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A REVIEW OF THE INFLUENCE OF LIVWEIGHT AND FLUSHING ON FERTILITY MADE IN THE CONTEXT OF EFFICIENT SHEEP PRODUCTION

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SUMMARY

The assumption that the increases in efficiency of feed conversion normally associated with increases in fertility will accrue when the increase in fertility is achieved via increased liveweight is questioned. The biological components of fertility are reviewed as the possible limiting stages in lamb production. These are the oocyte populations and their development, ovulation rate, embryonic loss, lamb mortality and lamb growth. The interdependence of these stages is emphasized and the possible genetic relationships are illustrated from the results of published mouse selection experiments.

The current evidence on relationships between fertility and ovulation rates and liveweight is summarized. Possible developmental origins of relationships between size and ovulation rate are listed.

The remainder of the review is concerned with the dynamic effects of liveweight and summarizes the evidence on how body reserves and their hormonal control might be related to ovulation rate and the annual cycle of lamb production. The final section suggests some experimental approaches which could be used to follow up some of the ideas reviewed.

INTRODUCTION

It is the purpose of this paper to review possible underlying factors which could account for the varying relationships reported for liveweight or for nutritional effects with ovulation rates and fertility in sheep and mice. The discussion will be from the point of view of genetic and management objectives for efficient production, with the underlying conviction that these are interdependent. Cockrem (1965) indicated some of the problems and interpretations which can arise from an uncritical use of animal weights. That discussion was mainly concerned with results within a flock where liveweight reflects differences between animals which may be of genetic or environmental origin. Larger relationships are usually found between flocks or between years, when liveweight reflects a multitude of management and environmental factors which are so confounded as to be very difficult to sort out. The present review is mainly concerned with animal effects within a flock, with specific emphasis

on the possibility of maintaining lamb production when there are autumn droughts, *i.e.*, low mating liveweights.

OBJECTIVES

As efficient production is the objective, the first point to consider is the relative efficiencies of increasing lamb production with or without increasing liveweight.

Table 1 illustrates the type of information which needs to be considered. The data used are as an example only, and a full computer simulation to study the effects of varying inputs is required. For the particular exercise illustrated, the relative returns

TABLE 1: RELATIVE EFFICIENCIES OF SINGLE AND TWIN-BEARING EWES OF TWO LIVEWEIGHTS

Ewe Wt (kg)	Relative Units Lamb	Units Wool	Annual Energy (MJ)	Efficiency	Relative Output per ha*
45	1.0	0.8	2500	7.2	25.9
	2.0	0.7	2800	9.6	34.7
75	1.5	1.0	3300	7.6	27.2
	2.6	0.9	3600	9.6	35.0

* At total available energy of 36 000 MJ/ha.

assumed for the 45 kg sheep are shown as 0.8 units for wool relative to 1.0 units for a lamb. Other wool returns are adjusted arbitrarily according to increased ewe size or lamb production. The annual energy is based on maintenance requirements (0.29 MJ/kg liveweight^{0.75}) for 6 months of the year, maintenance plus additional pregnancy requirements for 3 months (Sheenan *et al.*, 1977), maintenance plus an additional lactation requirement for 3 months, and for lamb feed, apart from milk, up to weaning. The requirements are greater for ewes with twins than for those with singles. Efficiency is total unit production over total energy. The increase in lambing with liveweight is based on results summarized by Hight and Jury (1973). On these assumptions there are obvious advantages in increasing lamb numbers within a liveweight range. However, the advantage of a twin-bearing ewe is by no means twice that of a single bearer, and this could be relevant to hard hill country or a drought-prone area where limiting and not total energy determines policy.

The efficiency of meat production was examined in this way by Large (1970), who concluded that one or two lambs from

a small ewe were as efficient as three or four lambs from a large ewe.

While there may be management methods which can improve lambing percentages *within a liveweight range*, the most likely method is by genetic improvement. At present the general implication seems to be that, because there is a small genetic correlation between fertility and liveweight, we have to have larger or heavier sheep in order to get more lambs. Unless the correlation is unity this is quite untrue. Figure 1 illustrates how selection can be made within the variation round the straight line which represents a genetic or phenotypic relationship. The lower the correlation, the greater the deviations available for selection. Cockrem (1959) has shown that considerable progress can be made in six generations to obtain short-tailed, high body weight mice, and vice versa, although the genetic correlation (of the order of 0.6) is much higher than any fertility relationships. What could be more important are the results of Baker and Cockrem (1970) which showed that there was no correlated response of tail length when body weight was selected for in a specific environment (cold).

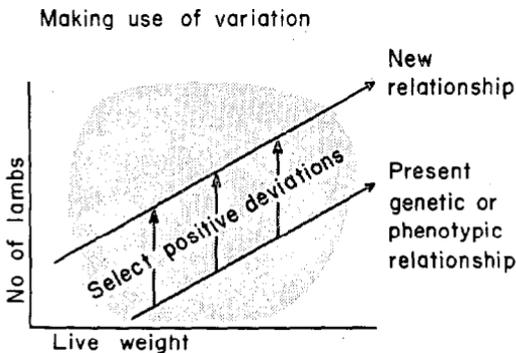


FIG. 1: *The use of variation to select for new relationships.*

More recently Eisen (1978) selected mice for increased litter size and decreased 6-week body weight, and for the traits separately. Litter size was increased without increasing body weight, but the increase was less than when the correlated response of body weight was allowed to occur.

Selection for deviations can be achieved directly or by using the appropriate weights in a selection index. However, progress would depend on the heritability of the primary factor of fertility and would therefore be very slow unless other factors of higher

heritability can be found. Along with these, a knowledge of their biological relationships with both fertility and liveweight or flushing effects could enable direct selection for the deviations required. Roberts (1979) reviewed correlated responses from selection for growth in laboratory animals and the implications for livestock.

For practical purposes such factors need to be easily measured, although this is not necessarily a good criterion for research planning. Those variables which contribute most to the productive end point, weight of lamb weaned, should have priority for consideration for genetic and management research. However, the nature of the process makes the usual ways of apportioning variation invalid, as ovulation rate, lamb loss, etc., are inter-related and sequential.

FACTORS LIMITING LAMB PRODUCTION

Figure 2 indicates key biological areas which may be or are known to be limiting in lamb production. The first main determinant is the ovulation rate (the number of eggs shed). This is clearly a limiting factor as two lambs rarely come from the shedding of one egg. Furthermore, when results are presented as averages, it is important to remember that the individual events are discrete so that the same averages may represent differing proportions of 0, 1, or more eggs shed. Although the events are discrete, underlying endocrine scales may be continuous with threshold effects, and if this is so the averages are meaningful.

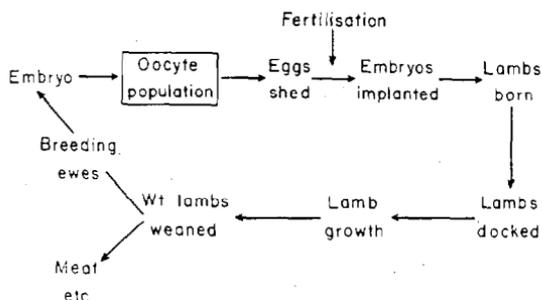


FIG. 2: Key points in lamb production.

The number of eggs shed will depend on the sensitivity of the follicle(s) to endocrine stimulation and on the extent of the stimulation itself. It may also depend on the distribution of the number of oocytes. A conceptual framework of this aspect has been given by Schwarz and Hoffman (1972). Evidence for most mammals studied so far suggests that, with a few exceptions, the

number of oocytes is determined early in foetal life and that subsequent degeneration or atresia determines the number at any particular ovulation. This aspect was discussed by Baker (1972), and all aspects of mammalian ovarian development have recently been reviewed by Guraya (1978).

Most of the work on oocyte populations has been in rodents as the number of eggs shed is sufficient to indicate differences. Pedersen (1970) described a technique for studying follicle populations and their development in the mouse and gave results on the timing of development and decrease in the pool of small follicles with age. He concluded that the growth of follicles is continuous and occurs at all times, and that the number of growing follicles depends on systems within the follicle, but that the number of these which finally ovulate is determined externally by the gonadotrophins.

For sheep, the timing of development to ovulation has been described by Dzuik (1965), while Turnbull *et al.* (1977) examined the ovine ovary but were unable to use Pedersen's technique because of "expense and practical difficulties". They concluded that, for the sheep (Merino), follicle development is continuous throughout the luteal cycle. This agrees with Allen (1961), who found that PMSG treatment did not alter the size distribution of ovarian follicles. However, Hay and Moor (1977) have found that pregnant mare's serum gonadotrophin (PMSG) acts by preventing atresia of mature follicles. Whether this size distribution of developing follicles is dependent on the primordial numbers is not known for certain, but Mauléon (1977) reviewed these and other quantitative aspects of oocyte populations and quoted evidence for genetic differences in the numbers of primordial follicles in rats. For sheep, he quoted results indicating inverse relationships between primordial follicle numbers and growing follicle numbers, with higher ovulation rates being associated with less of the former and more of the latter. This agrees with results for Merino ewes from flocks selected for and against multiple births (Turner, 1978). Trounson *et al.* (1974) examined primordial follicle numbers at birth, 7 days and 5 months. The low twinning group had more follicles but the high twinning group a higher plasma LH, and the results imply that some oocytes were formed after birth.

Once the egg is shed and fertilized, the limitation is the implantation and early development of the embryo. This can be affected by intra-uterine factors which may be related to those affecting ovulation rate. As ovulation rate increases so does loss

at this next stage; so the relationship between the two is fundamental to the study of the former. In the extreme case of selection for ovulation rate in the mouse (Land, 1970), the increase in embryo loss was balancing so that litter size remained unchanged. External factors such as temperature (Dutt, 1960) can increase loss, as can body temperature as a characteristic of the ewe itself (Cockrem and McDonald, 1969).

The next major losses are at lambing from dystocia or from "physiological starvation" in the 48 hours after birth. Both these are influenced by foetal nutrition. Hull (1977) has suggested that brown adipose tissue in the rabbit can be increased in offspring by short-period starvation of the mother. This has the effect of increasing the mother's mobilization of fatty acids and the venous-arterial gradient to the foetus. Alexander (1978) studied lipids and adipose tissue in foetuses from ewes fully or partially fed and effects of this type were not indicated. Hypophysectomized foetuses laid down considerable fat, while the normal foetuses of fully fed ewes lost subcutaneous fat during the last weeks of gestation. This suggests that there is a foetal role independent of that of the mother.

The final stage is that of the lamb growth, which is dependent on its birth weight, the milk production of the ewe, and the genetics of the lamb. Bradford (1972) discussed maternal effects, including lamb survival, and gave evidence suggesting that in a poor environment maternal effects can mask the genetic potential of lamb growth as shown in its weaning weight. He also discussed the problem of the smaller ewe being desirable for phenotypic efficiency but undesirable for passing on the genes required for the fast-growing lamb. The two objectives of fast growth for meat production and an efficient replacement ewe may not be compatible. From the efficiency point of view, twin lambs are not usually twice the weight of single lambs at weaning, although they may catch up at a later stage.

LIVEWEIGHT AND FERTILITY

While most recent work on liveweight relationships has centred on ovulation rates, this interest has arisen from possible relationships between fertility and liveweight. Within flocks it would appear that about 10%, at the most, of the phenotypic variation in overall fertility is attributable to liveweight, while the genetic correlation could be of the order of 0.2 (Young *et al.*, 1965). This latter figure may depend on selection methods or environment,

as Clarke (1972) reported no increase in weight in a Romney flock selected for high fertility, although the low fertility flock showed a downward response in weight. A major study of breed differences and liveweight relationships has been made for New Zealand hill-country flocks by Hight and Jury (1973), who included a review of work up to that date. Differences in liveweight occurred between ewes having 0, 1, or 2 lambs, but the variations accounted for by the regressions of various measures of fertility on liveweight are not given. Ewes having multiple births were lighter at weaning, although heavier at other stages.

The liveweights referred to above, being within flocks and measured at the one time, reflect differences in size and condition. Between-flock effects will reflect immediate differences in condition and long-term permanent effects on size. For these, about 40% of the differences in lambing percentages may be reflected in those factors which underlie liveweight (Coop and Hayman, 1962), frequently described as liveweight *per se* (Coop, 1966). These between- and within-flock liveweights may be related to any stage of the lambing cycle, but "flushing" effects arising from nutritional treatments prior to mating are likely to have their immediate effects on ovulation rates and embryo survival, although there could well be carryover into pregnancy or even lamb survival.

The basic data on flushing and liveweight "*per se*" are those of Coop (1966). His data from the Ashley Dene farm for first cross Border-Corriedale ewes have been recalculated as lambs born/ewes mated and are shown in Table 2. There were 200 to 250 ewes per treatment. Treatments in 1962 and 1963 were

TABLE 2: COOP'S (1966) ASHLEY DENE RESULTS AS LAMBS BORN/100 EWES MATED

	HH	HL ¹	LH	LL	Wt. Diff. HH-LL (kg)	Total Ewes
1962	162	146	152	132	11	709
1963	157 (L) ²	151 (L)	152 (H)	140 (H)	7 (max.)	728
1964	134	122	130	123	5	863
1965	125	121	116	121	7	1080
Mean 64/65	129.5	121.5	123.0	122.0		

¹H as high plane of nutrition, and L a low plane.

²3rd treatment in parentheses.

started in the December prior to mating, with an additional treatment in 1963 from the time the rams were joined.

In 1964 and 1965, treatments started for a fortnight prior to rams joining, with a changeover at this time. Overall, it would appear that the inclusion of a low treatment can decrease the lambing percentage. In general, effects were on twinning, but the Low-Low treatments increased the number of barren ewes in 1962 and 1963. However, over all the experiments the greatest number of barren ewes (10.4%) was for the High-Highs in 1965, in which year all groups showed more barren ewes. For these experiments the main differences are between years and presumably arose from causes unrelated to the flushing treatments which are summarized by the liveweight changes, although 1962 is quoted as an exceptional year for pasture growth and lambing percentage. The results can best be summarized by the author's comment ". . . it is quite clear what should not be done. That is that the ewes should not be losing condition at mating."

OVULATION RATES

The differences found by Coop (1966) could be the result of effects on ovulation rate or on later stages of the fertility cycle. While the main interest has been on ovulation rate and twinning, it should be remembered that the barren ewe problem may not just be an extreme of this scale to zero. It could also be a problem of high embryo loss. Bindon and Piper (1977) suggested a linear relationship with ovulation rates of 1, 2 or 3 leading to 1, 1.47 and 2.0 lambs, respectively — *i.e.*, increased losses with increased ovulation rates. As the laparotomy techniques to determine ovulation rates can affect losses. Hight *et al.* (1976) looked at the ovulation rate in aged ewes in relation to previous lambing performance. Their results showed that Romney ewes had lower ovulation rates and higher loss up to parturition than F1 Border Leicester-Romney cross ewes. They also found evidence of a possible relationship of liveweight and ovulation rate between years.

Relationships between ovulation rate, liveweight at autumn mating and changes in liveweight have been reviewed, summarized and reanalysed by Morley *et al.* (1978). They concluded that the main effect is of liveweight (as reflecting body condition) at the time, and that weight gain or "flushing" is likely to be effective only for animals initially in poor condition. From published evidence on ovulatory responses to lupin seed supple-

ments, they suggested that protein deficiency could be the major limiting factor.

As Morley *et al.* (1978) summarized liveweight relationships, further evidence here will be confined to other possible sources of variation in ovulation rate. McDonald and Ch'ang (1966) found a small effect on ovulation rate of oestrous cycle order (first 1.71 to third 1.88) but a larger effect from the environment in which the sheep were reared. The ewes were random bred of the same genetic origin and were brought together in December prior to the breeding season from a hill farm and a lowland farm. They were fed so as to maintain weight. Initial weights were not given. The hill-reared animals shed 4.86 eggs over three cycles and the lowland 5.76. Allison (1968) compared Romney and Border Leicester-Romney cross ewes each on two planes of nutrition from December to February to give differences of about 9 kg at first oestrus. Effects on ovulation rate were: breed 0.31, first or second oestrus 0.25, nutrition 0.1. In the experiment of McDonald and Ch'ang, the hill ewes had been moved and the experiment run in the environment of the lowland animals. Doney *et al.* (1973) reported differences in ovulation rates between homebred and purchased ewes (Scottish Blackface) and an interaction with a stress effect (6-hr daily wetting) such that this reduced ovulation rates in homebred but not purchased ewes. Stress also delayed the onset of oestrus in both groups. The experiment involved small numbers and is difficult to interpret, but it certainly suggested that management factors other than nutrition may be important. In particular, planes of nutrition leading to rapid weight losses could act through a stress effect independently of any direct nutritional effect.

Overall, the evidence would suggest that there is considerable variation in ovulation rate and lambing which is not reflected in liveweight. In particular, the importance of the effect of oestrous cycle number should always be considered in surveys and in experimental work. For sheep, Land (1974) discussed the physiological bases of possible methods of indirect selection for lambs born which do not involve liveweight. He concluded that genetically increasing ovulation rate is likely to be the quickest method of increasing lamb production.

EVIDENCE FROM MOUSE SELECTION EXPERIMENTS

Genetic studies of mice by Land and Falconer (1969) showed that selection for natural ovulation rate gave no increase of litter size because of greater embryo loss, whereas selection for induced

ovulation rate (constant gonadotrophin dose) increased litter size. Induced and natural ovulation rates had a genetic correlation of only 0.3. These results and those of Land (1970) are summarized in Fig. 3, which is based on selection experiments for litter size and body weight as well as the two ovulation rates. Selection for litter size increased body weight, pituitary activity and ovarian sensitivity (assessed by induced ovulation). Selection against litter size increased uterine losses and slightly increased ovulation rate. Ovulation rate increase on selection arose from increased pituitary activity. While body-weight increases could be associated with increased pituitary activity, this does not explain the genetic correlation with induced ovulation which must act through increased ovarian sensitivity. The whole picture is complex but suggests that ovarian sensitivity is an important factor in increasing litter size, and that natural ovulation rate is, in the mouse, to some extent in balance with uterine losses.

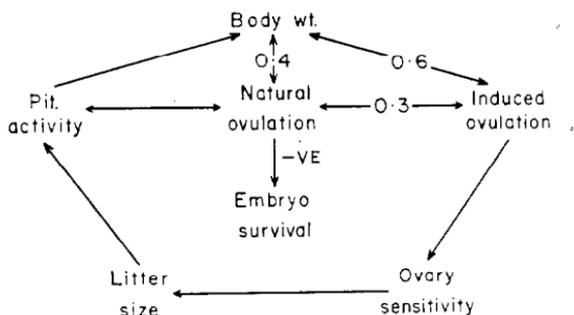


FIG. 3: Relationships between body weight, ovulation rate and litter size in mice.

Also in the mouse, Fowler and Edwards (1960) found relationships between egg number and body weight, but egg number: body weight ratio differed in the two strains being studied. However, Rahnefeld *et al.* (1962) found a zero genetic correlation between growth rate and litter size in mice.

Meyer and Bradford (1974) found that plane of nutrition affected ovulation rate similarly in three lines genetically different for this character. However, the line (G) resulting from selection for high weight gain, which also had the highest ovulation rates, had a lower proportion of females successfully mated. Bradford (1971) had already found that selection for high weight gain, while increasing ovulation rate, did not increase litter size. In experiments similar to those of Land (1970), Bradford

(1968) selected for litter size with and without gonadotrophin stimulation, and also (Bradford, 1969) for ovulation rate and for embryo survival. Selection for ovulation rate using gonadotrophin stimulation gave no response in litter size. This contrasts with Land's (1970) results. However, the normal selection for ovulation rate gave a similar result of increased embryo loss negating the increased ovulation rate, while litter size selection also increased ovulation rate. The additional experiment of selecting for embryo survival gave a direct response and a correlated response in litter size.

In contrast to all these results, Dalton and Bywater (1963) obtained no response to selection for litter size or litter weights on normal or diluted diets. Their stocks were of the same origin as Land and Falconer's (1969) and the differentials as great as Bradford's (1968). Population size and random sampling of genes could possibly account for the different results.

A recent experiment used larger populations of mice than previously for selection for and against litter size in mice for 15 generations, (Joakimsen and Baker, 1977). The results were in line with those of Land and Falconer in that increased fecundity resulted from an increase in ovulation rate alone but decreased fecundity was due to both ovulation rate and embryonic loss effects. Body-weight responses were such that they were probably associated with ovulation rate but not with embryonic loss.

Overall, these mouse experiments illustrate:

1. Variability between experiments, in particular with respect to correlated responses. There appears to be an important source of variation, interacting with other factors, which is not being taken into account.
2. The interdependence of those factors measured and the necessity of keeping a balance in order to optimize litter size.
3. That to show that a particular response (such as ovulation rate) has resulted from selection for litter size does not mean that the reverse situation is true (that selection for ovulation rate will increase litter size). In other words, the general concept of genetic correlation being independent of cause and effect does not hold for fertility problems.

LIVEWEIGHT AS SIZE EFFECTS

With this general background it is possible to consider where genetic and environmental factors might contribute to relationships between liveweight and fertility or ovulation rate. Morley

et al. (1978) pointed out that early generations of breed crosses could lead to genetic relationships from linkage effects. However, any genetic effects considered here will be those from possible pleiotropy.

Figure 4 illustrates some possibilities whereby relationships could arise biologically.

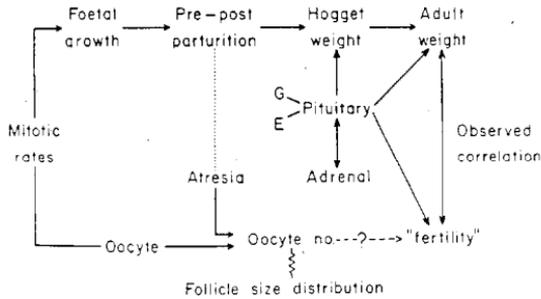


FIG. 4: Some possible origins of phenotypic relationships between fertility and liveweights.

If oocyte numbers affect the distribution of follicle size and hence ovulation rate, then key areas could be:

1. Common genetic determinants of mitotic rates affecting oocyte numbers and animal size. Falconer *et al.* (1978) has shown that for organs, such as the lung, which are related to the size of an animal, increase on selection for size results about half from increasing cell number and half from an increase of cell mass.
2. If atresia of oocytes before and after parturition is as important in sheep as in some other mammals, then growth checks at this point could result in greater atresia leading to fewer oocytes and a smaller animal.
3. Oocyte numbers may also affect pituitary relationships by feedback effects; these were reviewed by Karsch *et al.* (1977).

There is little evidence as to the importance of these aspects for sheep, and the difficulties in the techniques mean that progress in these areas is likely to be slow.

In addition, there is the necessity to explain the possible inverse relationship between primordial and developed follicles and ovulation rate in sheep. Follicle development is clearly of prime importance.

Ovarian sensitivity may reflect cell reactions to hormone stimulation, an aspect discussed by Moor and Warnes (1977). This

could be a common factor in increasing ovulation rate and total embryo survival if ovarian and uterine "sensitivity" were related as suggested by Land's results. Relationships with body growth, however, would seem more likely to arise from common pituitary effects, increasing both gonadotrophins and those hormones affecting growth. Some common effects could occur with hormones of the pituitary and adrenal which control general metabolism. Kordon (1977) reviewed the role of neurotransmitters with nor-adrenaline and serotonin (5 hydroxytryptamine) possibly having key roles in the control of hormone feedback mechanisms for ovulation. As these amines are also concerned with the regulation of many other homeostatic mechanisms, factors affecting them could have widespread effects. A possible role of such transmitters in the face cover-fertility syndrome has been suggested by Cockrem (1967). These pituitary-mediated effects could have a role in determining the onset of puberty in the hogget and hence relationships between measures of onset of puberty and subsequent fertility in the adult (Ch'ang and Rae, 1970). These effects could be genetic or environmental but are likely to differ from those caused by an extremely low plane of nutrition which could have numerous other effects.

LIVEWEIGHT AS "DYNAMIC" EFFECTS

The relationships shown in Fig. 4 are those which could lead to the association between the size of an animal and fertility, in particular from selection. This would be a part of the background to Coop's (1966) liveweight *per se*. The other part and the possible dynamic effect are shown in Fig. 5. This illustrates the annual cycle of liveweight in relation to events associated with fertility.

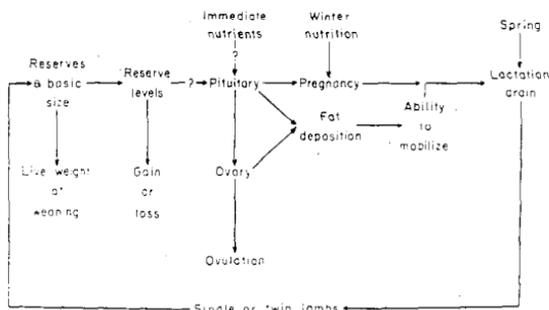


FIG. 5: The annual cycle of adult ewe liveweight in relation to lambing.

Taking the weaning of the previous year's lambs as the start of the cycle, then there is a ewe of a basic size of muscle and bone and a variable addition of fat and water which will determine its liveweight, along with a variable gut content correlated with current intake. However, the key variable will be the energy reserves, which will be mainly fat. At the point of starting the cycle, under New Zealand farming conditions there will usually have been adequate feed and the energy reserves will be dependent on previous events over the winter, the lactation drain and the number of lambs the ewe has reared. A key factor may be the animal's ability to metabolize and put on more reserves as the lactation drain decreases. Early weaning practices could be relevant here from this point of view and from the possibility of prolactin secretion levels affecting subsequent ovulation (Thorner, 1977).

Depending on feed availability and the animal's ability to use feed over the summer, the reserves at weaning will be related to those during the mating season; thus the liveweight *per se* will reflect the basic size of the animal together with these reserves. This effect of reserves versus size can be seen in the results of a trial by Inkster reported by Wodzicka-Tomaszewska *et al.* (1968). Ewes on high and low planes of nutrition on the hills for 4½ years were brought together for fat lamb production. Liveweights for first 4½, next 1, and next 4 years were: high plane 48, 52, 50 kg; low plane 35, 41, 46 kg. The low plane sheep were smaller but they probably had the greater reserves in these last 4 years, when animals reared on high and low planes had the same lambing percentages and proportion barren in spite of large differences in the earlier years. For extremely low planes of nutrition, stress effects on ovulation may be as important as nutritional effects, particularly if the starved grazing sheep has the much higher maintenance requirement suggested by Farrell *et al.* (1972).

Frisch (1977) has suggested that the proportion of fat in the body is associated with puberty and reproduction in the human and the rat, and that this is more important than size. Bentley (1976) compared the endocrinology and reproduction of a wide range of mammals and showed how gonadal growth and fat deposition may be related through the hypothalamus in birds. While this has evolved in relation to the breeding and migratory patterns in the avian species investigated, the broad outline of control mechanisms is fairly similar in all vertebrates. Feral sheep had to deal with a fluctuating food supply, and considerable

migrations occurred even after early domestication. It would seem a reasonable hypothesis that pituitary release of gonadotrophins at the luteinizing phase might be affected by the level of fat reserves in the animal. The anabolism and catabolism of body reserves may well be affected by the light and temperature periodic effects which control breeding in a sheep. In this context it is of interest that Radford (1959) found a major annual variation in the incidence of twin ovulations in Merino sheep although they were kept at a constant body weight.

This is a complex area, as the total endocrine balance will not only be affected by the level of feeding, the season, and the body reserves, but will also vary with the genetic makeup of the animal. When the egg is implanted and the *corpora lutea* maintained, then the changed hormone balance is such that fat deposition occurs, presumably as an adaptation for possible feed shortages late in pregnancy.

These possible body-reserve effects could be separate from an immediate flushing effect of a short-term, high energy, high-protein or specific amino acid intake. Morley *et al.* (1978) discussed possible effects of protein and suggested that it can be limiting, but that an excess has no effect. This agrees with the results of Corbett and Edey (1977), who used formaldehyde-treated casein to increase blood urea and amino acid concentrations in the plasma but found no increase in ovulation rates or mean follicle diameters.

Smith *et al.* (1979) showed that liveweight changes do not reflect all the nutritional effects that may have important influences on ovulation rate.

Cumming *et al.* (1975) found higher embryo survivals at maintenance feeding than at 25% of maintenance or twice maintenance. The latter could have increased embryonic mortality by a raised metabolism and body temperature. They also found that survival was higher in crossbred sheep than in purebred sheep.

As pregnancy proceeds, reserves will be built up and then used, with the major use coming in the period of early lactation. Thus, from the stage of early embryo development onwards, the key attributes for the ewe are, first, ability to lay down reserves, then a minimum maintenance requirement as feed becomes short, and then an ability to mobilize the reserves. Panaretto (1964) has found variation between sheep in this latter ability, and this could be important for lactation and possibly for maintaining gradients of fatty acids to the lamb for its build-up of reserves prior to birth, as suggested by Hull (1977). Apart from these

physiological considerations, the use of actual liveweight could obscure the fact that the large ewe with limited reserves is the one requiring the most feed. A further important point is that increased hydration of tissues in late pregnancy can mask losses of body fat (Robinson *et al.*, 1978).

The combination of the ewe's phenotype, the number of lambs it has produced and reared, and the feed available over the period then brings us back to the starting point of the reserves available at the time the lamb(s) are weaned. Thus the concept offered is one of the ability of the ewe to lay down and mobilize body reserves in relation to feed available and the breeding cycle. This replaces liveweight *per se* and dynamic effects of an infinite variety of feeds. Under this concept the basic size of the animal should be considered as a separate problem in relation to fertility and production, in that we can probably breed for any size relationship that we require. In this context the key determinant of size is probably the genotype passed on to a lamb whose optimal size is determined by the meat market rather than biological requirements.

POSSIBLE EXPERIMENTAL APPROACHES

Discussion of this sort offers explanations for observed relationships and data, and while it offers a background to interpretation it is of real use only if the important hypotheses arising from the discussion can be tested in both field and experimental conditions. More knowledge is needed of the factors limiting lamb production in those New Zealand Romney ewes which have low fertility, as genes from this breed will be a major part of the gene pool for a long time, whatever outcrossing programme is practised. However, information and possibly some genes from elsewhere will enable faster progress. Knowledge comes from contrasts and differences, in particular in relationships.

Thus studies of sheep which differ from the Romney may give us methods and variables for use with the Romney or its crosses. Information from research on the Booroola (Allison, 1979; Piper *et al.*, 1979) could be as important as the genes contributed by this strain to the national flock. The Ruakura fertility selection flock also has further potential as a source of information (Clarke, 1972).

There are also sheep which breed as hoggets at a low liveweight, which rarely have twins but may also rarely be infertile, and which are likely to be highly efficient at handling their body reserves. These are the feral sheep which have been running under

natural conditions for up to 50 years and been subjected solely to natural selection. Examples are those from Campbell Island and from the Hokonui area, north of Invercargill. Studies of their metabolism over the annual cycle could produce valuable information on the things to look for in commercial sheep. There are some feral Romney sheep also available, while the Marshall Romney sheep are reputed to result from mainly natural selection with respect to lamb survival.

The interaction of these breeds with different environments in terms of feed and other factors such as environmental temperature should be informative if the various techniques discussed by Land (1974) are used to look at the physiological pathways involved. It seems unlikely that oocyte populations can be looked at in more than a small number of sheep, but their importance might be assessed in terms of the developing larger follicles only, in order to study breed and treatment differences. Ovary sensitivity could be studied by the use of unilateral ovariectomy and the use of exogenous hormone treatments. LH, FSH and other endocrine levels can be assessed in the plasma with suitable sampling precautions. For larger-scale experiments, ovulation rates and lambs born can be informative if considered together.

For liveweight relationships, the key measurements are those which distinguish basic size from fat storage (which will vary over the year). The simplest of such measurements is the height at withers, which is not strongly related to liveweight. The relationship of such measurements to weight either between experimental groups or within groups at different times would be a simple method for large-scale field experiments, but the interpretation would be difficult unless more detailed data were collected on smaller groups. For example, studies using the "Danscan" system (Bass, 1979) would enable the changes in fat in individual animals to be followed over the year.

More detailed techniques will give indications of the protein or energy status of an animal and of whether reserves are being mobilized. Payne and Laws (1978) have shown that certain tissue enzyme levels can reflect the protein status of a sheep, but at present these determinations require liver biopsy and would be unsuitable for repeated sampling. Cholesterol is a common factor in lipids and hormones and could be of particular interest. Genetic variation in and relationships with concentrations in plasma of cattle have been discussed by Edfors-Lilia *et al.* (1978). Changes in plasma concentration of this compound and of urea

and albumin could be informative on genetic and metabolic responses to seasonal feed changes and should be reasonably easy to obtain. Plasma can be obtained a number of times from the same animal and interpretation based on changes rather than the absolute values which have caused difficulties with the "metabolic profile" approach (Wolff *et al.*, 1978). Results of this type require care in interpretation as blood volumes affect all concentrations and these can also change with feed and season. Sykes and Field (1974) have demonstrated the effect of blood volume variations in hill sheep in Scotland, but also showed that there were effects of stage of pregnancy and feed on albumin levels.

The relationships of this type of parameter to the known components of litter size for different breeds, groups, and treatments could be very informative in finding appropriate measurements for selecting highly fertile animals for a variety of environmental conditions.

With this type of information it might be possible to make an accurate selection of the types of sheep required for widely differing environments and determine the biological requirements for their optimum productivity.

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