFERENCES BETWEEN MALE AND FEMALE FOETUSES

Measurement	Group means				Overall mean	C.V. %	S.E.	Mean differences	
	HP/Ram L	HP/Ram S	LP/Ram L	LP/Ram S				Plane of nutrition (HP-LP)	Rams (Ram L - Ram S)
__Body length__									
Curved crown-tail	34.8	35.4	32.3	32.6	33.9	2.5	0.43	2.7 ***	-0.5
Curved crown-rump	24.9	25.6	23.8	24.1	24.6	3.2	0.39	1.3 **	-0.5
Straight crown-rump	26.8	27.8	25.9	26.1	26.7	2.9	0.39	1.3 **	-0.6
Tail length	10.1	9.7	8.8	8.3	9.3	4.7	0.22	1.4 ***	0.5
__Head__									
Face width	4.4	4.4	4.2	4.5	4.4	3.4	0.08	0.1	-0.2
Face length	4.2	4.3	4.1	4.3	4.2	2.1	0.05	0.1	-0.2
Head width	4.5	4.6	4.2	4.1	4.4	4.8	0.10	0.4 ***	0
Head depth	4.8	4.9	4.6	4.7	4.8	4.1	0.10	0.2 *	-0.1
__Neck__									
Length	5.8	5.5	6.1	5.4	5.7	6.9	0.20	-0.1 *	0.5 *
Girth	8.5	8.6	7.8	7.7	8.2	2.2	0.09	0.8 ***	0
__Trunk__									
Length	16.0	16.2	15.4	15.8	15.8	2.7	0.21	0.5 *	-0.3
Chest depth	6.3	6.4	5.8	5.8	6.1	2.2	0.07	0.6 ***	-0.1
Heart girth	16.6	16.4	15.2	15.2	15.9	2.1	0.16	1.3 ***	0.1
Navel girth	17.7	17.8	16.5	16.3	17.1	2.1	0.18	1.4 ***	0.1
__Pelvis__									
Length	4.6	4.6	4.5	4.5	4.5	6.0	0.14	0.1	0
Width	2.9	2.9	2.7	2.6	2.8	9.9	0.14	0.3	0.1
__Limbs__									
Metacarpus									
length	3.7	3.6	3.5	3.5	3.6	2.7	0.05	0.3 ***	-0.1
depth	0.6	0.6	0.5	0.5	0.6	7.5	0.02	0.1 *	0
width	0.5	0.5	0.5	0.4	0.5	5.5	0.01	0.1 **	0.1
Radius/ulna length	5.3	5.2	4.9	4.8	5.1	5.6	0.14	0.4 *	0.1
Humerus length	4.3	4.5	3.9	3.8	4.1	5.1	0.11	0.6 ***	-0.1
Tibia/fibula length	5.8	6.3	5.6	5.3	5.8	9.2	0.27	0.6 (*)	-0.1

TABLE 4:18. MEAN FOETAL BODY MEASUREMENTS (cm) AT 140-DAYS OF GESTATION AFTER ADJUSTMENT FOR DIFFERENCES BETWEEN MALE AND FEMALE FOETUSES

Measurement	Group means				Overall mean	C.V. %	S.E.	Mean differences	
	HP/Ram L	HP/Ram S	LP/Ram L	LP/Ram S				Plane of nutrition (HP-LP)	Rams (Ram L - Ram S)
Body length									
Curved crown-tail	75.3	70.8	62.1	59.2	66.9	3.4	1.16	12.4 ***	3.7 *
Curved crown-rump	57.6	53.7	48.2	46.5	51.5	3.9	1.03	8.3 ***	2.8 *
Straight crown-rump	52.0	48.3	41.6	40.6	45.6	2.8	0.66	9.1 ***	2.4 **
Tail length	18.1	16.6	13.2	13.4	15.3	12.4	0.97	4.1 **	0.7
Head									
Face width	6.1	5.9	5.5	5.4	5.7	4.0	0.12	0.6 **	0.2
Face length	7.5	7.5	6.6	6.3	7.0	5.7	0.20	1.1 ***	0.2
Head width	6.0	5.9	5.8	5.6	5.8	9.9	0.30	0.3	0.2
Head depth	8.3	8.3	7.8	7.8	8.0	5.1	0.21	0.5 *	0
Neck									
Length	12.3	10.4	10.8	9.6	10.8	10.7	0.59	1.2 (*)	1.6 *
Girth	17.7	17.0	14.5	13.3	15.6	5.0	0.40	3.5 ***	1.0 *
Trunk									
Length	34.3	31.3	27.0	25.7	29.6	2.4	0.36	6.5 ***	2.2 ***
Chest depth	12.7	12.4	10.4	9.8	11.3	3.5	0.20	2.5 ***	0.5 (*)
Heart girth	34.3	33.4	28.2	26.2	30.5	2.7	0.42	6.7 ***	1.5 **
Navel girth	36.4	34.3	28.9	26.9	31.6	5.0	0.80	7.5 ***	2.1 *
Pelvis									
Length	10.5	10.2	8.5	8.2	9.4	3.3	0.16	2.0 ***	0.3 (*)
Width	6.0	5.7	4.7	4.5	5.2	4.8	0.13	1.3 ***	0.3
Limbs									
Metacarpus length	10.2	9.5	8.5	8.0	9.0	3.1	0.15	1.6 ***	0.6 **
depth	1.5	1.4	1.2	1.0	1.3	5.9	0.04	0.4 ***	0.2 (*)
width	1.3	1.3	1.0	1.0	1.2	5.9	0.04	0.3 ***	0
Radius/ulna length	12.4	11.9	11.0	10.4	11.4	5.5	0.32	1.5 ***	0.6
Humerus length	11.2	10.7	9.2	8.9	10.0	4.4	0.22	1.9 ***	0.4 (*)
Tibia/fibula length	14.0	13.4	11.5	11.1	12.5	4.4	0.281	2.4 ***	0.5 (*)

TABLE 4:19. TREATMENT EFFECTS ON FOETAL BODY MEASUREMENTS (cm) AT 90- AND 140-DAYS OF GESTATION AFTER ADJUSTMENT(1) FOR FOETAL BODY WEIGHT AND SEX

Measurement	Variance ratios					
	After 90-days			After 140-days		
	Nutrition (N)	Rams (R)	N x R	Nutrition (N)	Rams (R)	N x R
Body length						
Curved crown-tail	2.86	0.08	0	0.08	0	0.88
Curved crown-rump	0.42	0.27	0.20	0.04	0.06	1.01
Straight crown-rump	0.13	1.10	0.45	3.17	1.06	3.87
Tail length	0.31	0.02	0.15	0.36	1.02	0.09
Head						
Face width	1.58	4.90	2.63	0.93	0.58	0.38
Face length	0.33	1.43	0.70	0.01	0.17	0.78
Head width	0.01	0.49	0.30	0.85	0.16	0.12
Head depth	0.08	0.18	0.14	0.59	1.02	0.04
Neck						
Length	1.36	5.90*	0.96	3.43	0.06	0.36
Girth	14.74**	0.05	0.42	1.29	0.57	2.87
Trunk						
Length	0	0.72	0.36	7.81*	7.07*	7.46*
Chest depth	14.41**	1.19	1.42	0.20	0.60	3.12
Heart girth	10.56**	0.41	0.25	3.45	0.10	14.94**
Navel girth	5.36*	0.82	0.57	0.01	0.01	0.09
Pelvis						
Length	0.77	0.12	0.36	0.42	0.65	0.38
Width	0.06	0.25	0.14	0.35	0.04	0.10
Limbs						
Metacarpus						
Length	0.79	0	0.06	0.16	1.73	0.66
Depth	0	0.38	2.89	0.02	0.01	1.94
Width	0.96	8.70*	7.58*	0.63	7.67*	0.92
Radius/ulna length	0.07	0.78	0	3.74	0.84	0.12
Humerus length	2.32	0.22	2.69	2.45	0.68	0.26
Tibia/fibula length	4.19	1.25	4.62	0.68	0.12	0.04

Note:

(1) Covariance analysis of logarithmic transformed data:

9 degrees of freedom at 90-days of age

10 degrees of freedom at 140-days of age

(tibia/fibula) was 2.39 for HP foetuses and 2.34 for LP foetuses. The dished appearance of the face in undernourished or prematurely born young at birth is also borne out by the ratio of face width : face length; this ratio was 0.80 and 0.85 for HP and LP foetuses respectively.

(b) Measurements after Adjustment for Differences in Foetal Body Weight

Treatment effects on foetal body measurements at 90- and 140-days of age after adjustment, by covariance of logarithmic transformed data, for differences in foetal body weight as well as for foetal sex are recorded as variance ratios in Table 4:19.

At both ages it is clear that differences in foetal body conformation due to nutrition and sires reflected differences in foetal body weight. Foetuses of the same age and, statistically, the same weight, possessed the same conformation, irrespective of the treatments applied, with the possible exceptions of the neck girth and chest dimensions.

(c) Sex Effects on Foetal Body Measurements

Fig. 4:16 illustrates the pattern of sex effects on body dimensions of foetuses of the same body weight. The logarithmic regression coefficient appropriate to each measurement, derived from covariance analysis, has been multiplied by 10^2 so that the values shown indicate the percentage difference between males and females. Positive and negative coefficients show that males were larger or smaller respectively than females at the same body weight.

Sex differences in body conformation were, in general, manifested to a greater extent at 90- than 140-days of age. Some of the differences were small, attaining no more than 1-2 per cent. in either direction, and need accepting with reserve.

At both ages, males, compared with females, were longer in overall body length, larger in all head dimensions, shorter but thicker in the neck, larger in all trunk dimensions, smaller in the pelvis and shorter in the limbs.

(d) Allometric Growth of Foetal Body Dimensions

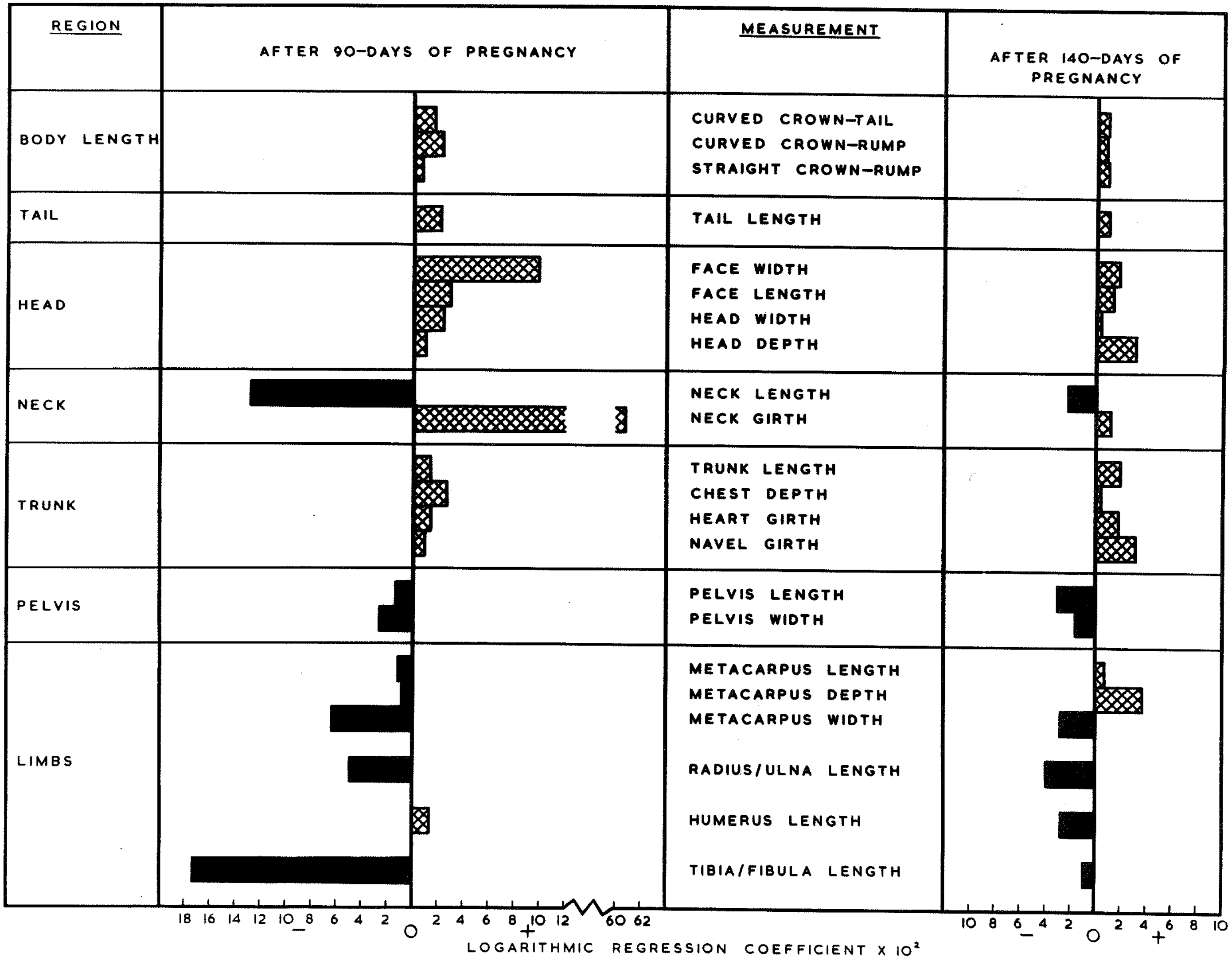
The relation of the increase in foetal body dimensions with increase in foetal body curved crown-rump length at each of the two stages is depicted in Fig. 4:17. The regression coefficients, again shown on a percentage basis, were derived from covariance analyses of logarithmic transformed data using crown-rump length and foetal sex as the two covariates.

(i) After 90-days : Over the range of body length encompassed by foetuses of 90-days of age, the limbs and tail were increasing in length at a much faster rate than body length. On the other hand, the depth of the head, neck girth, chest depth and pelvis width were increasing at a much slower rate than body length.

(ii) After 140-days : The rates of increase in the width of the head and length of the neck exceeded the rate of increase

Fig. 4:16.- Sex effects on foetal body measurements after 90- and 140-days of gestation. Positive and negative coefficients indicate that males were larger or smaller respectively than females at the same body weight. All the coefficients shown were significant ($P < 0.05$).

SEX EFFECTS ON FOETAL BODY MEASUREMENTS



in body length. The relative growth rates of the limbs, and the tail, had reduced substantially compared with earlier rates and were now growing at a rate a little less than the rate of increase in body length. Chest depth, and the width of the pelvis, showed little change in their relative growth rate over the two ages examined. The girth of the neck showed an increased rate of relative growth over the later compared with the earlier age.

VIII. Weights of Foetal Body Components

(a) Actual Weights

Mean weights of foetal body components at 90- and 140-days of age are recorded in Tables 4:20 and 4:21 respectively. These weights have been adjusted, by covariance, for the effects of foetal sex but not for differences in foetal body weight.

(i) After 90-days : All components, except the skull, the rumen and the adrenals, were heavier in HP than LP foetuses, the differences attaining significance in 23 out of the 32 recorded parts.

Foetuses sired by Ram S were lighter in all recorded components, except the skin, blood, abomasum and adrenals, than foetuses sired by the larger ram. This agrees with the recorded foetal weights at this age (Table 4:15). The differences attained statistical significance, however, for only 6 components.

The large relative variability (C.V. %) of some components may be noted, particularly the thyroids.

TABLE 4:20. MEAN WEIGHTS (g) OF FOETAL BODY COMPONENTS AT 90-DAYS OF GESTATION AFTER ADJUSTMENT FOR DIFFERENCES BETWEEN MALE AND FEMALE FOETUSES

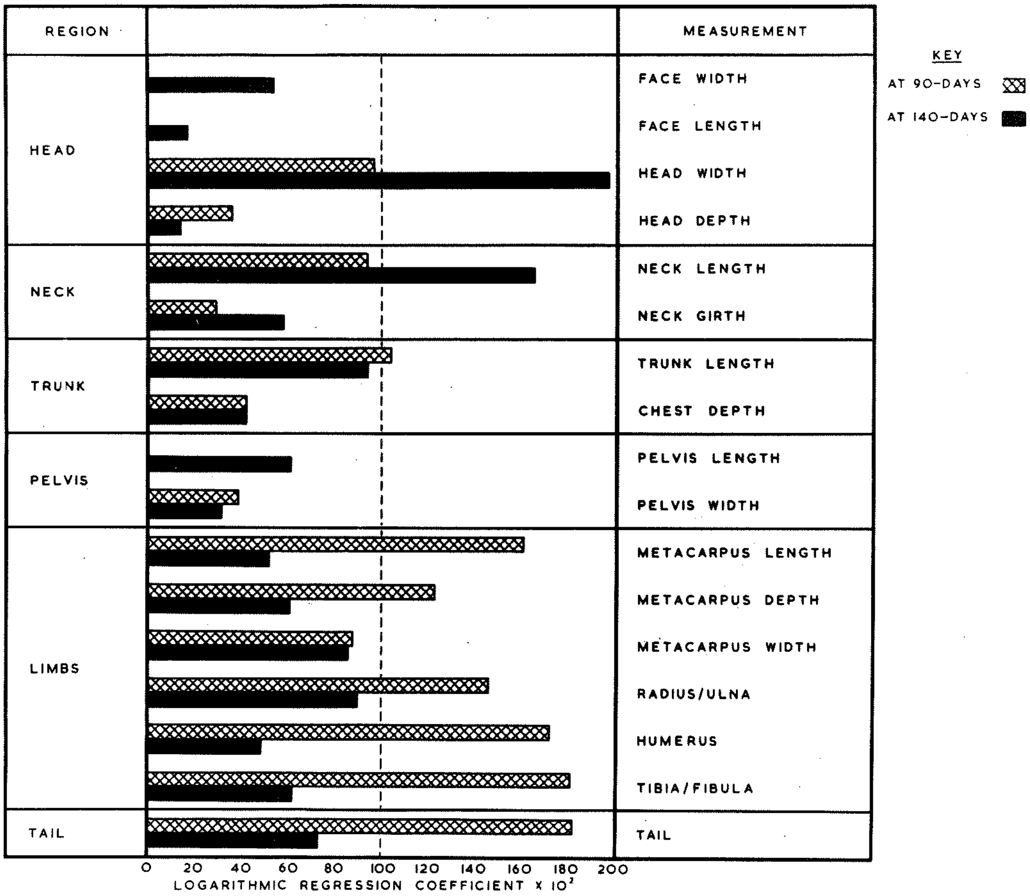
Component	Group means				Overall mean	C.V. %	S.E.	Mean differences	
	HP/Ram L	HP/Ram S	LP/Ram L	LP/Ram S				Plane of nutrition (HP-LP)	Rams (Ram L - Ram S)
Skull	65.64	67.07	64.24	68.74	66.27	7.0	2.67	- 0.13	- 2.97
Fore-feet	6.55	6.71	5.80	6.08	6.30	7.8	0.29	0.69 *	- 0.22
Hind-feet	6.28	6.45	5.28	5.74	5.95	7.4	0.25	0.81 **	- 0.32
Tail	1.14	1.25	0.81	1.06	1.07	23.1	0.14	0.26 (*)	- 0.18
Skin	45.22	46.01	40.82	40.09	43.23	7.6	1.89	5.16 *	0.03
Blood	35.65	31.03	27.48	25.39	30.19	14.7	2.58	6.90 *	3.36
Brain	8.39	8.40	7.69	8.19	8.17	3.6	9.17	0.46 **	- 0.26
Eyes	4.86	4.99	4.10	4.16	4.55	6.1	0.16	0.80 ***	- 0.10
Ears	1.50	1.53	1.42	1.56	1.50	9.2	0.08	0.03	- 0.09
Oesophagus	1.51	1.53	1.11	1.23	1.35	19.5	0.15	0.35 *	- 0.07
Rumen	1.39	1.50	1.51	1.59	1.49	10.6	0.09	- 0.10	- 0.10
Reticulum	0.42	0.49	0.38	0.37	0.42	14.2	0.03	0.08 *	- 0.03
Omasum	0.48	0.50	0.54	0.40	0.43	18.3	0.05	0.12 *	- 0.04
Abomasum	1.46	1.42	1.39	1.36	1.41	5.8	0.05	0.06	0.04
Small intestine	3.72	4.07	3.49	3.40	3.69	10.6	0.23	0.45 *	- 0.13
Large intestine/rectum	1.11	1.28	1.16	1.22	1.19	15.4	0.11	0.01	- 0.11
Total (gastro-intestinal tract)	10.01	10.81	9.38	9.56	9.99	4.5	0.26	0.94 **	- 0.49 *
Heart	4.62	4.81	4.01	4.11	4.40	7.7	0.19	0.66 **	- 0.14
Lungs/trachea	21.03	21.41	18.54	18.04	19.87	6.4	0.73	2.93 **	- 0.44
Pericardium	1.41	1.67	1.20	1.51	1.44	16.2	0.13	0.18	- 0.28 *
Diaphragm	2.30	2.28	1.59	1.96	2.04	11.6	0.13	0.51 **	- 0.17
Liver/gall bladder	42.06	43.64	26.80	37.58	37.52	14.9	3.24	10.66 **	- 6.18 *
Spleen	0.88	0.93	0.65	0.80	0.82	9.2	0.04	0.18 ***	- 0.10 *
Kidneys	6.56	6.59	5.46	6.09	6.18	14.0	0.50	0.79 (*)	- 0.33
Bladder	0.33	0.27	0.20	0.26	0.27	23.7	0.03	0.07 *	-
Caul/mesenteric fat	0.49	0.64	0.44	0.50	0.52	14.9	0.04	0.10 *	- 0.10 *
Neck thymus	1.368	1.488	0.941	0.951	1.203	9.9	0.069	0.482 ***	- 0.065
Heart thymus	0.513	0.528	0.325	0.279	0.420	11.6	0.028	0.219 ***	- 0.030
Thyroids	0.167	0.164	0.092	0.163	0.147	81.4	1.133	0.038	- 0.034 *
Adrenals	0.135	0.140	0.160	0.134	0.143	12.5	0.010	- 0.009	0.011
Pancreas	0.534	0.574	0.477	0.507	0.524	8.4	0.031	0.062 *	- 0.035
Carcass	224.6	234.1	200.4	212.8	218.3	5.0	6.3	22.8 **	-11.0 (*)

TABLE 4:21. MEAN WEIGHTS (g) OF FOETAL BODY COMPONENTS AT 140-DAYS OF GESTATION AFTER ADJUSTMENT FOR DIFFERENCES BETWEEN MALE AND FEMALE FOETUSES

Component	Group means				Overall mean	C.V. %	S.E.	Mean differences	
	HP/Ram L	HP/Ram S	LP/Ram L	LP/Ram S				Plane of nutrition (HP - LP)	Rams (Ram L - Ram S)
Skull	290.4	261.7	218.0	190.4	240.1	9.7	12.2	71.9 ***	28.1 *
Fore-feet	92.3	79.8	54.8	45.6	68.1	9.3	3.3	35.9 ***	10.9 **
Hind-feet	86.7	72.6	50.5	42.9	63.2	9.4	3.1	33.0 ***	10.8 **
Tail	11.5	9.3	5.0	3.6	7.4	15.8	0.6	6.1 ***	1.8 *
Skin	724.5	644.7	383.6	319.5	518.1	11.8	32.3	333.0 ***	72.0 (*)
Blood	170.9	148.9	110.2	79.6	127.4	10.0	6.7	65.0 ***	26.3 **
Brain	41.9	36.9	32.9	29.5	35.3	7.1	1.3	8.2 ***	4.2 **
Eyes	10.4	10.5	9.1	8.7	9.7	5.2	0.3	1.6 ***	0.2
Ears	19.3	17.6	12.5	10.4	15.0	17.1	1.4	7.0 ***	1.9
Oesophagus	5.4	5.3	3.2	3.0	4.3	20.9	0.5	2.3 ***	0.1
Rumen	12.5	10.9	6.9	5.7	9.0	10.4	0.5	5.4 ***	1.4 *
Reticulum	4.4	4.3	2.5	1.8	3.2	17.5	0.3	2.2 ***	0.4
Omasum	3.1	2.9	2.3	1.7	2.5	18.9	0.3	1.0 **	0.4
Abomasum	25.2	19.7	12.1	10.1	16.8	14.0	1.2	11.4 ***	3.8 *
Small intestine	42.5	35.2	23.7	19.2	30.2	10.2	1.6	17.4 ***	5.9 **
Large intestine/rectum	16.6	15.1	8.7	7.8	12.0	14.5	0.9	7.5 ***	1.2
Total (gastro-intestinal tract)	109.9	93.4	59.4	49.2	78.0	9.4	3.9	47.4 ***	13.4 **
Heart	31.2	27.9	21.9	17.9	24.8	9.4	1.2	9.7 ***	3.7 *
Lungs/trachea	142.8	141.7	85.8	71.4	110.5	8.8	5.1	63.7 ***	7.7
Pericardium	12.4	11.9	9.2	8.4	10.5	7.2	0.4	3.4 ***	0.6
Diaphragm	15.5	13.9	6.4	6.0	10.5	13.7	0.8	8.5 ***	1.0
Liver/gall bladder	132.0	110.6	72.0	59.7	93.6	7.4	3.6	55.4 ***	16.8 ***
Spleen	8.5	6.9	3.1	2.4	5.2	25.8	0.7	4.9 ***	1.1
Kidneys	29.7	22.8	17.4	14.4	21.1	18.9	2.1	10.4 ***	5.0 *
Bladder	3.9	3.4	1.9	2.1	2.8	14.9	0.2	1.7 ***	0.1
Caul/mesenteric fat	6.4	4.6	2.4	2.2	3.9	15.1	0.3	3.2 ***	1.0 **
Neck thymus	21.34	19.21	8.21	7.11	13.97	11.8	0.87	12.62 ***	1.62
Heart thymus	9.54	9.10	3.51	2.53	6.17	12.8	0.42	6.30 ***	0.71
Thyroids	1.01	0.83	0.85	0.34	0.76	33.8	0.14	0.32 *	0.34 *
Adrenals	0.84	0.80	0.51	0.48	0.66	11.7	0.04	0.32 ***	0.04
Pancreas	4.94	4.08	2.47	1.96	3.36	12.9	0.23	2.29 ***	0.69 *
Carcass	2032.4	1666.2	1009.7	792.7	1375.3	10.9	79.4	948.1 ***	291.6 **

Fig. 4:17.- Relative growth of foetal body dimensions : regression coefficients in the relations between body measurements and curved crown-rump length at 90- and 140-days of gestation after adjustment for the effects of foetal sex. All the coefficients shown were significant ($P < 0.05$).

RELATION OF INCREASE IN FOETAL BODY LINEAR MEASUREMENTS WITH INCREASE IN FOETAL BODY LENGTH



(ii) <u>After 140-days</u> : Table 4:21 shows that HP foetuses were significantly heavier than LP foetuses in all components. Foetuses sired by Ram L were heavier than Ram S foetuses in all components, the differences attaining significance in 17 components. These results are in agreement with the nutritional and sire effects on foetal body weights (Table 4:16).

(b) Weights after Adjustment for Differences in Foetal Empty Body Weight

Treatment effects on foetal body component weights at 90- and 140-days of age after adjustment, by covariance analysis of logarithmic transformed data, for differences in foetal body weight, as well for foetal sex effects, are recorded as variance ratios in Table 4:22.

It is clear that, at both ages, differences in component weights between HP and LP foetuses, and between those sired by Ram L or Ram S, were proportional to the differences in foetal body weight. Anatomical components of foetuses of the same age and body weight were very similar indeed in weight, irrespective of the treatments applied. The increase in experimental precision through inclusion of foetal body weight in these comparisons was of a high magnitude, especially after 140-days when body weight differences were largest. In the case of <u>foetal carcass weight</u> at 140-days, for example, a ninefold reduction in the size of the error mean square, associated with the adjustment for body weight differences, was

TABLE 4:22. TREATMENT EFFECTS ON THE WEIGHT (g) OF FOETAL BODY COMPONENTS AT 90- AND 140-DAYS OF GESTATION AFTER ADJUSTMENT(1) FOR FOETAL EMPTY BODY WEIGHT AND SEX

Component	VARIANCE RATIOS					
	After 90-days			After 140-days		
	Nutrition (N)	Rams (R)	N x R	Nutrition (N)	Rams (R)	N x R
Skull	6.38*	0.06	1.47	9.02*	1.42	0.21
Fore-feet	2.47	0.22	1.02	0.06	0.36	0.01
Hind-feet	0.01	0.34	[illegible]	0.64	0.02	0.62
Tail	2.58	2.82	0.56	0.60	1.12	0.01
Skin	4.75	5.47*	0.03	0.70	2.28	0.36
Blood	0.97	1.92	0.17	1.68	3.74	1.91
Brain	0.01	1.20	4.96	4.13	0.16	0.55
Eyes	5.00	0.28	0.02	0.05	0.80	1.29
Ears	1.17	0.23	0.84	0	0	0.14
Oesophagus	7.25*	1.48	0.06	0.06	0.25	0.11
Rumen	3.67	0.30	0.09	2.16	1.46	0.79
Reticulum	1.16	0.85	0.93	1.85	0.62	2.18
Omasum	0	0.02	0.37	3.06	2.61	0.86
Abomasum	0.01	1.30	0.03	1.52	1.16	0.89
Small intestine	0	0.09	0.82	0.78	1.09	0.08
Large intestine/rectum	0.09	1.73	0.38	1.37	0	0.04
Total (gastro-intestinal tract)	1.34	2.82	1.04	1.61	0.76	0.03
Liver/gall bladder	2.37	2.85	3.22	2.25	1.71	0.02
Spleen	5.07	4.70	2.27	0	0.22	0.17
Kidneys	1.64	0.29	1.36	0.85	1.60	0.38
Bladder	2.88	0.41	4.11	5.80*	0.25	2.28
Caul/mesenteric fat	0.02	5.96*	1.37	1.07	0.31	1.83
Neck thymus	13.52**	1.03	0.86	0.61	0.97	0.02
Heart thymus	5.65*	5.29	1.74	0.43	2.29	4.12
Thyroids	1.10	10.22*	1.10*	1.02	0.38	4.15
Adrenals	1.13	1.27	2.25	0.18	1.50	0
Pancreas	0.07	1.21	0.02	0.02	0	0
Carcass	0	2.90	1.25	0.21	0.30	0

Note:

(1) Covariance analysis of logarithmic transformed data:

9 degrees of freedom at 90-days of age

10 degrees of freedom at 140-days of age

recorded - from 13.5 to 1.5 (Appendix II : Example C.).

After 90-days, 4 components recorded a significant nutritional effect after adjustment, 3 components a significant sire effect, with 2 significant interactions. After 140-days, only 2 components recorded a significant treatment effect; the skull and the bladder appeared affected by nutrition. This number of significant effects, as a proportion of the total number of comparisons made, might reasonably be expected to arise by chance, as was the case for the foetal body dimensions.

(c) Sex Effects on the Weight of Foetal Body Components

Fig. 4:18 depicts the pattern of sex effects on the weights of foetal body components of foetuses of the same empty body weight. As with the examination of sex effects on foetal body dimensions, the logarithmic regression coefficient appropriate to each component has been derived from the covariance analysis, and is shown on a percentage. Positive and negative coefficients indicate that males were heavier or lighter respectively than females at the same foetal empty body weight.

In general, sex differences in the weights of components were greater at the younger of the two ages examined. A clear pattern of developmental differences due to foetal sex is difficult to discern at either age. Several components show a reversal of the sex effect between 90- and 140-days; the most striking is the thyroid gland. Most components show a diminished sex effect between the two ages although the sign remained the same; for example, males had heavier *tails* than females at both ages, but the *tail* was 39 *per cent*. heavier at 90-days compared with 7 *per cent*. at 140-days. The very small sex effects of 1-2 *per cent*. in either direction, as for example the *skull*, *brain* and *carcass* at both ages, need cautious acceptance.

(d) Allometric Growth of Foetal Body Components

Growth coefficients of the foetal body components at each of the two stages are illustrated in Fig. 4:19. The coefficients were derived from covariance analyses of logarithmic transformed data using foetal empty body weight and foetal sex as the two covariates.

(i) *After 90-days* : The *fore*- and *hind-feet*, *skin*, *heart*, *lungs and trachea*, *diaphragm*, *liver*, *kidneys*, *caul/mesenteric fat*, and *heart thymus* were increasing in weight at a faster rate than the empty body. On the other hand, growth coefficients of the *pericardium*, *spleen* and *adrenals* were substantially less than unity, indicating that their relative rates of growth were much less than that of the body as a whole. Other organs and parts, such as the *skull*, *liver* and *carcass*, were growing at much the same rate as the body.

(ii) *After 140-days* : The relative rates of growth of the *tail*, *skin*, *spleen*, *neck thymus*, *heart thymus*, *pancreas* and *carcass* exceeded that of the empty body. All these organs were growing at a faster relative rate after 140-days than they were after 90-days. Growth coefficients of remaining organs after 140-days were less than

Fig. 4:18.- Sex effects on foetal body components after 90- and 140-days of pregnancy. Positive and negative coefficients indicate that males were heavier or lighter respectively than females at the same empty body weight. All the coefficients shown were significant ($P < 0.05$).

SEX EFFECTS ON FOETAL BODY COMPONENTS

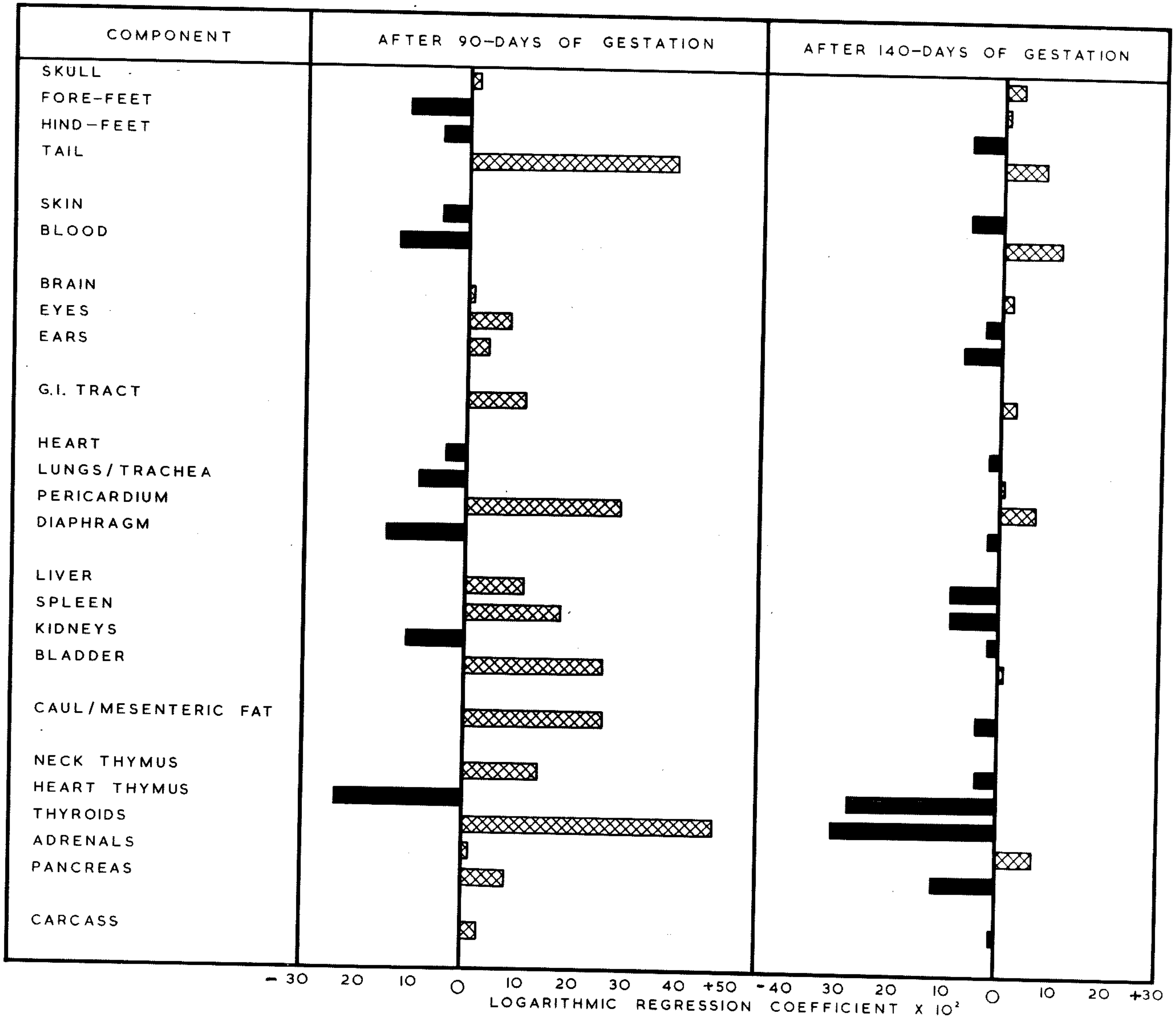


Fig. 4:19.- Relative growth of foetal body components : regression coefficients in the relations between the weight of body components and empty body weight at 90- and 140-days of gestation after adjustment for the effects of foetal sex. All the coefficients shown were significant ($P < 0.05$).

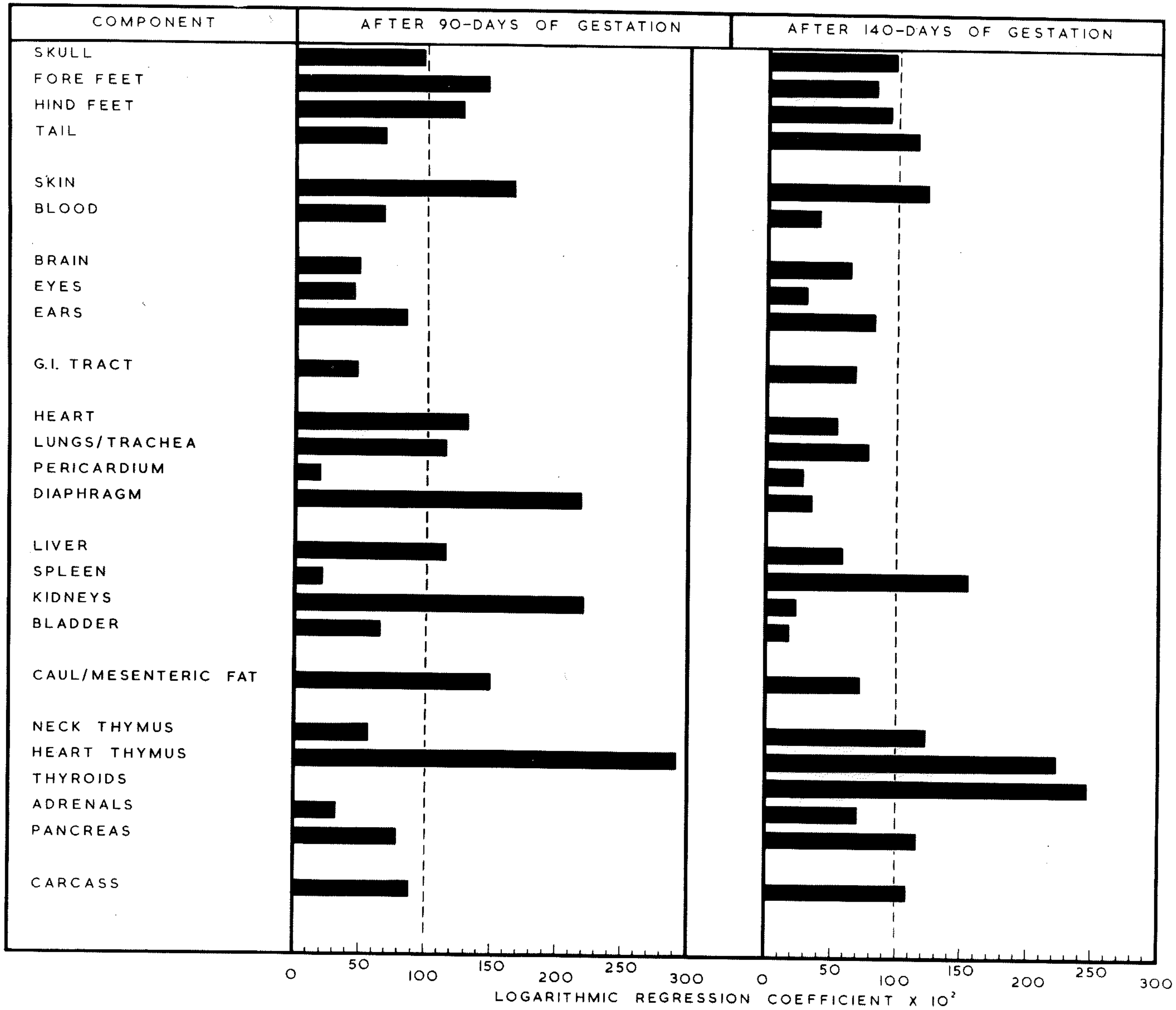

COMPONENT
AFTER 90-DAYS OF GESTATION
AFTER 140-DAYS OF GESTATION
SKULL
FORE FEET
HIND FEET
TAIL
SKIN
BLOOD
BRAIN
EYES
EARS
G.I. TRACT
HEART
LUNGS/TRACHEA
PERICARDIUM
DIAPHRAGM
LIVER
SPLEEN
KIDNEYS
BLADDER
CAUL/MESENTERIC FAT
NECK THYMUS
HEART THYMUS
THYROIDS
ADRENALS
PANCREAS
CARCASS
0
50
100
150
200
250
300
0
50
100
150
200
250
300
LOGARITHMIC REGRESSION COEFFICIENT X 10²

TABLE 4:23. RELATIVE GROWTH OF COMPONENTS OF THE FOETAL GASTRO-INTESTINAL TRACT : LOGARITHMIC PARTIAL REGRESSION COEFFICIENTS(1) IN THE RELATIONSHIPS BETWEEN THE WEIGHT (g) OF COMPONENTS AND FOETAL EMPTY BODY WEIGHT (g) AFTER ADJUSTMENT FOR DIFFERENCES BETWEEN MALE AND FEMALE FOETUSES

Component	Regression coefficient ± S.E.	
	After 90-days	After 140-days
Oesophagus	- 1.506 ± 1.105	0.701 ± 0.360
Rumen	0.847 ± 0.438	1.304 ± 0.039 ***
Reticulum	0.362 ± 1.004	0.465 ± 0.247
Omasum	2.581 ± 0.880 *	- 0.409 ± 0.354
Abomasum	0.417 ± 0.132 *	0.603 ± 0.162 **
Small intestine	0.973 ± 0.424 *	0.712 ± 0.059 ***
Large intestine	- 0.324 ± 1.062	0.568 ± 0.149 **
Total (gastro-intestinal tract)	0.438 ± 0.072 ***	0.673 ± 0.059 ***

Note:

(1) Coefficients derived from covariance analysis of logarithmic transformed data.

unity. Relative growth rates of the limbs, skin, blood, heart, lungs and trachea, diaphragm, liver, kidneys and the caul/mesenteric fat were less after 140-days than after 90-days.

Differences in the differential growth ratios of the components within and between each stage appear to reflect functional necessity. This is more clearly shown from an examination of the growth coefficients of individual components of the gastro-intestinal tract recorded in Table 4:23. The coefficients did not attain significance for all components. It is nevertheless interesting to note the changes in the relative growth rates between the two ages. The omasum attained the highest relative growth rate after 90-days, and the rumen after 140-days. The relative growth rate of the former part decreased in late gestation, but the differential growth ratio of the abomasum increased, and that of the rumen markedly so, as the time of birth drew near.

IX. Wool Follicle Development

(a) Actual Numbers of Follicles and their Ratios

Mean numbers of wool follicles and follicle ratios for foetuses after 90- and 140-days are given in Table 4:24. Sire effects were not significant at either age, although density and total population estimates tended to favour foetuses sired by the larger (L) of the two rams.

(i) After 90-days : The significantly higher density of primary (Pf) follicles, coupled with a greater skin area, of HP as compared with LP foetuses, led to a greater estimated total population of Pf follicles per animal under HP nutrition.

(ii) After 140-days : Foetuses from LP ewes had a significantly higher density of Pf follicles and a higher, but not significant, density of immature secondary follicles (Si) than HP foetuses. On the other hand, the density of mature secondary follicles (Sf) was significantly higher in HP foetuses. The difference in density of total follicles (Pf + Si + Sf) was not significant, but tended to favour HP foetuses.

Both the Sf/Pf, and the Si + Sf/Pf ratios were significantly lower, but the Si/Sf + Pf ratio higher, in LP foetuses.

The estimated total Pf population favoured HP foetuses but the nutritional effect was not significant. HP foetuses had significantly greater total populations of Si, Sf, and therefore Si ± Sf, follicles than foetuses born to LP ewes. The total populations of Pf + Si + Sf, Si and Sf follicles of LP foetuses, as percentages of comparable estimates for HP foetuses, were 58, 70 and 35 per cent. respectively; the maturation of secondary follicles was thus most affected by maternal undernutrition.

(b) Follicle Numbers after Adjustment for Differences in Foetal Body Weight

Wool follicle numbers at each stage were adjusted, by covariance analyses of natural data, for differences in foetal body weight and for the effects of foetal sex. Coefficients for foetal

TABLE 4:24. MEAN WOOL FOLLICLE NUMBERS AND FOLLICLE RATIOS OF FOETUSES AFTER 90- AND 140- DAYS OF GESTATION

Character		Group means				Overall mean	C.V. %	S.E.	Mean differences	
		HP/Ram L	HP/Ram S	LP/Ram L	LP/Ram S				Plane of nutrition (HP-LP)	(Ram L - Ram S) Rams
After 90-days of gestation										
Skin area (cm^2)		451	463	414	412	437	7.5	17.0	44*	5
No. of Pf follicles/mm^2		84.1	85.4	79.2	73.5	81.0	8.8	3.67	8.4*	2.2
Total no. of Pf follicles/foetus (millions)		3.80	3.96	3.30	3.05	3.56	14.4	0.264	0.71*	0.05
After 140-days of gestation										
Skin area (cm^2)		2235	2029	1380	1255	1725	7.3	63.0	815***	166*
No. of follicles/mm^2	Pf	13.6	14.4	20.0	23.5	17.9	15.4	1.38	- 7.8***	-2.2
	Si	132.5	132.1	145.1	138.7	137.1	14.6	10.02	- 9.6	3.4
	Sf	74.8	63.7	37.9	41.9	54.6	12.4	3.39	29.4***	3.6
	Si + Sf	207.3	195.8	183.0	180.6	191.6	10.5	10.02	19.8(*)	7.0
	Pf + Si + Sf	220.9	210.2	203.0	204.1	209.5	9.7	10.16	12.0	4.8
Follicle ratios										
	Sf/Pf	5.53	4.42	1.91	1.89	3.44	15.6	0.268	3.08***	0.57(*)
	Si + Sf/Pf	15.26	13.59	9.16	8.04	11.51	13.2	0.763	5.83***	1.40(*)
	Si/Sf + Pf	1.50	1.72	2.53	2.14	1.97	19.6	0.192	- 0.73**	0.09
Total no. of follicles/foetus (millions)										
	Pf	3.03	2.93	2.77	2.92	2.91	12.9	0.187	0.14	-0.03
	Si	29.60	26.76	20.12	17.42	23.47	17.2	2.023	9.41***	2.77
	Sf	16.771	12.98	5.25	5.28	10.07	18.3	0.923	9.61***	1.88(*)
	Si + Sf	46.37	39.74	25.37	22.70	33.54	14.7	2.462	19.02***	4.65(*)
	Pf + Si + Sf	49.40	42.67	28.14	25.62	36.45	14.0	2.548	19.16***	4.63(*)

TABLE 4:25. MEAN WOOL FOLLICLE NUMBERS OF FOETUSES AT 90- AND 140-DAYS OF GESTATION AFTER ADJUSTMENT FOR FOETAL BODY WEIGHT

Character	Adjusted means				Variance ratios		
	HP/Ram L	HP/Ram S	LP/Ram L	LP/Ram S	Nutrition	Rams	Interaction (N x R)
<u>After 90-days of gestation</u>							
No. of Pf follicles/mm^2	82.2	82.0	81.9	76.7	0.19	0.51	0.71
Total no. of Pf follicles/foetus (millions)	3.61	3.63	3.57	3.37	0.36	0.32	0.79
<u>After 140-days of gestation</u>							
No. of follicles/mm^2							
Pf	19.3	17.2	17.1	17.8	0.02	0.13	1.15
Si	114.4	123.3	154.4	156.3	0.53	0.10	0.10
Sf	57.8	53.8	49.5	57.1	0.04	0.16	3.98
Si + Sf	172.2	177.1	203.9	213.4	0.56	0.20	0.05
Pf + Si + Sf	191.5	194.3	221.0	231.2	0.50	0.15	0.12
Total no. of follicles/foetus (millions)							
Pf	2.88	2.77	3.00	3.00	0.06	0.04	0.13
Si	21.08	22.02	25.58	25.22	0.19	0.01	0.10
Sf	10.57	9.37	9.52	10.81	0.01	0.01	6.12*
Si + Sf	31.65	31.39	35.10	36.03	0.22	0.01	0.09
Pf + Si + Sf	34.53	34.16	38.10	39.03	0.23	0.01	0.10

Note:

Regression coefficients, derived from covariance analyses, for body weight were all significant ($P < 0.05$); coefficients for foetal sex were not significant.

weight attained significance ($P < 0.05$) in all cases, but coefficients for foetal sex were not significant.

Adjusted mean values and variance ratios (of adjusted mean squares) are recorded in Table 4:25. Differences due to maternal nutrition or sires in any of the parameters were not significant; there was, however, evidence of interaction in the estimated total population of Sf follicles at 140-days of age.

X. Development of the Semitendinosus Muscle

(a) Muscle Weights and Actual Number of Muscle Fibres

Mean weights of the Semitendinosus muscle, and the estimated total number of fibres in a cross-section of the muscle, at each age are given in Table 4:26.

(i) After 90-days : The weight of the muscle in HP foetuses exceeded that in LP foetuses, but the difference due to sires was small and not significant.

HP foetuses had a greater total number of muscle fibres/cross section; the sire effect was small but tended to favour the smaller ram (S).

(ii) After 140-days : An eight-fold increase in the mean weight of the muscle between 90- and 140-days was recorded under HP feeding compared with a four-fold increase under poor nutrition. Foetuses from HP ewes had a heavier muscle than those from LP ewes; the mean weight of the latter represented 51 per cent. of the former. Foetuses sired by Ram L had a heavier muscle than those sired by Ram S, the difference in mean weights being similar

TABLE 4:26. MEAN MEASUREMENTS OF THE SEMITENDINOSUS MUSCLE AFTER ADJUSTMENT FOR THE EFFECTS OF FOETAL SEX

Character	Group Means				Overall mean	C.V. %	S.E.	Mean Differences	
	HP/Ram L	HP/Ram S	LP/Ram L	LP/Ram S				Plane of nutrition (HP-LP)	Rams (Ram L - Ram S)
<u>At 90-days of age</u>									
Muscle wt. (g)	1.0007	1.1280	1.0127	0.8851	1.0614	3.6	0.0220	0.1155***	0.0001
Est. no fibres/cross-section (1000)	64.87	62.75	53.90	56.64	59.73	9.1	3.167	8.54*	-0.31
<u>At 140-days of age</u>									
Muscle wt. (g)	8.4380	7.4923	4.3742	3.7311	6.0089	10.1	0.3138	3.9125***	0.7944*
Est. no. fibres/cross-section (1000)	84.24	87.02	64.14	54.07	72.37	9.6	3.587	26.52***	3.64

under both planes of nutrition.

The mean number of muscle fibres/cross-section increased between 90- and 140-days of age under HP feeding; under poor nutrition the mean number increased over this interval in foetuses sired by Ram L but decreased in foetuses sired by Ram S. Maternal undernutrition throughout pregnancy significantly reduced the total number of fibres/cross-section; the mean value for LP foetuses representing 69 per cent. of the mean value for HP foetuses. Foetuses sired by Ram L had a slightly, but not significantly, greater number of fibres/cross-section than foetuses sired by the smaller ram.

(b) Muscle Fibre Numbers after Adjustment for Differences in Muscle Weight.

The numbers of muscle fibres/cross-section were adjusted, by covariance of logarithmic transformed data, for differences in muscle weight and foetal sex.

(i) After 90-days : The number of fibres was not significantly associated with muscle weight. The regression coefficient for foetal sex (0.1830 ± 0.0125 : $P < 0.001$) indicated that males had approximately 18 *per cent*. more fibres in the cross-section than females.

(ii) After 140-days : Both regression coefficients attained significance ($P < 0.001$). The coefficient for muscle weight was 0.7135 ± 0.0600, and for foetal sex was 0.1489 ± 0.0021, the latter indicating the greater number of fibres for males than females. Adjusted mean values ($\times 10^3$) were : HP/Ram L, 63.27; HP/Ram S, 70.88; LP/Ram L, 76.44; LP/Ram S, 72.38. Treatment effects were not significant.

(c) Relationships of Muscle Fibre Numbers to Estimates of Muscle Length and Body Length

Further definition of relationships between fibre numbers, muscle weight and muscle length was attempted. However, muscle fibre number/cross-section was not significantly correlated with either the length of the tibia/fibula (as a measure of muscle length) or with foetal crown-rump length, as measured externally (see Fig. 4:2).

XI. Factors Affecting Foetal Growth

Foetal body weights after 90- and 140-days have been related to a number of independent variables in multiple regression models, with progressive elimination of non-significant variables. Each variable in the model assumes independence of others.

The following abbreviations are used in the equations presented:-

F.W. = Foetal weight (g.)

F.S. = Foetal sex (discontinuous variable : female = 0; male = 1).

R. = Ram (discontinuous variable : Ram S = 0; Ram L = 1).

F.I. = Feed intake (D.O.M./day/g.)

B.W. = Ewe body weight (kg.) at mating (wool-free).

E.W.C. = Ewe body weight change/day/g. (wool-free; conceptus-free).

(a) After 90-days: The derived equation was:-

$$\begin{array}{lllll} \text{F.W.} = 405.4 + & 79.7\ \text{F.S.} + & 2.35\ \text{B.W.} + & 0.504\ \text{E.W.C.} \\ (\text{s.e.}) & (\pm\ 9.2) & (\pm\ 0.65) & (\pm\ 0.075) \\ & {*}{*}{*} & {*}{*} & {*}{*}{*} \end{array}$$

with residual coefficient of variation of 8 per cent. This equation accounts for 80 per cent. of the variation in foetal weight at 90-days of age (R = 0.896, based on 11 d.f.)

The regression coefficients indicate that male foetuses were heavier than females; that foetal weight increased by 2.35 g. for each 1 kg. of increase in ewe body weight at mating, and by 0.504 g. for each 1 g./day of ewe body weight change over the first 90-days of pregnancy.

(b) After 140-days : The derived equation was:-

$$\begin{array}{llll} \text{F.W.} = 446.7 + & 236.9\ \text{R} + & 3.503\ \text{F.I.}\ (0\text{-}140\ \text{days}) \\ (\text{s.e.}) & (\pm\ 58.1) & (\pm\ 0.909) \\ & {*}{*} & {*}{*} \end{array}$$

with a residual coefficient of variation of 6 per cent. These variables account for 85 per cent. of the variation in foetal weight at 140-days of age (R = 0.922, based on 13 d.f.).

The coefficients indicate that foetuses sired by the larger ram (L) were heavier and that each 1 g. of D.O.M. intake/day over 140-days of pregnancy was associated with an increase in foetal weight of 3.503 g.

(c) At birth : Birth weight of lambs was significantly associated with the ram and feed intake over the whole of pregnancy in the following equation:-

$$\text{F.W.} = 1390.0 + \underset{\substack{(\pm\ 124.4)\\ ***}}{509.8\ \text{R}} + \underset{\substack{(\pm\ 0.894)\\ ***}}{4.800\ \text{F.I.}}$$

(s.e.)

This equation accounts for 84 <u>per cent</u>. of the total variation in birth weight (R = 0.917, based on 18 d.f.), with a residual coefficient of variation of 6 <u>per cent</u>.

Birth weight of lambs increased by 4.80 g. for every 1 g. of D.O.M. intake/day during pregnancy. Ram L left heavier progeny than the smaller ram S.

D. DISCUSSION

In this experiment foetal growth in early gestation depended upon the level of nutrition supplied to the ewe after mating. This noteworthy result contrasts with others (Wallace 1948; El Sheikh *et al*. 1955; Foote *et al*. 1959) and challenges the high priority for available nutrients ascribed to the foetus by Hammond (1944). It is interesting that Schinckel (1963) recently reported a significant difference in the weight of single and multiple Merino foetuses at 90-days of age, from which he implied that maternal nutrition might be a limiting factor in early prenatal growth.

A reduction in foetal weight at 90-days of age may have been

been recorded in this study and not in others for several reasons. Firstly, the ewes were subjected to very severe nutritional stress in early pregnancy. Although the low plane ewe in Wallace's (1948) study suffered much the same proportional body weight loss without appreciably affecting the weight of twin foetuses, his ewes were relatively heavy at mating. Granted the breed difference, the mature Merino ewes in this experiment were, by comparison, light at mating and in generally poor condition. Body fat, as a source of catabolisable energy, may buffer the effect of restricted feed intake in early pregnancy. Secondly, the feed intake and concomitant degree and rate of body weight gain and loss could be strictly controlled, even though the animals were subjected to the rigours of the field environment. Lastly, examination of a greater number of foetuses than in Wallace's (1948) work permitted statistical analysis of the data.

Further experiments are clearly necessary to determine, for example, critical levels of feed restriction and weight loss before the growth of single and multiple foetuses is affected. Discrimination between the academic and practical importance of retarded early foetal growth is also needed.

Embryonic loss in early pregnancy slightly increased under good feeding of the ewe after mating in the studies of Foote et al. (1959) and Bellows et al. (1963). On the other hand, a marked reduction in the number of lambs born to maiden ewes ill-fed in early pregnancy was recorded by Bennett et al. (1964); the stage at which losses occurred was not defined. A sensitive balance between embryonic loss and retardation of foetal growth is suggested, for placental development was restricted to a greater extent than foetal growth in this experiment. This supports Hammond's (1944) proposal and agrees with other investigations (Wallace 1948; El-Sheikh et al. 1955; Foote et al. 1959; Bellows et al. 1963). Drastic curtailment of feed intake after conception and prior to completion of implantation may lead to embryonic loss; incipient undernutrition of a less precipitous nature may permit completion of implantation but restrict full placental development and thus foetal growth.

Caruncles of the non-pregnant uterus probably develop into functional cotyledons following pressure from the early blastocyst (Huggett & Hammond 1952), arising from accumulated allantoic fluid (reviewed by Pomeroy 1960). The smaller number of cotyledons involved in the vacant horn (where initiation of placentation would occur later than in the pregnant horn) of LP ewes, indicates an effect of maternal nutrition on early blastocyst development. The sire, and possibly the sex, effects on the number of functional cotyledons may also reflect rapidity of blastocyst growth. Ovine foetal growth can be markedly depressed by surgical reduction of the number of caruncles (Alexander 1964b), even though individual cotyledons display compensatory development.

Placental and foetal weights at 90-days of age were closely associated after elimination of other variables. At 140-days a greater amount of variation in the positive relationship remained unexplained. Alexander (1964*b*) found very little placental tissue (cotyledons only) was necessary to permit gestation to reach 100 days, but the size which the placenta had attained limited subsequent foetal growth. Compensatory growth of the foetus in late pregnancy, following nutrient restriction of the ewe in early gestation, requires examination. Placental weight, however, as Alexander (1964*a*) and Holm (1964) stress, represents only a crude estimate of placental efficiency and further explanation of the phenomena must be sought in other parameters, such as those suggested by Moustgaard (1959).

Continuation of maternal undernutrition through late pregnancy dramatically increased the difference in weight between HP and LP foetuses from approximately 12 *per cent*. at 90-days of age, to 46 *per cent*. at 140-days and 39 *per cent*. at birth. Wallace (1948) reduced the weight of 144-day old *twin* foetuses by 46 *per cent*. through underfeeding the ewe in late pregnancy. This comparison, together with the 16 *per cent*. mortality of LP ewes in late pregnancy, emphasises the severe stress imposed in late gestation of this trial; and also in the studies of Schinckel & Short (1961) and Taplin & Everitt (1964) who recorded reductions of 34 *per cent*. and 43 *per cent*. respectively in the birth weight of single lambs derived from undernourished Merino ewes. The lack of an appreciable nutritional effect on the weight of single foetuses at 140-days of age in the investigation of Bellows _et al_. (1963), and on birth weight of lambs in other studies (reviewed by Thompson & Aitken 1959; Schinckel 1963) may be accounted for by the lesser degree of stress applied.

These results therefore support the view (Schinckel 1963) that the effects of poor maternal nutrition will be manifested to the greatest degree when foetal mass is increasing most rapidly. It is, however, necessary to recall the much lower feed intake of LP ewes in late as compared with early pregnancy.

Undernutrition markedly increased the weight of uterine fluids and caused abdominal and thoracic oedema. The latter is a recognised characteristic of undernutrition (Keys _et al_.1950; Morris, Howard & Macfarlane 1962; Panaretto 1964), and under such conditions gross body weight becomes a very misleading parameter of performance. Nett body weight loss of these ewes was substantial, but would be much exceeded by weight loss on a moisture-free basis. Changes in the chemical composition of the ewes are intended for later study.

Cotyledon morphology was also profoundly affected by underfeeding. After 140-days of pregnancy cotyledons from LP ewes presented a thrombosed, senile appearance perhaps associated with an abbreviated gestation. Eversion of the foetal component of the cotyledon suggests that the foetus attempts compensation for a restricted placental area. Bellows _et al_.(1963) also noted this effect in their nutritional study, as did Alexander (1964_b_) after surgical reduction of placental development. A differential pattern of placental retardation was indicated by the cotyledon weights and numbers in each horn, and the weight and morphology of individual cotyledons according to their position within the horn. Further study of these characteristics is required, perhaps employing the technique of foetal exclusion described recently by Lehr *et al.* (1964). This might lead to application of a local haemodynamic control of prenatal growth (McLaren & Michie 1960) in the sheep, as distinct from the solely systemic principle proposed by Hammond (1944).

Marked effects of prenatal undernutrition on parameters of foetal development were recorded, but these were strikingly proportional to the effects recorded on foetal body mass. Patterns of allometric growth of foetal body components, and of body dimensions, conformed with other expositions (Wallace 1948; Joubert 1956*a*; Stephenson 1962*a*) and appeared little disturbed by the level of maternal feeding. The evidence adduced strongly suggests that undernutrition in prenatal life retards growth processes in a general, and not differential, manner.

While full support is thus offered for the allometric growth principle (Huxley 1932), the concept of a *differential* effect of undernutrition on growth and development (reviewed by Palsson 1955) seems untenable. The two interpretations depend upon whether or not differences incurred in body weight are taken into account. Adoption of the methods used by the Hammond or Cambridge school necessitates presentation of data as in Fig. 4:20. Interpretation of this type of analysis leads inevitably to the conclusions forwarded by Pålsson (1955) in his review of the Cambridge contributions.

When, however, adjustment is made for empty body weight differences nutritional effects become negligible, with a few exceptions in the mature animal such as the reduced weight of the gastro-intestinal tract (especially the stomachs), the skin, kidneys and carcass, and adrenal enlargement, in LP ewes. Comparisons yet to be made on a fat-free empty body weight basis should prove illuminating, for it is upon this basis that the traditional Cambridge concepts are under critical review (Tulloh 1963; Elsley et al. 1964). The data on foetal body dimensions substantiate the view (Taplin & Everitt 1964) that the undernourished lamb at birth appears malproportioned in relation to a well-fed lamb simply because it is lighter and at an earlier stage of the differential growth and development process. The foetal body component evidence corroborates this proposal. Although the foetal carcasses were not dissected into tissue components, it is interesting to note that Stephenson (1964) found that 99.8 per cent. of variation in skeletal muscle of ovine foetuses could be accounted for by differences in body weight.

A strong genetic influence on foetal weight operated in late gestation, the larger of the two rams (L) producing heavier off-spring at 140-days of age and at birth. The sire effect cannot be entirely dissociated from differences in feed intake of the ewes. Nevertheless,

Fig. 4:20.- Relative effects of plane of nutrition on components of the empty body of ewes and foetuses after 90- and 140-days of pregnancy. Mean weights of components of Low Plane animals expressed as percentages of mean weights of High Plane animals.

Abdominal organs = liver, gall bladder, spleen, kidneys, urinary bladder.

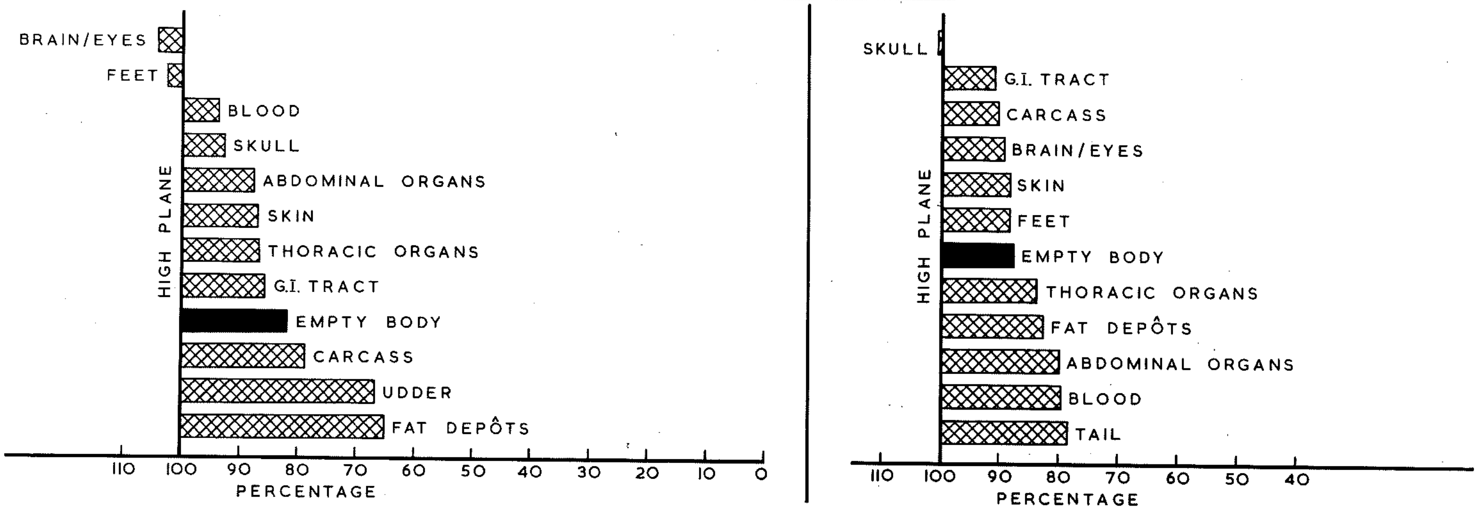
Thoracic organs = heart, lungs and trachea, diaphragm.

Feet = fore- + hind-feet.

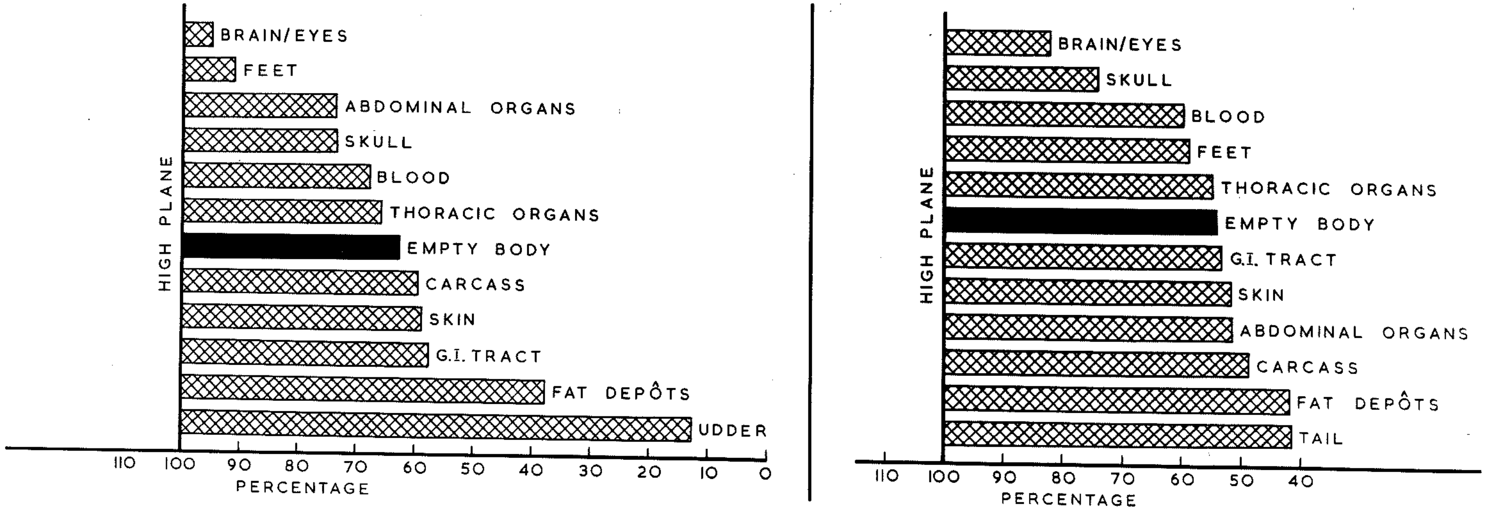
RELATIVE EFFECTS OF PLANE OF NUTRITION ON COMPONENTS OF THE EMPTY BODY

EWES FOETUSES

AFTER 90-DAYS OF PREGNANCY



AFTER 140-DAYS OF PREGNANCY



lighter lambs were born to ewes mated to the smaller ram (S), although the ewes consumed more feed than those in lamb to Ram L. Unequivocal reference to the inheritance of growth rate is not permissible, for the two rams were not reared under identical conditions. The data do suggest, however, that the inheritance of large body size within a breed is a characteristic amenable to selection.

Foetal development, on the other hand, was scarcely influenced by the size of the sire after adjustment for differences in foetal weight. Examination of skeletal muscle tissue, as one component of foetal size, failed to reveal significant differences in cell number. This is hardly surprising with such a small number of animals for study. Further investigation along these lines might be profitable, especially if differences in muscle cell size are also recorded.

The effect of sex on the growth of the foetus, unlike the sire influence, became apparent early in gestation, subsequently diminishing with age. Stephenson (1962a) suggested that the greater variability of foetal body dimensions in late gestation may obscure the sex effect. The same proposal may apply to this study, but it is interesting that the weights of body components showed the same trend with time. Ram lambs are generally reported to be heavier than ewe lambs at birth (reviewed by Everitt & Jury 1966a). In this study, with relatively small numbers, females were slightly heavier at 140-days of age, and at birth.

In postnatal life the difference in body weight between rams and ewes, favouring the former, is much diminished under poor nutrition (Pålsson & Verges 1952). This principle held true for foetuses at 140-days of age, and at birth, but there was little such evidence at 90-days. On the contrary, females at 90-days suffered more from poor maternal feeding than did males. The sex effect on foetal growth may assume a cyclical nature with fluctuations of somatic activity associated with the maturation of different endocrine organs and the integration of the endocrine system as a whole.

Body conformation, as described by the linear measurements, of male foetuses at the same body weight as females, tallies with Stephenson's (1962a) description, with only minor differences. The pattern of sex effects on the weights of body components was not so clear. Male foetuses had a greater number of muscle fibres/cross-section of the Semitendinosus muscle than females of the same age and (statistically) the same weight. This interesting result supports Hammond's (1932) proposal and helps to explain the plump, blocky shape of males as described here and by Stephenson (1962a) for the ovine foetus, and by Keller (1920) and Beer (1925) for the bovine foetus. To what extent this finding relates to the superior growth rate of males in postnatal life and sex differences in body composition (reviewed by Turton 1963; Everitt & Jury 1965a,b) is not known.

Comparison of the estimated muscle fibre numbers at each age suggests that hyperplasia continued past 90-days of age in HP foetuses. This contrasts with the inference drawn by Joubert (1956a). Under poor nutrition of the ewe, however, there appeared very little change in fibre numbers with advancing age, and LP foetuses at birth had substantially fewer muscle fibres than HP foetuses. Muscle cell division in such restricted animals may be prolonged into postnatal life given adequate feeding after birth. Additional study of this topic is needed, for it may assist explanation of the retarded postnatal growth and restricted mature size of animals ill-fed in early life (Schinckel & Short 1961; Taplin & Everitt 1964). Its possible importance in meat production is obvious.

Wool follicle development in foetuses of 140-days of age showed a similar pattern of nutritional effects to those described for lambs at birth by Schinckel & Short (1961) and Taplin & Everitt (1964). The smaller LP foetuses had fewer follicles per animal with less matured Sf follicles, in agreement with Schinckel (1955), Short (1955) and Schinckel & Short (1961). Initiation of secondary follicles in LP foetuses is not continued after birth even under adequate nutrition (Schinckel & Short 1961) so that the reduced secondary follicle population represents a permanent effect. The population of primary follicles at 140-days of age, on the other hand, was not significantly affected by maternal undernutrition, and at 90-days the nutritional effect appeared proportional to the effects on foetal body weight. This suggests that the initiation and maturation of primary follicles is related to body weight and continues past 90-days of age in retarded foetuses.

Wool growth of the ewes was reduced in late as compared with early pregnancy. These results may reflect, in part, the effects of pregnancy per se. However, the bare maintenance of nett body weight under HP feeding, and substantial loss under LP, coupled with the increased adrenal weights, lends support to the proposal (Lindner & Ferguson 1956) that wool growth may be limited by adreno-cortical activity. Efficiency of wool growth increased as feed intake decreased as reported by Ferguson (1962) but there was a suggestion that efficiency was little affected at the highest levels of intake. Panaretto (1964) found that severely underfed ewes almost ceased to grow wool after 200 days of undernutrition.

The estimates of nutritional requirements for body maintenance of the ewes generally exceed those for pen-fed and yard-fed animals (Table 2:2). Higher maintenance requirements than those for housed sheep are not unexpected for these ewes must have expended additional energy in combatting the environment and in locomotion. On the other hand, they were saved the considerable energy expense of harvesting their food (Graham 1964c). The latter cost may represent a big proportion of the difference between these estimates and those for grazing animals. This suggestion is in line with others (Coop 1961, 1962a; Coop & Drew 1964; Lambourne 1955, 1961), while the increased adrenal weights lend support to an endocrine stress effect on feed requirements (Lambourne & Reardon 1963). Estimated requirements for weight gain are lower than those given by other studies (reviewed by Coop 1962a). The increasing weight gain due to conceptus growth undoubtedly plays an important role in the reported relationships. Neither can an improvement in anabolic efficiency resulting from pregnancy *per se* (Newton 1952) be dissociated. Nevertheless, these estimates, together with those of nutrient requirements for foetal growth, may assist in formulation of more valid recommendations than exist at present (N.R.C. 1959). The chemical composition of the weight gains is intended for further study and the results should be helpful in this connexion.

Finally, the factors shown to affect foetal growth and development at the two ages may be summarised. Variation in foetal weight at 90-days was largely accounted for by foetal sex, the body weight of the ewe at conception, and the body weight change of the ewe. The last variable may, in fact, reflect maternal feed intake. In late gestation (140-days of age and at birth) the sire influence and maternal feed intake appeared of greatest importance. Ambient temperature seems unlikely to have exerted any direct influence, the recorded temperatures being considerably less than the critical one (44.5°C for 7 hours each day over 3-4 months of late pregnancy) for Merino ewes reported by Yeates (1956). It is, however, possible that the additive effect of high ambient temperature and poor nutrition (Yeates 1958) may have operated. This question cannot be resolved satisfactorily from these data.

5. EXPERIMENT B

THE INFLUENCE OF EWE BODY WEIGHT AT MATING, AND OF SEVERE MATERNAL UNDERNUTRITION DURING EARLY PREGNANCY, ON FOETAL GROWTH AND DEVELOPMENT

A. INTRODUCTION

The body weight of the ewe at mating is important in the formulation of a grazing management programme for it dictates the policy to be adopted between weaning and mating. It impinges also upon the level of feeding during pregnancy, especially the degree of feed restriction, and concomitant body weight loss, which may be enforced in early pregnancy.

On the average, ewes of relatively heavy body weight at mating show a superior reproductive performance, in terms of ovulation rate and lambing percentage, to lighter ewes (Wallace 1961; Coop 1962b). Coop (1964) suggests a twofold contribution to this positive association; one of heavy body weight (fatness) per se (a "static effect"), and the other of increasing body weight at the time of mating (a "dynamic effect"), the latter being related to the practice of "flushing" (reviewed by Moule 1962c). Marked reduction in the number of lambs born to ewes suffering severe nutritional restriction in early pregnancy

(Bennett, Axelson & Chapman 1964) appears greater in maiden than older ewes; this age effect may, in fact, be related to differences in body weight at mating, in much the same way as barrenness and twinning rate (Coop 1962b, 1964).

Experiment A provided evidence that maternal undernutrition in early pregnancy retarded placental development and foetal growth; this effect was somewhat greater in ewes which were lighter in body weight at mating than in heavier ewes.

However, Experiment A did not distinguish the relative roles of skeletal frame size and of body tissue reserves as determinants of body weight. Secondly, foetuses retarded in growth by poor maternal nutrition in early pregnancy were given no opportunity to display powers of compensatory growth and development in late pregnancy under an abundant feeding regime generally advocated for ewes at this time (Wallace 1948).

Experiment B was therefore undertaken to provide information about:-

(a) the effects of body weight, condition (fatness) and skeletal size of the ewe at the time of mating, and of maternal undernutrition in early pregnancy, on foetal growth and development;

(b) the ability of the foetus for compensatory growth and development in late pregnancy following a period of poor maternal feeding;

and (c) the response of the ewe to realimentation after a period of undernutrition.

The experiment was conducted under similar field conditions to those operating in Experiment A.

B. MATERIALS AND METHODS

I. Experimental Design

A 2 x 2 factorial design was employed. The first factor compared the performance of ewes differing markedly in body weight at the time of mating, i.e. between ewes which were relatively heavy (He) or light (Li). The second factor compared the effects of two relative levels of maternal nutrition during the first 90-days of pregnancy - High Plane (HP) and Low Plane (LP).

Ewes were randomised into two groups after weaning their lambs in September 1963. Animals of one group were offered feed *ad libitum* until mating (He), while the feed intake of animals in the other group (Li) was severely restricted causing substantial body weight loss. After mating, ewes of each group were allocated alternately to the two nutritional regimes so that the gross body weight of each animal either increased (HP) or decreased (LP) by 15 *per cent*. over 90-days of pregnancy. From 91- to 140-days of pregnancy all sheep were offered feed *ad libitum*, permitting realimentation of previously restricted sheep.

Thus, after mating, four groups of ewes were studied : sheep which were heavy at mating and subsequently well-fed (He/HP) or poorly-fed (He/LP) for the first 90-days of pregnancy; and ewes which were relatively light at mating and subsequently well-fed (Li/HP) or poorly-fed (Li/LP) in early pregnancy.

Six randomly selected He ewes and 6 Li ewes were killed at joining time. Six ewes from each of the four groups were slaughtered after 90-days of pregnancy, and 3 from each of the four groups after 140-days of pregnancy.

Remaining ewes continued on to lambing.

II. Experimental Animals

(a) Ewes

Table 5:1 summarises the classifications of the ewes.

Sixty-six 3-year-old South Australian Merino ewes were selected for the experiment from 82 animals available after weaning their lambs in September 1963. Each selected ewe had successfully reared a single lamb in the 1963 season.

(b) Ram

All ewes were mated to the same South Australian Merino ram; this was the larger (Ram L) of the two sires used in Experiment A.

III. Management

(a) General

The animals were held under similar field conditions to those described in Experiment A.

All ewes were drenched with 1 million I.U. Vitamin A and 250,000

I.U. Vitamin D_3 in October 1963, and again in February 1964.

Ewes were also drenched with thiabendazole in October, 1963 and in February, 1964.

(b) Mating

The system of mating and the determination of the first day of pregnancy followed the procedures described for Experiment A.

(c) Feeding

Ewes were fed twice daily in individual stalls located adjacent to the area - see Fig. 4:1. Feeding operations, illustrated in Plates 5:1 and 5:2, were similar to those used in Experiment A. The more enclosed individual feeding bins than those used initially for Experiment A eliminated the opportunity for ill-fed ewes to steal food from neighbouring sheep.

The composition of the pelleted diet used throughout the experiment is recorded in Table 5:2. Apparent digestibility coefficients were derived from a digestibility trial with 3 two-year-old Merino wethers as described for Experiment A.

Ewes were weighed twice weekly and the feed offered quantitatively adjusted after each weighing in order to achieve the desired curve of body weight gain or loss. After 90-days of pregnancy under controlled feeding, all ewes were offered the pelleted diet *ad libitum.*

Drinking water was available at all times.

TABLE 5:1. SUMMARY OF CLASSIFICATION OF EWES

Classification	Number of ewes						Total	Remarks
	Group							
	He/HP	He/LP	Total	Li/HP	Li/LP	Total		
Weaning	-	-	-	-	-	-	66	
Served by teaser ram	-	-	32	-	-	32	64	
No display of oestrus	-	-	-	-	-	2	2	
Mated to entire ram:								
No. of services required for conception:								
1.	11	9	20	8	6	14	34	
2.	5	6	11	6	6	12	23	
3.	-	1	1	2	4	6	7	
Total	16	16	32	16	16	32	64	
Absence of oestrus after mating to entire ram, followed by later return to teaser ram	-	-	-	-	1	1	1	1 Li/LP ewe returned after 67 days
Slaughtered:								
Mating	-	-	6	-	-	6	12	
After 90-days of pregnancy								
Ewes with a single foetus	6	6	12	6	6	12	24	
Ewes with twin foetuses	2	1	3	-	-		3	He/LP ewe with foetus resorbing
After 140-days of pregnancy								
Ewes with a single foetus	3	3	6	3	3	6	12	
Ewes with twin foetuses	-	1	1	-	-	-	1	
Premature labour	-	-	-	-	1	1	1	134 days of pregnancy : twin foetuses
	-	1	1	-	-	-	1	107 days of pregnancy : bloat
Lambing	1	2	3	3	3	6	9	All single lambs

Plate 5:1.- The design and operation of the pens used for individual feeding in the 1963-64 experimental period. Ewes waiting for rations. The numbered feed containers can be seen. Body weight scales are in the central background.

Plate 5:2.- Ewes receiving rations.

TABLE 5:2. SUMMARY OF THE PRINCIPAL DIETARY CONSTITUENTS

Constituent	Proportion(2)
Pelleted feed (1)	
Lucerne %	45
Barley %	50
Common salt %	2
Sterilised bone meal %	3
Dry matter %	95.2 (78)
Composition (% dry matter)	
Ash	6.5
Organic matter	93.5
Ether extractives	4.6 (83)
Crude fibre	14.2 (78)
Crude protein (N x 6.25)	15.0 (84)
Nitrogen-free extractives	57.4 (77)
Ca	1.80
P	0.63
Ca/P ratio	2.86
Na	0.62
Cl	1.31
Digestible organic matter (%)	72
Digestible energy (Cals/g)(3)	3.446

Note: (1) Pellets approximately 1 cm long and 0.4 cm diameter.

(2) Apparent digestibility coefficients, derived from feeding trials with three wethers, are shown in parentheses.

(3) Derived from regression equation of Moir (1961) :

$$y = 0.0462\, x - 0.158$$

where,

y = Digestible energy in Cals/g

x = Dry matter digestibility %

IV. Wool Production of Ewes

Techniques used in Experiment A were adopted for the study of wool growth by the ewes. Harvests were taken from the tattooed midside patch after 90- and 140-days of pregnancy and each sheep was shorn immediately before slaughter.

V. Body Condition of Ewes

A single subjective condition (fatness) score was applied to each ewe at weaning, mating and on all subsequent weighing occasions, using the same observer as in Experiment A.

VI. Body Measurements of Ewes

Linear body (skeletal) measurements of ewes recorded at mating and immediately prior to slaughter were: body length (withers to pins), withers height, chest depth, pelvis width (width at hips) and length (hips to pins), width at ribs, and length of the upper and lower fore-leg, as defined by Turner *et al.* (1953).

VII. Slaughter Procedure and Dissection of the Gravid Uterus

Similar techniques and definitions to those described for Experiment A were used.

VIII. Radiography of Foetuses

Each foetal body was X-rayed in a lateral recumbent position, while the fore-feet were photographed in dorsal-volar view.

At 90-days of age, for both the foetal body and fore-feet, "Kodirex" envelope-pack film was used with an instrument setting of 50 Kv, 20 mA and 3 secs. and a tube-film distance of 80 cm.

At 140-days of age, for the foetal body, a "Kontak" cassette (37.5 x 30.0 cm.), with Hi-speed screens, carrying Du Pont (type 508) film, and settings of 55 Kv, 40 mA and 0.75 secs. with a tube-film distance of 80 cm. was employed. Two pictures of each foetus were recorded, the dividing line lying in the lumbar region. Fore-feet at 140-days of age were X-rayed with the same equipment and settings as those used at 90-days of age.

IX. Foetal Measurements from X-ray Negatives

Crown-rump length was measured from each X-ray negative using a map measurer. Lengths of the metacarpus, radius, ulna, humerus, scapula, metatarsus, tibia-fibula and femur were measured with micrometer calipers.

X. Biometrical Methods

Statistical analyses of data relating to the ewes and foetuses followed the procedures described in detail for Experiment A.

Standard analyses of variance and covariance appropriate to a 2 x 2 factorial design, and of regression analysis, were used (Snedecor 1956). Variation due to the initial weight of the ewes at mating time, to maternal nutrition, and to their interaction (each with a single degree of freedom) was isolated. Mean differences of main treatment effects (initial weight of ewe, maternal nutrition) have been presented.

C. RESULTS

I. General Progress of the Experiment

(a) Climatic Conditions

Meteorological records covering the period of field activity are illustrated in Fig. 5:1.

Ambient temperatures increased from a monthly average of 58.0°F (14.4°C) in September 1963 to 70.1°F (21.2°C) in December 1963 and 69.9°F (21.1°C) in January 1964, and then declined to 58.3°F (14.6°C) in May 1964. The maximum daily air temperature exceeded 90°F (32.2°C) on 3 days in November and 7 days in December 1963, and on 6, 6 and 2 days in January, February and March 1964, respectively. There were 3 days in January, and 1 day in March 1964, when the maximum daily air temperature exceeded 100°F (37.8°C).

Rainfall did not exceed 0.5 in. per month between early November 1963, and early April 1964, when field activities of the experiment were terminating. A total of 4.62 in. of rain fell in April 1964 (including 2.99 in. during the third week), and 2.10 in. in May 1964.

Pasture re-growth in the area was negligible, the experimental animals subsisting on their pelleted rations.

(b) General Performance of Experimental Animals

Table 5:1 shows that 64 ewes out of the 66 available at weaning were mated to the fertile ram. Two ewes made no display of oestrus and one Li/LP ewe returned to the ram after a period covering 4 oestrous cycles.

One Li/LP ewe entered upon labour after 134 days of pregnancy (after 43 days of ad libitum feeding). She was slaughtered after 24 hrs. and found to be carrying twin foetuses. One member of the pair was lodged in the cervix, but of otherwise normal presentation for parturition; the other member lay in the uterine horn with no obvious evidence of abnormality.

One He/LP ewe carrying a single foetus died from bloat after 107 days of pregnancy, i.e. after 17 days of ad libitum feeding. This was the first animal to be re-fed after undernutrition in early pregnancy. Rations were subsequently offered to animals in this category on a gradually increasing basis, ad libitum feeding being achieved approximately 7 days after the change of routine.

Three He ewes killed after 90-days of pregnancy, and 1 He ewe killed after 140-days, carried twin foetuses. One member of the pair of twin foetuses taken from the He/LP ewe after 90-days showed signs of resorption, although this foetus weighed (478 g.) more than its mate (452 g.).

Single lambs were born to a total of 9 ewes, 6 of them to Li ewes. All the lambs born were reared successfully by their dams.

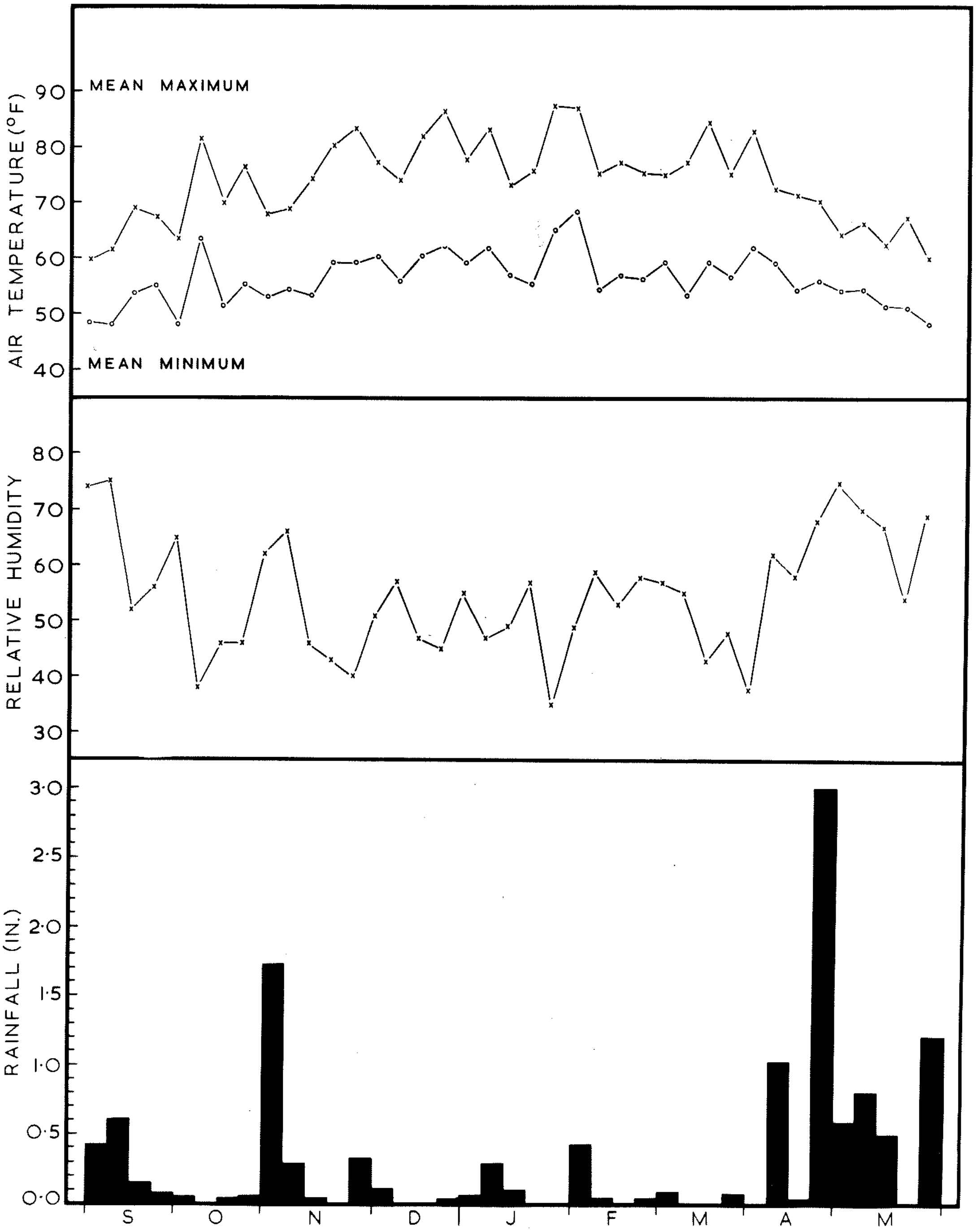
II. Performance of Ewes

(a) Body Weights and Condition Scores

Mean gross body weights of all ewes during the 7

Fig. 5:1.- Climatological records for the Waite Agricultural Research Institute during the 1963-64 experimental period.

METEOROLOGICAL RECORDS FOR THE 1963-64 EXPERIMENTAL PERIOD



weeks before mating are portrayed in Fig 5:2, while Fig. 5:3 displays comparable information for those ewes slaughtered during pregnancy each carrying a single foetus. Mean body condition scores are recorded in Table 5:3.

Seven weeks before mating the mean weight of all ewes was 44.2 kg. ± S.D. 3.2. Ewes ill-fed before mating (Li) lost more body weight, on average, than well-fed ewes (He) gained (Fig. 5:2). At mating, the mean gross body weight of all He ewes was 48.6 kg. ± S.D. 3.9, and of all Li ewes was 38.1 kg. ± S.D. 4.1.

Associated with these significant changes in gross body weight were alterations in body fatness, as judged by the condition scores (Table 5:3). He ewes improved in condition immediately before mating, achieving considerable fatness (mean score 8.2). Li ewes were depleted in tissue reserves so that they were in lean condition (mean score 4.5) by mating time.

Views of representative He and Li ewes slaughtered at mating time are shown in Plate 5:3, while carcasses of representative animals are illustrated in Plate 5:4.

Fig. 5:3 shows that the recorded gross body weights of ewes during pregnancy approximated the desired weights. Light ewes well-fed in early pregnancy (Li/HP) tended to gain more weight than desired, and better accuracy in the control of LP animals was achieved. Body weights recorded after 90-days of pregnancy, expressed as percentages of the appropriate weights recorded at mating (see Fig. 5:3) indicate

Fig. 5:2.- Mean gross body weights of all experimental ewes during the seven weeks before mating.

MEAN LIVE WEIGHTS (kg) OF EWES PRIOR TO MATING

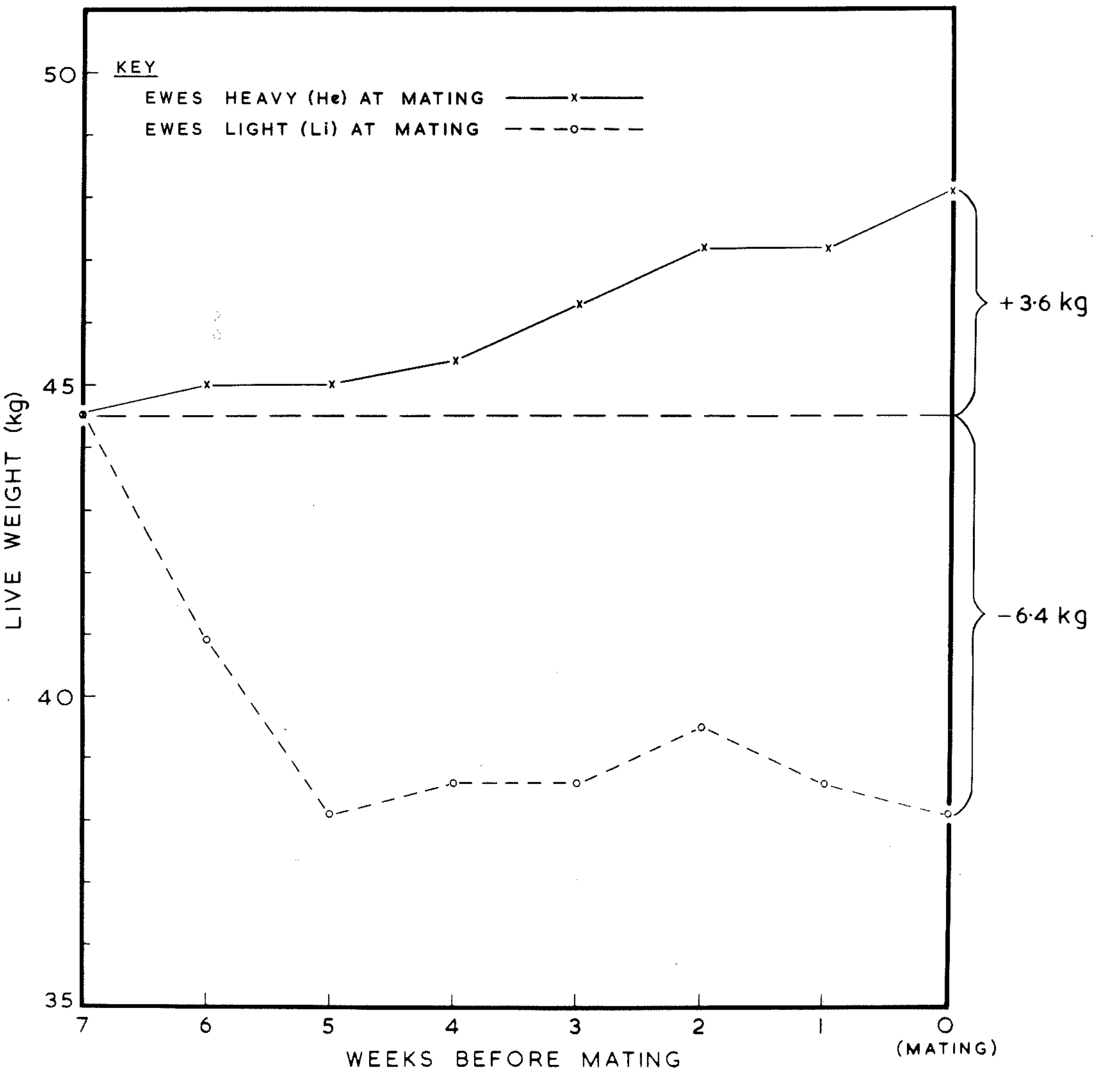


Fig. 5:3.- Mean gross body weights during pregnancy of ewes which were slaughtered and carried a single foetus. The desired weight gain or loss over 90-days of pregnancy (± 15 *per cent*. of the weight recorded at mating) is shown by the solid lines; broken lines represent recorded mean body weights. From 90- to 140-days of pregnancy all ewes were offered feed *ad libitum*.

MEAN LIVE WEIGHTS (kg) OF EWES IN PREGNANCY

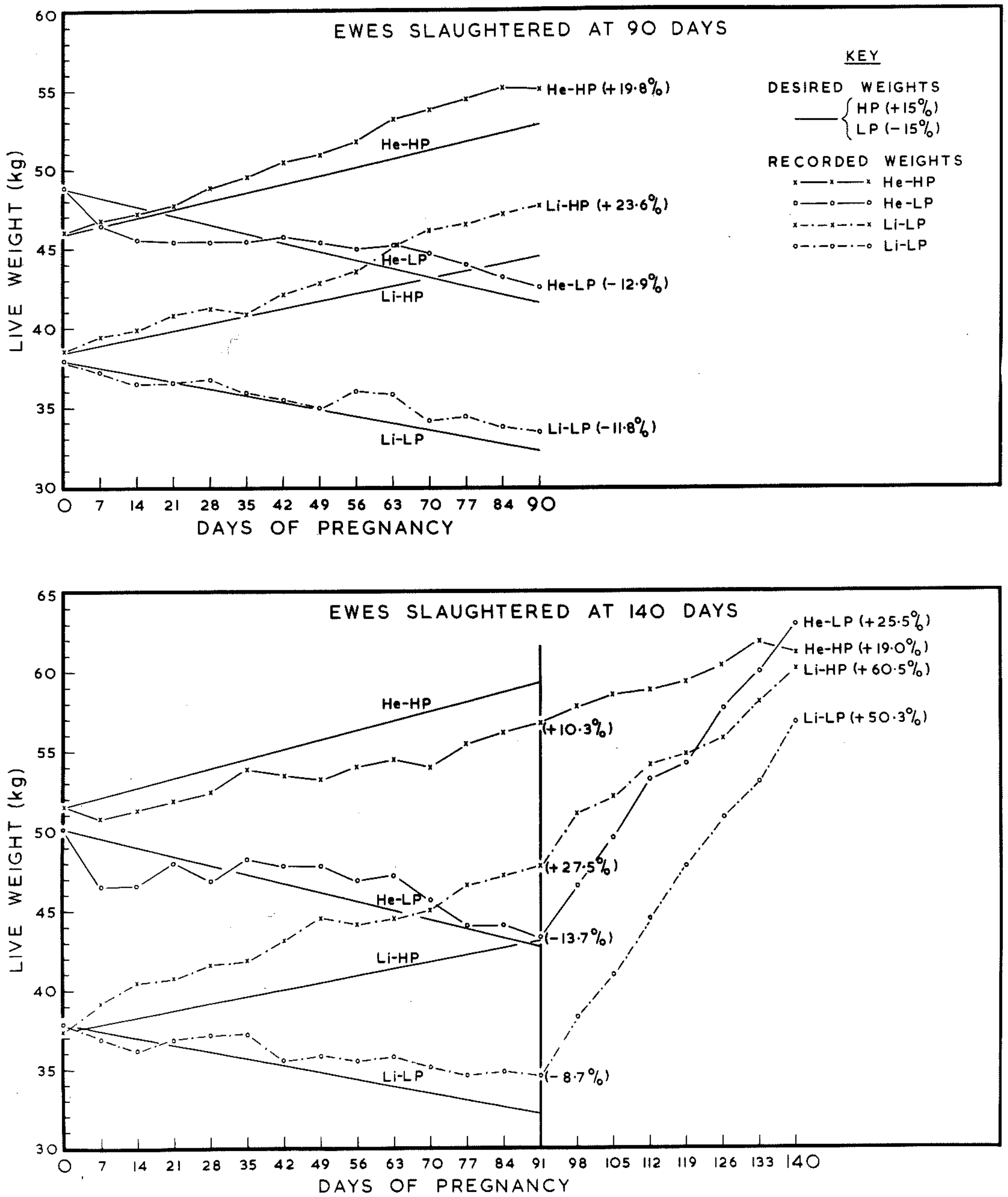


TABLE 5:3. MEAN BODY CONDITION SCORES OF EWES

Time of scoring	Group means				Overall mean	C.V. %	S.E.	Mean differences	
	He/HP	He/LP	Li/HP	Li/LP				Initial wght. (He-Li)	Plane of nutrition (HP-LP)
Weaning	-	-	-	-	7.3	11.3	0.26	-	-
Mating	8.2		4.5		6.4	10.0	0.24	3.7***	-
Ewes slaughtered after 90-days of pregnancy	8.0	6.0	6.7	3.5	6.0	9.7	0.24	1.9***	2.6***
Ewes slaughtered after 140-days of pregnancy:									
At 90-days	8.0	5.0	5.7	2.7	5.3	12.1	0.37	2.3***	3.1***
At 140-days	8.7	7.3	6.7	5.3	7.0	13.0	0.53	2.0**	1.4*

Note : Score 10 = very fat; Score 1 = emaciated.

that the desired weight gain or loss, of 15 per cent., was exceeded by Li/HP ewes and not attained by either He/LP or Li/LP ewes. The noticeable body weight reduction of He/LP ewes in the first week after mating reflects reduction of gastro-intestinal contents. Li/LP animals did not show this effect, probably because their meagre rations before mating had already stabilised gut contents at a low level.

Under the ad libitum feeding after 90-days of pregnancy the rate of body weight increase of previously underfed ewes was very marked, and substantially greater than that of ewes well-fed in early pregnancy. After 140-days of pregnancy He/LP ewes were heaviest and Li/LP ewes lightest. Although the latter gained most in late pregnancy they had a greater leeway to make up in a limited time.

The marked differences existing after 140-days of pregnancy in the percentages that the gross body weights represented of the respective weights at mating (Fig. 5:3) are much reduced when final weights are related to weights recorded at weaning. This draws attention to a synonomous terminology; for example, He/HP animals well-fed before and after mating could be described as HP/HP animals; while Li/LP ewes could be described by the notation of LP/LP. The experiment, in effect, was concerned with the duration, as well as the time and degree, of undernutrition imposed on breeding ewes.

Condition scores of the ewes (Table 5:3) show that after

Plate 5:3.- Side and rear views of representative heavy (He) and light (Li) ewes slaughtered at mating (10 x 10 cm. grid).

EWES SLAUGHTERED AT MATING

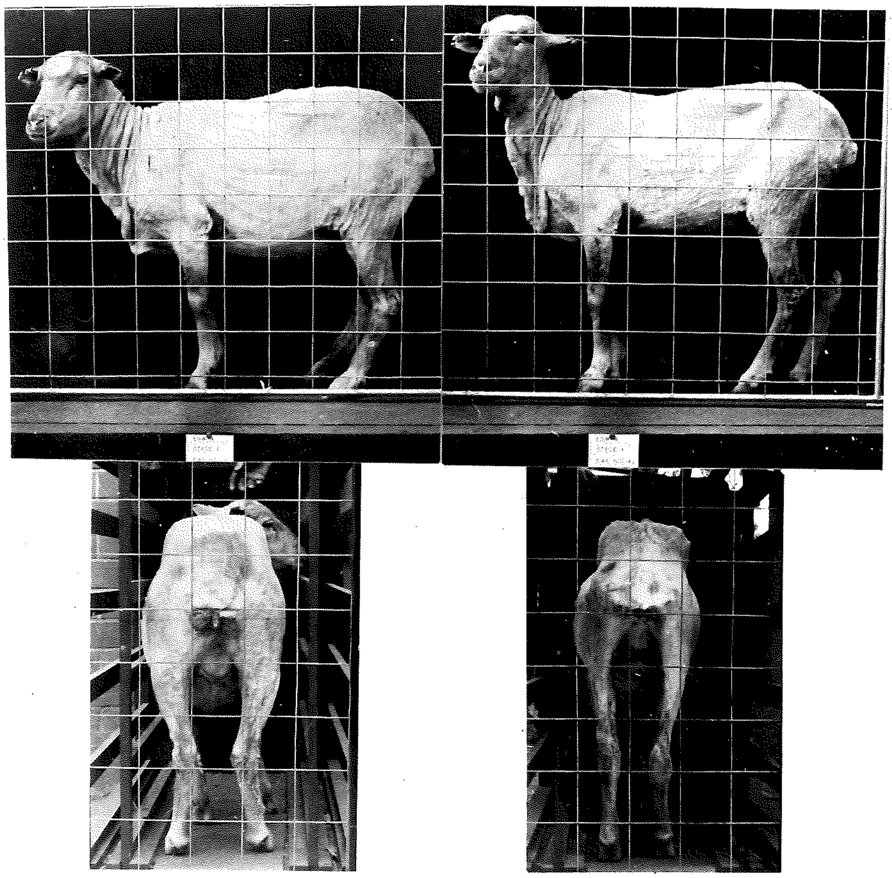
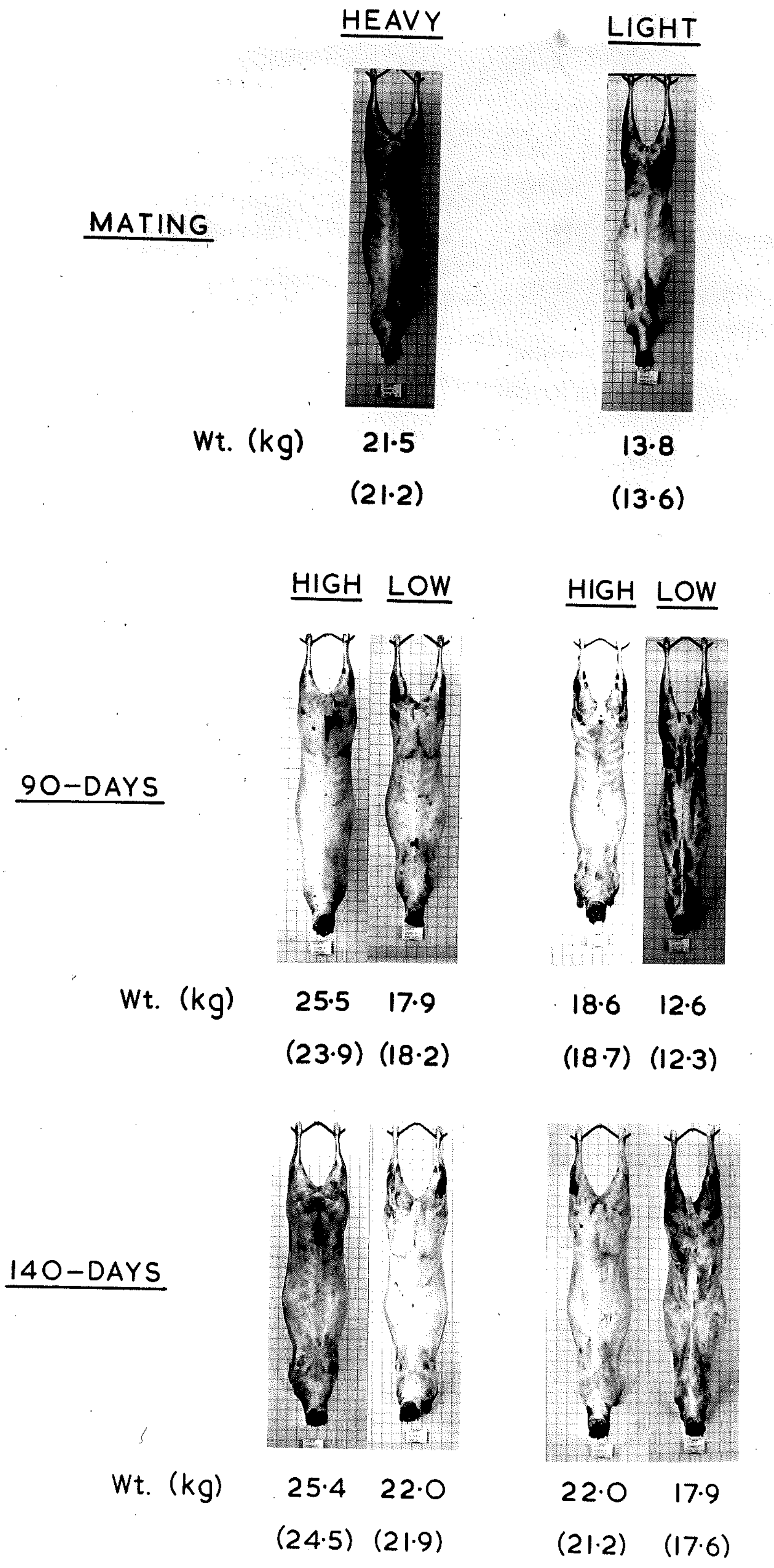


Plate 5:4.- Carcasses of representative ewes slaughtered at mating, and after 90- and 140-days of pregnancy. Individual carcass weights are shown and, in parentheses, the mean weight of each group (5 x 5 cm. grid).

EWE CARCASSES OF SLAUGHTER SAMPLES



90-days of pregnancy Li/LP ewes had become very lean with He/LP and Li/HP ewes of comparable fatness. At the end of ad libitum feeding (140-days) significant differences existed in the condition of ewes, Li/LP animals recording the lowest mean score.

(b) Body Measurements

Mean body measurements of ewes recorded at mating, and after 90- and 140-days of pregnancy are given in Table 5:4; mean differences of treatment effects are provided in Table 5:5. Coefficients of variation associated with the measurements are comparable in magnitude with those given by Turner *et al*. (1953).

At mating, and after 90-days of pregnancy, He ewes were wider across the ribs than Li ewes, and HP ewes wider than LP ewes. This is interpreted as a greater depth of soft tissues overlying the ribs in heavier and better-fed animals. Differences in all other measurements did not attain significance, except for a greater length of the lower fore-leg in Li, as compared with He, ewes after 90-days of pregnancy.

Body weight differences between He and Li ewes at mating and subsequent stages, as well as differences due to nutrition during pregnancy (HP-LP), therefore reflected variation in soft body tissues rather than skeletal frame size.

(c) Food Intake

Mean weekly amounts of dry matter (D.M.) offered, rejected and consumed by the slaughtered ewes carrying a single foetus are shown in Fig. 5:4.

He/HP ewes were offered feed greatly in excess of appetite throughout the whole of pregnancy. The tendency for their intake to decline as pregnancy proceeded may be noted with interest.

Li/HP ewes slaughtered after 90-days were also fed, in effect, ad libitum. Those Li/HP ewes slaughtered after 140-days were somewhat restricted in their intake during early pregnancy, reflecting the attempt to keep them at the desired level of weight increase. Feed consumption of these animals increased steadily as pregnancy proceeded.

Feed offered to, and consumed by, ewes ill-fed in early pregnancy (He/LP and Li/LP) reached very low levels indeed after 90-days of pregnancy. During the last week (13) of feed restriction Li/LP ewes consumed, on the average, 95 g./D.M./day. The tendency for feed consumption to rise and fall again in early pregnancy is associated with the stabilisation of gut-fill and the necessity to meet the desired weight curves.

In the last 7 weeks of pregnancy the amount of feed offered to ewes previously underfed in early pregnancy was in excess of their appetite. The feed consumption of Li/LP ewes, in particular, attained very high levels in late pregnancy, much exceeding the intake of He/HP and Li/LP ewes.

Trends of feed intake during pregnancy are more clearly seen

TABLE 5:4. MEAN BODY MEASUREMENTS (cm) OF EWES AT MATING, AND AFTER 90- AND 140-DAYS OF PREGNANCY

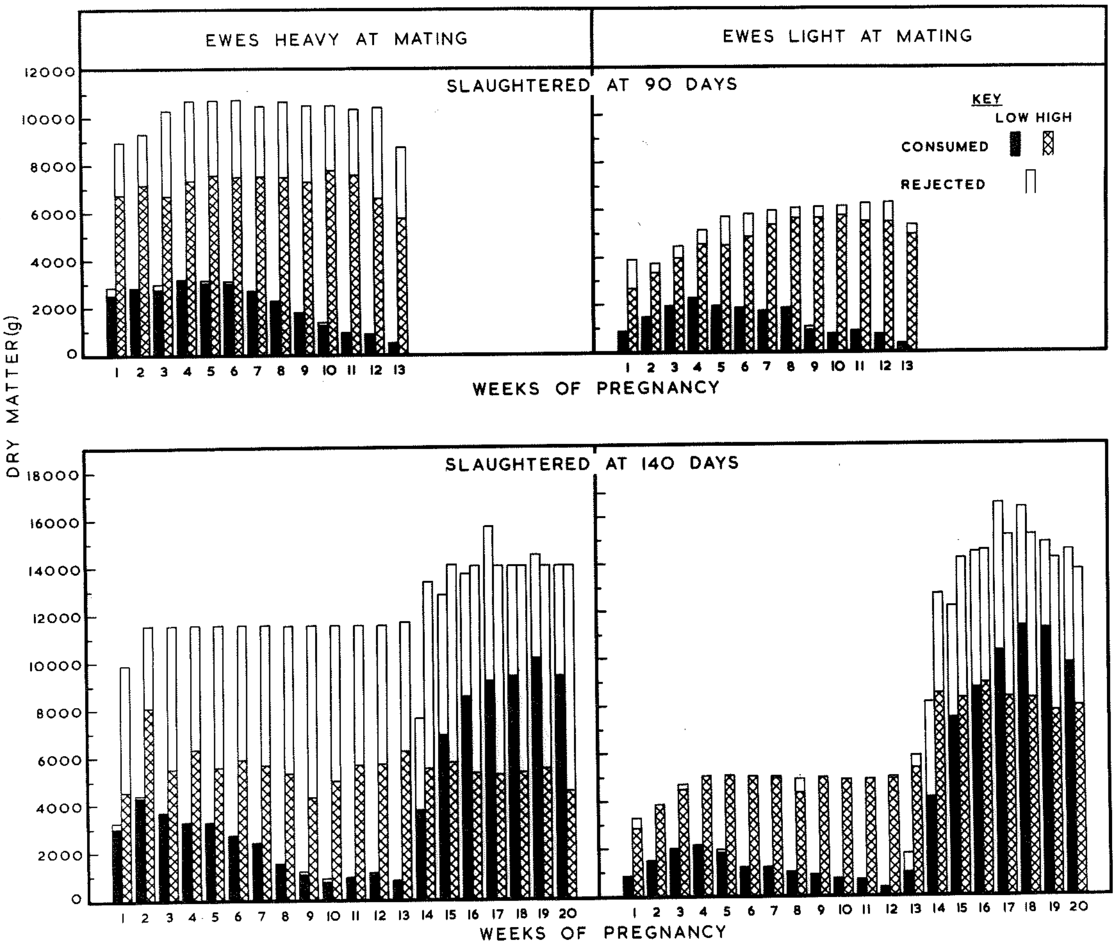
Measurement	At mating					After 90-days of pregnancy							After 140-days of pregnancy						
	Group means		Overall mean	C.V. %	S.E.	Group means				Overall mean	C.V. %	S.E.	Group means				Overall mean	C.V. %	S.E.
	He	Li				He/HP	He/LP	Li/HP	Li/LP				He/HP	He/LP	Li/HP	Li/LP			
Body length	71.1	70.8	71.0	4.3	0.62	73.8	71.0	71.5	70.1	71.6	3.8	1.12	72.3	72.5	72.2	72.0	72.2	4.2	1.74
Withers height	64.6	65.4	65.0	4.0	0.52	64.1	62.7	61.9	66.2	63.7	4.5	1.18	62.6	64.0	64.2	64.2	63.8	3.5	1.31
Chest depth	31.6	31.6	31.6	3.1	0.20	30.9	30.9	31.7	30.9	31.1	4.8	0.61	31.3	31.0	31.5	31 5	31.3	2.4	0.44
Pelvis																			
width	18.3	18.6	18.5	4.0	0.15	18.8	18.8	19.1	19.2	19.0	4.8	0.37	18.5	19 1	19.0	19.2	19.0	4.6	0.51
length	22.1	21.9	22.0	3.6	0.16	22.2	21.5	22.0	22.2	22.0	2.8	0.25	22.3	22.8	22.3	22.7	22.5	4.5	0.58
width x length	404.8	406.9	405.9	6.4	5.32	417.6	404.2	419.9	425.2	416.7	5.1	10.27	412.2	437.1	424.6	434.3	427.1	7.2	17.72
Width at ribs	24.0	22.0	23.0	8.1	0.38	26.5	23.3	25.4	21.3	24.1	4.7	0.46	28.3	28.7	28.5	28.7	28.5	6.3	1.04
Upper fore-leg length	22.2	22.1	22.2	4.2	0.19	22.3	22.3	21.4	22.5	22.1	3.1	0.28	22.2	22.7	22.5	22.7	22.5	3.1	0.41
Lower fore-leg length	15 8	16.1	16.0	4.0	0.13	16.0	15.8	16.3	16.5	16.1	2.5	0.16	16.2	16.7	16.5	16.7	16 5	4.8	0.46
Body weight: chest depth ratio	1.53	1.18	1.36	5.8	0.16	1.80	1.38	1.51	1.09	1.44	5.9	0.93	1.96	2 01	1.91	1 80	1.92	8.3	0.09
Number of observations	24	24	48	-	-	6	6	6	6	24	-	-	3	3	3	3	12	-	-

TABLE 5:5. BODY MEASUREMENTS OF EWES: MEAN DIFFERENCES (cm) OF TREATMENT EFFECTS AT MATING, AND AFTER 90- AND 140-DAYS OF PREGNANCY

Measurement	At Mating	After 90-days of pregnancy		After 140-days of pregnancy	
	Initial weight (He-Li)	Initial weight (He-Li)	Plane of nutrition (HP-LP)	Initial weight (He-Li)	Plane of nutrition (HP-LP)
Body length	0.3	1.6	2.1	0.3	0
Wither height	-0.8	-0.7	-1.5	-0.9	-0.8
Chest depth	0	-0.4	0.4	-0.4	0.2
Pelvis					
width	-0.3	-0.3	0	-0.3	-0.4
length	0.2	-0.3	0.3	0.1	-0.5
width x length	2.1	-17.0	4.6	-4.8	-17.3
Width at ribs	2.0 ***	1.6 **	3.7 ***	-0.1	-0.3
Upper fore-leg length	0.1	0.4	-0.6	-0.2	-0.4
Lower fore-leg length	-0.3	-0.5	0	-0.2	-0.4
Body weight : chest depth ratio	0.35 ***	2.9 ***	4.2 ***	1.3	0.3

Fig. 5:4.- Mean weekly amounts of dry matter offered, rejected and consumed by the ewes during pregnancy.

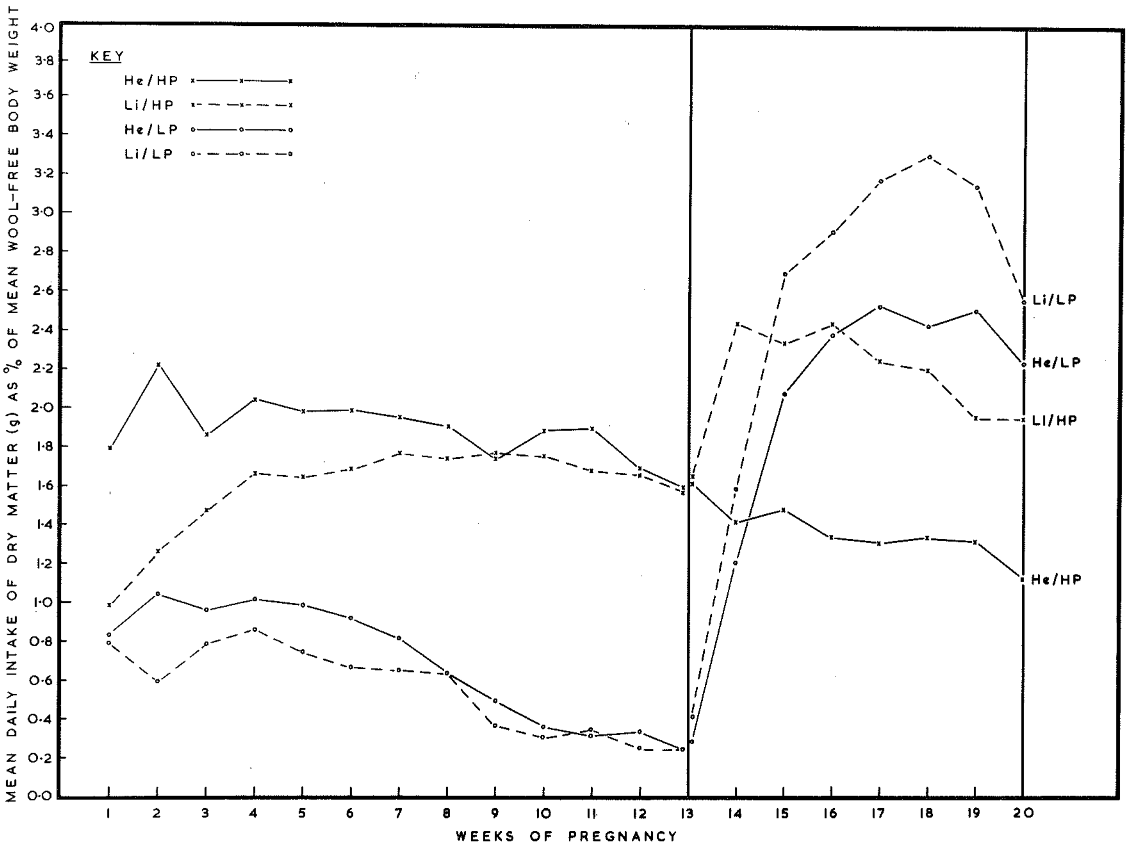
MEAN FOOD CONSUMPTION



in Fig. 5:5 where mean daily intakes of D.M. are expressed as percentages of mean wool-free body weights of the ewes. Curves for the first 90-days of pregnancy represent the mean values of 9 animals/group, but 3 ewes/group in the last 7 weeks. The progressive decline of intake of the relatively fat He/HP ewes as pregnancy proceeded is noteworthy. Feed consumption of He/HP and Li/HP ewes, and of He/LP and Li/LP ewes, attained similar proportions of body weight after 90-days of pregnancy. During the last 7 weeks of pregnancy, under _ad libitum_ feeding, the feed consumption of all ewes, except He/HP animals, increased; the increase being greatest for animals which had previously been restricted the most. This compensatory intake reached a peak in week 14 of pregnancy for Li/HP ewes, in week 17 for He/LP ewes and in week 18 for Li/LP ewes; subsequently declining in each instance to week 20 of pregnancy.

Mean daily intake of digestible organic matter (D.O.M.) is recorded for the slaughtered ewes carrying a single foetus in Table 5:6. Intake of D.O.M. in early pregnancy of He/LP ewes slaughtered after 90-days approximated less than one-third of the intake of He/HP ewes and less than one-half in the case of ewes killed after 140-days. Intake of Li/LP ewes in early pregnancy as a percentage of the intake of Li/HP ewes represented 28 _per cent_. for ewes killed after 90-days, and 25 _per cent_. for ewes killed after 140-days. In the last 7 weeks of pregnancy the D.O.M. intake of ewes previously ill-fed (He/LP and Li/LP) was significantly greater than previously well-fed ewes (He/HP and Li/HP). Li/LP ewes consumed the most D.O.M./day in late preg-

Fig. 5:5.- Mean daily intake of dry matter during pregnancy as a percentage of the mean wool-free body weight of the ewes.


KEY
He/HP
Li/HP
He/LP
Li/LP
MEAN DAILY INTAKE OF DRY MATTER (g) AS % OF MEAN WOOL-FREE BODY WEIGHT
4·0
3·8
3·6
3·4
3·2
3·0
2·8
2·6
2·4
2·2
2·0
1·8
1·6
1·4
1·2
1·0
0·8
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0·4
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1
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10
11
12
13
14
15
16
17
18
19
20
WEEKS OF PREGNANCY
Li/LP
He/LP
Li/HP
He/HP

TABLE 5:6. MEAN DAILY INTAKE (g) OF DIGESTIBLE ORGANIC MATTER

Period	Group means				Overall mean	C.V. %	S.E.	Mean differences	
	He/HP	He/LP	Li/HP	Li/LP				Initial weight (He - Li)	Plane of nutrition (HP - LP)
Ewes slaughtered after 90-days									
0-90 days	744.3	222.0	496.8	139.7	400.7	9.9	16.2	164.9 ***	439.7 ***
Ewes slaughtered after 140-days									
0-90 days	589.3	231.0	483.7	121.7	356.4	25.9	53.2	107.5	360.2 ***
91-140 days	533.0	824.0	832.7	904.3	773.5	12.8	56.9	-190.0 *	-181.3 *
0-140 days	569.7	442.7	608.7	401.3	505.6	15.9	46.5	1.2	167.2 **

nancy. Over the whole of pregnancy there was no significant difference in D.O.M. intake/ day between He and Li ewes, but HP ewes consumed significantly more feed than LP ewes.

(d) Wool Production and Efficiency of Wool Growth

(i) Production

Mean wool production data of slaughtered ewes are summarised in Table 5:7.

More greasy fleece wool of higher yield was produced by He than Li ewes and more by HP than LP ewes. Clean wool production was thus also greater in the initially heavier and the better-fed ewes. The ranking order of daily clean fleece production over 140-days of pregnancy was He/HP, He/LP, Li/HP and Li/LP. The production of the last group represented approximately half that of He/HP ewes. Less clean wool/day was produced by He/HP ewes in the last 7 weeks of pregnancy than in the first 13 weeks, with the converse for the other three groups of ewes.

(ii) Efficiency

Table 5:8 records estimates of the mean efficiency of wool growth. Efficiency of production in early pregnancy was greatest by ewes receiving the least feed. In late pregnancy the ranking order of the groups for efficiency reflected the reverse order of feed intake, with He/HP ewes producing wool most efficiently on least feed as compared with Li/LP ewes producing wool least efficiently

TABLE 5:7. MEAN WOOL PRODUCTION (g) OF EWES KILLED AFTER 90- AND 140-DAYS OF PREGNANCY

Character	Group means				Overall mean	C.V. %	S.E.	Mean differences	
	He/HP	He/LP	Li/HP	Li/LP				Initial weight (He-Li)	Plane of nutrition (HP-LP)
<u>Ewes killed after 90-days</u>									
Midside clean wool/10 cm^2/90 days	15.927	8.942	9.320	6.102	10.073	20.7	0.852	4.724***	5.102***
Greasy Fleece/90 days	2945	2288	2013	1652	2225	15.9	144.6	784***	509**
Yield %	64.4	54.0	54.0	56.2	57.2	14.6	3.4	4.1	4.1
Clean Fleece/day	21.0	13.7	11.8	10.3	14.2	17.1	0.99	6.3***	4.4***
<u>Ewes killed after 140-days</u>									
Midside clean wool/10 cm^2									
0-90 days	10.367	7.830	10.310	5.803	8.578	17.5	0.866	1.042	3.522***
91-140 days	4.758	5.136	6.258	3.982	5.034	22.4	0.650	-0.173	0.949
0-140 days	15.125	12.966	16.568	9.685	13.612	18.0	1.406	0.958	4.562*
Greasy fleece/140 days	3375	2857	2287	2250	2692	14.7	229.0	848**	278
Yield %	63.9	56.0	61.7	49.2	57.7	7.4	2.5	4.5	10.2**
Clean fleece/day									
0-90 days	16.6	10.9	9.8	7.4	11.2	23.0	1.48	5.2**	4.1*
91-140 days	13.4	12.6	10.6	9.2	11.4	16.8	1.11	3.1*	1.1
0-140 days	15.5	11.5	10.1	8.0	11.3	19.5	1.27	4.5**	3.1*

TABLE 5:8. MEAN EFFICIENCY OF WOOL GROWTH(1)

Period	Group means				Overall mean	C.V. %	S.E.	Mean differences	
	He/HP	He/LP	Li/HP	Li/LP				Initial weight (He - Li)	Plane of nutrition (HP - LP)
<u>Ewes slaughtered after 90-days</u>									
0-90 days	2.84	6.16	2.37	7.62	4.74	23.8	0.460	-0.50	-4.29 ***
<u>Ewes slaughtered after 140-days</u>									
0-90 days	3.08	4.90	2.02	6.58	4.14	47.8	1.144	-0.31	-3.19 *
91-140 days	2.55	1.53	1.34	1.01	1.61	22.9	0.213	0.87 **	0.68 *
0-140 days	2.87	2.62	1.69	2.01	2.30	31.0	0.411	0.90	-0.04

(1) Efficiency = $\frac{\text{Clean dry wool/g/day} \times 100}{\text{Intake D.O.M./g/day}}$

on the most feed intake. Differences in the efficiency of production over the whole of pregnancy were not significant.

Efficiency of wool growth is related to feed intake (on a per unit body weight basis) in Fig. 5:6. As feed intake increased so efficiency of wool growth fell but, in early pregnancy at least, at a decreasing rate at the higher levels of feed intake.

(e) Nutrient Requirements for Maintenance and Body Weight Gain of Ewes

Mean daily intake of D.O.M./g. has been related in multiple regression to mean wool-free conceptus-free body weight$^{0.75}$ (B.W.) in kg., and to mean wool-free conceptus-free weight gain/g./day (W.G.).

The relationship (based on 20 d.f.) for ewes slaughtered after 90-days of pregnancy is shown in equation (1):-

$$\begin{array}{llll} (1) & D.O.M. = -569.0 & + 38.3\ B.W. & + 2.001\ W.G. \\ & (s.e.) & (\pm 13.8) & (\pm 0.255) \\ & & * & *** \end{array}$$

Maintenance requirement of a ewe weighing 45.4 kg. was therefore estimated at 684 g. D.O.M./day, with 1 g. of weight gain (between 33.6 - 513 kg. body weight) requiring 2.00 g. D.O.M./day.

Equation (2) shows the relationship (based on 8 d.f.) for ewes slaughtered after 140-days of pregnancy:-

$$\begin{array}{lllll} (2) & \text{D.O.M.} & = -460.8 & + \; 36.6 \text{ B.W.} & + \; 1.379 \text{ W.G.} \\ & (\text{s.e.}) & & (\pm 10.1) & (\pm 0.592) \\ & & & ** & * \end{array}$$

Over 140-days of pregnancy, therefore, the maintenance requirement of a ewe weighing 45.4 kg. was estimated at 654 g. D.O.M./day with 1.38 g. D.O.M. being required for 1 g. body weight gain (ewes weighing 37.1 - 63.7 kg. body weight).

(f) Lamb Birth Weights and Length of Gestation

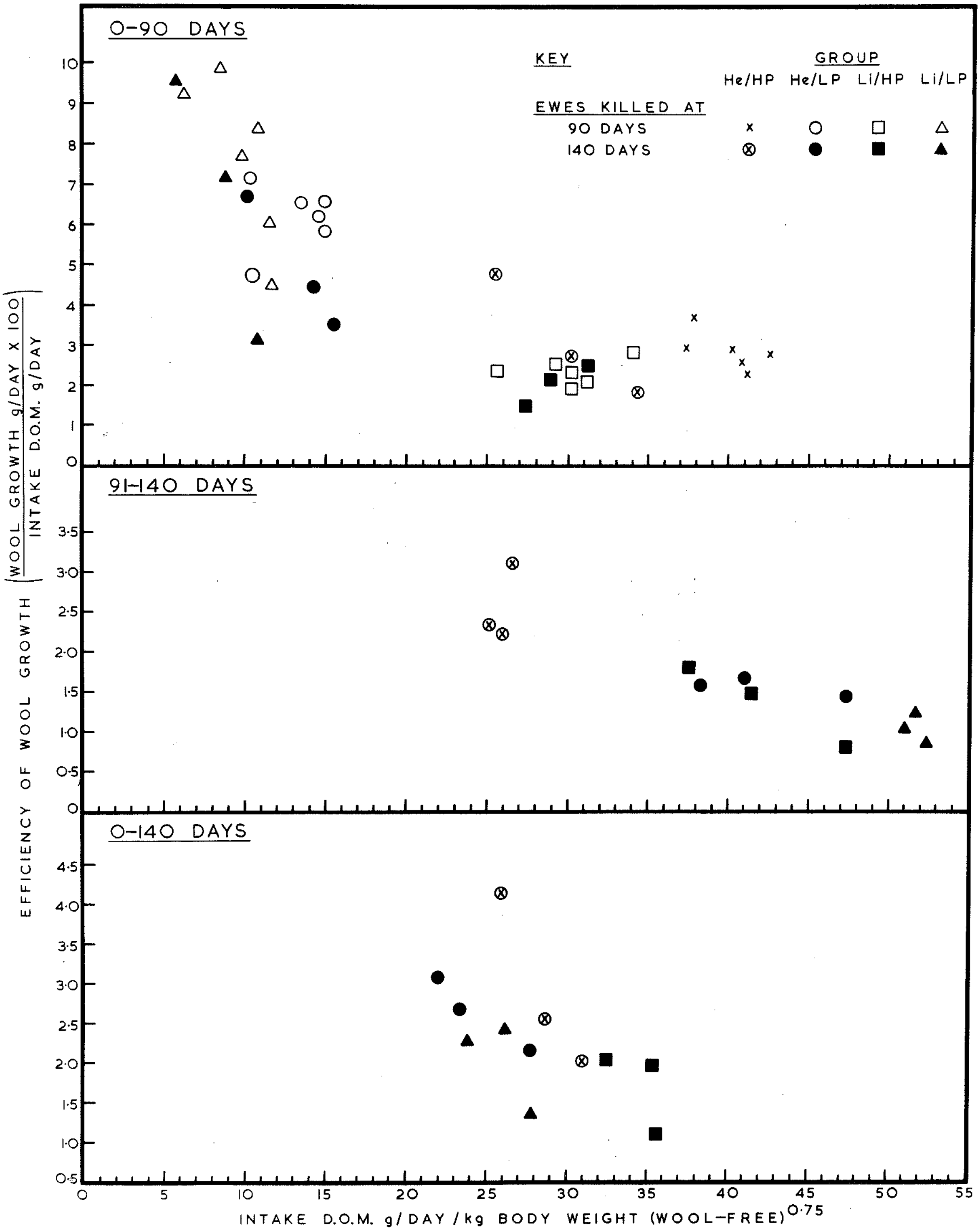
Table 5:9 records individual and mean birth weights of the 9 lambs. The mean length of gestation for these lambs was 149.8 days ± S.D. 2.1.

TABLE 5:9. INDIVIDUAL AND MEAN BIRTH WEIGHTS (g) OF SINGLE LAMBS

Sex	Group means				Overall mean
	He/HP	He/LP	Li/HP	Li/LP	
Male	4580		5125 5370	4980	
Mean	4580	-	5248	4980	5014
n	1	-	2	1	4
Female		4325 4480	5055	4475 4560	
Mean	-	4403	5055	4518	4579
n	-	2	1	2	5

Fig. 5:6.- Efficiency of wool growth related to feed intake (data relating to ewes slaughtered).

EFFICIENCY OF WOOL GROWTH RELATED TO FEED INTAKE



The number of lambs per subclass is too small to permit more than passing comment. Ram lambs, overall, were heavier than ewe lambs; the mean weight of the latter representing 91 per cent. of the former. Ignoring sexes, the mean weight of lambs born to He ewes (4462 g.) represented 91 per cent. of the mean birth weight of Li lambs (4928 g.); mean birth weight of HP lambs (5033 g.) was 110 per cent. of the mean weight of LP lambs (4564 g.)

III. Slaughter Records

(a) Body Weights and Weight Gains

(i) Body weights

Mean body weights of ewes killed at joining time and after 90- and 140-days of pregnancy are recorded in Table 5:10. The relation between empty body weight (or corrected empty body weight, where applicable) and wool-free final weight for all slaughtered ewes is shown in Fig. 5:7. A regression, pooled over all groups, could be fitted to this relationship and the equation used to estimate initial mean empty body weights recorded in Table 5:10.

At joining time, He ewes were significantly heavier than Li ewes in wool-free live weight, empty body weight and hot carcass weight.

After 90-days of pregnancy, significant differences existed between He and Li ewes, and between HP and LP ewes, in all the parameters.

After 140-days of pregnancy, He ewes were heavier than Li ewes,

TABLE 5:10. MEAN BODY WEIGHTS (kg.) OF EWES KILLED AT JOINING TIME, AND AFTER 90- AND 140-DAYS OF PREGNANCY

Weight	Group means				Overall mean	C.V. %	S.E.	Mean differences	
	He/HP	He/LP	Li/HP	Li/LP				Initial weight (He - Li)	Plane of nutrition (HP-LP)
<u>Ewes killed at joining time</u>									
Wool-free live wt. at slaughter	47.2		35.4		41.3	5.9	1.0	11.8***	-
Empty body wt.	36.8		25.5		31.2	7.1	0.9	11.3***	-
Hot carcass wt.	21.2		13.6		17.4	8.4	0.6	7.6***	
<u>Ewes killed after 90-days</u>									
Wool-free live wt. at mating	46.1	48.9	38.6	38.0	42.9	3.9	0.7	9.2***	-
Estimated initial empty body wt.(1)	33.8	35.4	29.3	29.0	-	-	-	-	-
Wool-free final live wt. at slaughter	52.1	40.3	45.7	31.8	42.5	4.3	0.8	7.5***	12.9***
Final empty body wt.	41.2	33.6	37.2	26.5	34.6	5.3	0.8	5.6***	9.2***
Final corrected empty body wt.	38.8	31.3	34.6	24.1	32.2	5.8	0.8	5.7***	9.0***
Hot carcass wt.	23.9	18.2	18.7	12.3	18.3	6.3	0.5	5.6***	6.1***
<u>Ewes killed after 140-days</u>									
Wool-free live wt. at mating	51.5	50.2	37.5	37.8	44.3	8.1	2.1	13.2***	-
Estimated initial empty body wt.	37.0	36.2	28.7	28.8	-	-	-	-	-
Wool-free live wt. after 90-days	56.8	43.3	47.8	34.5	45.6	13.9	3.7	8.9*	13.4*
Estimated corrected empty body wt. after 90-days	40.1	32.1	34.8	26.9	33.5	-	-	-	-
Wool-free final live wt. at slaughter	58.0	60.2	57.9	54.5	57.6	9.7	3.2	2.9	0.6
Final empty body wt.	49.1	48.9	47.3	43.6	47.2	9.0	2.4	3.6	2.0
Final corrected empty body wt	41.0	39.7	38.2	35.4	38.6	10.6	2.4	3.6	2.1
Hot carcass wt.	24.5	21.9	21.2	17.6	21.3	14.0	1.7	3.8	3.1

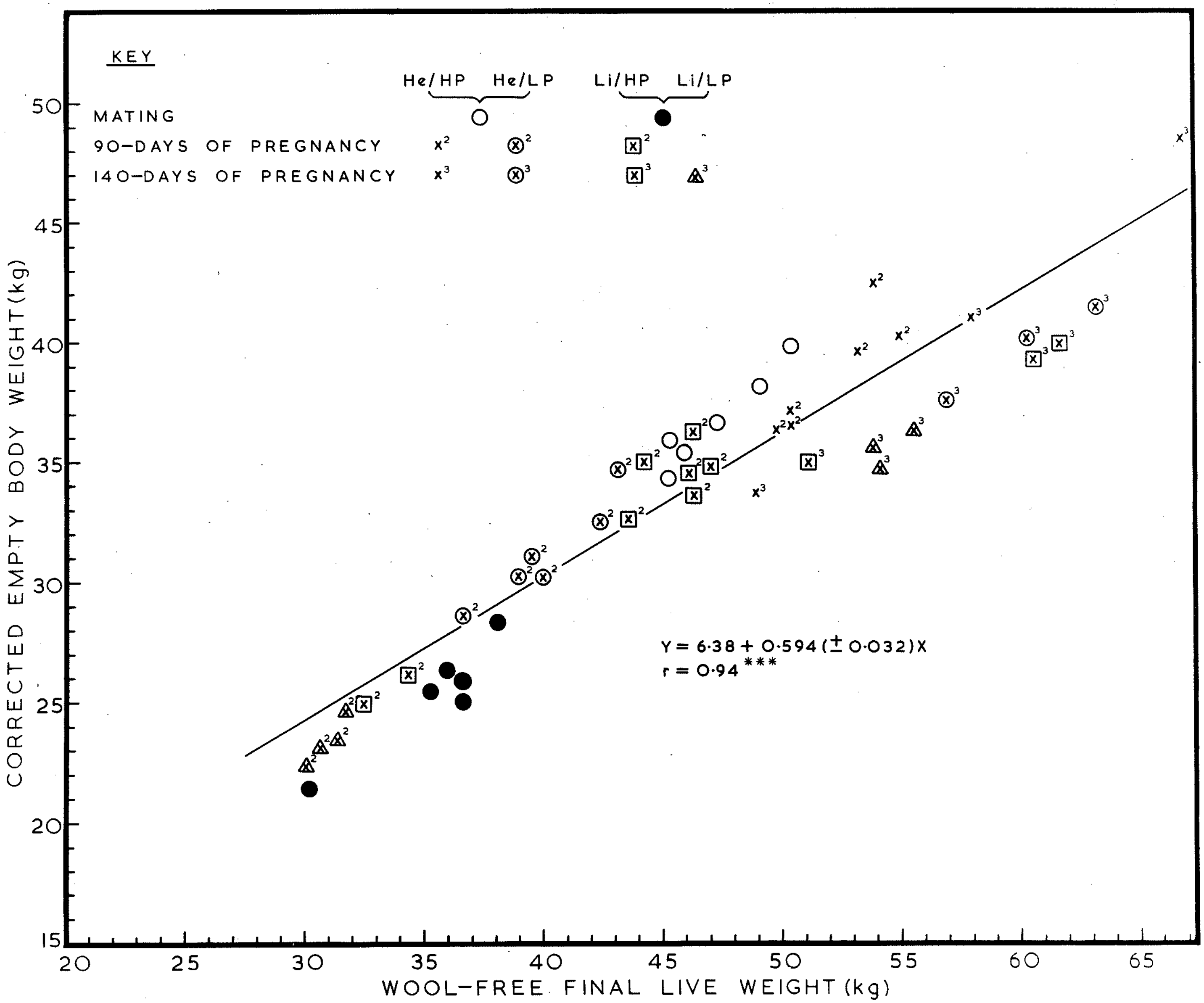
Note:

Empty body wt. = Wool-free live wt. <u>minus</u> gastro-intestinal contents

Corrected empty body wt. = Empty body wt. <u>minus</u> conceptus

(1) Estimated by regression - see Fig. 5:7 and text.

Fig. 5:7.- The relationship between corrected empty body weight (empty body weight *minus* conceptus) and wool-free final live weight in ewes killed at mating, and after 90- and 140-days of pregnancy.


KEY
He/HP
He/LP
Li/HP
Li/LP
MATING
90–DAYS OF PREGNANCY
140–DAYS OF PREGNANCY
Y = 6·38 + 0·594 (± 0·032) X
r = 0·94***
CORRECTED EMPTY BODY WEIGHT (kg)
WOOL–FREE FINAL LIVE WEIGHT (kg)
15
20
25
30
35
40
45
50
20
25
30
35
40
45
50
55
60
65

and HP ewes heavier than LP ewes, in all parameters; but in no instance was the weight difference significant. It may be noted that the mean corrected empty body weight of Li/LP ewes after 140-days was 5.6 kg. less than for He/HP ewes. Plate 5:4 illustrates the marked treatment effects on the ewe carcasses, and may be related to the condition scores given to the live animals (Table 5:3).

(ii) Gastro-intestinal contents

Contents of the gastro-intestinal tract averaged 10.4 kg. and 9.9 kg. in He and Li ewes respectively at joining time. These weights represented 22 per cent. and 28 per cent. of wool-free body weight for He and Li ewes respectively. Differences in gut-fill at this stage were not significant.

After 90-days of pregnancy, gut contents weighed 11.0, 6.7, 8.5 and 5.3 kg. for He/HP, He/LP, Li/HP and Li/LP ewes respectively; these weights, as percentages of wool-free body weights, were 21.0, 16.6, 18.6 and 16.2 respectively. The differences in absolute and proportionate values due to initial weight of ewe and to nutrition attained significance ($P < 0.01$).

After 140-days of pregnancy, differences in absolute and relative values of the gut contents were not significant, but tended to be heavier in Li and LP ewes. The contents weighed 8.9 kg. (15.3 per cent.) in He/HP ewes, and 11.3 kg. (18.8 per cent.), 10.7 kg. (18.2 per cent.) and 10.9 kg. (20.1 per cent.) in He/LP, Li/HP and

Li/LP ewes respectively. These differences may be related to trends of feed intake in late pregnancy (Figs. 5:4 and 5:5). The rapid weight gains during late pregnancy of previously undernourished animals (Fig. 5:3) reflected, in large part, increased intake. This was still apparent after 50-days of rehabilitation feeding in the case of those ewes most severely restricted in intake before mating and in early pregnancy (Li/LP).

(iii) Weight gains

Differences between the mean weights recorded in Table 5:10 have been assembled in Table 5:11, where the mean weight gains or losses are also expressed as percentages of appropriate mean initial weights.

The different estimates of weight gain and loss reveal the inadequacies of gross body weight as a parameter of performance under such radically different regimes.

After 90-days of pregnancy, the well-fed ewes (He/HP, Li/HP) had gained, on average, approximately 5 kg. in nett body weight compared with 9 kg. in gross body weight. The undernourished ewes (He/LP, Li/LP) lost approximately 4.5 kg. in nett weight over this period.

The estimated gains in nett body weight over 140-days of pregnancy show that Li/HP ewes gained most and He/LP ewes least. Those ewes initially of light body weight at mating (Li) gained more in nett weight than He ewes. It is interesting that He/HP ewes barely

TABLE 5:11. MEAN BODY WEIGHT GAINS (kg.) OF EWES KILLED AFTER 90- AND 140-DAYS OF PREGNANCY

Weights	Mean differences				Mean difference as percentage of initial value			
	He/HP	He/LP	Li/HP	Li/LP	He/HP	He/LP	Li/HP	Li/LP
<u>Ewes killed after 90-days</u>								
Final <u>minus</u> wool-free live wt. at mating	9.0	-6.3	9.1	-4.5	19.5	-12.9	23.6	-11.8
Wool-free final <u>minus</u> wool-free live wt. at mating	6.0	-8.6	7.1	-6.2	13.0	-17.6	18.4	-16.3
Final empty body <u>minus</u> initial empty body(1)	7.4	-1.8	7.9	-2.5	21.9	- 5.1	27.0	- 8.6
Final corrected empty body <u>minus</u> initial empty body(1)	5.0	-4.1	5.3	-4.9	14.8	-11.6	18.1	-16.9
<u>Ewes killed after 140-days</u>								
Final <u>minus</u> wool-free live wt. at mating	9.8	12.8	22.7	19.0	19.0	25.5	60.5	50.3
Wool-free final <u>minus</u> wool-free live wt. at mating	6.5	10.0	20.4	16.7	12.6	19.9	54.4	44.2
Final empty body <u>minus</u> initial empty body(1)	12.1	12.7	18.6	14.8	32.7	35.1	64.8	51.4
Final corrected empty body <u>minus</u> initial empty body(1)	4.0	3.5	9.5	6.6	10.8	9.7	33.1	22.9
Final corrected empty body <u>minus</u> corrected empty body after 90-days of pregnancy(1)	0.9	7.6	3.4	8.5	2.2	23.7	9.8	31.2

Note:

Empty body wt. = Wool-free final live wt. <u>minus</u> gastro-intestinal contents
Corrected empty body wt. = Empty body wt. <u>minus</u> conceptus

(1) Estimated by regression - see Fig. 5:7 and text.

maintained nett body weight over the last 50 days of pregnancy, whereas other ewes gained substantially.

IV. The Genital Tract

(a) Weights of Components

Mean weights of the genital tract, and components, after 90- and 140-days of pregnancy are recorded in Tables 5:12 and 5:13 respectively.

(i) After 90-days.- The complete genital tract was a little heavier in Li than He ewes, and heavier in HP than LP ewes, but in neither case did the difference attain significance.

The placenta was significantly heavier in HP than LP ewes, the difference originating more from the cotyledonary component than the membranes. The foetus and uterus were significantly reduced in weight by undernutrition in early pregnancy.

Uterine fluids, on the other hand, were heavier in Li than He ewes and, to a lesser extent, heavier in LP than HP ewes. In both comparisons the differences are reflected most in the weight of amniotic fluid.

The vulva/vagina/cervix complex, and the ovaries, were significantly heavier in Li than He ewes.

(ii) After 140-days.- The complete genital tract was lighter in He/HP than He/LP ewes, but heavier in Li/HP than Li/LP ewes. This interaction between the initial weight of the ewe and the plane of

TABLE 5:12. MEAN WEIGHTS (g) OF COMPONENTS OF THE GENITAL TRACT AFTER 90-DAYS OF GESTATION

Component	Group means				Overall mean	C.V. %	S.E.	Mean differences	
	He/HP	He/LP	Li/HP	Li/LP				Initial weight (He-Li)	Plane of nutrition (HP-LP)
Fluids									
Allantoic	190.5	158.2	209.5	193.3	187.9	19.2	14.7	- 27.1(*)	24.3
Amniotic	487.3	553.8	623.7	780.2	611.3	36.1	90.1	-181.4(*)	-111.5
Total	677.8	712.0	833.2	973.5	799.2	28.9	94.4	-208.5*	- 87.3
Placenta									
Cotyledons	690.7	591.2	644.8	480.2	601.7	16.9	41.5	78.5	132.1**
Membranes	145.8	128.3	155.0	114.5	135.9	28.7	15.9	2.3	29.0(*)
Total	836.5	719.5	799.8	594.7	737.6	17.6	53.0	80.8	161.1**
Foetus	620.2	587.3	621.8	561.2	597.6	7.9	19.2	12.3	46.8*
Uterus	234.5	227.0	254.2	205.5	230.3	13.2	12.4	0.9	28.1*
Necrotic tissue and dissection loss	56.0	58.5	88.0	61.2	65.9	54.7	14.7	- 17.4	12.2
Uterus + contents	2425.0	2304.2	2596.2	2396.0	2430.3	14.1	140.0	-131.5	160.5
Vulva/Vagina/Cervix	36.0	39.3	42.1	45.1	40.6	11.5	1.9	- 5.5**	- 3.2
Ovaries	3.354	3.356	3.843	3.621	3.588	8.4	0.123	- 0.287*	0.020
Fallopian tubes	1.060	1.033	1.078	1.020	1.048	10.1	0.043	- 0.003	0.043
TOTAL (Complete Genital Tract)	2465	2348	2643	2445	2475	13.9	140.3	- 138	158

TABLE 5:13. MEAN WEIGHTS (g) OF COMPONENTS OF THE GENITAL TRACT AFTER 140-DAYS OF GESTATION

Component	Group means				Overall mean	C.V. %	S.E.	Mean differences		
	He/HP	He/LP	Li/HP	Li/LP				Initial weight (He-Li)	Plane of Nutrition (HP-LP)	Interaction
Fluids										
Allantoic	1716.7	1976.7	1173.3	1445.0	1727.9	13.9	138.4	237.5	34.2	- 294.2
Amniotic	693.3	1196.7	791.7	1283.3	991.3	61.8	353.4	- 95 2	- 497.5	- 5.9
Total	2410.0	3173.4	2565.0	2728.3	2719.2	24.3	381.3	145.3	463.3	- 300.1
Placenta										
Cotyledons	597.7	486.6	525.1	368.4	494.4	19.8	56.4	95.4	133.9*	- 22.8
Membranes	266.0	287.7	360.3	255.7	292.4	11.3	19.0	- 31.2	41.5 (*)	- 63.2*
Total	863.7	774.3	885.4	624.1	786.8	9.7	43.9	64.2	175 4**	- 86.0
Foetus	4135.0	4643.3	4920.0	4190.0	4472.1	5.0	128.3	- 165.9	110.9	- 619.2**
Uterus	551.3	525.0	596.3	549.3	555.0	11.1	35.5	- 34.7	147.5	- 10.4
Necrotic tissue and dissection loss	106.0	95.0	119.0	116.7	109.2	40.6	25.6	- 17.4	6.7	4.4
Uterus and contents	8065.0	9210.0	9085.0	8207.3	8641.8	7.7	382.8	- 8.7	- 133.7	-1011.4*
Vulva/Vagina/Cervix	47.6	45.1	46.6	40.9	45.1	7.1	1.9	2.6	4.1	- 1.6
Ovaries	3.390	3.692	3.637	3.480	3.550	7.2	0.147	- 0.018	- 0.073	- 23.0
Fallopian tubes	1.113	1.065	0.968	0.975	1.030	9.6	0.057	0.118	0.021	0.028
TOTAL (Complete Genital Tract)	8117	9260	9137	8253	8692	7.6	382.8	- 7	- 130	- 102 *

Note: Interaction effect = (He/HP - He/LP) - (Li/HP - Li/LP) nutrition in pregnancy was significant for the gravid uterus, foetal weight and the foetal membranes; approached significance ($P < 0.10$) for the weight of allantoic fluid; and was noticeable for other components.

The placenta as a whole, and the cotyledons as a component, were significantly heavier in HP than LP ewes.

(b) Proportionate Composition of the Gravid Uterus

The mean weight of each component of the gravid uterus, expressed as a percentage of the total weight, at both 90- and 140-days of pregnancy, is illustrated in Fig. 5:8. Mean differences between the percentages at each stage are recorded in Table 5:14.

The foetus comprised 25 per cent. and 52 per cent. of the gravid uterus after 90- and 140-days of pregnancy respectively. Treatment effects were not significant.

The placenta (as a proportion) after 90-days represented 35 per cent. in He/HP as compared with 32 per cent. in He/LP ewes; and 31 per cent. in Li/HP ewes as compared with 25 per cent. in Li/LP ewes. Comparable treatment effects on the placenta after 140-days of pregnancy were indicated ($P < 0.10$). The placenta represented approximately one-third of the gravid uterus at 90-days, but approximately one-tenth at 140-days.

Uterine fluids represented a significantly greater proportion of the gravid uterus after 90-days in Li/LP ewes (41 per cent.) than in other animals (30 per cent.). This difference stemmed from

Fig. 5:8.- Proportionate composition by weight of the gravid uterus after 90- and 140-days of pregnancy.

PROPORTIONATE COMPOSITION OF THE GRAVID UTERUS

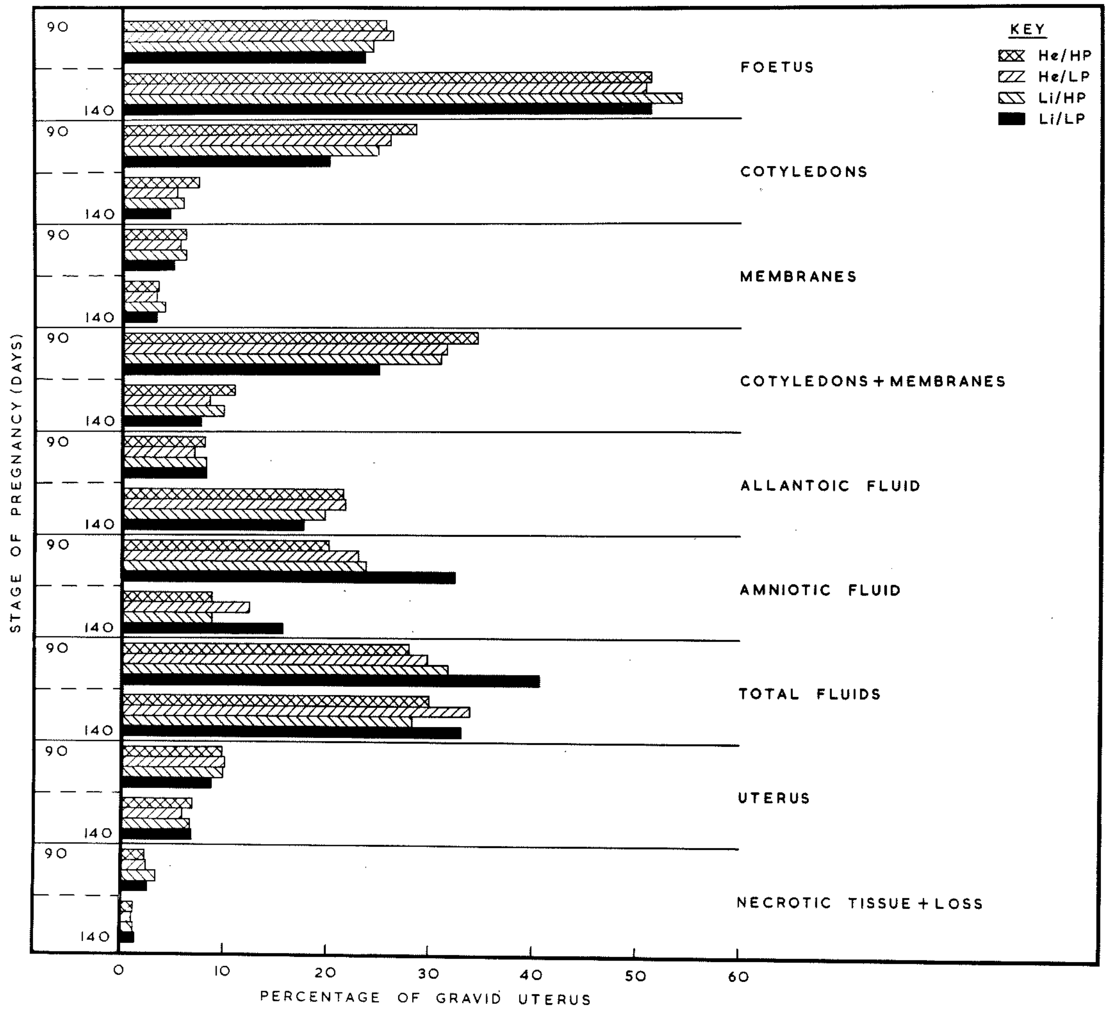


TABLE 5:14. MEAN DIFFERENCES BETWEEN PERCENTAGES OF COMPONENTS OF THE GRAVID UTERUS AFTER 90- AND 140-DAYS OF PREGNANCY

Component	Mean differences			
	After 90-days		After 140-days	
	Initial weight (He-Li)	Plane of nutrition (HP-LP)	Initial weight (He-Li)	Plane of nutrition (HP-LP)
Fluids				
Allantoic	-0.7	0.5	2.9(*)	0.9
Amniotic	-6.6*	-5.8*	-1.6	-5.3
Total	-7.3*	-5.3(*)	1.3	-4.4
Placenta				
Cotyledons	4.9***	3.7**	1.2(*)	1.8*
Membranes	0.3	0.8	-0.3	-0.5(*)
Total	5.2**	4.5*	0.9(*)	2.3**
Foetus	2.1	0.1	-1.7	1.8
Uterus	0.6	0.4	-0.4	0.4
Necrotic tissue / dissection loss	0.6	0.4	-0.2	0.1

the proportion of amniotic fluid. Allantoic fluid, on the other hand, represented a greater proportion of the gravid uterus in He than Li ewes after 140-days, although the difference was barely significant ($P < 0.10$).

Differences in the proportions of other components were not significant.

V. Foetal Weights, and Cotyledon Weights and Numbers

Mean single foetus weights, together with mean weights and numbers of functional cotyledons, after 90-days of pregnancy are recorded in Table 5:15, and after 140-days of pregnancy in Table 5:16.

(a) Foetal Weights

(i) After 90-days.- IP foetuses were lighter, by approximately 8 *per cent.* on the average, than HP foetuses (Table 5:15). Males were heavier, by 11 *per cent.*, than females. The initial weight of the ewe had no significant effect on foetal weight at 90-days of age.

(ii) After 140-days.- Foetuses from Li ewes were heavier than those from He ewes (Table 5:16), but a high plane of maternal nutrition in early pregnancy gave heavier foetuses than a low plane. This significant interaction ($P < 0.01$) was noted previously (see Table 5:13) and appears consistently in all subsequent data related to foetal growth and development. The sex effect on foetal weight at 140-days of age was not significant. A crude measure of foetal growth efficiency is to express foetal weight (g.) at 140-days of age as a proportion of the body weight of the ewe at mating (kg.). Using mean values, the index for the He/HP ewes was 80.3 g. foetus/kg. ewe body weight (wool-free) at mating, and 92.5 (He/LP), 131.2 (Li/HP) and 110.9 for Li/LP ewes.

Foetal weights at 90- and 140-days of age were not significantly associated with various measures of skeletal frame size, or the condition scores (fatness), of the ewes recorded at mating time.

(b) Cotyledons

(i) Total weights of cotyledons

(1) After 90-days.- Table 5:15 shows that poor nutrition of the ewe in early pregnancy reduced the total weight of functional cotyledons. The total weight of cotyledons in the pregnant horn from LP ewes represented 84 per cent. of the comparable total weight from HP ewes; and 73 per cent. in the vacant horn. Under HP feeding the total weight of cotyledons in the pregnant horn represented 62 per cent. of the weight for the combined horns, and 65 per cent. in LP ewes. These comparisons, together with the significant reduction in the total weight of cotyledons in the vacant, but not pregnant horn, indicate that poor nutrition of the ewe restricted placental development to a greater extent in the vacant horn.

He ewes had a heavier total weight of cotyledons than Li ewes, significantly so in the vacant horn.

TABLE 5:15. MEAN SINGLE FOETUS WEIGHTS (g), TOGETHER WITH MEAN WEIGHTS (g) AND NUMBERS OF FUNCTIONAL COTYLEDONS, AFTER 90-DAYS OF GESTATION

Character	Group means						Overall mean	C.V %	S.E.	Mean differences		
	Initial weight		Plane of nutrition		Foetal sex					Initial wgt. (He-Li)	Plane of nutrition (HP-LP)	Foetal sex (Male-Female)
	He	Li	HP	LP	Male	Female						
Foetal weight	603.8	591.5	621.0	574.3	620.8	559.0	597.6	7.9	18.8	12.3	46.7*	61.8**
Cotyledons												
<u>Total weight</u>												
Pregnant horn	395.8	369.0	414.8	350.0	395.7	344.6	382.4	22.1	34.6	26.8	64.8	51.1
Vacant horn	245.1	193.6	253.0	185.7	228.9	201.3	219.3	25.0	22.3	51.5*	67.3**	27.6
Combined horns	640.9	562.6	667.8	535.6	624.6	545.9	601.7	16.9	41.5	78.3	132.2**	78.7
<u>Numbers</u>												
Pregnant horn	41.4	46.9	45.4	42.9	44.8	43.1	44.1	13.5	2.4	- 5.5*	- 2.5	1.7
Vacant horn	32.3	29.1	32.9	28.5	31.1	29.4	30.7	25.7	3.2	3.2	4.4	1.7
Combined horns	73.6	76.0	78.2	71.4	75.9	72.6	74.8	14.5	4.4	- 2.4	6.8	3.3
<u>Average weight</u>												
Pregnant horn	9.64	7.98	9.28	8.34	8.83	8.00	8.81	23.6	0.85	1.66	0.94	0.83
Vacant horn	7.82	6.71	8.06	6.47	7.36	6.85	7.26	28.9	0.86	1.11	1.60	0.51
Combined horns	8.84	7.52	8.71	7.66	8.23	7.52	8.18	21.8	0.73	1.32	1.05	0.71
Number of observations	12	12	12	12	15	9	24	-	-	-	-	-

TABLE 5:16. MEAN SINGLE FOETUS WEIGHTS (g), TOGETHER WITH MEAN WEIGHTS (g) AND NUMBERS OF FUNCTIONAL COTYLEDONS, AFTER 140-DAYS OF GESTATION

Character	Group means						Overall mean	C.V. %	S.E.	Mean differences (1)		
	Initial weight		Plane of nutrition		Foetal sex					Initial weight (He-Li)	Plane of nutrition (HP-LP)	Foetal sex (Male-Female)
	He	Li	HP	LP	Male	Female						
Foetal weight	4389.2	4555.0	4527.5	4416.7	4486.7	4457.5	4472.1	5.0	121.8	- 165.3	110.8	29.2
Cotyledons												
<u>Total weight</u>												
Pregnant horn	311.0	276.4	329.7	257.7	312.2	275.2	293.7	20.6	35.0	34.6	72.0	37.0
Vacant horn	231.2	170.3	231.7	169.8	199.1	202.4	200.8	22.7	26.3	60.9*	61.9*	- 3.3
Combined horns	542.2	446.7	561.4	427.5	511.3	477.6	494.5	19.6	56.4	95.5	133.9*	33.7
<u>Numbers</u>												
Pregnant horn	44.2	41.4	41.9	43.7	43.5	42.0	42.8	16.9	4.2	2.8	- 1.8	1.5
Vacant horn	32.7	31.5	30.5	33.7	33.2	31.0	32.1	23.5	4.4	1.2	- 3.2	2.2
Combined horns	76.9	72.9	72.4	77.4	76.7	73.0	74.8	17.7	7.6	4.0	- 5.0	3.7
<u>Average weight</u>												
Pregnant horn	7.15	6.87	8.11	5.92	7.18	6.55	7.02	21.2	0.86	0.28	2.19*	0.63
Vacant horn	7.31	5.69	7.86	5.14	6.00	6.53	6.50	25.1	0.94	1.62	2.72*	- 0.53
Combined horns	7.18	6.33	7.93	5.58	6.67	6.54	6.75	21.4	0.83	0.85	2.35*	0.13
Number of observations	6	6	6	6	6	6	12	-	-	-	-	-

Note: (1) For foetal weight, the interaction between initial weight of the ewe x plane of nutrition was significant ($P < 0.01$) ; other interactions did not attain significance at $P < 0.05$ and values therefore are not presented.

Male foetuses were associated with a greater total weight of cotyledons, particularly in the pregnant horn, than females.

Distributions of cotyledon weights after 90-days of pregnancy are illustrated in Figs. 5:9 and 5:10. Substantial variation in the weight of individual cotyledons can be seen (C.V. 16.9 per cent. for combined forms - see Table 5:15). Cotyledons of the largest sizes were recorded from both Li ewes and LP ewes.

(2) After 140-days.- The significant differences between the total weights of cotyledons at 140-days approximated those recorded at 90-days. Total cotyledon weights were less at 140-days than 90-days of pregnancy.

Figs. 5:11 and 5:12 show the distributions of cotyledon weights after 140-days of pregnancy. Marked differences in the histograms can be seen, especially for Li/LP ewes as compared with Li/HP ewes (Fig. 5:12). Cotyledons of the heaviest weights were recorded from He/HP, He/LP (Fig. 5:11) and Li/HP (Fig. 5:12) ewes, but not Li/LP ewes.

Comparison of Figs. 5:11 and 5:12 reveals the regression in cotyledon weights between 90- and 140-days noted for mean weights (Tables 5:15 and 5:16). There is a suggestion that the largest cotyledons regressed most over this period of pregnancy.

(ii) Numbers of cotyledons

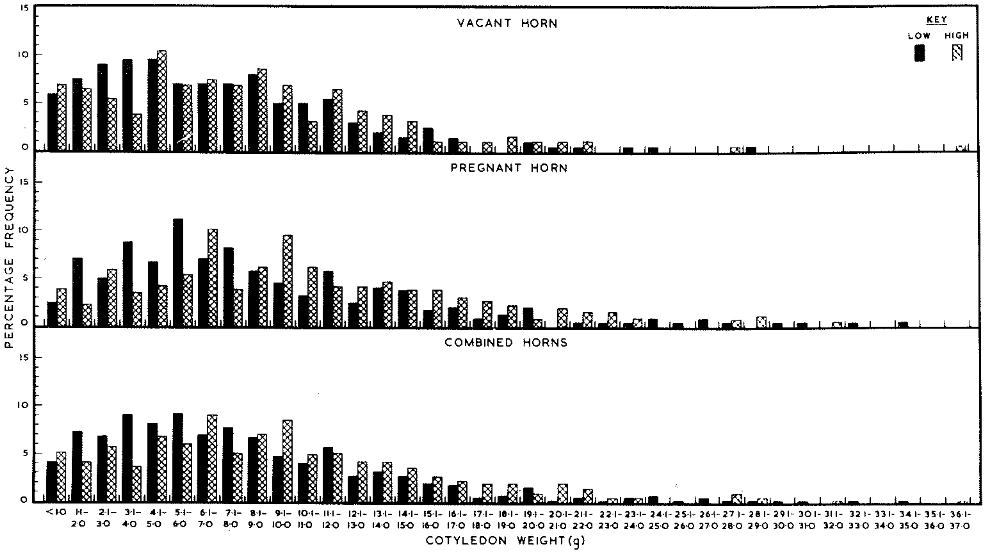
(1) After 90-days.- The total number of functional cotyledons (Table 5:15) was significantly less in the pregnant horn of

Fig. 5:9.- Mean distributions of functional cotyledon weights after 90-days of pregnancy in ewes which were heavy at mating.

Fig. 5:10.- Mean distributions of functional cotyledon weights after 90-days of pregnancy in ewes which were light at mating.

DISTRIBUTION OF COTYLEDON WEIGHTS AT 90 DAYS OF PREGNANCY

EWES HEAVY AT MATING



DISTRIBUTION OF COTYLEDON WEIGHTS AT 90-DAYS OF PREGNANCY

EWES LIGHT AT MATING

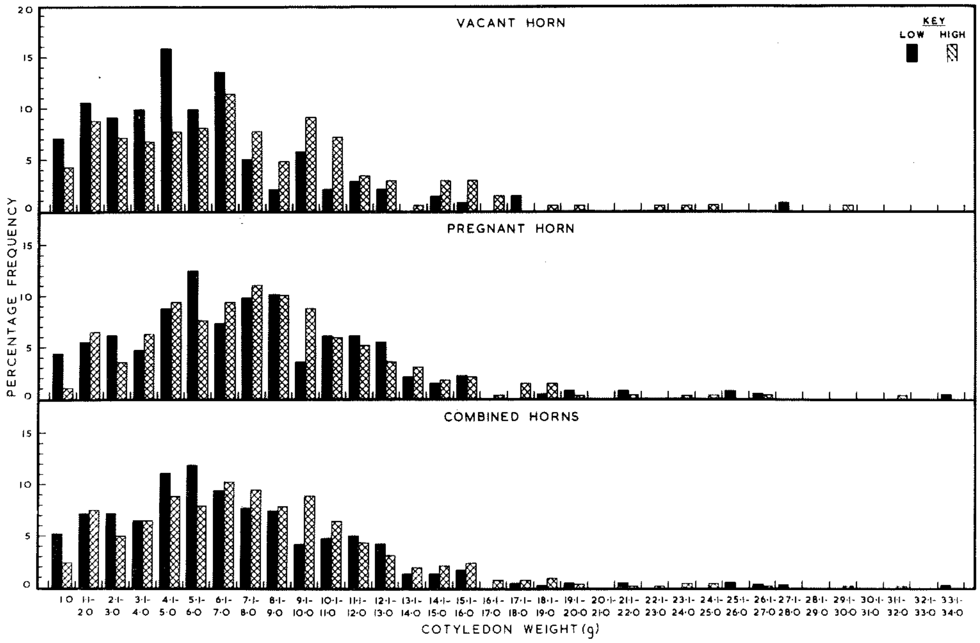
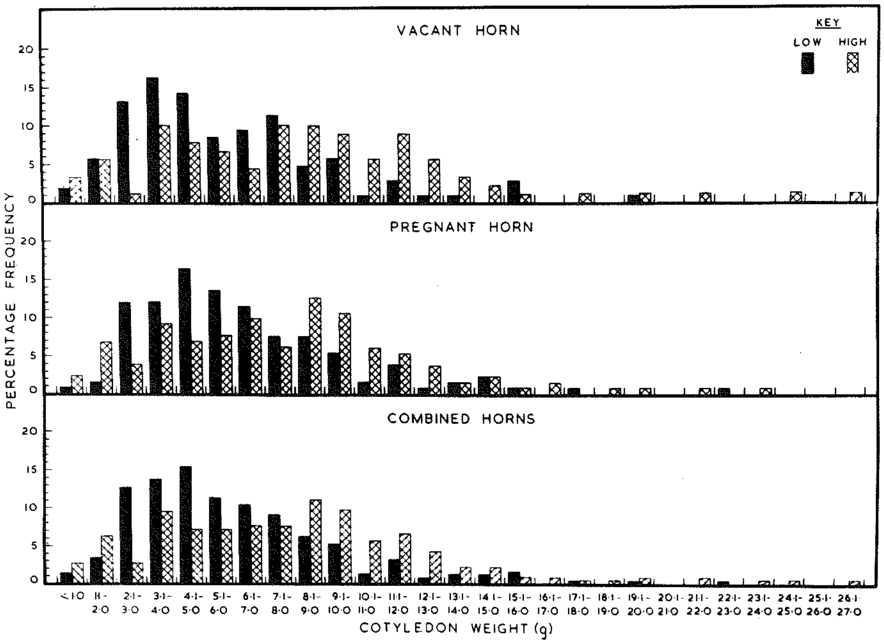


Fig. 5:11.- Mean distributions of functional cotyledon weights after 140-days of pregnancy in ewes which were heavy at mating.

Fig. 5:12.- Mean distributions of functional cotyledon weights after 140-days of pregnancy in ewes which were light at mating.

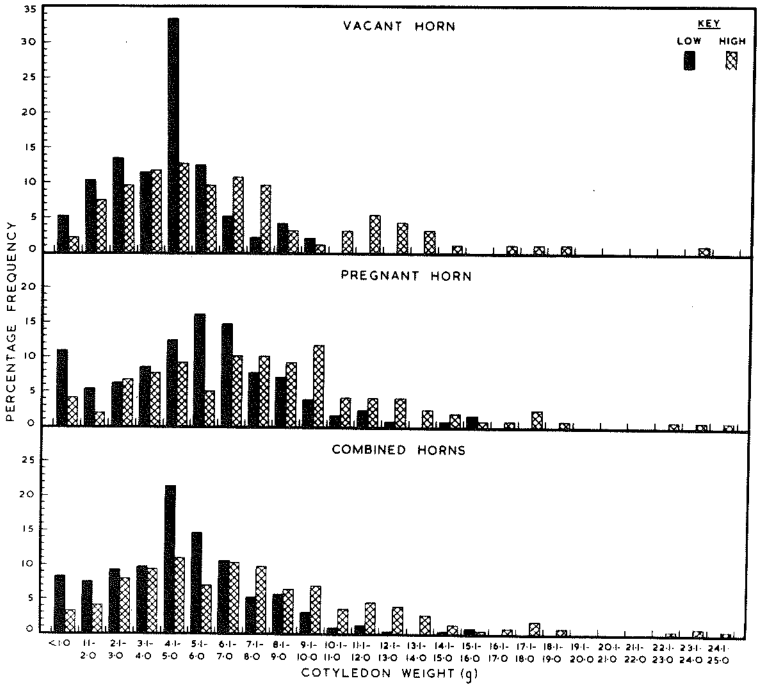
DISTRIBUTION OF COTYLEDON WEIGHTS AT 140-DAYS OF PREGNANCY

EWES HEAVY AT MATING



DISTRIBUTION OF COTYLEDON WEIGHTS AT 140-DAYS OF PREGNANCY

EWES LIGHT AT MATING



He than Li ewes. Other differences in the number of cotyledons were not significant, although LP ewes had a smaller number, especially in the vacant horn, than HP ewes.

(2) After 140-days.- Differences in the number of cotyledons (Table 5:16) were not significant, the overall mean number (74.8) equalling the comparable number recorded after 90-days (Table 5:15).

(iii) Average weight of cotyledons

(1) After 90-days.- Differences in the average weights of cotyledons (Table 5:15) were not significant, but tended to be heavier for He than Li ewes, heavier in HP than LP ewes, and heavier for male than female foetuses.

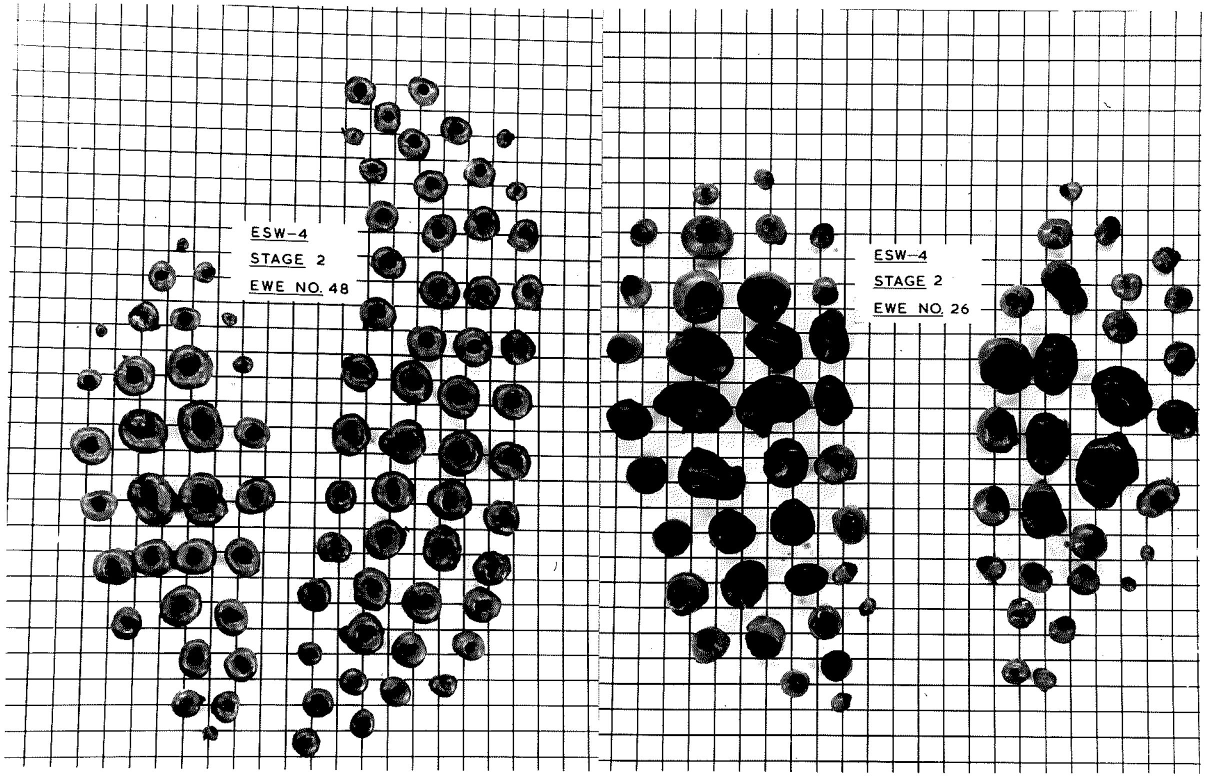
(2) After 140-days.- HP ewes had cotyledons of significantly greater average weight than LP ewes (Table 5:16). Other differences were small and not significant.

(iv) Morphology of cotyledons

Plate 5:5 is a semi-schematic representation of the functional cotyledon array after 90-days of pregnancy from selected Li/HP and Li/LP ewes. The profound effect of poor nutrition in early pregnancy on the appearance of the cotyledons can readily be seen. Moreover, the distorted cotyledons of the Li/LP ewe appeared to be concentrated more towards the centre of each horn, with diminishing effects towards more distal locations. This suggests an association with the directional flow of the uterine blood supply.

Plate 5:5.- Semi-schematic representation of the functional cotyledon array after 90-days of pregnancy from selected HP and LP ewes which were both light at mating. The distorted cotyledons of the LP ewe tend to lie more towards the centre of each uterine horn (2 x 2 cm. grid).

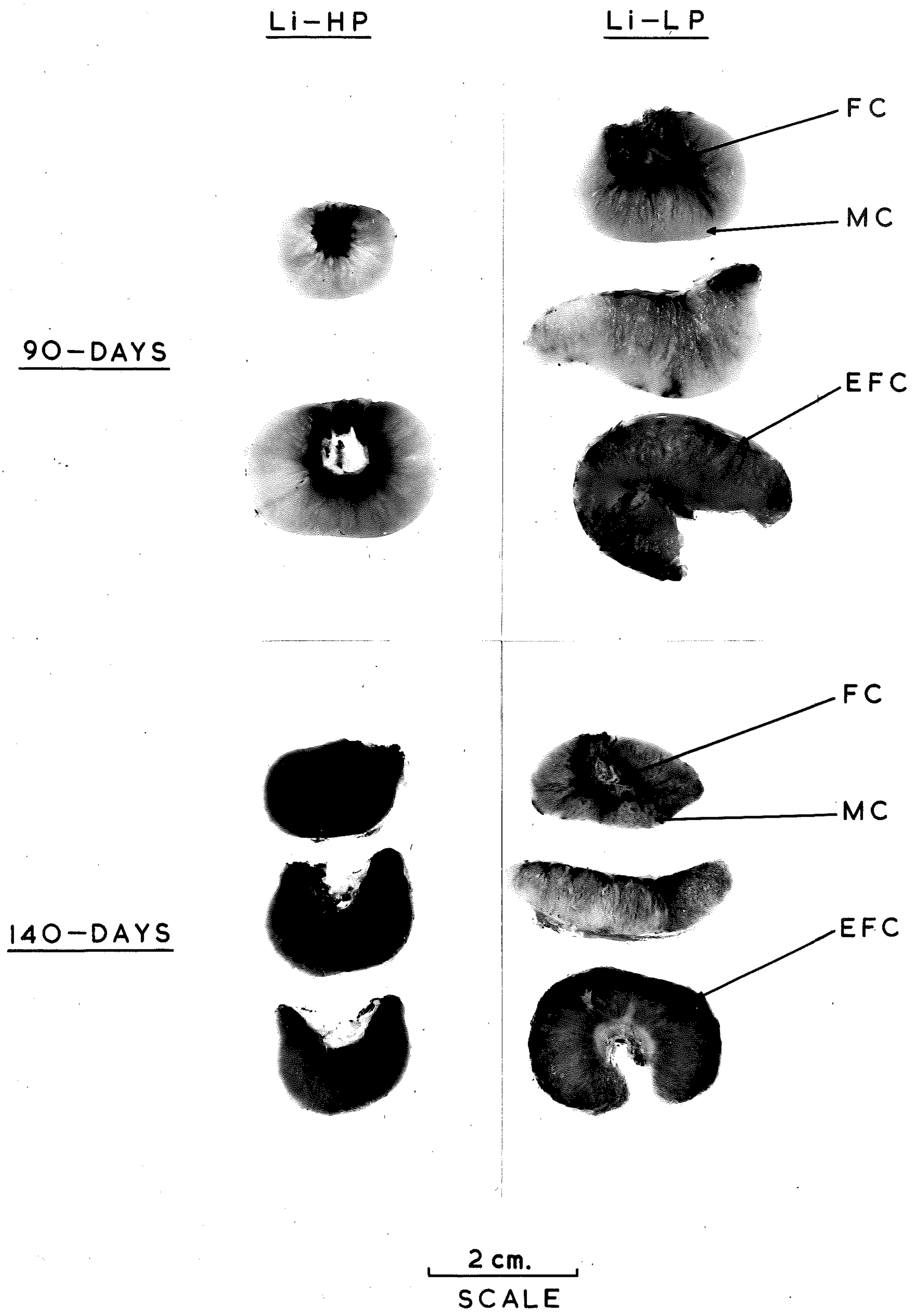
90–DAYS OF PREGNANCY



	Li–HP		Li–LP	
	VACANT	PREGNANT	PREGNANT	VACANT
No.	31	53	37	30
Wt. (g)	320·4	409·0	314·0	287·9
	729·0		601·9	

Plate 5:6.- Vertical sections of cotyledons from HP and LP ewes after 90- and 140-days of pregnancy. FC = foetal component, MC = maternal component, EFC = everted foetal component. Cotyledons at 140-days are generally smaller and darker than those at 90-days.

VERTICAL SECTIONS OF COTYLEDONS



Vertical sections of some of the cotyledons shown in Plate 5:5, and other cotyledons taken from ewes of comparable groups after 140-days of pregnancy, are displayed in Plate 5:6. Cotyledons taken from ill-fed ewes show the remarkable eversion of the foetal component which, in the extreme condition resemble a bovine cotyledon (Amoroso 1952) or an inverted "normal" ovine cotyledon. Separation of these cotyledons into maternal and foetal components proved impossible without damaging the structure; it is therefore not known to what extent the distortion reflected compensatory growth of foetal tissue, or marked regression of maternal tissue. Foetal membranes could be easily detached from cotyledons after 140-days, but not after 90-days, of pregnancy.

(c) Relationships between Foetal Weight and Placental Components

(i) Foetal weight and the number of cotyledons

Foetal weights at 90- and 140-days of age were not significantly associated with the number of cotyledons in either the pregnant or vacant horn, or the combined horns.

(ii) Foetal weight and the weights of placental components

The relationships between foetal weight and the weight of the placenta (cotyledons and membranes) after 90- and 140-days of pregnancy are depicted in Fig. 5:13.

The relationship at 90-days of age could be described by the following equation:-

$$\begin{array}{lccc} \text{F.W.} = 465.3 + & 30.1\ \text{F.S.} + & 1.49\ \text{C.W.} + & 6.14\ \text{M.W.} \\ \text{(s.e.)} & (\pm 7.7) & (\pm 0.80) & (\pm 2.79) \\ & *** & (*) & * \end{array}$$

where,

F.W. = Foetal weight (g.) at 90-days of age.

F.S. = Foetal sex (discontinuous variable; female = 0, male = 1).

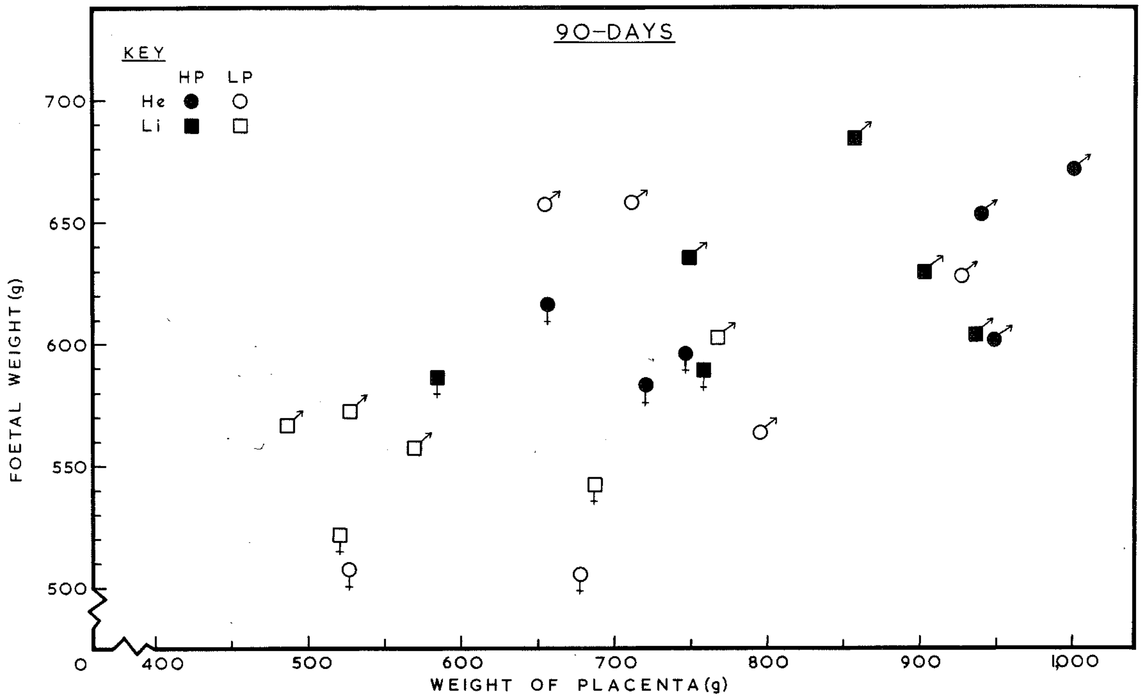
C.W. = Total weight (g.) of cotyledons.

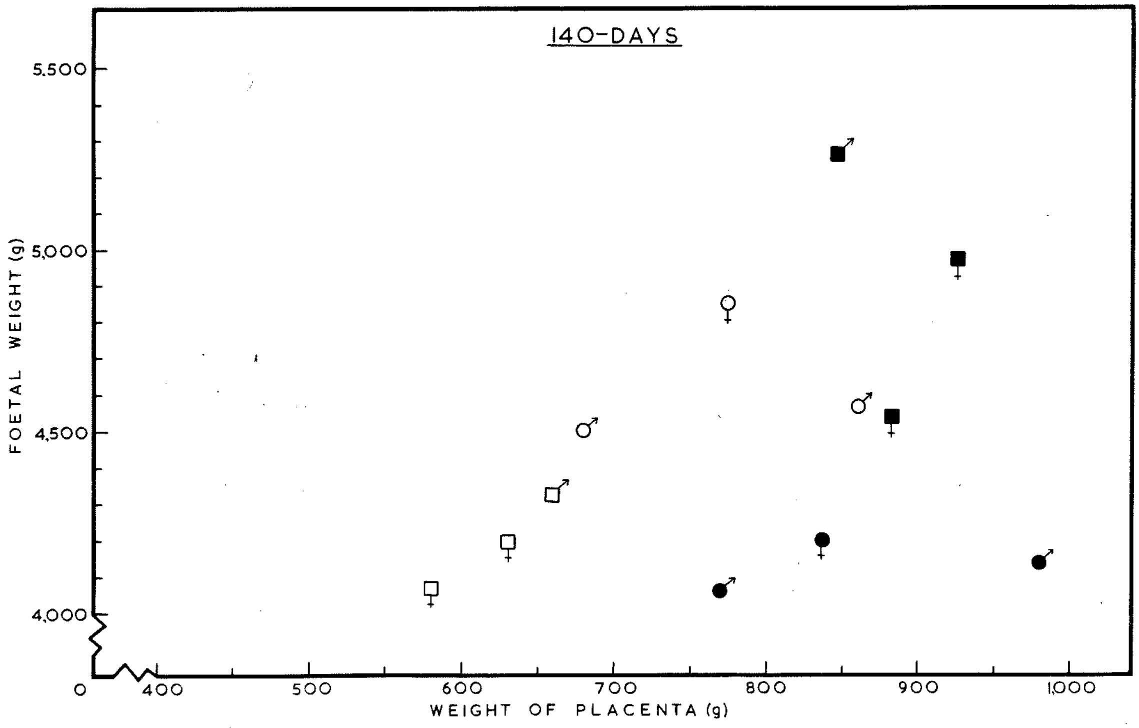
M.W. = Total weight (g.) of membranes.

This equation, based on 20 d.f., has a residual coefficient of variation of 10.2 <u>per cent</u>. and accounts for 62 <u>per cent</u>. of the variation in foetal weight (R = 0.79). When the variance due to foetal sex was eliminated, each g. of cotyledons supported 1.17 g. of foetus, and each g. of membranes supported 6.14 g. of foetus. On extrapolation, the regression line intercepts the foetal weight axis above the origin, at approximately 0.5 kg.

After 140-days, no significant association between foetal weight and the weight of placental components, either within groups or overall, could be detected. This may reflect the small number of foetuses at this age. It is, nevertheless, interesting to note that the three He/HP foetuses were exceptionally light in weight although their placentae were relatively heavy (Fig. 5:13).

Fig. 5:13.- The relationship between foetal weight and the weight of the placenta (cotyledons + membranes) after 90- and 140-days of pregnancy.


90-DAYS
KEY
HP LP
He ● ○
Li ■ □
FOETAL WEIGHT (g)
700
650
600
550
500
0
400
500
600
700
800
900
1,000
WEIGHT OF PLACENTA (g)
♂
♀


140-DAYS
FOETAL WEIGHT (g)
5,500
5,000
4,500
4,000
0
400
500
600
700
800
900
1,000
WEIGHT OF PLACENTA (g)
♂
♀

VII. Foetal Radiographs

(a) General observations

X-ray positives of selected HP and LP female foetuses after 90-days of gestation are illustrated in Plate 5:7. A composite print of a foetus after 140-days of gestation is shown in Plate 5:8.

At 90-days of age the epiphyseal growth centres of the lower limb bones are retarded in their appearance in the light foetus derived from an ill-fed ewe. Closer examination shows, too, the unfused state of the two lateral pieces of the sternum in the He/LP foetus; this effect, however, was observed in this foetus only.

Comparison of Plates 5:7 and 5:8 shows the very striking skeletal development occurring in late gestation. In no case was an absence or obvious retardation of growth centres observed in the foetuses of this age, whatever their history.

Skeletal development with increasing age and weight is particularly well demonstrated in the X-ray photographs of the fore-limb. Plate 5:9 shows positive prints of foetal fore-limbs at three ages. The poor development of the limb taken from the He/LP foetus (506 g.) at 90-days of age may be noted.

(b) Foetal Bone Measurements taken from X-ray Negatives

Mean measurements of foetal bones taken from X-ray negatives at 90- and 140-days of gestation are recorded in Tables 5:17 and 5:18 respectively.

Plate 5:7.- X-ray positives of selected HP and LP female foetuses after 90-days of gestation. The absence of carpal nuclei, the unfused state of the sternal pieces and the lower general density of the LP foetus may be noted.

90-DAYS OF AGE

613 (g)
FEMALE
He/HP

506 (g)
FEMALE
He/LP

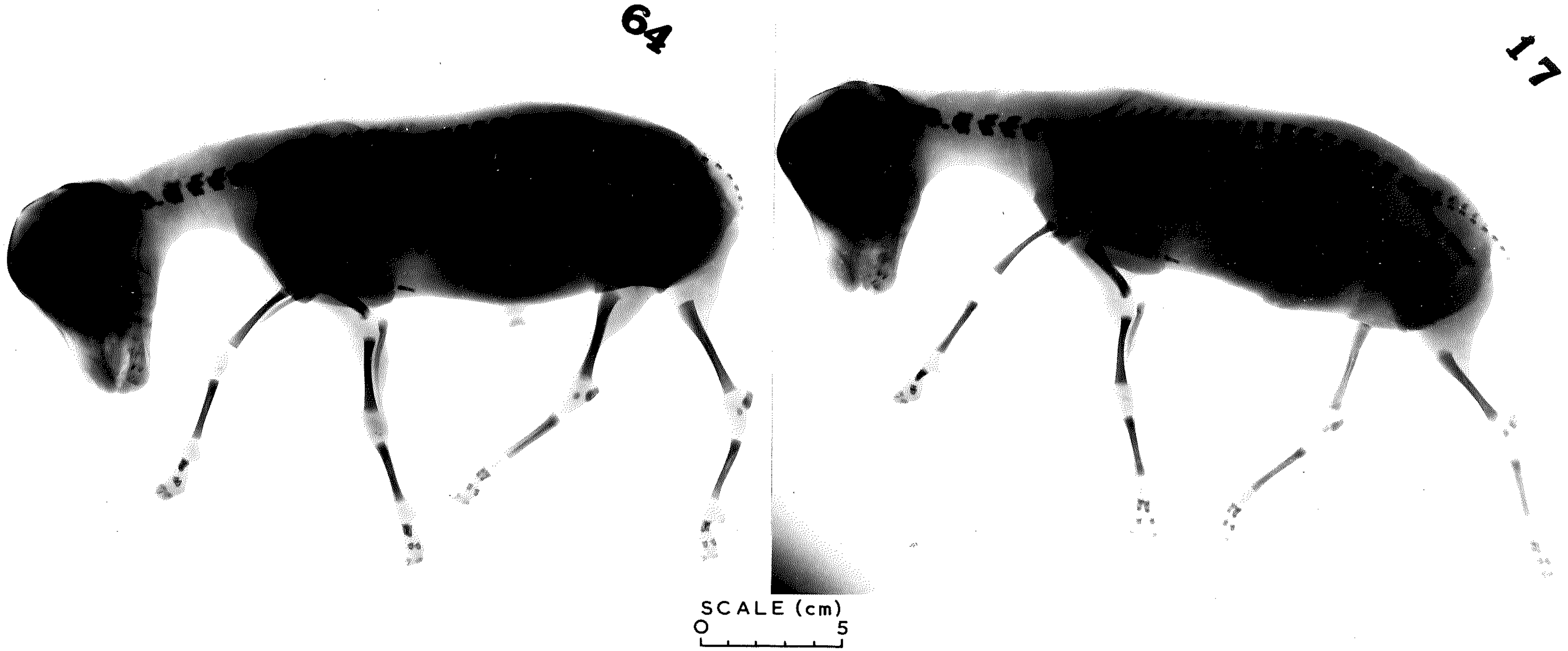


Plate 5:8.- X-ray positive of a selected foetus (He/HP) after 140-days of gestation. The fore and hind ends of the animal were photographed separately and the two prints butted together; consequently there is some distortion at the level of the last rib.

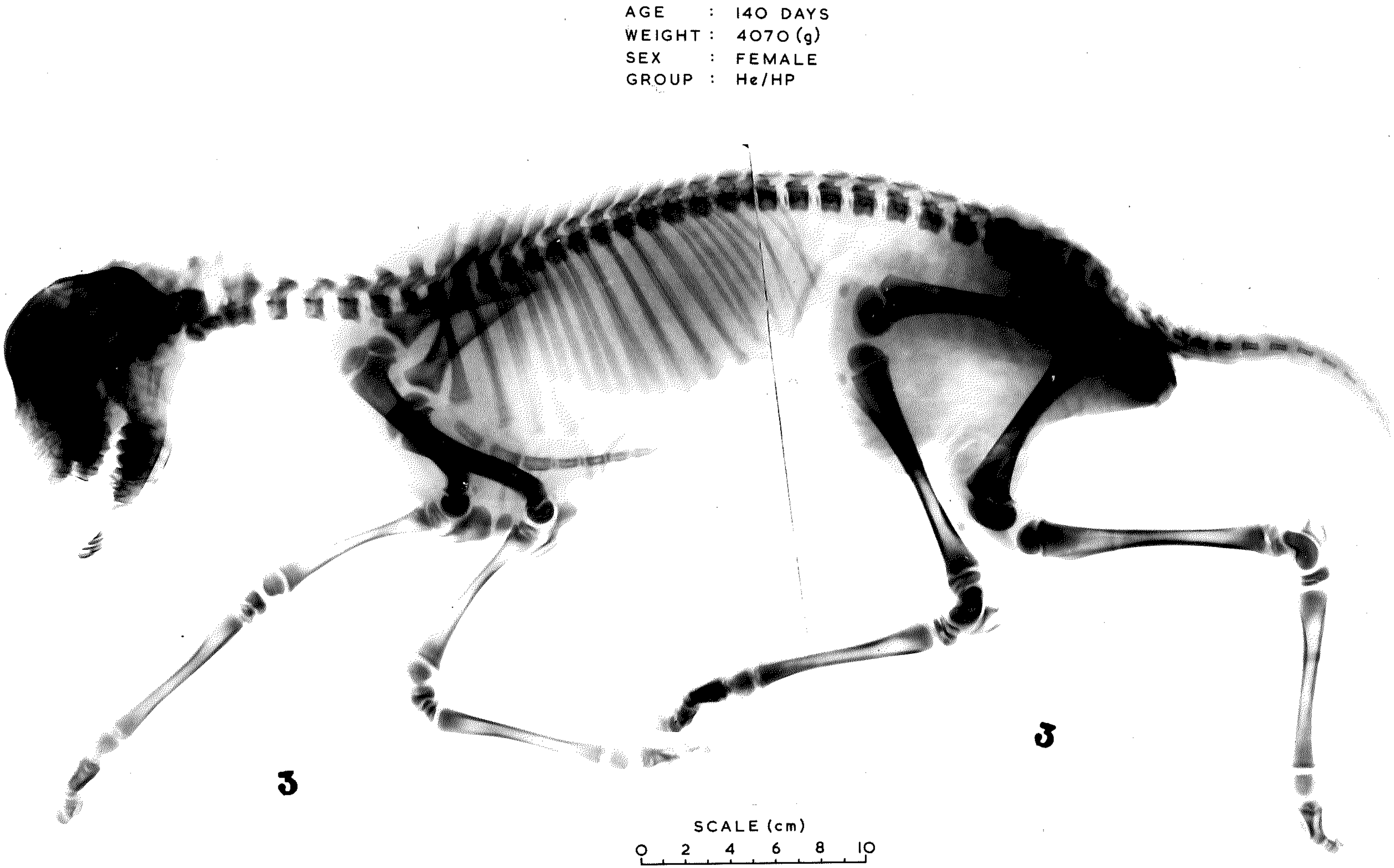

AGE : 140 DAYS
WEIGHT : 4070 (g)
SEX : FEMALE
GROUP : He/HP
3
3
SCALE (cm)
0 2 4 6 8 10

Plate 5:9.- X-ray positives to illustrate skeletal development of the fore-leg during foetal life. At 506 g. body weight (Li/LP : 90-days of age) nuclei of the carpals and proximal sesamoids are absent; at 655 g. body weight (Li/HP : 90-days of age) carpal nuclei can be seen; at 1385 g. body weight (107-days of age) proximal sesamoid nuclei are clearly seen. The unfused state of the metacarpal bone at the lighter weights, the general increase in bone density with increasing body weight and age, and the appearance of the distal end of the ulna at heavier weights may also be noted.

SKELETAL DEVELOPMENT OF THE FORE-LEG

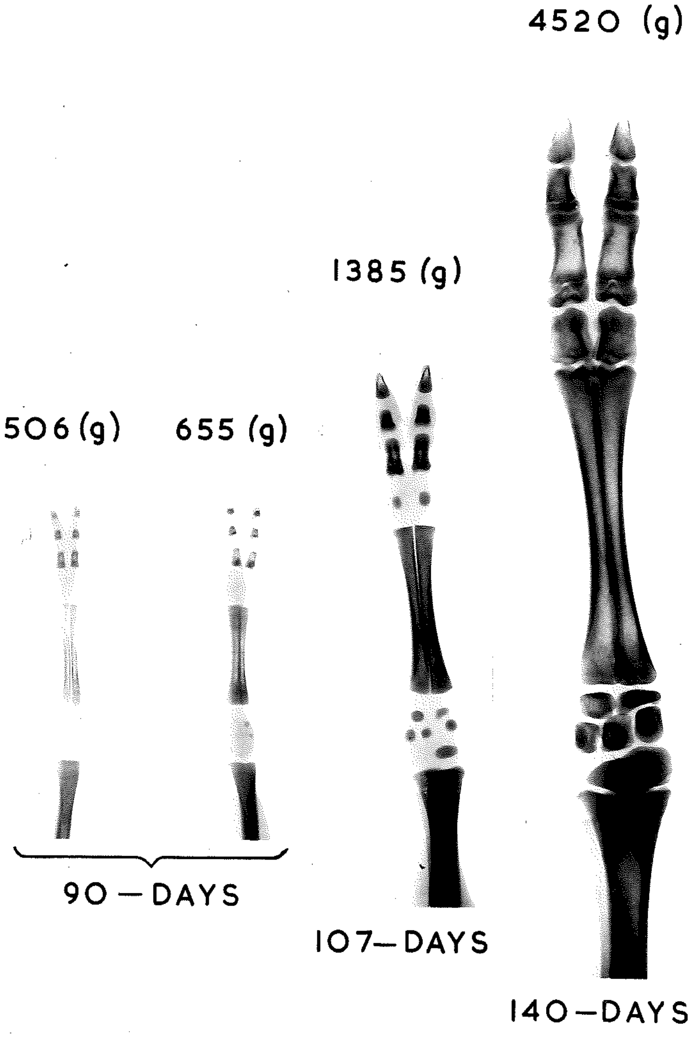


TABLE 5:17. MEAN MEASUREMENTS OF FOETAL BONES, TAKEN FROM X-RAY NEGATIVES, AT 90-DAYS OF GESTATION AFTER ADJUSTMENT FOR THE EFFECTS OF FOETAL SEX

Measurement	Group means				Overall mean	C.V. %	S.E.	Mean differences	
	He/HP	He/LP	Li/HP	Li/LP				Initial weight (He-Li)	Plane of nutrition (HP-LP)
Body length									
Curved crown-tail	29.29	29.26	29.62	29.29	29.37	2.2	0.27	-0.18	0.18
Curved crown-rump	37.94	37.77	37.78	37.25	37.67	2.5	0.39	0.34	0.35
Tail length	8.64	8.45	8.16	7.96	8.30	7.8	0.26	0.49	0.20
Fore-limb length									
Metacarpus	2.50	2.39	2.49	2.27	2.41	4.7	0.05	0.07	0.17**
Radius	2.91	2.81	2.85	2.64	2.80	3.9	0.04	0.12	0.16**
Ulna	3.32	3.22	3.32	3.05	3.23	4.0	0.05	0.09	0.19**
Humerus	2.62	2.53	2.62	2.42	2.55	4.2	0.04	0.06	0.15**
Scapula	2.93	2.83	2.88	2.57	2.80	4.4	0.05	0.16**	0.21***
TOTAL	14.28	13.78	14.16	12.95	13.79	3.8	0.21	0.48*	0.86***
Hind-limb length									
Metatarsus	2.45	2.52	2.52	2.36	2.46	8.1	0.08	0.05	0.05
Tibia/fibula	3.70	3.59	3.67	3.34	3.57	4.8	0.07	0.14	0.22**
Femur	2.85	2.77	2.85	2.58	2.77	4.2	0.05	0.10	0.18**
TOTAL	9.00	8.88	9.04	8.28	8.80	5.1	0.19	0.28	0.44*

TABLE 5:18. MEAN MEASUREMENTS OF FOETAL BONES, TAKEN FROM X-RAY NEGATIVES, AT 140-DAYS OF GESTATION AFTER ADJUSTMENT FOR THE EFFECTS OF FOETAL SEX

Measurement	Group means				Overall mean	C.V. %	S.E.	Mean differences	
	He/HP	He/LP	Li/HP	Li/LP				Initial weight (He-Li)	Plane of nutrition (HP-LP)
<u>Body length</u>									
Curved crown-tail	53.42	55.96	57.58	54.21	55.29	2.9	0.94	-1.21	0.42
Curved crown-rump	72.46	76.13	78.20	73.07	74.97	2.0	0.87	-1.34	0.73
Tail length	19.04	20.17	20.63	18.86	19.68	6.7	0.77	-0.14	0.32
<u>Fore-limb length</u>									
Metacarpus	7.52	7.73	7.77	7.50	7.63	1.2	0.05	-0.01	0.03
Radius	8.73	9.04	9.17	8.72	8.92	0.5	0.03	-0.06	0.07
Ulna	8.64	8.85	9.02	8.65	8.79	1.8	0.09	-0.09	0.08
Humerus	8.55	8.93	8.89	8.56	8.73	1.5	0.08	0.02	-0.03
Scapula	7.01	7.19	7.39	6.93	7.13	1.6	0.07	-0.06	0.14
TOTAL	40.45	41.74	42.24	40.36	41.20	1.1	2.75	-0.21	0.30
<u>Hind-limb length</u>									
Metatarsus	7.89	8.25	8.47	7.97	8.14	2.0	0.10	-0.15	0.07
Tibia/fibula	12.05	12.34	12.62	12.07	12.27	0.7	0.05	-0.15	0.13
Femur	9.37	9.48	10.08	9.44	9.59	2.3	0.13	-0.34	0.27
TOTAL	29.311	30.07	31.17	29.48	30.00	1.5	2.56	-0.64	0.47

TABLE 5:19. RELATIONSHIPS BETWEEN EXTERNAL BODY MEASUREMENTS (cm) AND MEASUREMENTS (cm) TAKEN FROM X-RAY NEGATIVES AT 90- AND 140-DAYS OF GESTATION

External body measurement (y)	X-ray negative measurement (x)	Correlation coefficient (r)		Regression coefficient (b)		Residual standard deviation	
		90-days	140-days	90-days	140-days	90-days	140-days
Curved crown-tail	Curved crown-tail	0.72 ***	0.98 ***	0.83	1.08	0.874	0.642
Curved crown-rump	Curved crown-rump	0.64 **	0.99 ***	0.34	1.00	0.581	0.381
Tail length	Tail length	0.55 **	0.89 ***	0.62	0.93	0.617	0.708
Metacarpus length	Metacarpus length	0.63 **	0.82 ***	0.94	1.23	0.011	0.223
Radius/ulna length	Radius length	0.55 **	0.57 *	0.82	1.21	0.207	0.377
Humerus length	Humerus length	0.58 **	0.54 *	0.83	1.05	0.182	0.373
Tibia/Fibula length	Tibia/Fibula length	0.48 *	0.83 ***	0.67	2.02	0.291	0.919

At 90-days of age, a low plane of maternal nutrition significantly reduced the length of all limb bones, except the metatarsus. The fore-limb, especially the scapula, of Li/LP foetuses was significantly shorter than in other foetuses.

At 140-days of age, main treatment effects on any of the measurements were not significant; but significant ($P < 0.05$) interactions were recorded for all measurements except those of the hind-limb. Foetuses from He/HP ewes had shorter measurements than foetuses from He/LP ewes, but Li/HP foetuses had longer measurements than Li/LP foetuses. This reflects differences in foetal body weights (Table 5:16).

The association between external body measurements and measurements derived from X-ray negatives is of interest. Table 5:19 records the relationships between selected measurements. All the relationships were significantly correlated. Regression coefficients at 90-days were less than unity in all cases; this reflects the difficulty of defining points of reference in X-ray negatives of foetuses at this age when bones are still very cartilaginous in nature (see Plate 5:7). At 140-days of age, on the other hand, regression coefficients all exceed unity, except for tail length. At this age bone lengths are over-estimated by external body measurements because of the skin and other soft tissues overlying points of reference.

VIII. Factors Affecting Foetal Growth

Foetal body weights at 90- and 140-days of age have been related to a number of independent variables in multiple regression models.

(a) After 90-days.- The derived equation was:-

$$\begin{array}{lcccc} & \text{F.W.} = 429.3 + 70.5\ \text{F.S.} & + 3.18\ \text{B.W.} & + 0.354\ \text{E.W.C.} \\ (\text{s.e.}) & (\pm 13.1) & (\pm 1.31) & (\pm 0.0832) \\ & *** & * & *** \end{array}$$

where,

F.W. = Foetal weight (g.) at 90-days.

F.S. = Foetal sex (discontinuous variable : female = 0, male = 1).

B.W. = Ewe body weight (wool-free) at mating (kg.).

E.M.C. = Ewe body weight change/day/g. (wool-free, conceptus-free).

with a residual coefficient of variation of 12 per cent. These variables account for 71 per cent. of the variation in foetal weight at 90-days of age (R = 0.84, based on 20 d.f.). The regression coefficients indicate that males were heavier than females; that foetal weight increased by 3.18 g. for each 1 kg. increase in ewe body weight at mating, and by 0.354 g. for each 1 g./day of ewe body weight change over the first 90-days of pregnancy.

(b) After 140-days.- No significant within-group associations between foetal weight and any of the following variables could be detected: foetal sex; ewe body weight at mating; ewe weight change/day between mating to 90-days of pregnancy, or 91 to 140-days, or mating to 140-days: feed intake in early or late pregnancy, or over the whole of pregnancy.

This may reflect the small number of foetuses per group.

D. DISCUSSION

Feed intake of the fat ewes fed *ad libitum* throughout pregnancy (He/HP) declined as pregnancy proceeded, both absolutely (Table 5:6, Fig. 5:4) and in proportion to body weight (Fig. 5:5). In late pregnancy nett body weight of the ewes was barely maintained (Table 5:11), and the weight of their single foetuses at 140-days of age concomitantly reduced. On the other hand, gross body weight steadily increased as pregnancy continued (Fig. 5:3), reflecting conceptus growth. Use of gross body weight as the sole parameter of performance in pregnant ewes can therefore be misleading.

These observations help to explain the report (Jeffries & Fern 1956) that overfat ewes at pasture gave birth to light single and twin lambs. Unfortunately, their report provides insufficient information on the body weights or degree of fatness of the ewes at mating and during pregnancy. The authors state only that their "very fat" ewes weighed 131 lb. (59.5 kg.) one month before lambing, compared with an average weight of 119 lb. (54.0 kg.) for their "forward store to fat condition" ewes. Neither was the breed specified.

A reduction in feed intake of twin-bearing Border Leicester x Merino ewes over the last 50 days of pregnancy was reported by Reid & Hinks (1962). Birth weight of the lambs was reduced, but so also was their period of gestation. These workers adduce evidence that the decline of intake could not be ascribed solely to a mechanical restriction of gastrointestinal tract capacity by the expansive conceptus, coupled with large depots of abdominal fat (Mäkelä 1956; Tayler 1959). Metabolic changes associated with advancing pregnancy and physiological processes of fattening as alternative or additional agencies were favoured.

In this study, feed intake of the He/HP ewes declined from early pregnancy onwards. This suggests that the ewes may have been considerably fatter than those animals investigated by Reid & Hinks (1962). The latter authors comment in this connexion, ".... monotocous ewes may show a similar decline in feed intake to that recorded here in polytocous ewes if they are fatter than in the present experiments". Tayler (1959) reported a significant negative relationship between the feed intake of cattle at pasture and the amount of internal (perinephric) body fat. Moreover, the gross body weight increase of these He/HP ewes prior to mating under ad libitum feeding was not as great as expected. By the time of mating the ewes may have reached an early stage of the inappetence phenomenon reported for very fat sheep fed to appetite (Schinckel 1960). Ambient temperature, too, may have played some part in the curtailment of feed intake by affecting the physiological processes of heat dissipation (Macfarlane 1961) under the field conditions of the experiment.

On the other hand, the weight of foetuses at 140-days of age carried by fat ewes ill-fed in early pregnancy but later abundantly fed (He/LP) compared favourably with those born to thin ewes continually well-fed during pregnancy (Li/HP). The former ewes consumed less feed over 140-days of pregnancy than the latter (Table 5:6), with superior efficiency in wool production (Table 5:8). Furthermore, a superior ovulation rate of He ewes was indicated by the number of twin sets recorded, as might be expected from the work of Wallace (1961) and Coop (1962<u>b</u>, 1964).

Thin ewes poorly-fed in early pregnancy (Li/LP) consumed the least feed over 140-days of pregnancy (Table 5:6), displaying a spectacular compensatory intake in late pregnancy under <u>ad libitum</u> feeding. Their foetuses at 140-days of age were not unduly restricted in weight, the deficit being of greater academic than practical importance. Nevertheless, this system of management for breeding ewes cannot be recommended for several reasons. Firstly, a poor ovulation rate and increased barrenness can be expected from ewes of relatively light body weight at mating (Wallace 1961; Coop 1962<u>b</u>, 1964). Secondly, Li/LP ewes have little opportunity to accumulate needful body tissue reserves before the onset of lactation and concomitant increase of metabolic demand. Thirdly, the profound effects of undernutrition on placental development of these ewes (Plates 5:5 and

5:6) strongly suggests the need for caution until more is known about the physiological causes and possible sequelae. Taplin & Everitt (1964), for example, recorded abortion in late pregnancy of ewes severely undernourished in early pregnancy but abundantly fed thereafter (LH ewes). The rapidly increasing weight of the foetus in late gestation (Fig. 2:3) under a LH feeding regime may overload a tenuous maternal: foetal placental adherence. The premature labour of the Li/LP ewe carrying twins in this experiment lends support to this suggestion, but further study is clearly needed. Fourthly, foetal growth and development in early gestation was retarded to the greatest extent in the Li/LP ewes. Differences in skeletal frame size of the ewes played no obvious role in foetal growth, and the effects of ewe body weight must be attributed to differences in soft body tissues, largely body fat as a source of catabolisable energy. The lighter the body weight of the ewe at mating time the greater is the risk of damage to the conceptus through undernutrition in early pregnancy. Lastly, wool was produced less efficiently over 140-days of pregnancy by Li/LP than He/LP ewes (Table 5:8).

Foetal weights at 90-days of age were reduced by maternal undernutrition in early pregnancy, with a greater reduction in placental weight. Alexander (1964b) found that while very little placental tissue in the ovine was needed to permit gestation to reach the 100th day of gestation, subsequent foetal growth was limited by placental size. The ill-fed light ewes (Li/LP) still possessed

Continued on p. 297

considerable placental tissue after 90-days of undernutrition (as compared, for example, with the LP ewes of Experiment A), and presumably sufficient to permit foetal growth to proceed unhindered under the generous feeding in late pregnancy. This may also explain the comparable birth weight of LH and HH lambs in the work reported by Taplin & Everitt (1964), and of a larger number of lambs in the same experiment (Everitt : unpublished data). In other words, placental size must be restricted by undernutrition in early pregnancy below a critical threshold level before subsequent foetal growth is retarded. Granted that placental size or efficiency has not been retarded by undernutrition in early pregnancy, then compensatory foetal growth in late gestation appears probable under good feeding conditions. Prolongation of undernutrition past 90-days of pregnancy may lead to further restriction of placental development, with adverse effects on subsequent foetal growth, and with less time available before parturition for any degree of compensation.

The evidence presented on placental development, and the factors affecting it, is consistent with the earlier study (Experiment A). The total number of cotyledons, in both studies, is comparable with the number recorded by Alexander (1964a) for the Australian Merino and less than for other breeds. As Alexander (1964a) points out, this may place the Merino foetus at a disadvantage in terms of uterine nutrition. The distribution of the functional cotyledons appeared affected by maternal nutrition and foetal sex, as in Experiment

A, and emphasises the need for studies of factors influencing blastocyst development. The number of animals available for study in late pregnancy was regrettably small due to the larger number of ewes killed at mating and after 90-days of pregnancy than in Experiment A; further investigations in this period of pregnancy are also necessary. The effects of protracted undernutrition beyond 90-days of gestation followed by good feeding in the remainder of the prenatal existence, and in postnatal life, needs particular study.

Foetal development, as studied by the radiographs, substantiated the findings of Experiment A, insofar as ossification of the skeleton was more closely allied to body weight than age. In rabbit foetuses of the same age, Appleton (1929) found ossification to be more advanced in heavier foetuses. Ovine foetuses from ewes fed on a low plane of nutrition were found by Wallace (1948) to be in a less advanced state of ossification than foetuses of the same age from well-fed ewes. Pomeroy (1960) studied ossification in the porcine foetus; bones of a light foetus were small, and ossification less advanced, than in a foetus of the same age but three times heavier. Appearance of ossification centres did not appear retarded in the undersized pig foetuses, but there was evidence that this was the case in the 90-day foetuses of this study (Plates 5:7 and 5:9). This is not inconsistent with the lack of fusion of the two lateral strips of sternal pieces in the lightest foetus. A radiographic study of lambs taken from well-fed and ill-fed ewes at several stages of gestation, and in postnatal life, might throw light on the phenomenon of retarded postnatal performance of lambs undernourished in prenatal life (Schinckel & Short 1961; Taplin & Everitt 1964).

Finally, it may be noted that the estimated nutrient requirements for body maintenance of the ewes exceeded the estimates recorded in Experiment A. Reasons for the greater requirements of ewes in this trial are not clear. Environmental conditions and quality of the feed were very similar in the two investigations. However, while the experimental animals were of the same age, the ewes in this present experiment were generally heavier and fatter than those of Experiment A. Energy requirements for heat dissipation may be increased in fat pregnant sheep under high ambient temperatures; the work of Graham (1964a) suggests this possibility. On the other hand, Lambourne (1961) and Lambourne & Reardon (1963) found that maintenance requirements were greater for thin than fat sheep at pasture. Estimated requirements for weight increase approximated those recorded in Experiment A, and were less than those generally quoted (reviewed Coop 1962a).

6. GENERAL DISCUSSION AND CONCLUSIONS

" .... and surely we are all out of the computation of our age, and every man is some months older than he bethinks him. For we live, move, have a being and are subject to the actions of the elements and the malice of diseases in that other world, the truest microcosm .... " (Browne 1642).

This quotation summarises two of the three major themes running through these studies. It is hardly possible, in the first place, to remain unimpressed by the beauty of the uterine microcosm, the co-ordination of activity inherent in the formation of new life. Secondly, the sensitivity of the foetal body mass to nutritional regimes imposed upon the material organism is most impressive. Thirdly, however, the ability of the foetus to sustain imposed stresses, with remarkable preservation of the "interieur mileau", is an equally eminent theme. Growth proceeded along its inevitable course, attaining developmental horizons with a biological flexibility essential to survival.

Experiment A revealed the important fact that the foetus is not inviolate in early gestation. This was confirmed by Experiment B, which also demonstrated the resilience ofthe maternal organism and the way in which she offers substantial protection to her developing offspring. The energy balance between the intake of food and catabolism of body tissues on the one hand, with pregnancy requirements on the other, represents a profitable source of future investigation.

Gestation tests the integrity of every structure in the body. The foetus, however, is not entirely at the mercy of the microcosm in which it exists. Both Experiment A and B showed quite clearly that under severe stress the foetus attempts augmentation of its nutritional supply by compensatory development of placental components. Moreover, Experiment B suggested that, given the opportunity to do so, the restricted foetus possesses powers of compensatory growth and development. Time, however, dictates the issue. Premature senility of the placenta advances parturition, with the early expulsion of young into the hazards of an independent existence. Time also limits the degree of compensatory prenatal growth which is possible before birth.

The severely retarded lamb at birth is thus at a marked disadvantage in a developmental sense. These studies, particularly Experiment A, indicate that two of the tissues of importance to productivity in later life - the skin and skeletal muscle - have a restricted cell number in underfed animals. Cell size has an upper limit beyond which it cannot pass for physical reasons. It seems not unlikely, therefore, that the poor postnatal performance of animals ill-fed _in utero_ may reflect restricted cell numbers. Examination of other organs and tissues, and particularly endocrine glands, is needed to test this hypothesis. The extent to which the development of retarded tissues can continue after birth also requires careful examination. In this connexion it is necessary to recall that, under field conditions, residual effects of poor nutrition in pregnancy are manifested in the suckling period, prolonging the stress laid upon the young animal. Absence of udder development in the LP ewes of Experiment A characterises the effect of poor nutrition in late pregnancy. Experiment B, on the other hand, revealed the equally striking benefits to ewe and foetus of abundant feeding in late pregnancy.

These studies have also helped to clarify the manner in which undernutrition is manifested in terms of growth and development. Little or no evidence could be adduced from Experiment A to support the principle of a differential effect on the foetus. In the case of the ewe, further study is required of nutritional effects on a fat-free body basis. Even with the inclusion of fatty tissue, however, there was no strong evidence to support the concept of the Cambridge school. This may reflect a close association between body weight and fatness in mature animals of similar history.

Foetal sex exerted a noticeable effect on placental development and prenatal growth in both the experiments. The earliest stage of gestation at which the sex effect is manifested needs defining. Blastocyst development may proceed at a more rapid rate in males than in females; if this be true, then a genetic sex-linked action is implicated.

The larger of the two sires used in Experiment A produced larger lambs near term, with some suggestion of a genetic influence on the cell number of the Semitendinosus muscle. A larger number of animals is required for further investigation of this interesting result, for it may have important applications in genetic progress with meat producing animals.

Finally, the application of these studies to the grazing management of breeding ewes may be briefly reviewed. Experiments A and B illustrate the profound effects of the level of nutrition in late pregnancy on the ewe and, particularly, the foetus. In this connexion these results substantiate well-known facts. On the other hand, severe undernutrition in early pregnancy leads to some reduction in foetal growth rate with marked effects on the placenta. From a practical point of view it is, in fact, the latter effect which may prove of greatest importance, for restricted placental size may have repercusions later in pregnancy. Experiment B showed that fat ewes at mating could be underfed in early pregnancy with less risk of damage to the ewe and her foetus. Comparison of the results of the two experiments suggests that the ewes in Experiment A were depleted of tissue reserves by the time of mating; and that undernutrition after mating had more marked effects than in the Li/LP ewes of Experiment B. Under conditions of heavy stocking rates, a cumulative depression of the body weight of the breeding ewe can be expected, the ewe being mated in progressively poorer condition with succeeding seasons. On the other hand, the poor performance of the very fat ewes well-fed throughout pregnancy in Experiment B (He/HP) appears equally dangerous, as well as wasteful in resources.

In terms of a grazing management programme, therefore, these results strongly suggest that the breeding ewe should be fed after weaning so as to achieve the heaviest body weight possible at mating time. Advantage should be taken of both "static" and "dynamic" factors known to favour high ovulation rates. After mating, ewes should neither be fed to appetite nor subjected to gross restriction; a degree of restriction is clearly desirable but the critical level needs establishing. From 90-days of pregnancy to term the ewe requires abundant feeding to provide for the requirements of the foetus and lactation.

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APPENDIX I

PUBLISHED PAPERS RELATING TO THE THESIS

Paper No.

1. EVERITT, G.C. (1962*b*). On the assessment of body composition in live sheep and cattle. *Proc. Aust. Soc. Anim. Prod.* *4*, 79-89.

2. EVERITT, G.C. (1963). Component analysis of meat production using biopsy techniques. Section 10, pp. 1-10, In *Selected papers of Aust. C.S.I.R.O. Symposium on "Carcase Composition and Appraisal of Meat Animals"*, Melbourne, August 1963 :

3. EVERITT, G.C. (1963). Beef carcase appraisal by jointing. Section 16, pp. 1-12, In *Selected papers of Aust. C.S.I.R.O. Symposium on "Carcase Composition and Appraisal of Meat Animals"*, Melbourne, August 1963.

4. EVERITT, G.C. (1964). Maternal undernutrition and retarded foetal development in Merino sheep. *Nature* (*Lond.*) *201*, 1341-1342.

5. TAPLIN, D.E.* & EVERITT, G.C. (1964). The influence of prenatal nutrition on postnatal performance of Merino lambs. *Proc. Aust. Soc. Anim. Prod.* *5*, 72-81.

   * A graduate student contributing to the research programme of the Animal Production section in his 5th (Honours) year of candidature for the degree of Bachelor of Agricultural Science.

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Everitt, G. C. (1962). On the assessment of body composition in live sheep and cattle. *Proceedings of the Australian Society of Animal Production ... biennial conference, 4*, 79-89.

NOTE:

This publication is included in the print copy
of the thesis held in the University of Adelaide Library.

Everitt, G. C. (1964). Component analysis of meat production using biopsy techniques. In D. E. Tribe (Ed.), *Carcase composition and appraisal of meat animals : selected papers*. East Melbourne, Vic.: Commonwealth Scientific and Industrial Research Organization.

Everitt, G. C. (1964). Beef carcase appraisal by jointing. In D. E. Tribe (Ed) *Carcase composition and appraisal of meat animals : selected papers*. East Melbourne, Vic.: Commonwealth Scientific and Industrial Research Organization.

Everitt, G. C. (1964). Maternal Undernutrition and Retarded Fœtal Development in Merino Sheep. *Nature, 201*, 1341.

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APPENDIX II

EXAMPLES OF STATISTICAL ANALYSES

The tables presented in this appendix carry the following abbreviations:-

d.f. = degrees of freedom

m.s. = mean square

a.m.s. = adjusted mean square

b. = regression coefficient

v.r. = variance ratio

c.v. % = coefficient of variation as a percentage

s.e. = standard error

*** = $P < 0.001$

** = $P < 0.01$

* = $P < 0.05$

EXAMPLE A.

Treatment effects on components of ewe empty body weight after 140-days of pregnancy (2 x 2 analysis of variance).

EYES (g)

(i) Variance Analysis

Source of Variation	d.f.	m.s.	v.r.
Treatment	3	2.917	0.777
Error	12	3.750	

(ii) Effects

	Response	v.r.
HP v. LP	- 1.250	1.666
Ram L v. Ram S	0.750	0.600
Interaction	- 0.250	0.066

(iii) Mean Values

		Nutrition		
		HP	LP	Pooled
Sires	Ram L	33.5	32.5	33.0
	Ram S	34.5	33.0	33.8
	Pooled	34.0	32.8	33.4

c.v. % = 5.8

s.e. of mean ± 0.9682

EXAMPLE B.

Foetal curved crown-tail measurement (cm.) at 90-days of gestation after adjustment for the effects of foetal sex (2 x 2 covariance analysis with 1 covariate : natural data)

(i) Variance Analysis

Source of Variation	d.f.	Curved crown-tail		
		m.s.	a.m.s.	v.r.
Material nutrition (N)	1	27.977	25.929	34.763***
Sires (S)	1	0.947	1.480	2.033
N x S	1	0.305	0.071	0.096
Error$^{(1)}$	11	1.725	0.728	-

b (foetal sex) = 1.786 ± s.e. 0.4455**

(ii) Mean Values

Group	Actual Mean ± s.e.	Adjusted Mean ± s.e.
HP/Ram L	34.85 ± 0.657	34.79 ± 0.427
HP/Ram S	35.43 ± 0.657	35.37 ± 0.427
LP/Ram L	32.40 ± 0.657	32.34 ± 0.427
LP/Ram S	32.40 ± 0.758	32.64 ± 0.496

Note: (1) Error d.f. reduced to 10 for a.m.s.

EXAMPLE C.

Foetal carcass weight (g) at 140-days of gestation after adjustment for foetal sex and foetal empty body weight (2 x 2 covariance analysis with 2 covariates : $\log_e$ data)

(i) Variance Analysis

Source of Variation	d.f.	Foetal Carcass Weight			
		m.s. (x 10^3)	v.r.	a.m.s. (x 10^3)	v.r.
Material nutrition (N)	1	1971.1	146.007***	0.3285	0.213
Sires (S)	1	106.0	7.852*	0.4607	0.299
N x S	1	0.5	0.037	0.0029	0.002
Error(1)	12	13.5	-	1.5413	-

b_1 (foetal sex) = -0.00295 ± s.e. 0.000592***

b_2 (foetal body weight) = 1.0799 ± s.e. 0.1229***

(ii) Mean Values (logarithmic)

Group	Actual Means ± s.e.	Adjusted Means ± s.e.
HP/Ram L	7.596 ± 0.0581	7.184 ± 0.0527
HP/Ram S	7.421 ± 0.0581	7.167 ± 0.0344
LP/Ram L	6.882 ± 0.0581	7.147 ± 0.0346
LP/Ram S	6.731 ± 0.0581	7.132 ± 0.0531

Note: (1) Error d.f. reduced to 10 for a.m.s.