The influence of maternal nutrition on ovine foetal growth

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In recent years considerable information on ovine foetal growth has emanated from both medical research, in which the sheep has been used as a convenient experimental animal, and agricultural research, in which the main interest has been in improving the efficiency of the sheep as a meat and wool producer (Alexander, 1974). In the present paper an attempt is made to draw together some of the main findings, in particular those relating to the effects on foetal growth of under- and over-nutrition at different stages of gestation.

In reviewing the results of experiments made in early and mid pregnancy, nutritional treatments are described as either 'high' or 'low', since in many early reports this is the only description of the treatments. In an attempt at more accurate definition, where possible body-weight changes are included in the present review.

Nutrition in early pregnancy

Although the absolute increase in foetal weight in early pregnancy is very small, specific growth rates are greatest at this stage with daily weight increases of over 20% (Robinson, McDonald, Fraser & Crofts, 1977). Much of the recent work on the effects of maternal nutrition during this part of pregnancy has been done in Australia (Edey, 1966), New Zealand (Coop & Clarke, 1969) and at the Hill Farming Research Organisation in Edinburgh (Gunn, Doney & Russel, 1972). Interest has centred mainly on the degree of food restriction that can be applied before a significant increase in embryo loss is recorded. The general conclusion from the studies is that if ewes are in good body condition at mating, their embryo loss, almost all of which takes place in the first month of pregnancy, is increased only by severe undernutrition involving dietary energy intakes as low as 15% of maintenance for periods of up to 7 d. This is in keeping with the more recent studies (Blockey, Cumming & Baxter, 1974) in which fasting for up to 3 d from either day 1, 5, 8, 10 or 12 after mating (i.e. up to implantation) was found to have no deleterious effect on fertility in twin ovulating ewes. On the other hand there are isolated instances of overfeeding in early pregnancy having significantly decreased embryo survival (El-Sheikh, Hulet, Pope & Casida, 1955; Foote, Pope, Chapman & Casida, 1959*a*).

In view of the small size of the foetus in early gestation (approximately 0·3 and 5 g at 25 and 40 d, respectively; Joubert, 1956), it is perhaps not surprising that

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there are few observations on the effects of maternal nutrition on foetal weight at this stage. Hulet, Foote & Price (1969) offered ewes either 75 or 150% of their estimated maintenance energy requirements from mating until slaughter at 21 or 30 d of pregnancy without effect on foetal weight. In studies in which nutrient intakes were not accurately defined, El-Sheikh *et al.* (1955), while failing to find a significant effect of plane of nutrition at 40 d of gestation on foetal weight and crown–rump length, observed a significantly higher chorion weight in ewes offered a high as compared with a low level of feeding in early pregnancy. A similar, though not significant effect, was recorded by Foote, Pope, Chapman & Casida (1959*b*). Since it is recognized that undernutrition in late pregnancy has a greater influence on placental than on foetal size (Wallace, 1948), the above observations may well represent the first indications of undernutrition affecting the growth of the conceptus.

Nutrition during the first 90 *d of gestation*

The introduction of supplementary feed at about 90 d of gestation is widely recommended in practice. At this stage foetal weight is only about 15% of that attained at parturition some 8 weeks later; specific growth rates have declined to around 6% but absolute growth is increasing rapidly, the value at 90 d being approximately double that at 75 d. Since the studies of Wallace (1948), who found no decrease in foetal weight in ewes which lost 7% of their gross body-weight in the first 90 d of gestation through underfeeding, it has been generally assumed that feeding level in the first three months of pregnancy does not affect early foetal growth. However, Everitt (1964) exposed the danger in this assumption by recording a 10 and 30% reduction in foetal and functional cotyledon weight, respectively, at 90 d of gestation in single-bearing Merino ewes which, as a result of undernutrition, lost 12% of their gross body-weight in the first three months of pregnancy. Similarly, Curet (1973) observed that protein undernutrition in early pregnancy has an adverse effect on foetal weight at 90 d.

Unequivocal proof that the effect recorded by Everitt could be eliminated by a high plane of nutrition in late pregnancy was not obtained, in that some of the recuperated ewes aborted (Taplin & Everitt, 1964), though later results (Everitt, 1966, 1967) suggest that at least a partial compensation can occur. This is of particular interest in that it implies either an improvement in placental function, or a compensatory development of the foetal cotyledonary component (see reviews by Everitt, 1968 and Alexander, 1974), or an increase in the weight of the placenta beyond the stage of gestation at which maximum placenta weight (Stegeman, 1974) is normally observed, i.e. 90 d. Young ewes which have not reached their mature body size at mating may be less capable of compensating. Bennett, Axelsen & Chapman (1964) found that a restriction in food intake in the first 90 d of gestation sufficient to reduce body-weight by 25%, followed by a high level of feeding in late pregnancy, had no effect on lamb birth weight in mature ewes but decreased it in young ewes by 0·8 kg (24%).

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In view of the very small growth rates and nutrient requirements of the foetus up to 90 d of gestation, one questions whether the effects on growth rates of undernutrition during this period are directly due to an inadequate supply of nutrients per se or are mediated through an effect of undernutrition on the endocrine status of the dam. An increase in plasma progesterone concentration in early pregnancy as a result of undernutrition has been observed by Cumming, Mole, Blockey, Winfield & Goding (1971), and increased progesterone is known to reduce both uterine blood flow and oxygen consumption in ewes in early gestation (Caton, Abrams, Lackore, James & Barron, 1974).

Nutrition during late pregnancy

Knowledge of the degree and duration of body tissue mobilization that can be tolerated beyond 90 d of gestation without impairing the compensatory effects on birth weight of a high level of feeding in late pregnancy is of value in the management of sheep flocks under a wide range of environmental conditions, yet this is a topic that has received little attention. The only published findings would appear to be those of McClymont & Lambourne (1958), who recorded a depression in lamb birth weight in ewes subjected to an approximate 20% reduction in gross body-weight from mating to 4 weeks before lambing, followed by high plane feeding until parturition. This can only be described as very severe undernutrition and represents a weight loss double that normally observed in harsh hill environments in Britain (Russel, Gunn & Doney, 1968). Clearly more information is needed on the influence of ewe size, body fat reserves at mating and foetal load on the stage of gestation to which specific degrees of undernutrition can be applied without causing reductions in birth weight and viability.

Nutrition and foetal development. There have been conflicting interpretations of the effect of maternal nutrition on the development of the foetus. Blaxter (1957) expressed the results of Wallace (1948) on an age basis and concluded that there was a disturbance of the normal growth relationships in the lamb from the undernourished ewe. Everitt (1968), using the same results augmented with those of Taplin & Everitt (1964), regressed organ weight against foetal weight and concluded that no differential effect occurred. A similar change in interpretation was proposed for foetal growth by Fowler & Livingstone (1972) who re-analysed the prenatal growth data of Pomeroy (1960*a*,*b*) for the pig.

With this in mind further examination of Wallace's relationships between specific organ or tissue weights or both and foetal weight shows that apart from the liver and spleen, the weights of which are highly sensitive to transitory nutritional and physiological states in postnatal life anyway, there is no convincing evidence for differential effects of undernutrition on development. Similarly, observations on the size of the tissue and organs in relation to foetal weight for the undernourished lambs (64% of the weight of controls) born from ewes kept in high environmental temperatures (Cartwright & Thwaites, 1976) are in agreement with the view that evidence for differential effects of undernutrition on foetal tissues or organs is lacking. A similar conclusion can be deduced from the findings of Creasy, De Swiet, Kahanpaa, Young & Rudolph (1973), in which a 30% reduction in foetal weight through embolization of the maternal uteroplacental blood stream was observed. Even when undernutrition of specific dietary nutrients, such as protein and calcium, was sufficient to cause a 25% reduction in birth weight (Sykes & Field, 1972*a*) no evidence of differential effects on the foetus was apparent. This apparent inability to distort by nutritional means the allometric relationships which exist between specific organs or tissues and the total foetus also holds for observations made within anatomical units, e.g., the skeleton (Wallace, 1948) and the skeletal muscle (Swatland & Cassens, 1973). Thus all the evidence supports the view expressed by Everitt (1968) 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'. It should not be assumed, however, that the anatomical similarity of the undernourished newborn lamb and the well-nourished one of similar weight in utero implies that they are biochemically identical. Jones (1976) draws attention to the hormonal and biochemical changes which occur very rapidly just before natural parturition and which are intimately related to postnatal viability.

Energy intake and lamb birth weight. A useful statistic for foetal growth in late pregnancy is that irrespective of litter size a fairly constant proportion of birth weight is attained at specific stages during late pregnancy. For example, the newborn lamb from an adequately nourished ewe acquires approximately 85, 50 and 25% of its birth weight in the last 8, 4 and 2 weeks of gestation, respectively, regardless of litter size (Robinson *et al.* 1977). Estimates of the metabolizable energy (ME) requirements for pregnant ewes with a mating weight of 55 kg were presented by Rattray (1974). They were based on energy balance findings obtained by the comparative slaughter procedure (Rattray, Garrett, East & Hinman, 1974) and refer to total birth weights of 4·9, 7·9 and 9·1 kg for single, twin and triplet lambs respectively. When expressed as multiples of maintenance the requirements at days 100, 120 and 140 of gestation, respectively, are 1·2, 1·4 and 2·0 for a single foetus, 1·5, 1·9 and 2·6 for twins and 1·6, 2·1 and 2·8 for triplets. These high energy requirements are seldom satisfied in practice; indeed attempts to do so, particularly in the overfat polytocous ewe, are likely to lead to a loss in appetite, hyperketonaemia, hypoglycaemia and premature parturition (Reid, 1968).

The difference between absolute requirement for energy and that intake which, although inadequate to meet absolute requirement, does not result in a reduction in lamb birth weight and viability (see review by Thomson & Aitken, 1959) is crucial in commercial production systems; yet the differences found in experiments on the extent to which the ewe can mobilize her body reserves in late pregnancy without detriment to foetal weight are striking. This point is illustrated in Fig. 1 which presents results taken from recent publications in which both the energy intake of ewes in late pregnancy and the birth weight of their lambs are given. Three breeds contrasting in size and fecundity were chosen; the small Welsh Mountain of approximately 30 kg producing a single lamb, the Scottish Blackface weighing

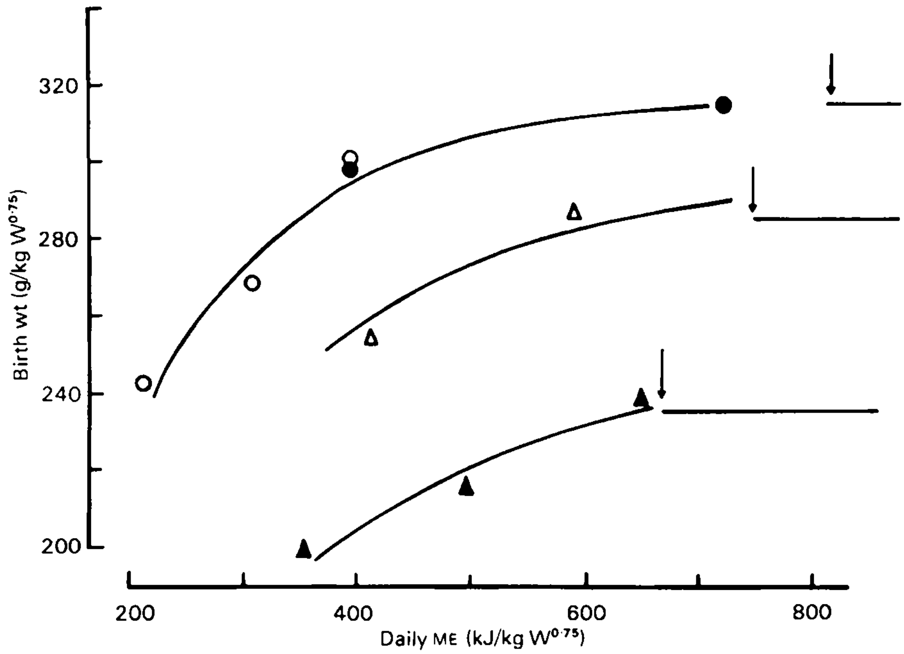

Fig. 1. The effect of metabolizable energy (ME) intake by the ewe during late pregnancy on lamb birth weight for three contrasting breeds. The data used are those of Robinson *et al.* (1973) for the Welsh Mountain (▲); Russel *et al.* (1967) for the Scottish Blackface (△); and Valdez Espinosa *et al.* (1977) (○) and Shevah *et al.* (1975) (●) for the Finnish Landrace×Dorset Horn. The horizontal lines represent the expected birth weight in relation to weight of ewe at mating (Donald & Russell, 1970). Arrows indicate the estimated ME requirements of the ewes (Rattray, 1974).

approximately 55 kg, with a mean litter size of 1·5, and the prolific Finnish Landrace×Dorset Horn weighing 68 kg with a mean litter size of 2·25. The results for each breed together with estimates of their energy requirements during late pregnancy are presented. The clearest suggestion of an immediate response in lamb birth weight to reductions in ME intake below absolute requirements is apparent in the results for the Welsh Mountain and Scottish Blackface. There is some suggestion that the Finnish Landrace×Dorset Horn may be able to tolerate a greater degree of undernutrition than either of the other breeds before a significant drop in birth weight is observed. With the limited results available for each breed it would be unwise to speculate as to whether this represents a breed difference. In fact it could be related to the body reserves of the animals for, although no information on this aspect is given in the original publications, it may be more than coincidental that of the three breeds the Finnish Landrace×Dorset Horn is likely to have the greatest internal fat depots (McClelland & Russel, 1972). Irrespective of the reason for this difference, this exercise reveals the danger of using lamb birth weight as the sole index of the adequacy or otherwise of dietary energy in late pregnancy.

Protein intake and lamb birth weight. Until relatively recently little attempt has been made to assess the specific effect of protein undernutrition on foetal growth in the sheep. Robinson & Forbes (1968) presented findings illustrating the separate effects of dietary crude protein and metabolizable energy intake on lamb birth weight and on maternal body-weight change in ewes of about 70 kg body-weight which produced twin lambs. Fig. 2 gives their results in a format which allows a ready assessment of the relative effects on birth weight and maternal body-weight change of altering dietary crude protein intake. The response was calculated at a constant daily ME intake of 12·5 MJ. For comparative purposes the effect in the same experiment of reducing dietary ME intake, while keeping digestible crude protein intake at a constant 100 g/d, is also shown. Both forms of undernutrition had a more dramatic effect on the maternal body than on the foetus, an observation which reinforces the earlier reference as to the ability of the ewe to sustain foetal growth at the expense of her own body tissues.

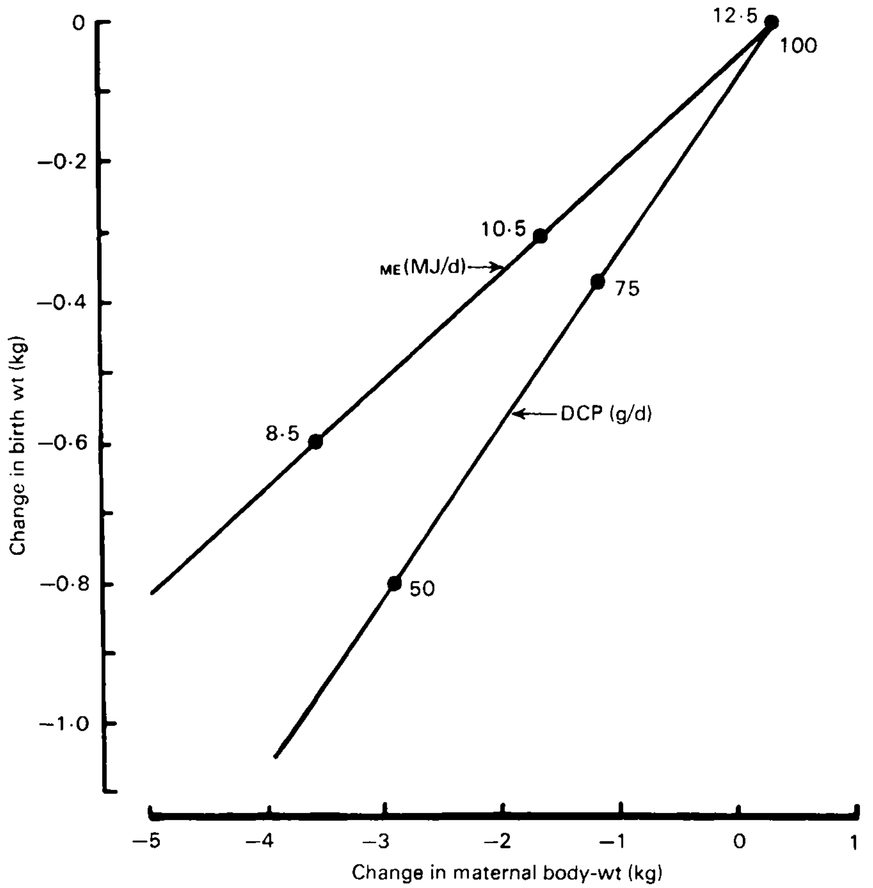

Fig. 2. The effect on lamb birth weight of altering maternal body-weight change by reducing the dietary digestible crude protein (DCP) and metabolizable energy (ME) intake of the ewe on late pregnancy. The relationships are calculated from the results of Robinson & Forbes (1968).

Evidence that the detrimental effect of low maternal crude protein intake on lamb birth weight is accentuated at low levels of energy intake has been presented by McClelland & Forbes (1968) and Sykes & Field (1972*b*). In the latter experiments the ability of the ewe to catabolize maternal tissue protein is clearly apparent in that ewes given the low protein diet lost 364 g more protein than those given the high. The corresponding reduction in the protein content of the lambs at birth was 199 g which was associated with a reduction in lamb birth weight of 809 g. An interesting feature of these experiments was that protein undernutrition had a greater effect on foetal size and thus skeletal size (Sykes & Field, 1972*a*) than had the reduction of the calcium content of the diet to a value equivalent to 18% of that recommended by the ARC (1965). This is of interest in view of the suggestion by Twardock, Symonds & Sansom (1971) that the rate at which calcium crosses the placenta in late pregnancy may limit foetal size in ewes bearing large litters.

Research into practice

The information presented in this review may well give the impression that existing knowledge on the effects of maternal nutrition on ovine foetal growth is such that gross under- or overnutrition to a degree sufficient to impair normal prenatal growth is unlikely to occur in practice. This, however, is not the case. The management as one unit of ewe flocks comprising animals with different foetal numbers inevitably leads to under- or overnutrition of individuals. Even where attempts are made to divide ewes into groups with similar foetal numbers and to feed accordingly, the competition between individuals for a limited amount of supplementary food is such that some are overfed while others are underfed (Foot, Russel, Maxwell & Morris, 1973). Similarly, a change to a higher output system involving, for example, more frequent breeding can result in early and mid pregnancy coinciding with peak grass production and may well lead to the, as yet, inexplicable phenomenon that gross overnutrition in early and mid pregnancy can cause reductions of up to 40% in lamb birth weight (D. Scott, T. E. C. Weekes & J. J. Robinson, unpublished results). For these reasons the importance of effectively integrating research findings on the effect of maternal nutrition on foetal growth and lamb viability into commercial practice cannot be overemphasized.

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