Review

Litter size, ovulation rate and prenatal survival in relation to ewe body weight: genetics review

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Abstract

Lamb’s birth weight and litter weight were found to be related to ewe weight. Deviations from generally applicable formulae indicated an interaction between the genotype of the lamb and the maternal environment, as suggested in egg transfer experiments. Land’s (1977) hypothesis on the spare conceptus capacity, when comparing large and small breeds within a species, with respect to prolificacy, was more applicable to genetically homogeneous groups within a breed than between breeds and lines within a breed. A hypothesis suggests that variation in the within breed genetic correlation between ewe weight and prolificacy may largely depend on the relative uniformity of selection criteria applied. It can further be argued whether selection based on body weight or growth rate, compared to selection on reproductive performance, could be important sources of within breed as well as among breed variations in the genetic correlation estimates between ewe weight and prolificacy. The dynamics of the genetic correlation between ewe weight and prolificacy has an effect of long-term selection for body weight, growth rate and reproduction traits. This leads to the problem of the relative incompatibility of selection of an association between body proportions with reproductive traits, especially in meat type breeds. There is a parallelism or antagonism in the genetic correlations between ewe weight and prolificacy as compared to those between ewe weight and other reproduction traits. The within breed relationship between ewe weight and ovulation rate was found to be positive in some breeds. The effects of body condition at mating were contradictory. Genotype × environment interactions were observed in certain cases. Among most breeds, differences in ewe weight were unrelated to differences in ovulation rate. There were no relationships between ewe weight and prenatal survival within breeds or in lines within a breed. However, there exists a differential relationship between ovulation rates and prenatal survival rates in relation to ewe weight, depending on the selection criteria applied. A clearcut relationship between litter weight components and ewe weight cannot be generalized but may vary among differentially selected breeds and lines within them. This is a final, unifying and unresolved question.

Keywords: Ovulation; Survival; Prolificacy; Body weight; Sheep

1. Introduction

In a review of the genetic variation associated with prenatal survival and ovulation rate in sheep, Michels et al. (1998) concluded that the hypothesis which assumes the presence of a substantial genetic variation in the ovulation rate of ewes but not in their ability to carry to full term a given number of fertilized eggs, cannot be generalized. There was a significant variation in prenatal survival within breeds, mainly due to differences among lines within breed, and in the uterine efficiency among breeds and their crosses.
resulting from a marginal increase in prolificacy due to increased ovulation. The relationships among prolificacy, ovulation rate, prenatal survival and ewe weight before or during mating have been extensively reviewed (Cumming et al., 1975; Bradford et al., 1974, 1986a,b; Meyer and Clarke, 1982; Meyer, 1985; Hare and Bryant, 1985; Dodds et al., 1991; Nawaz and Meyer, 1991). A number of reviews have been limited to either the relationships between body weight of the ewe at mating and of their newborn offspring (Donald and Russell, 1970), or the more general relationship between maternal effect and neonatal weight among and within mammalian species (Leitch et al., 1959; Land, 1977). The objective of the present study is to review prolificacy, ovulation rate and prenatal survival in relation to ewe weight. The biological basis of the relationships between prolificacy and ewe weight among and within sheep breeds will be assessed. Ovulation rate and prenatal survival will be examined in relation to ewe weight, taking into consideration the possible effects of body condition and plane of nutrition, between and within breeds, lines and their crosses.

2. Litter weight and lamb weight at birth in relation to ewe weight

There was a relationship found between ewe weight after lambing and the birth weight of their newborn offspring when comparing Border Leicester and Welsh Mountain ewes. When fertilized eggs were transferred from Border Leicester ewes weighing 64–82 kg at maturity to Welsh Mountain ewes weighing 36–46 kg and vice versa, the mean birth weight of three Border Leicester lambs born to Welsh Mountain ewes was 19% lower than the three Border Leicester lambs born to Border Leicester ewes. Correspondingly, the mean birth weight of five Welsh Mountain lambs born to Border Leicester ewes was 15% greater than the four Welsh Mountain lambs born to Welsh Mountain ewes. These results showed that breed of the lamb and the maternal effect arising from changing the intra-uterine maternal environment by transferring the ova were important factors while the sex of the lamb had no significant effect (Hunter, 1957).

In another study involving egg transfer (Dickinson et al., 1962), the size of the lambs from a larger genotype (Lincoln: 74–90 kg body weight) was affected to a larger degree by the different maternal environments than were lambs of a smaller genotype (Welsh Mountain: 40–46 kg body weight). In the maternal environment of Lincoln ewes, lambs were on an average 22% heavier compared to those derived from egg transfer to Welsh ewes. In contrast, Welsh lambs were 9% heavier compared to those derived from egg transfer to Lincoln ewes. When eggs were transferred to the common maternal environment of 1.5-year old nulliparous Scottish Blackface ewes weighing 46–51 kg, the Lincoln lambs derived from egg transfer were smaller than not-transferred Lincoln lambs at birth. Correspondingly, the Welsh lambs derived from egg transfer were similar in size to not-transferred Welsh lambs. Comparatively, the larger Lincoln lambs were still invariably heavier at birth than the smaller Welsh lambs in this same maternal environment. This suggests the presence of an interaction between the genotype of the lamb and the maternal environment.

In an egg transfer study of seven sheep breeds of varying mature weight, Bradford et al. (1974) compared birth weights predicted from mature ewe weights in each breed using the formula developed by Dickinson et al. (1962), according to which lamb weight at birth and litter weight were related to the mature weight of the donor \(D^{0.83}\) and the recipient \((R/D)^{0.83}\). There was a good agreement between predicted and observed litter weights in a number of groups. In contrast, Finnish Landrace lambs had litter weights that were on an average more than a kg lighter than the predicted weight, a highly significant difference. The deviation in birth weight of Finnish Landrace lambs was evident in pregnant Finnish Landrace as well as Welsh Mountain ewes. When compared at a constant prolificacy in their native uterine environment or in a common recipient breed, Finnish Landrace lambs were consistently lighter at birth than Southdown and Merino lambs although mature weight of the Finnish Landrace was higher. The Merino exceeded its predicted litter weight at birth by more than a kg, a difference approaching significance in spite of small numbers.

In another study of 15 breeds of sheep from naturally mated flocks (Donald and Russell, 1970), average regression coefficients between litter weight and ewe weight were 0.721 for singles and 0.741 for twins.
Corresponding estimates in the triplets from a smaller number of ewes and a fewer breeds were 0.773. Although ewe weight at mating increased from small to large breeds, litter weight at birth did not increase proportionally, at least in singles and twins. Consequently, the predicted birth weight of a lamb born as a single was 9.6% of a 25 kg ewe but was only 6.5% of a 100 kg ewe. Corresponding values for lambs born as twins were 15 and 11%, respectively. In general, the ratio of litter weight among singles, twins and triplets were 1.0, 1.6 and 1.85, respectively at constant ewe weight.

In the Romney (65.4 kg) and Corriedale (68.1 kg) ewes, 2.5-years old at breeding, the relationships between litter weight and ewe weight were 7.0 and 7.6%, respectively, for singles, and 11.6 and 11.5%, respectively, for twins. Corresponding values in the 2.5-year old Welsh Mountain ewes (25 kg) were 10.0% for singles and 15.8% for twins (Leitch et al., 1959). According to Land (1977), individual birth weight, expressed as a percentage of the dam’s body weight among most species, was about 5% varying from 3 to 10%. However, the pig was an exception to that generalization. This relatively constant relationship between individual birth weight ($Y_1$) and the dam’s body weight ($X$) among species can be expressed as $Y_1 = aX$, where the empirical relationship between litter weight ($Y_2$) and the dam’s body weight for 114 mammalian species could be predicted as follows: $Y_2 = 0.5408X^{0.8323}$ (Leitch et al., 1959). Land (1977) assumed that among species, one of the consequences of litter weight being related to a lower power of the dam’s body weight than was individual birth weight was that litter size must decrease as the dam’s weight increases. Within species however, where larger breeds tended to produce larger litters, the reverse relationship occurred. The answer to this paradox was found in the duration of pregnancy. Since the gestation length of a species is positively related to adult body weight, the foetuses of larger species take longer to grow from conception to around 5% of their adult weight than those of smaller species. A species, however, is potentially an interbreeding group. Therefore, within a species, the duration of pregnancy remains constant. The range of the body weights between breeds among most of the species should, therefore, be restricted by the ability of the foetus to grow rapidly to achieve more than 3% of maternal weight, and survive. Furthermore, it should also be restricted by the ability of the foetus to grow slowly to achieve less than 10% of the maternal weight and avoid difficulties during parturition. With larger breeds giving birth to relatively smaller offspring and small breeds to relatively larger offspring, there would be spare conceptus capacity in the large breeds, but inadequate capacity in the small breeds. With this relationship it was argued that natural selection would favor the birth of numerically larger litters from the heavy breeds and vice versa.

3. Prolificacy in relation to ewe weight

3.1. Comparison between breeds

The prolificacy in the Welsh Mountain sheep, the smallest hill breed, was 1.22, 1.58 and 1.73 in the first, second and third parities, respectively. In contrast, the prolificacy in the Lincoln sheep, with double the body weight of the Welsh Mountain, was 1.38, 1.73 and 1.74, respectively. Correspondingly, Lincoln ewes were less prolific with higher body weight than either the Scottish Blackface (1.75, 1.95 and 2.11) or the South Country Cheviot (1.46, 1.86 and 1.89). The South Country Cheviot and Scottish Blackface ewes with similar body weight were significantly different in prolificacy (Wiener, 1967). Prolificacy at first breeding in 3-year old ewes was similar in three breeds of Javanese sheep (1.54, 1.55 and 1.20) weighing 25.6, 24.9 and 22.2 kg, respectively (Bradford et al., 1986a). The New Zealand Oxford ewes were heavier than Texel and Finish Landrace ewes at weaning (100:92:89%, respectively) and as yearlings (100:93:88%). However, the prolificacy of hoggets was higher in Finnish Landrace ewes (2.1) than in Texel (1.3) and Oxford (1.0) ewes, after being subjected to the same gonadotrophic treatment (McMillan et al., 1988).

In a study of ewes from three synthetic (Canadian, Outaouais and Rideau) breeds and purebred Suffolk and Finnsheep (Demirören et al., 1995), Suffolk ewes that weighed significantly more than the synthetic Canadian ewes were similar in prolificacy. Finnsheep ewes weighed 8.9 kg less at breeding than Rideau ewes, but were significantly more prolific and 19% higher in fecundity. Suffolk ewes weighing 15.7 kg
more than Finnsheep ewes were significantly lower in prolificacy, fertility and fecundity (1.0 lamb, 24 and 106%, respectively). The Outaouais, Rideau and Finnsheep ewes (189, 190 and 209%, respectively) were more fecund than the Canadian and Suffolk ewes (128 and 103%, respectively). This is consistent with results from an earlier crossbreeding study (Shrestha et al., 1992). There appeared to be no clear relationships between prolificacy and ewe weight among breeds. Moreover, there appeared to be a negative relationship when fecund type ewes were compared with meat type ewes.

3.2. Relationships among and within breeds

The weighted average genetic correlations between ewe weight and prolificacy at various ages ranged from −0.46 to 0.78 with a mean value of 0.41 (Fogarty, 1995). Corresponding estimates in the Norwegian breeds and the Cheviot breed weighed at weaning were −0.46 (Gjedrem, 1996) and −0.11 (Eikje, 1975). Similarly, in New Zealand Romney ewes the genetic correlation was −0.20, but between ewe weight at 13 months and prolificacy for 2-year old ewes it was 0.13 (Baker et al., 1982). Majority of these estimates had higher standard errors and were not significant. In Merino sheep selected for high and low weaning weight, no difference in multiple births was observed (Pattie, 1965). Brien (1986) concluded that estimates of genetic correlation between reproductive performance and body weights at weaning or before weaning were probably unreliable, as these weights were confounded with maternal effects.

In other Merino ewes there was a positive genetic correlation of 0.35 between ewe weight at weaning and prolificacy and of 0.60 between hogget weight and prolificacy (Davis, 1987). In the same breed, Mortimer and Atkins (unpublished, see Fogarty, 1995) reported lower estimates of 0.03 between hogget weight and prolificacy compared to 0.10 for ewe weight at weaning. In crossbred ewes derived from the Romanov and Berrichon du Cher breeds, estimates between ewe weight at 70–90 days and prolificacy at first lambing were 0.15–0.11 in F2 ewes and 0.17–0.15 in F3 ewes (Ricordeau et al., 1982).

Though not significant, the genetic correlation between ewe weight after weaning and prolificacy was 0.37 in the Lacaune breed (Ricordeau et al., 1986), 0.65 in a synthetic sire strain and two dam strains (Shrestha and Heaney, 1987), 0.30 in the Rambouillet (Waldron and Thomas, 1992), 0.41 in the Blackface and 0.78 in the Welsh Mountain (Purser, 1965), 0.65 in the Scottish Blackface (Atkins, 1986). In a study of nearly 1300 Clun Forest ewes with about 4800 lambing records over 5 years, the genetic correlation between premating ewe weight and prolificacy was 0.21 (P > 0.05). Nevertheless there was a tendency for premating ewe weight to be positively correlated with prolificacy, whereas the estimate for fecundity was 0.04 and possibly independent (Forrest and Bichard, 1974).

In mature ewes from the Cambridge breed selected for prolificacy and milking ability, the genetic correlation between ewe weight at mating and prolificacy was 0.40, based on a multiple age analysis over a 12-year period (Owen et al., 1986). In the Tygerhoek Merino flock the genetic correlation between mature premating ewe weight and the subsequent number of lambs per ewe conceived ranged from 0.36 to 0.89 in the selection population. Corresponding estimates from the selection and control populations were lower, ranging between −0.07 and 0.69. There was a tendency for similar estimates between premating ewe weight at 1.5 years and average lifetime performance per ewe conceived (Cloete and Heydenrych, 1987). This difference is in line with the contradictory results in Galway ewes from Hanrahan (1976) and More O’Ferrall (1976), although it should be mentioned that the latter author studied ewe weight at 18 months in relation to the number of lambs born per ewe mated at the subsequent lambing. The correlation of 0.85 was estimated from a selection flock of Galway ewes maintained over a 6-year period. Hanrahan (1976) on the contrary compared the average prolificacy of selected Galway ewes with the mean prolificacy of contemporary control flock ewes and found no evidence of a genetic correlation.

On the contrary, in unselected ewes of the Hyfer breed, a new composite breed that varied considerably in ewe weight, the genetic correlation between ewe weight at 12–18 months and prolificacy in an accelerated eight monthly lambing system was −0.19 (Fogarty et al., 1994). Correspondingly, in Canadian ewes, a meat-type sire breed developed from a crossbred foundation and selected primarily on indi-
individual lamb growth, the estimate was $-0.28$. Corresponding estimates in Outaouais and Rideau ewes, both fecund-type dam breeds also developed from a crossbred foundation and selected primarily for prolificacy with lesser emphasis on lamb growth, were 0.12 and 0.21, respectively. The ewes were also held under conditions of an 8 month breeding cycle and artificial rearing of lambs (Hansen and Shrestha, 1999).

3.3. Relationships among lines within breeds

In three fertility lines (prolificacy, high $= 1.67$; low $= 1.17$; control $= 1.28$) initiated from a flock of 1,000 Romney ewes (Clarke, 1972), the body weights at mating in mature ewes were 2–3 kg higher in the high fertility line than those in the low line. But the control line was the heaviest, probably because heavier sheep were selected in the earlier years, whereas the high and low lines were selected exclusively on reproduction performances (Meyer and Clarke, 1982).

In grade Targhee ewes allocated at random for selection at 120 day body weight and the control groups, both of them in two different environments (Lasslo et al., 1985a), fertility and lamb survival decreased in the weight-selected lines, especially in the last four generations (Lasslo et al., 1985b). In the subsequent generations, the lines began to diverge in prolificacy from each other and from the control lines, only after 18 years of selection (Quirke et al., 1985). In a follow-up study of mature ewes, prolificacy in one weight selected line was 1.43 compared to 1.26 in the other line ($P < 0.05$). Prolificacy in the former line was similar to that in a line selected for multiple births and higher ($P > 0.05$) than the two control lines, 1.33 and 1.37 (Bradford et al., 1986b). These data on the Targhee breed reinforce the fact that differences between lines and genotype environment interactions can occur only after many years of selection.

The deviations and variations in the weight of individual offspring as a proportion of the dam’s weight found among and within breeds probably explain why Land’s hypothesis on the spare conceptus capacity in large and small breeds within a species, with respect to prolificacy, was not unequivocally confirmed in the comparison among breeds and lines studied. Probably, the possibility of producing more and smaller offspring from smaller breeds was underestimated, as shown in three Javanese sheep breeds with mature weights under 30 kg and a prolificacy up to 4 or 5.

3.4. Fecundity compared to prolificacy in relation to ewe weight

There have been a number of estimates published on the genetic correlation between ewe weight and fecundity (Young et al., 1963; Kennedy, 1967; Shelton and Menzies, 1968; Chang and Rae, 1972; Forrest and Bichard, 1974; More O’Ferrall, 1976; Blair, 1981; Baker et al., 1982; Cloete and Heydenrych, 1987; Davis, 1987; Fogarty et al., 1994). Fecundity is a complex trait containing fertility and prolificacy, therefore trends on these two components are of interest.

In Romney ewes the genetic correlation between ewe weight and fertility was $-0.46$ at weaning, and $-0.34$ as yearling. Corresponding estimates with prolificacy were $-0.20$ and 0.13, respectively (Baker et al., 1982).

In Merino ewes on the contrary the genetic correlation between fecundity and ewe weight was 0.25, but 0.09 for adult weight, which was lower. In contrast, for prolificacy the estimate increased from 0.35 for ewe weight at weaning to 0.66 for adult weight. In this breed, a negative genetic correlation of $-0.30$ was estimated between adult body weight and fertility (Davis, 1987).

In the Hyfer ewes, a genetic correlation of 0.01 between adult body weight and fecundity probably is a consequence of a negative estimate of $-0.19$ for prolificacy and a positive estimate of 0.63 for fertility (Fogarty et al., 1994). In the Tygerhoek Merino flock, however, the estimates for the number of lambs per ewe conceived and fecundity were similar in the two sets of data (Cloete and Heydenrych, 1987).

In the synthetic Canadian Arcott, Outaouais and Rideau ewes the genetic correlation estimates between ewe weight at mating and fecundity were 0.29, $-0.55$ and 0.33, respectively, and not significant (Hansen and Shrestha, 1999). The negative estimate in the Outaouais ewes compared to the positive estimate for prolificacy (0.12) was in agreement with earlier reports on fertility and prolificacy in this breed. Similarly, fertility was significantly lower and prolificacy
significantly higher than in the Rideau ewes (Demirören et al., 1995). As a result fecundity did not differ between these two synthetic breeds, both selected primarily for prolificacy, although body weight at mating was significantly lower in the Outaouais ewes.

4. Ovulation rate in relation to ewe weight

4.1. Relationships within and between breeds, lines within a breed and crosses

In mature Merino ewes, ovulation rate was relatively constant when the ewe weight was below 35–37.5 kg at mating. In heavier ewes, an increase of 2.5 kg was associated with a 5% increase in ovulation rate up to 53.5 kg, and a 10% increase per 2.5 kg within the range 40–48 kg. A 3% gradient still existed at 55 kg but the numbers of ewes above this weight were considered inadequate to allow firm conclusions (Edey, 1968). Among mature Targhee ewes, the ovulation rate as a deviation from the two control lines was 0.20 and 0.19 \((P < 0.05)\) at first oestrus in two lines selected for increased 120 day body weight, and 0.16 in a line selected for multiple births. Body weight within line had a significant influence on ovulation rate, the number of \(\text{corpora lutea}\) increased by 0.024 and 0.034 per kg body weight for first and second cycles, respectively (Quirke et al., 1985).

In Barbados ewes the ovulation rate was 1.86 at first and 2.04 at second oestrus. Corresponding estimates in the Barbados × Targhee ewes were 1.93 and 2.04, respectively, and in Barbados × Dorset-Targhee ewes 1.72 and 1.80, respectively. In Targhee ewes they were lower: 1.29 and 1.40, respectively \((P < 0.01)\). Targhee ewes (54.4 kg) were significantly heavier at sponge removal than Barbados ewes (30.9 kg), the crossbreed ewes being intermediate (44.9, 43.5 kg). The significant regression estimate of ovulation rate on body weight was 0.049 \(\text{corpora lutea/kg at first, and 0.046 at second oestrus (Bradford and Quirke, 1986). In three Javanese sheep breeds, there was a significant difference in ewe weight at sponge removal but ovulation rate at first or second oestrus did not vary (Bradford et al., 1986a).}

Body weight of ewes with two ovulations was 3.6 kg heavier at 1.5 years of age, 5.1 kg at older ages compared to ewes with one ovulation in prolific flocks of Romney, Coopworth and Perendale sheep. The 1.5-year old ewes with three ovulations were 0.6 kg heavier than ewes of the same age with two ovulations \((P > 0.05)\). Older Romney and Perendale ewes with three ovulations were 3.3 kg heavier than ewes with two ovulations but in older Coopworth ewes the difference of 0.6 kg was not significant (Davis et al., 1987).

There have been two reports of genetic correlation between ewe weight and ovulation rate (Fogarty, 1995). The genetic correlation between ewe weight and ovulation rate at 6–7 months of age in the Ramboullet breed was estimated at 0.21 when weight records of all ewes were included. Deletion of body weights from ewes with no record on prolificacy or ovulation resulted in an estimate of 0.36 (Waldron and Thomas, 1992). In Merino ewes, the corresponding estimate between ewe weight after weaning and ovulation rate was −0.13 (Mortimer and Atkins, unpublished; see Fogarty, 1995).

4.2. Ovulation rate in relation to ewe weight, size and condition and/or plane of nutrition at mating

Ducker and Boyd (1977) argued that ewe weight ‘per se’ was not a good indicator of ovulation rate in Greyface ewes. In spite of the larger ewes being 25% heavier than the smaller ewes, the mean ovulation rates of the two groups were almost identical. At the same body weight, the smaller ewes in improved body condition had a significantly higher mean ovulation rate than the larger ewes in poor body condition. The scoring procedure was based on the degree of fatness (Meat and Livestock Commission, 1973).

In Australia (Guerra et al., 1972), large Merino ewes had more multiple ovulations than the smaller ewes (14/47 versus 6/53; \(P < 0.01)\). To examine the effects of ewe weight on ovulation rate, the ewes were divided into five weight classes ranging from 27.5 to 64 kg. There was a significant linear relationship between ovulation rate and ewe weight or body size \((\text{width} \times \text{length} \times \text{depth})\), but not between ovulation rate and body condition \((\text{body weight/body size} = g/10 \text{cm}^3)\). Ewe weight proved to be a more effective predictor of ovulation rate than either body size or body condition. However, partial correlation analysis indicated that body size and condition influenced ovulation rate.
According to Ducker and Boyd (1977) a possible explanation for the difference in the findings with Guerra et al. (1972) may be because Merino ewes with small body size, weighing 30–40 kg, characteristic of 1–1.2 ovsulations per ewe and a high incidence of barren ewes (34–51%) were used in that study. In their experiment a selected group of 50 small and 50 large Greyface ewes, based on their body size, were used. Most of the Greyface ewes weighing 60–75 kg, characteristic of 1.8 ovsulations per ewe, conceived and lambed after their first service.

Cumming (1977), based on 11 experiments, reported an increase in mean ovulation rate from 0 to 0.44 for every 10 kg increase in ewe weight. In most flocks, the increase was in the order of 0.25–0.30 for every 10 kg increase. Differences in the body weight-ovulation rate relationships between Saxon Merino and Border Leicester × Merino ewes in the January–February mating were absent in the April–May mating. An interaction between ewe weight and January–February mating in relation to ovulation rate was observed within the Border Leicester × Merino flock. In general, ewe weight independently was as accurate a predictor of ovulation rate as a combination of ewe weight and body condition. When the variability associated with ewe weight was adjusted, body condition score (Russel et al., 1969) did not account for any variation. Therefore, plane of nutrition did not appear to have any significant influence on ovulation rate. Over all breeds and crosses studied by Morley et al. (1978) ovulation rate increased by 2% for every kg of increase in ewe weight. In the Scottish Blackface the response was 6.7% and curvilinear. The level of nutrition prior to and at mating had no effect on ovulation rate when ewes were in moderately good body condition.

The pooled regression of ovulation rate on ewe weight at mating was 0.013 corpora lutea/kg (P < 0.01) in six genotypes. Corresponding estimate in the Polypay ewes was 0.024 corpora lutea/kg (Nawaz and Meyer, 1991). The Polypay breed with 25% Finnish Landrace (Hulet et al., 1984) responded to improved body condition with higher ovulation rate. Meyer and Bradford (1973) reported that ovulation rate was more responsive to nutritional improvement in Finnish Landrace × Targhee yearling ewes than in purebred Targhees yearlings, since the breed × treatment interaction approached significance for pre-flushing ovulation rate. The lower average regression estimate of 0.013 corpora lutea/kg compared to the average estimate of 0.048 ova/kg for ewes of the Targhee and Barbado, and their crosses (Bradford and Quirke, 1986) may be because ewes were younger and of poor body condition in the latter experiments. The mean ewe weight of 64 kg reported by the former authors suggests that body condition levels were above the critical level, therefore, reproductive performance did not vary.

5. Prenatal survival in relation to ewe weight

5.1. Within and among genetic groups

In mature Romney ewes of medium and high ewe weight there was no evidence of an association between ewe weight and survival of ova at days 19–22, 18–30 or 35–38 post coitum, after egg transfer or in mated ewes (Cumming and McDonald, 1970). In 120 Merino ewes from different treatment groups a significant negative regression of prenatal mortality (% of ova not resulting in lambs) on ewe weight at mating was observed, but not on body condition. These ewes were about 10 kg lighter during early pregnancy than in an earlier experiment, because of draught conditions (Edey, 1970). In groups of Merino ewes selected on the basis of either large or small body size there was a 44% ovum wastage and lambs born from ewes mated did not vary significantly with ewe weight, body size or body condition (Guerra et al., 1972). In Merino and Border Leicester × Merino ewes at different nutritional levels from day 2 to day 16 post coitum, ewe weight, condition score and face wool cover were not significant factors in determining the number of foetuses surviving to days 26–30, when ewes with low body weight were excluded (Cumming et al., 1975). Ewe weight at mating had no effect on the percentage of young crossbred ewes with live 25–30 day foetuses (Hare and Bryant, 1985).

The effects of ewe weight or weight change during mating on partial failure of multiple ovulation were small and not significant in twin ovulating ewes from 21 farms in four South Island districts of New Zealand (Kelly and Johnstone, 1982). Variation in ewe weight at mating over 6 genetic groups had no effect on uterine efficiency (the marginal increase in prolificacy
as ovulation rate increases) of ewes that conceived from twin ovulations (Nawaz and Meyer, 1991). On the contrary, ewes in a Booroola Merino flock with a higher premating body weight had lower prenatal mortality when adjusted to similar ovulation rates (Dodds et al., 1991).

### 5.2. Differences among breeds, lines within a breed, and crosses. Genotype × environment interactions

In Scottish Blackface ewes, the proportion of corpora lutea represented by living foetuses at day 26 was higher in the heavier line (source B) compared to the lighter line (source A), although the confounding effects of the differential ovulation rates among body conditions and source of ewe made it difficult to make a firm conclusion (Gunn et al., 1972). In a later experiment, the numbers of living foetuses at day 28 per ewe mated was 1.40 at Glensaugh station and 1.12 at Lephinmore station ($P < 0.05$). The ewes from Glensaugh were significantly heavier than those from Lephinmore before and at mating. A maintenance level of feeding followed by a higher plane of nutrition prior to mating resulted in a loss of 0.16 ova at day 28 at Glensaugh compared with 0.32 at Lephinmore. On the contrary, a higher plane of nutrition at the start followed by maintenance level prior to mating showed no difference (Gunn et al., 1984).

In the Targhee breed, on the contrary, numbers (%) of lambs per corpus luteum for all ewes mated were significantly lower in the lines selected for a high body weight at 120 days of postnatal age ($W$ lines = 54 and 58%), compared to the control lines ($C$ lines = 73 and 82%) and to the line selected for multiple births ($T$ line = 68%). Ewes of the $W$ lines weighed 61.5 and 60.4 kg and were significantly heavier at mating than those from Lephinmore weighing 53.5 and 53.8 kg, respectively. The ewes of the $T$ line weighing 56.5 kg were intermediate. Calculations on yearling ewes indicated that the ewes of the $W$ lines were inferior in uterine efficiency (Bradford et al., 1986b).

Offspring of Polypay ewes were more prolific than those of Coopworth-type ewes due to a significant increase in both ovulation rate (1.94 versus 1.77) and uterine efficiency for twin ovulators (0.94 versus 0.76), although mating weights were similar in both (63.6 versus 64.7 kg). In the six genotypes studied, variation in ewe weight had no effect ($P > 0.50$) on uterine efficiency of ewes conceiving to twin ovulations (Nawaz and Meyer, 1991).

The proportion of multiple ova lost at 4 weeks was significantly greater in Welsh Mountain ewes (35–40 kg) on a low–high pattern of nutrition compared to those on a high–low pattern, 5 weeks prior to a synchronized mating. The difference between the two treatments was not significant in the heavier Brecknot Cheviot ewes weighing 40–45 kg. The proportion of single ova failing to produce a viable foetus was 0.04 in Brecknot Cheviot ewes with a condition score of 2.5 compared to 0.28 in those with scores $\geq 2.75$ ($P < 0.05$). In the Welsh Mountain ewes, the proportions were 0.04 and 0.02, respectively, and not significantly different (Gunn et al., 1991). These results suggest an interaction between breed and plane of nutrition before mating or condition score on the mortality of 4 weeks old ova. Further studies within and among breeds may be of value in confirming breed × nutrition interaction.

The uterine efficiency estimate for twin-ovulating Coopworth × Polypay ewes on the low plane of nutrition before mating was 0.38 compared to 0.77 for ewes on high plane of nutrition. Corresponding values for Polypay ewes were 0.80 and 0.75, respectively. Among triple ovulating Coopworth × Polypay ewes, low plane of nutrition reduced prolificacy by 0.4 lambs, however, there was no effect for Polypay ewes. Low postmating nutrition of triple ovulating Coopworth × Polypay ewes reduced prolificacy by 0.6 lambs, compared to a reduction of 0.3 in Polypay ewes. Average mating weights of ewes on high and low planes of nutrition were 74.2 and 58.6 kg, respectively, whereas Coopworth × Polypay and Polypay ewes across treatments weighed 65.8 and 67.0 kg, respectively, (West et al., 1991). The relationships between ewe weight at mating and uterine efficiency or litter prolificacy in twin or triple ovulating ewes within or across breeds and nutrition need to be assessed.

Body condition and/or nutritional levels before, at or after mating were shown to be important variable factors for prenatal survival, interacting with ovulation rate and/or with breeds or lines within a breed. These effects indicate, again, the existence of genotype × environment interactions, but no clear picture about the relationship between prenatal survival and ewe weight can be derived from these
experiments. On the basis of the data reviewed, especially when relating them to those on ovulation rate in the Targhee breed (Quirke et al., 1985) there seems to exist a differential relationship between ovulation rate and prenatal survival rates in relation to ewe weight, depending on criteria along which the different breeds or lines within a breed were selected.

6. Conclusion

The hypothesis can be made that variation in the within breed genetic correlation between ewe weight and prolificacy may largely depend on the relative uniformity of selection criteria applied within each breed. This is an unresolved question, since no precise information on this aspect was reported. It can further be questioned whether selection on growth rate, compared to selection on reproduction performance, could be an important source of within breed as well as among breed variation in the genetic correlation between ewe weight and prolificacy. Indications as to the inefficiency of body weight as a general reference were given in the comparison of three fertility lines in the Romney breed, the comparison of ewes from the Oxford and Finnish Landrace breeds and among three synthetic breeds, one selected primarily on lamb growth, the remaining two on prolificacy. This leads to the problem of growth, more specifically proportional growth, in relation to reproduction performance, in both types of breeds or lines within breeds.

It can be questioned as to what degree the genetic relationship can change and revert as a consequence of long-term selection for body weight, body growth or reproduction parameters. This leads to the problem of the relative incompatibility of selection on body proportions with the selection on reproductive performance traits, especially in meat type breeds. An unresolved question relates to the possibility of a parallelism or an antagonism in the genetic correlations between ewe weight and prolificacy, as compared to that between ewe weight and fecundity. The literature suggests that the answer depends largely on the genetic relationship between ewe weight and fertility.

The genetic relationship between litter weight and ewe weight, compared within and among breeds, may vary with body proportions and possibly related prenatal development processes in prolific and meat type sheep breeds and in differentially selected lines within a breed. Moreover, the components of both litter weight and ewe weight are multiple and probably interact with each other. Since ewe weight can influence the litter weight components, a clear cut relationship between the litter weight components and ewe weight can probably not be considered as general but may vary among differentially selected breeds and lines within them. This is a final, unifying, unresolved question.

References


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