MONTANA STATE UNIVERSITY

Direct and correlated responses to selection for reproductive rate in Rambouillet sheep
by Susan Gail Schoenian

A thesis submitted in partial fulfillment of the requirements for the degree of Master of Science in Animal Science
Montana State University
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Abstract:
Data were reported for a flock of Rambouillet sheep established in 1968 as a long term divergent selection experiment consisting of animals selected for high reproductive rate (H line) or low reproductive rate (L line). A random bred control line (C line) was added in 1972. Selection was based on the dam's past reproductive performance using the following index: I=no. lambs born/ (age of ewe-1).

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The H line had higher ($P<.05$) overall reproductive performance than the L and C lines. Lambing rate was .98, 1.40 and 1.25 for the L, H, and C lines, respectively. High line ewes were significantly lower ($P<.05$) in first service fertility, but there were no differences in fertility over all services. High ewes were superior to L ewes in litter size, 1.61 compared to 1.17. The C line was intermediate between the two selected lines, 1.42, indicating that greater progress has been achieved in the downward direction. Selection produced a correlated response in ovulation rate, with H ewes significantly higher at all ages. Embryo survival was lowest in the H line. There were no differences ($P>.05$) in embryo survival when site of ovulation was taken into account.

There were no differences ($P>.05$) between the three Rambouillet lines for birth weight, weaning weight, ewe body weight, fleece weight or fleece grade. Each trait has declined over the duration of the experiment, but because the Targhee flock showed the same downward trend in production, it was concluded that environment, primarily the change in summer range, was the major cause. Fleece grade is the only trait that may have been adversely affected by selection for reproductive rate.

It was concluded that selection for reproductive rate has improved lambing rate and had a positive effect on several components of reproduction. Further, selection for reproductive rate did not have any adverse effect on several production traits.

DIRECT AND CORRELATED RESPONSES TO SELECTION FOR REPRODUCTIVE RATE IN RAMBOUILLET SHEEP

by

Susan Gail Schoenian

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ABSTRACT

Data were reported for a flock of Rambouillet sheep established in 1968 as a long term divergent selection experiment consisting of animals selected for high reproductive rate (H line) or low reproductive rate (L line). A random bred control line (C line) was added in 1972. Selection was based on the dam's past reproductive performance using the following index: I=no. lambs born/(age of ewe-1).

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It was concluded that selection for reproductive rate has improved lambing rate and had a positive effect on several components of reproduction. Further, selection for reproductive rate did not have any adverse effect on several production traits.

INTRODUCTION

Low lambing rates represent a major obstacle to sheep productivity in the United States. While selection for increased litter size has resulted in some improvement in lambing rate (the number of lambs born per ewe exposed), progress has generally been considered slow and not very effective. There is a continuing need to understand the mechanisms by which selection can influence lambing rate and its components, and to search for new and more effective ways of improving the reproductive performance of sheep.

The United States Department of Agriculture Crop Reporting Board (1988) reported 538,000 head of sheep in Montana at the beginning of 1988. Montana currently ranks sixth nationally in sheep numbers (USDA, 1988). Cash receipts from the sale of sheep, lambs and wool in 1986 were close to 30 million dollars (Montana Ag Statistics, 1987). Approximately 70 percent of the income from a sheep enterprise in Montana is derived from the sale of lambs (Verl Thomas, personal communication).

The lambing rate in the United States is low compared to the potential; the national average lambing rate was 106 percent in 1987. While lambing rate has improved slightly over the past few years, it is a figure which has remained virtually unchanged for the past several decades (USDA, 1988). The declining size of the national sheep flock over the past 45 years reflects the general poor economic health of the industry. However, with a stable per capita consumption of lamb and reduced supplies, prices have improved and continue to be strong for

the producer. In fact, in 1987 and 1988, sheep numbers increased (USDA, 1988). But, if sheep production is to remain a viable component of the United States and Montana agricultural industries, greater progress in the areas of production and marketing must be achieved.

Litter size or the number of lambs born per parturition is a major factor affecting sheep productivity, contributing much more to the pounds of lamb weaned per ewe than does the growth rate of individual lambs. Feed costs represent the majority of the costs in a sheep enterprise. One way to reduce feed costs is to increase the number and weight of lamb(s) weaned per ewe.

While nutrition and other environmental factors exert a great deal of influence on the relative reproductive rate in sheep, a permanent genetic change is more desirable. Heritability estimates for reproductive rate are relatively low, however, selection for increased litter size in sheep has resulted in positive changes in lambing rate.

Little is understood about the effects selection has on lambing rate, its various components, and correlated responses in other production traits. A sound knowledge is required if the sheep industry is to achieve rapid and effective changes in lambing rate.

The purpose of this study was to determine the effects selection for reproductive rate in Rambouillet sheep has had on: 1) Lambing rate, i.e. direct responses (lambs born per ewe exposed to ram); 2) Components of lambing rate (i.e. fertility, litter size, ovulation rate and embryo survival); and 3) Correlated responses in other production traits (i.e. birth weight, weaning weight, ewe body weight, fleece weight, and fleece grade). While it is well documented that the ram

exerts a great deal of influence on the reproductive level of a flock, the focus of this thesis will be on reproduction in the ewe.

LITERATURE REVIEW

Reproduction in sheep is a complex trait. It is largely a function of fertility (the number of ewes conceiving), fecundity or litter size (the number of offspring per pregnancy) and lamb survival (the viability of offspring) (Bindon and Piper, 1980). The definition may be expanded to include the interval between parities. Litter size depends on ovulation rate and embryo survival, and this paper will be primarily concerned with the genetic variation in these traits.

From a producer's standpoint, reproductive performance can be expressed as the number and/or weight of lamb(s) weaned per ewe exposed. Though maximum is not necessarily optimum, both biological and economic efficiency are improved with higher levels of reproduction. Increased reproductive rate spreads out the fixed costs associated with maintaining the breeding ewe flock. Feed costs per lamb produced are reduced. Flock reproductive rate also affects the generation interval and selection intensity and consequently the amount of genetic improvement that can be made in a flock.

There are many factors which can affect reproduction in the ewe. These include nutrition, age, birth type, season, stress and genotype, as a partial list (Gunn, 1983; Cahill, 1984). It is recognized that fecundity will be lowest in a ewe's first lambing, regardless of her age. In some flocks, ewes born as twins have lower reproductive performance than singles up until they are four years old, (Piper and McGuirk, 1976). This was probably due to the persistence of a birth and rearing handicap associated with the twin lambs. Basuthalkur et

al. (1973) reported higher lifetime production for ewes born as twins, and Turner (1969) summarized ten estimates in which nine out of ten showed superior lifetime production for ewes born in multiple litters. Further, nutrition exerts a great deal of influence on the reproductive performance of sheep, although the mechanisms are not fully understood. Ovulation rate appears to be under predictable nutritional control, but embryo mortality does not lend itself well to an acceptable level of control (Gunn, 1983).

Litter size generally varies among breeds from one to three lambs. Sheep may give birth to six lambs (Land et al., 1982). There is also considerable variation in the distribution of litter sizes, i.e. the proportion of single, twin and triplet births. Offspring survival declines substantially as birth rank increases (Bradford, 1985). Production and labor costs associated with animals giving birth to multiples or being born as a multiple are higher. In fact, increasing the variability of litter sizes in a flock can result in a reduction in the total weight of lamb weaned per ewe (Bradford, 1985). Increasing litter size inevitably means a growing proportion of litters higher than twins. Below a mean litter size of 1.7, Davis et al. (1983) reported differences in litter size were a result of the proportion of ewes having singles and twins. However, when litter sizes increased to 1.7 to 2.3, differences were due to the proportion of ewes having twins and triplets (Davis, 1983). Ewes with one copy of the Booroola gene (mean litter size of 2.5) generally give birth to 1, 3 or 4 lambs, but few sets of twins (Davis, 1983). In addition, popular prolific breeds, such as the Finn and Romanov, are said to have wide distributions of

birth ranks with a high percentage of triplet births (Lindsay, 1982). Two slightly less prolific breeds, the Barbados Blackbelly (though the literature is conflicting) and East Java Fat Tail, appear to have a narrow distribution of birth types with twins being the dominant (Lindsey, 1982).

There is a conflict between researchers' findings and producers' skeptical attitude towards highly prolific animals, primarily because producers are well aware of the high production costs associated with multiple births. Unfortunately, the superiority of prolific animals is generally described in terms of average litter size rather than distribution of litter size. It, therefore, seems logical that improvement of litter size should include the change of variance of litter size as well as improvement of its mean.

High fecundity sheep, in general, attain puberty earlier, although this would not be charactersistic of the Booroola Merino (Piper and Bindon, 1982). Most prolific sheep display an extended breeding season, have higher ovulation rates and substantial prenatal embryonic wastage (Bindon and Piper, 1982). Studying the endocrinology of sheep with genetic differences in prolificacy is important so that a physiological explanation can be provided. High fecundity sheep appear to be characterized by having a higher plasma FSH activity during the estrus cycle (Land, 1979). Reduced production of feedback hormones is one way in which a high ovulation rate may be achieved (Land, 1979). Recent studies have demonstrated that active immunization against steroids can increase ovulation rate by modifying feedback on the pituitary (Webb, 1985; Cummins et al., 1983; and Johnson et al., 1983).

Components of Reproduction

Ovulation Rate

Ovulation rate is the most important factor influencing litter size. It sets the upper limit to potential lambing performance since monozygous twins are rare in sheep (Scanlon, 1973). Ovulation rate is influenced by five factors: genetic effects, age of ewe, liveweight-nutrition complex, season and hormonal therapies (Cahill, 1984).

There is a considerable amount of genetic variation between breeds for ovulation rate (OR), ranging from one to over three (Hanrahan, 1985). This variation has provided the means for genetic improvement of ewe prolificacy through crossbreeding. Five genotypes recognized as having high OR (3.0 or greater) are the Booroola Merino, Finnish Landrace, Dahman, Romanov and Hu Yang (Cahill, 1984). Further, there are fundamental differences in how these breeds achieve their high OR. Considerable variation also exists in distribution of ovulation rates within a breed (Hanrahan, 1985). The distribution of ovulation rate will influence the distribution of litter size and therefore, selection programs should take this variability into consideration, Achieving uniformity in litter size should be a goal of any research or breeding program undertaken.

The low OR of maiden ewes (1.5 years old) and its subsequent increase in mature ewes is well documented. Ewes reach their peak OR at 3-5 years old and this is maintained until at least 10 years old (Bindon et al., 1980; as reported by Cahill, 1984). The relationship between liveweight and nutrition on OR in sheep has been studied on

many occasions, and there appears to be both a "static" and "dynamic" effect of liveweight on ovulation rate. For each kg of additional liveweight at mating, ovulation rate is increased by .03 (Kelly and Johnston, 1982; Kelly et al., 1983). The positive correlation between liveweight and ovulation rate may be partly explained by differences in age. There are few estimates of the relationship between liveweight change or "flushing" on ovulation rate. Kelly and Johnston (1982) suggested it may be as high as .07 CL per ewe ovulating for each kg of liveweight change in the pre-mating period. The time of mating (season) and its subsequent effects on OR are also well documented. In most breeds, ewes begin cyclic estrus activity in summer and OR rises to a maximum in mid-autumn followed by a decline as ewes approach anestrus (Cahill, 1984). Generally, the highest ovulation rates occur at the second and third estrus cycle of the breeding season (Thompson et al., 1985).

Embryo Survival

Embryonic mortality is usually taken to mean the deaths of fertilized ova and embryos up to implantation--about day 40 in the sheep (Edey, 1979). It is the main source of loss during pregnancy and losses are greatest one week after mating (Edey, 1979). On the farm level, the costs of embryo mortality are delayed lambing, a reduction in twinning rates, and a slight increase in the number of open ewes.

Embryo survival can be affected by a variety of factors: nutrition, temperature, stress, age of ewe, genotype, and the site and rate of ovulation (Edey, 1979; Wilmut, 1985). Season and age effects

on "uterine efficiency", a measure of embryo survival, are small relative to their typical effects on ovulation rate (Meyer and Clarke, 1983). Embryonic survival seems to be dependent in part on the age of the female, with uterine space being more limited in young females (Wilmut, 1985; Smith, et al., 1986;). Variation in nutrition before mating and body condition at the time of mating, both influence the number of ovulations and embryo survival, and the level of nutrition after mating can influence the survival of embryos (Wilmut, 1985). Nonetheless, embryonic survival seems to be less affected by varying levels of nutrition than does ovulation rate (Gunn, 1983).

In an assessment of reproductive wastage in sheep, it was shown that by increasing ovulation rate one unit, the average number of embryos surviving, lambs born, lambs marked and lambs weaned would be increased by .52, .46, .33 and .23 respectively (Shelton et al., 1986).

With increased ovulation rate, embryo survival is expected to at best remain the same (Bradford, 1985). It may decrease as in mice and pigs (Bradford, 1969; Land and Falconer, 1969; Cunningham and Zimmerman, 1975). Hanrahan (1982) reports estimates of .85, .75, .66 and .57 for embryo survival for 2 to 5 ova respectively. The probability of embryo survival declines in essentially a linear fashion as the number of eggs entering the uterus increases (Hanrahan, 1980; Fogarty, 1984). However, Hanrahan (1985) reasons that the observed pattern may not be genetically associated with ovulation rate and that because of the environmental effect of ovulation rate on embryo survival, consideration of genetic differences in embryo survival must be at equivalent ovulation rates. In fact, Bradford (1986) reported

that selection for litter size, which is accompanied by a correlated response in ovulation rate, maintains or improves prenatal survival rate.

The tendency for one embryo to migrate to the opposite uterine horn following a double ovulation on one ovary was seen as a possible source of loss by Casida et al. (1966). A detailed study by Doney et al. (1973) led to the conclusion that embryos which migrate to the horn having no corpus luteum have decreased rates of survival. This is more than offset by the non-migrating embryos' chances of survival which are enhanced by the subsequent removal of uterine crowding effects. Scanlon's (1973) data indicates than transuterine migration of embryos in ewes with two ovulations on one ovary is the rule rather than the exception (87.5% of the ewes). He reasons that the migration of embryos within the uterus is of importance to the outcome of pregnancy, insofar as migration can result in greater efficiency of utilization of intrauterine space. Failure to successfully complete migration may be a factor contributing to embryo mortality. The process of transuterine migration in sheep appears to be well organized with an overall tendency of equalizing the distribution of fetuses between the uterine horns (Scanlon, 1973). In another study, White (1981) reported more embryo losses by ewes with two CL's on one ovary than by ewes with one CL on each ovary. In cows, transuterine migration is rare, and perhaps the reason for failure of cows to initiate twin pregnancies (Scanlon, 1973).

The literature pertaining to the effect of site of ovulation on embryo survival is conflicting. Bradford et al. (1986) reported

survival values of 83 and 87% for unilateral and bilateral ovulating ewes, respectively. This difference was not significant, and was in agreement with other reports of little if any effect of site of ovulation on embryo survival in twin ovulating ewes (Meyer, 1985; Kelly and Johnston, 1983; Kelly and Allison, 1976; Sittman, 1972). However, more lambs appear to be produced by bilateral triplet (i.e. 2-1) ovulations than unilateral ovulations (Meyer, 1985). In cows with twin ovulations, fertilization failure and/or embryo mortality is greater for unilateral twins (Hanrahan, 1983).

Methods of Effecting Genetic Change in Reproductive Rate

There are several ways of effecting genetic change in litter size in sheep. Crossbreeding can affect reproduction through different routes. Crossing breeds that have similar litter sizes will take advantage of the complimentary nature of various desirable traits, as well as exploit the effects of heterosis. Nitter (1978) discussed the main findings of crossbreeding in the dam and offspring as it relates to reproduction. He reports that dam effects are the main cause of heterosis in number of ewes lambing (H^M = 9%), while offspring effects are largely responsible for heterosis in lamb survival to weaning (H^I = 10%). For prolificacy, both individual and maternal heterosis are rather low (Nitter, 1978). This is in agreement of reports of little if any effect of heterosis on ovulation rate and embryo survival (Nitter, 1978). Estimates for paternal heterosis during the normal breeding season are quite low, however, results from three studies indicate that the use of crossbred rams outside the normal breeding

season will result in more ewes lambing (Leymaster, 1987). Nitter (1978) concluded that, in general, heterosis effects for reproductive rate are greater, though more variable, than they are for growth.

The use of prolific genotypes seems to be the most efficient way of effecting genetic changes in litter size. Examples of these breeds include the Finnish Landrace, Romanov, Barbados Blackbelly and the Chios. Litter size behaves as an additive trait and thus, litter size can be set at any level between that of the less prolific breed and the prolific breed by varying the proportion of the two parent breeds in the genetic make-up of the ewe stock. This system is not without constraints, however. Many times the prolific breed has certain shortcomings that may limit its usefulness in certain production environments, e.g. fleece and carcass characteristics of the Finn, colored wool of the Romanov, and the lack of wool in the Barbados Blackbelly. It is assumed that the genetic effect on sheep fecundity is the result of an additive effect of a multitude of genes, each with a small and non-measurable effect. However, recent research suggests that the high fecundity of the Booroola Merino sheep is inherited by a single gene (Piper and Bindon, 1982). The mean litter size of ewes heterozygous for the "F" gene is approximately 1.0 lambs higher than in non-carriers (Piper and Bindon, 1982). Subsequent studies have shown than the gene acts through ovulation rate, an effect of about 1.5 ova (Piper and Bindon, 1985). There is indication that genes of similar effect are segregating in Javanese sheep (Bradford et al., 1986), the Cambridge breed (Hanrahan, 1986) and Icelandic sheep (Jonmundssun, 1985).

A final method of effecting genetic change in litter size in sheep is selection within breeds, either directly for litter size, or for traits correlated with litter size.

Selection for Reproductive Rate

Due to its low heritability, it has generally been thought that selection for increased reproductive rate in the sheep would not be effective. Bradford (1985) summarized 30 heritability estimates for reproductive rate for different breeds and methods of estimation. They ranged from -.15 to +.35 and a mean of .10, and though there was only one negative estimate, the distribution skewed toward zero, "suggesting that some negative values have not been published." A summary of eight repeatability estimates was given by Land et al. (1983). Estimates ranged from .06 to 0.26 with an unweighted mean of .15.

In mice, selection for litter size has been successful (Bradford, 1969; Land and Falconer, 1969; Joakimsen and Baker, 1977). Joakimsen and Baker (1977) reported a marked response to selection for both high and low litter size, with a difference of 7.6 mice between the high and low lines at generation 15. Realized heritabilities were .18 and .22 in the high and low lines respectively (Joakimsen and Baker, 1977). Bradford's (1969) data shows an increase from 9 to 12 mice for the high line after 10 generations. Quijandria et al. (1983) reported heritability estimates for litter size in guinea pigs of similar magnitude to those reported in the mouse.

Pig data is less conclusive. A few experiments have been conducted in recent years and none have been very successful in

increasing litter size in the sow (Bichard and David, 1986). Direct selection for eleven generations in France produced little response (Ollivier and Bolet, 1981; Ollivier, 1982; as noted by Bichard and David, 1986), and Cunningham (1979) reported no success for within-herd selection experiments for litter size in swine. Revelle (1975) suggests that the low heritability for litter size in swine is due to a negative environmental correlation between the litter size in the dam and daughter, and that if an optimal maternal environment were provided, successful selection for litter size could be accomplished. In cattle, the heritability, repeatability and variance for fecundity appears to be quite low, although considerable breed and within breed variation exists (Rutledge, 1978). In the goat, selection for litter size appears to be quite similar to the situation in sheep (Devendra, 1985).

Several selection experiments have been conducted to evaluate the realized response to selection for litter size or other measures of prolificacy in sheep. They are summarized in Table 1.

Selection criteria have varied somewhat between experiments and thus, may account for differences in results. Some studies, to varying degrees have used multiple records. Mann et al. (1978) selected rams only and the study was of the shortest duration. The Turner (1978) study screened a large population for prolific ewes, as did other studies (Clarke, 1972; Hanrahan, 1982; and Bradford, 1985). Control lines were not maintained in all experiments (Turner, 1978; Hanrahan, 1982; and Mann et al., 1978), and the ability to assess genetic change accurately is questionable.

TABLE 1. RESULTS OF SELECTING FOR PROLIFICACY IN SHEEP[a]

Country	Breed	Approx dates	Annual % response[b]	References
Ruakura New Zealand	Romney	1948-72	1.75	Wallace (1964) Clarke (1972)
CSIRO Australia	Merino	1954-72	2.40	Turner (1978)
Trangie Australia	Merino	1959-73	2.00	McGuirk (1976) Atkins (1980)
Ireland	Galway	1963-81	1.57	Hanrahan and Timon (1978)
Ireland	Mixed	1963-	.7-5.1	Hanrahan (1982)
Hopland California	Targhee	1963-	1.50	Bradford (1985)
South Australia	Merino	1965-75	little change	Mann et al. (1978)

[a]adapted from Bradford (1985)
[b]response is reported in terms of percent increase in number of lambs born per ewe lambing.

Experiments in several countries were summarized by Bradford (1985). The two most well known studies are with Romneys in New Zealand which began in 1948 (Wallace, 1964; Clarke, 1972) and Merinos in Australia which began in 1954 (Turner, 1978). In both experiments, foundation ewes were selected on the basis of high and low twinning rates and assigned to lines on that basis. Considerable response has been reported in both studies, although the experiments are somewhat different. In the Ruakura flock in New Zealand (Wallace, 1964; Clarke, 1972), selection of ewes and rams was from dams with high or low reproductive rates. The linear regression or divergence of the high and low lines from the control line indicated an annual rate of 1.75 lambs born per 100 ewes lambing in the high line, compared to little divergence in the low line. Although there is a continuing positive

and fairly linear response in the high line, there was little divergence in the low line until approximately 12 years into the study when the low line began to deviate in a downward direction (Clarke, 1976).

In the Australian experiment (Turner, 1978), there was only divergent selection with no control line. The T (twinning line) and 0 (no multiples) lines were selected on the basis of the percentage of ewes having at least one multiple birth in three years. The B (Booroola) line was also selected for number of lambs born. Turner (1978) reports a regression of divergence (T-0) on time of 2.39 $\pm$.58 ewes with one multiple birth in three years. Greater response was made in the downward direction (0 line; b = 2.55 P<.01) than in the upward direction, in contrast to the results observed in the New Zealand experiment (Clarke, 1972). The rate of increase (T-0) has slowed in recent years, while the B-0 difference has continued to increase (Turner, 1978). However, it is now known that the superiority of the B line is due to the presense of a gene with a large effect on ovulation rate (Piper and Bindon, 1982).

In other experiments, McGuirk (1976) gave some results of selection for increased reproductive performance in the fertility flock at Trangie, Australia. The flock was started in 1959 and twin-born ram and ewe hogget replacements were chosen in preference to singles. Ewes which failed to raise a lamb were also culled. This program, evaluated relative to a control line, has increased litter size by 2% per year. Hanrahan and Timon (1974) reported no response to selection for litter size in Galway sheep after a period of about three generations.

However, in another study, Hanrahan (1982) reported an increase of 1.57% per year in litter size (Hanrahan and Timon, 1978). Mann et al., (1978) showed that very little response was achieved in a South Australia flock, but selection was limited to ram replacements. In the California experiment, Bradford (1985) reported little change in reproductive rate after a significant increase from the initial screening.

With the exception of Mann et al. (1978), all studies show a remarkably uniform response and are in agreement with the expected response, considering the low heritability of the trait and the differences in experimental design. An increase of 1-2% or better per year can be realized by selection for multiple births.

The effect of screening the initial population appears to make an important contribution to the response achieved (Bradford, 1985). Ewes are assigned to selection lines on the basis of their past reproductive performance. In the Turner (1978) experiment, initial selection clearly made a major contribution (about 2/3's) to the superiority of the high lines, though there has also been a continuing response. In the Ruakura high fertility line (Clarke, 1972), screening contributed 1/4 of the total response, and in the California Targhee line, all of the direct response achieved to date was a result of the initial screening (Bradford, 1986). Further, in the Ireland high fertility line (Hanrahan, 1982), initial screening almost certainly contributed to development of the highly prolific stock, and initial screening resulted in a litter size of about 0.2 lambs above the control line in a Norwegian study (Steine, 1985). On the other hand, the Trangie

Merino (Atkins, 1980) and Galway (Hanrahan, 1976) experiments did not involve initial screening, yet good response was achieved.

Correlated Responses

An increase in fertility has been reported in several of the selection experiments (Wallace, 1964; Clarke, 1972; McGuirk, 1976; Turner; 1978; and Bradford et al., 1986). A positive correlated response appears to be the general pattern (Bradford, 1985). However, in the New Zealand experiment, Clarke (1972) reported no differences in fertilty when high and low fecundity ewes were mated to terminal sires, and Wallace (1964) reported more dry ewes at the two-tooth stage in the Ruakura high fertility line.

Hanrahan and Quirke (1985) summarized the correlated changes in ovulation rate for four experiments where selection was for number of lambs born. In each case, the correlated change in ovulation rate was greater than the change in litter size. Bradford et al. (1986) showed clear evidence for a correlated response in ovulation rate following selection for twinning. Meyer and Clarke (1982) reported no differences in uterine efficiency in the Ruakura flock. Bradford, et al., (1986) reported that prenatal survival was equal to or superior, though not significant, to the control line.

Other correlated responses have been investigated in the ram. Rams that have been selected for high reproductive rate excel in scrotal circumference and libido (number of mounts in a serving capacity test) than control rams and those selected for low reproductive rate (Tulley, 1981). Clarke (1972) reported fertility

rates of 93% and 79% when high and low fecundity ewes were mated to rams of their own selection lines, compared to no differences when outside rams were used, thus indicating that selection has had an influence on the rams' ability to get ewes bred.

There are many difficulties associated with direct selection for reproductive rate. First of all, the trait is sex-limited and can only be measured in the female. Fertility and fecundity require the male for expression, and the use of an infertile ram can cause a ewe to be barren or display a litter size below her potential. There are a variety of seasonal and environmental aspects which can mask the effects of genetic change. Low reproductive rate itself limits the amount of selection pressure that can be applied and consequently the amount of genetic gain that can be achieved. A low fecundity flock with the greatest need for improvement will likely have the lowest selection differential for reproductive rate (Hanrahan, 1980).

Selection for Components of Reproductive Rate

More rapid response to selection could be achieved by a better understanding of the relationship between components of reproduction and indirect selection traits that could be measured early in life in both sexes and are genetically correlated with reproductive performance. Examples are sex-limited traits such as testis size in the male and ovulation rate in the female and traits that can be measured in both sexes, i.e. hormone levels.

Ovulation Rate

Substantial evidence points to ovulation rate as the principal factor affecting litter size in sheep (Bradford, 1972; Hanrahan, 1982; Meyer and Clarke, 1982; Trounson and Moore, 1972). The correlation between ovulation rate and litter size appears very linear at ovulation rates up to four (Hanrahan, 1982). In more prolific breeds, such as the Finn, the relationship between ovulation rate and litter size is culvilinear, indicating that further increases in ovulation rate may actually lead to decreases in litter size (Hanrahan, 1976). Theoretical studies by Hanrahan (1974) led to the prediction that at least a two-fold increase in rate of genetic gain per generation would be achieved by selection for ovulation rate rather than litter size. In low fecundity breeds, increased litter size should accompany higher ovulation rates. Thus, it follows that selection for ovulation rate rather than litter size would result in greater annual genetic gain.

Repeatability estimates for ovulation rate have been reported for the Galway, .27, and a mixed group of Rambouillet, Targhee and Columbia ewes, .38, (Hulet and Foote, 1967). Quirke et al. (1985) gave a repeatability estimate for CL count of .27 and .25 for mature and yearling Targhee ewes respectively. Carrick et al. (1976) reported a repeatability coefficient of 0.50 for Merino ewes within the same breeding season. These estimates suggest that ovulation rate may be a trait of moderate heritability and hence, more sensitive to selection than litter size, which is known to have a low heritability (Bradford, 1985; Land et al., 1983). Heritability of ovulation rate is much higher than that of litter size (Hanrahan, 1980; Hanrahan and Quirke,

1985). Hanrahan and Quirke (1985) reported heritability estimates of .50 ±.09 and .32 ±.16 for the Finn and Galway breeds respectively. This compares to a low estimate of .05 ±.07 and .16 ±.07 for 18 month old Merino ewes (Piper et al., 1980). The low estimate reported for the Merino ewes is no doubt a result of the small variation in ovulation rate found in maiden ewes.

The evaluation of ovulation rate as a selection criterion for litter size is needed, however, before it is widely adopted by the industry. In both mice (Land and Falconer, 1969; Bradford, 1969) and pigs (Cunningham et al., 1979) successful selection for ovulation rate has not resulted in an increase in litter size. In Bradford's experiments (Bradford, 1968; Bradford, 1969) successful selection for ovulation produced no increase in litter size, yet response to selection for litter size was completely explained by change in ovulation rate. The Nebraska swine experiment (Zimmerman and Cunningham, 1975; Cunningham et al., 1979) did not include selection for litter size, but the direct and correlated responses to selection for ovulation rate were similar to the mice data. Thus, the correlation between ovulation rate and litter size appears to be quite low in mice and pigs (Hill, 1985).

Selection for ovulation rate in Finn sheep has been very successful, with a difference of over 1 ovulation between high and low lines and a realized heritability of .50 ±.07 (Hanrahan, 1982). But here too, litter size has not increased. There are apparently no published reports for any species (except for superovulated mice (Land and Falconer, 1969)) where selection for ovulation rate alone has

yielded an increase in litter size (Bradford, 1985). A positive correlated response in litter size is expected in sheep and cattle, but the experiments needed to confirm this hypothesis have yet to be carried out (Bradford, 1985). A second caution about selecting for ovulation rate alone is that it is expected to cause an increase in variability in litter size.

Embryo Survival

Selection for embryo survival has not previously been suggested as a means of increasing the genetic potential for litter size in sheep, although selection for litter size is in reality an indexed selection for fertility, ovulation rate and embryo survival. The reasons are an apparent lack of genetic variation in embryo survival in sheep (Hanrahan, 1980), and the difficulty in measuring the trait. Where ovulation rate can be measured several times within a breeding season and without the male influence, embryo survival can only be measured once per season, only on those ewes who conceive to the measured ovulation rate, and the trait is subject to the male influence. The evidence for lack of genetic variation in embryo survival comes largely from interbreed embryo transfer studies and the results of selection for litter size (Hanrahan, 1980). These data indicate that this component generally contributes little to the observed differences in litter size (Hanrahan, 1980; Hanrahan, 1982).

There is other evidence, some more recent, that at least in some situations, genetic variation in embryo survival does contribute to differences in litter size. Meyer, et al. (1983) showed significant

differences in litter size among twin-ovulating ewes of different genotypes. Ricordeau et al, (1982) reports that the Romanov breed and its crosses are strikingly superior to other genotypes in embryo survival. Burfening, et al. (1977) reported significantly more embryos when rams from lines selected for multiple births were used. In a line of mice, Bradford (1969) successfully selected for high embryo survival. However, despite evidence of breed variation, the contribution of embryo survival to litter size in sheep is considered minor compared to that of ovulation rate (Hanrahan, 1982), and the prospects for within breed selection appear limited since available evidence on the repeatability of embryo survival indicates a value of less than .10 (Hanrahan, 1986).

In contrast to the effects of an increase in ovulation rate, an increase in embryo survival will decrease variability in litter size (Hanrahan, 1980), and thus must be recognized as an important component of reproduction. Calculations on various combinations of embryo survival and ovulation rate distribution, suggest a mean prolificacy of 1.9 to 2.0 with a high percentage of twin births (.7) is feasable (Hanrahan, 1986). Bradford (1985) makes the following conclusions about embryo survival:

> 1) there is probably some genetic variation in embryo survival in sheep; 2) selection for increased embryo survival may be necessary to realize the benefits from increased ovulation rates; and 3) improvement in embryo survival can contribute to achieving the goal of increased uniformity in litter size.

Selection for prolificacy in sheep would be more effective if characteristics in the male could be found which are correlated to female reproduction. Two measures of male reproductive performance,

scrotal circumference and serving capacity, have been shown to be heritable, and there is evidence that these two traits are related to female reproduction (Kilgour et al., 1985). Land (1973) reported that testicular growth in young rams was greater in a breed of high ovulation rate than in a breed of low ovulation rate, and that in female mice selected for ovulation rate, there was a correlated response in testis size in the males. Mafizul Islam et al. (1976) reported a genetic correlation between testis weight and ovulation rate in mice, though there was not a correlated change in litter size.

Correlated Responses in Production Traits

Reproduction is just one component of the productivity of an animal. A question that must be asked is whether changes in reproduction have or might affect other economically important traits such as wool, growth or lactation. Selection for reproductive rate in sheep can lead to correlated responses in other traits. Estimates of genetic correlations between reproductive traits and other production traits are quite variable and the published estimates reflect this as shown in Table 2.

The unweighted estimate for adult body weight is + .25 showing expected increases in body size following selection for increased number of lambs (Land, et al., 1983). Clarke (1972) reported a small correlated response in this direction, and Hanrahan (1976) found the correlated response in ewe body weight to be negligible. Bradford et al. (1986) reported an increase in liveweight of mature ewes on the order of 5 percent, but he found no significant difference in body

weight between the twinning and control lines at the yearling stage, probably due to the persistence of a birth and rearing handicap. Further, selection for increased growth rate may have an adverse effect on several components of reproductive performance and lead to a net decline in fitness (Bradford, 1985).

TABLE 2. GENETIC CORRELATIONS BETWEEN REPRODUCTION AND:[a]

Body wt	Weaning wt	Fleece wt	Reference
0.29		0.27	Young, Turner, and Dolling (1963)
			Dolling (1963)
0.61		-0.02	Purser (1965)
	-0.12	-0.25	Gjedrem (1966)
0.20		-0.52	Kennedy (1967)
	-0.03	-0.14	Shelton and Menzies (1968)
0.30	0.24		Ch'ang and Rae (1972)
0.21			Forrest & Bichard (1974)
	0.06	0.05	Eikje (1975)
-0.07		-0.15	More O'Ferrall (1976)

[a]adapted from Land et al. (1983)

The genetic correlation with fleece weight gives mostly negative estimates, but they are on average very small (Land, et al., 1983). The unweighted mean is -.1. Clarke (1972) substantiates this finding in both direction and magnitude with the correlated response in hogget fleece weight in the Ruakura flock. Turner (1978) reports no change in average clean wool weight of the T group relative to the 0 group. This confirms the estimate of zero genetic correlation between clean wool

weight and reproductive rate and explains the lack of change in reproductive rate in Turner's (1978) S and MS lines of Merinos selected for high clean wool weight.

After preliminary results of selection for prolificacy in Polish Merino sheep, Radomska et al. (1984) concludes that selection for litter size has not led to adverse selection for either body weight or wool production, and thus these traits would not be expected to deteriorate.

There is no discernable genetic correlation between weaning weight and the number of lambs born, though there will be an obvious negative environmental correlation (Land et al., 1983). The effect of selection for litter size on weight of lamb weaned per ewe exposed has not been reported for many of the experiments, but the available evidence on numbers weaned indicates a positive change (Bradford, 1985). In the Ruakura flock, Wallace (1964) reported that the high fertility animals show up very favorably when compared to the control and low fertility lines on the basis of weight of lamb weaned per ewe. Bradford (1985) argues that there is little doubt that selection for multiple births will increase the production of weight of lamb per ewe mated in any environment where survival of twin lambs is satisfactory.

Selection for number of lambs born, in both theory and practice, appears to have small genetic consequences for other production traits. However, one cannot forget the environmental and management considerations associated with rearing twin lambs. Further, a ewe may produce more lambs, but what feed consumption will she require to do so? Jones (1982) points out that the allowance for increased feed

requirements that would accompany genetic changes in reproductive rate may reduce the contribution of number of lambs weaned to a large extent.

MATERIALS AND METHODS

Animals and Management

Sheep

In the fall of 1968, a selection experiment for reproductive performance in sheep was initiated at the Montana Agricultural Experiment Station. Rambouillet ewes were assigned at random within age to one of two selection lines: a high (H) line to be selected for high reproductive rate and a low (L) line to be selected for low reproductive rate. No initial screening of the ewe population was practiced. Rams were selected from the foundation ewes on the basis of a reproductive index, and were assigned at random to produce the first ewe lamb progeny (born in 1969). After this time, the lines were closed and all selection was from within line. In the fall of 1972, all remaining foundation ewes were removed from the H and L lines and a random sample of 8 rams from the H and L lines was selected to establish a random bred control (C) line. The H, L and C lines were maintained at approximately 100 ewes each.

Selection Procedures

Rams were selected within the H and L lines each fall at weaning based on their dam's past reproductive performance. Selection was based on the following simple index:

I = total number of lambs born in lifetime/(age of ewe - 1).

The index represents the average number of lambs born in a ewe's lifetime up until the time she gave birth to the lamb under

consideration. The index includes all years that a ewe was exposed for breeding, whether she lambed or failed to lamb. The four rams with the highest indexes within H and the four rams with the lowest indexes within L were selected for use the following year. In addition, four reserve rams were also selected within each line. In the C line, eight rams plus four reserve were selected at random. An added requirement was that selected rams could not be paternal half sibs. The only other restrictions placed on the rams was that they should not have horns or wool blindness. Selected rams were used for only one breeding season at approximately 1 1/2 years of age.

Ewes in the H and L lines were selected on similar basis as rams, with no restrictions, and selection occurred when the ewes were approximately 16 months of age. Ewes in the C line were also selected completely at random. Ewes were bred to lamb first at 2 years of age and all ewes were removed from the flock at 6 years of age. The only other reasons for disposal were for failure to lamb for two consecutive years or physical problems such as mastitis.

Targhee Flock

Records from the experiment station's registered Targhee flock were also included in some of the analyses. Management of the Targhees was similar to that of the three Rambouillet selection lines, however selection criteria differed. Selection of the females was related to the ewe's ability to meet registration requirements with the U.S. Targhee Sheep Association. Targhees are a polled breed and scurs are not approved or accepted. Wool blind sheep are not permitted for

registry. Desirable Targhee wool is 60's and 62's in spinning count or half-blood. Fleeces should not vary more than two spinning counts from side to britch, with 58's and 56's the coarsest acceptable shoulder and britch respectively. Sheep finer than 64's are acceptable with sufficient staple length. Rams were also selected to meet registration requirements, but in addition their individual performance records for fleece weight and post weaning gain were used as selection criteria. All selected Targhee rams were above average in both fleece production and post weaning rate of gain, but no index that combined these traits was used.

Management and Environment

The experiment was carried out at Red Bluff Research Ranch near Norris, Montana. Elevations at Red Bluff range from 1280 m at the ranch headquarters to 1900 m in the Cottonwood pasture. Precipitation ranges from 25 to 48 cm over the ranch with an average of 38 to 46 cm. Management of the sheep flock is similar to that of any commercial range sheep operation in Montana. Shed lambing is practiced, and the ewes are brought to the ranch headquarters only at breeding, lambing and data collection, such as weaning.

All ewes and lambs were managed as one group throughout the experiment except at breeding when the ewes were assigned to single sire breeding pens. The breeding season was generally from mid-November to early December with lambing occurring in April and May. Ewes were placed in single sire breeding pens with rams of their respective breed and line. They stayed in the breeding pens for about

20 days and at the end of the 20 day period, all ewes were returned to the range and exposed to blackface rams for an additional 15 days. All ewes were weighed prior to mating.

All ewes were maintained together on winter range, which was composed primarily of blue-bunch wheatgrass and Idaho fescue. While on winter range, ewes were supplemented with 0.15 kg of a 20 percent protein pellet. Although the supplementation varied some from year to year, the approximate composition of the protein supplement was 48% barley, 5% wheat millrun, 27% soybean meal, 5% dehydrated alfalfa, 6% molasses, 7.5% dicalcium phosphate and salt. Ewes were also fed mixed alfalfa and grass hay when the snow cover was too deep to permit grazing or sufficient feed was not available on the range (generally 5 to 7 days per winter).

Each year, ewes were shorn prior to lambing between March 15 and April, except in 1977 when shearing took place after lambing in June. Grease fleece weights were recorded for each ewe and the fleeces were transported to the Montana Wool Laboratory for grading. A subjective estimate of grade was made by one of two experienced wool technicians.

Up until 1977, fleeces were graded using the American Blood system, however, in recent years, the English Spinning Count System was utilized. As a result, all fleece grade data have been coded to correspond to the earlier blood system. Fine (≥64's), 1/2 blood (62's, 60's), 3/8 blood (58's, 56's) and 1/4 blood (54's, 50's) are coded 1, 2, 3, and 4 respectively.

Prior to lambing, ewes were moved to large pens and observed 24 hours a day for lambing. Lambing commenced approximately April 10 each

year. Upon lambing, ewes and lambs were placed in individual pens, approximately 1.3 m^2. All lambs were eartagged, weighed within 24 hours of birth and the data recorded. Ewes and lambs remained in pens for one to three days, depending upon the number and strength of lambs. Ewes and lambs were then moved to larger, mixing pens with six to eight other ewes and their lambs for an additional two to three days. Eventually, ewes and lambs were moved to outside lots. In general, ewes with twins were kept separate from those with singles for the first two to three weeks after lambing. Ewes nursing twins received extra grain.

Ewes and lambs were herded on unfenced areas of the research ranch until mid-June. Until 1977, ewes and lambs were then taken by truck to high mountain Forest Service grazing allotments for the remaining summer grazing, until about the last week of August when lambs were weighed and weaned. However, after 1977, ewes and lambs remained on the research ranch for the entire summer grazing season, until mid-August when lambs were weighed and weaned.

Following weaning, all replacement ewe lambs remained at Red Bluff and were managed as one group. Ewe lambs were supplemented with 0.3 kg of a 20 percent protein pellet and allowed to graze hay meadow aftermaths until November. During the winter, the ewe lambs were also fed a mixed alfalfa-grass hay. Replacement yearling ewes were herded with the main ewe flock during the summer grazing season. Replacement ram lambs were transported to the Fort Ellis farm, five miles east of Bozeman, Montana, following weaning. Rambouillet ram lambs were fed one pound of barley and free choice mix grass-alfalfa hay through the

winter, and grazed cultivated pastures during the following summer grazing season. Management of the Targhee rams differed. Following weaning, the Targhee rams were tested for post-weaning gain. Prior to 1978, rams were fed two pounds of barley per head per day, plus mixed hay. After 1978, the test ration was characterized by higher energy and lower rouphage. The performance test finished in February when the rams were shorn and preliminary selections were made. Rambouillet rams were shorn in mid-February and all final selection decisions were made in the fall.

Data

Direct and Correlated Responses in Components of Lambing Rate

Ovulation rate data were collected for three seasons (1985-1987). Breeding season commenced approximately November 15 each year and data were collected on all Rambouillet ewes which were observed in estrus during first 20 days of the breeding season. Estrus was detected by fitting each Rambouillet ram with a marking harness. The pens were checked once daily to check for ewes that had been marked by the ram. Estrus ewes were examined via mid-ventral laparoscopy 4-5 days post mating. The ewes were held off feed and water 24 hours prior to laparoscopy. Just prior to laparoscopy each ewe was injected with 1 cc acepromazine maleate (10 mg/ml) (Tech America) IM and local anesthesia was induced by use of 5 cc lidocaine (2%) (Tech America) at each probe site. The number of corpora lutea observed on each ovary was recorded and taken to represent the ovulation rate. The laparoscopy technique

does not reduce the reproductive performance of the ewes examined (Oldam, et al. 1976).

Following laparoscopy, the ewes were given an injection of 5 cc Penicillin G Procaine. They were returned to the range and exposed to blackface rams for the remainder of the breeding season. The birth of a cross-bred lamb indicated that the mating by the Rambouillet ram and the observed ovulation did not result in a viable pregnancy.

The subsequent lambing record for each ewe was examined to access fertility, lambing rate, and litter size and to estimate embryonic survival. Lambing rate was defined as the number of lambs born per ewe exposed and litter size as the number born per ewe lambing. Fertility, expressed as the percent lambing per ewe exposed, was also accessed, at first service and for all services. Embryonic survival was the percentage of corpora lutea represented by live lamb(s) and it was calculated for pregnant ewes and for all ewes ovulating during the first 20 days. Embryonic survival data from ewes giving birth to cross-bred lambs was taken to be zero. Ewes credited with giving birth to more lambs than the observed ovulation rate had their ovulation rate adjusted upward to match the lambing record.

Statistical Analyses. The data were analyzed using the General Linear Model procedure of SAS (1985). Independent variables in the analyses were line, year, age of ewe and all two-way interactions. The partial regression of ewe pre-breeding body weight was also included. Dependent variables were fertility, lambing rate, litter size,

ovulation rate, and embryonic survival. The effect of site of ovulation on embryo survival was also examined.

Heritability and repeatability estimates of ovulation rate were determined using a least-squares analysis of variance (Harvey, 1977). In addition to the independent variables mentioned above, also included were the random effect sire within year-line and between ewe within sire within year-line.

Heritability (h^2) was estimated from paternal half-sib analysis using the following equation:

$$h^2 = \frac{4\acute{o}^2s}{\acute{o}^2w + \acute{o}^2e + \acute{o}^2s}$$

where $\acute{o}^2s$ is the estimate of the sire variance component and $\acute{o}^2e$ between ewe and $\acute{o}^2w$ is the residual variance component.

Repeatability (r_e) was estimated from the between ($\acute{o}^2e$) and residual ($\acute{o}^2w$) variance components.

$$r_e = \frac{\acute{o}^2e}{\acute{o}^2e + \acute{o}^2w}$$

Correlated Responses in Production Traits

Data for this study were collected from the three selection lines of Rambouillet sheep (L, H, and C) and the Targhee (T) flock. The Targhee data were included as another assessment of the environmental trends, in addition to the effects of selection for body weight and fleece weight.

Traits measured on lambs were birth weight and weaning weight. Traits evaluated in the ewes were body weight prior to mating, fleece

weight and fleece grade. The data represented growth and weight traits during the entire duration of the selection experiment in the Rambouillet sheep.

Statistical Analyses. Data were analyzed using least- squares procedures (Harvey, 1977). Using group means, regression analyses were performed taking account of ewe categories. Independent variables for the lamb traits (birth and weaning weight) were year of birth of the lamb (1969-1986), breed or line (L, H, C or T), year of birth by breed or line interaction, sex of lamb (ewe or ram), type of birth and rearing and date of birth. Independent variables for the ewe traits (body weight, fleece weight and grade) were breed or line, year of birth, breed or line by year of birth interaction and lactation status. Lactation status was a variable created to indicate whether a ewe nursed any lambs in the year affecting the trait being studied, but did not take into account twin or single since that was one of the selection objectives. Linear contrasts were used to test for differences between the Targhees and three selection lines. Each age of ewe was analyzed separately because year of birth of the ewe, age of the ewe, age of dam and year of the record cannot all be included in the same analyses due to complete confounding. Therefore, it was decided that rather than adjusting the records for year the record was made or age of ewe, each age of ewe group would be analyzed separately.

RESULTS AND DISCUSSION

Direct Responses

Lambing Rate

Analyses of variance for lambing rate at first service and lambing rate at all services are presented in Table 3. Year affected lambing rate ($P<.01$) when assessed for all services. Lambing rate was 1.13 $\pm$.04 in 1986 compared to 1.29 $\pm$.04 in 1987. The difference was the result of a 10% lower conception rate in 1986. Age of ewe did not affect lambing rate at first service, but did for all services ($P<.05$), even when body weight was included in the model. In general, lambing rate increased up to age 5 and declined at age 6 (Figures 1 and 2). The linear regression of pre-breeding weight on lambing rate was significant (Table 3). Lambing rate increased as pre-breeding weight increased. For each 1 kg increase in body weight, lambing rate increased .0087 $\pm$.0027 first service and .0089 $\pm$.0022 for all services repectively.

Line affected ($P<.01$) lambing rate at first and all services. Lambing rate at first service was lowest ($P<.05$) for the L line (0.87), but not different ($P>.10$) for the H (1.09) and C (1.15) lines (Table 4). The lower lambing rate of the H line is the result of lower first service fertility. Figure 1 shows that there was a change in rank in lambing rate at first service as ewes increased in age. When assessed over all services, lambing rate was different ($P<.05$) for all three lines. High line ewes were clearly superior to the other selection lines, giving birth to 1.40 $\pm$.05 lambs per ewe exposed. Low line ewes

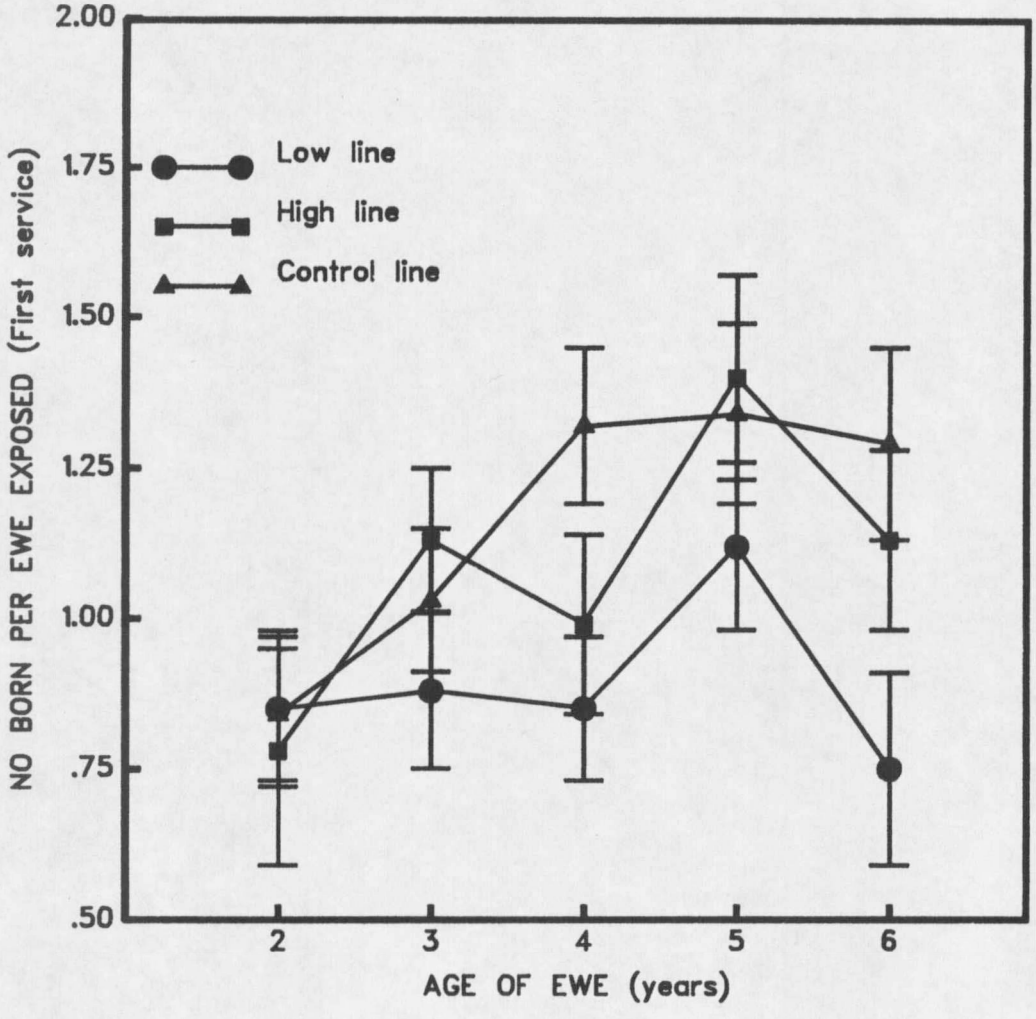


FIGURE 1. EFFECT OF LINE AND AGE ON LAMBING RATE (FIRST SERVICE).

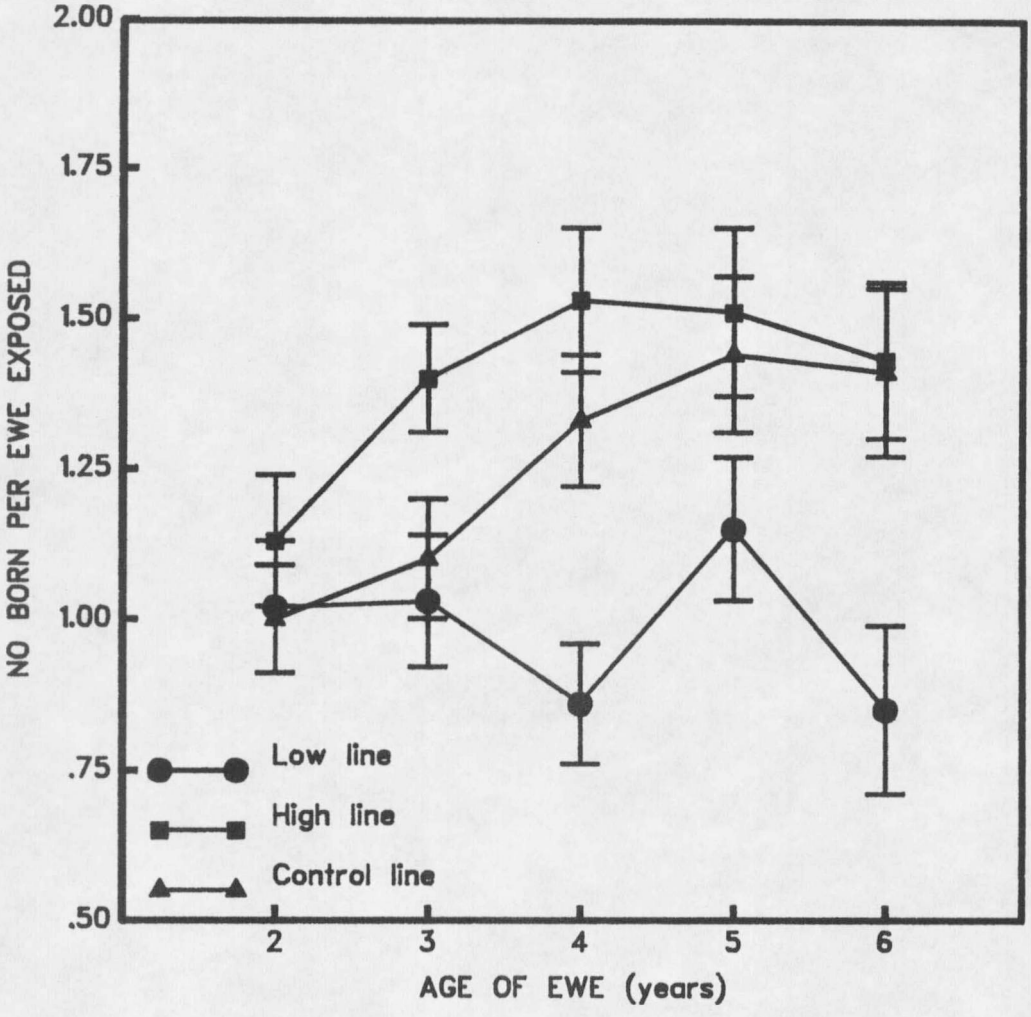


FIGURE 2. EFFECT OF LINE AND AGE ON LAMBING RATE (ALL SERVICES).

averaged less than one lamb, 0.98 ±.05, while C ewes were intermediate, showing an average rate of 1.25 ±.05 lambs born per ewe exposed (Table 4). There were no significant two-factor interactions for lambing rate at first service. For all services, a line x age interaction was observed (P<.10) and year x age approached significance (P = .125) (Table 3). Although the interaction of line x age was important, there did not appear to be a change in rank as the ewes became older (Figure 2). The H line was consistently higher than the L line and the C line was intermediate between the two selected lines.

TABLE 3. LEAST SQUARES ANALYSIS OF VARIANCE FOR LAMBING RATE (NUMBER OF LAMBS BORN PER EWE EXPOSED)

Source of variation	df	Mean squares	
		First service	All services
Line	2	3.15**	6.13**
Year	1	0.06	2.57**
Age	4	0.76	0.86*
Line x year	2	0.17	0.08
Line x age	8	0.54	0.60+
Year x age	4	0.33	0.66
Regression Weight	1	5.52**	5.68**
Error	427	0.51	0.36

+(P<.10) *(P<.05) **(P<.01)

Most of the literature reports response to selection for reproduction in terms of litter size. When the response is reported in terms of number of lambs born per ewe mated, the numbers are less impressive. Clarke (1972) reported an annual regression on years

(1948-1970) of 1.57 lambs per 100 ewes mated, compared to 1.75 lambs born per ewe lambing.

TABLE 4. LEAST SQUARES MEANS AND STANDARD ERRORS FOR LAMBING RATE (NUMBER OF LAMBS BORN PER EWE EXPOSED)

Line	No. of ewes	first service	All services
Low	147	$0.87^{a} \pm .06$	$0.98^{a} \pm .05$
High	149	$1.09^{b} \pm .06$	$1.40^{b} \pm .05$
Control	154	$1.15^{b} \pm .06$	$1.25^{c} \pm .05$

^{a,b,c}Means within the same column with different superscripts are significantly different ($P<.05$).

Correlated Responses in Reproductive Traits

Fertility

Fertility was 91.4 ± 2.3 percent in 1987 compared to 81.0 ± 2.5 percent for 1986 ($P<.01$). The linear regression of pre-breeding weight on fertility ($P<.01$) was .0278 ±.0161 percent (first service) and .0259 ±.0125 percent (all services) per kg increase in pre-breeding weight. Age did not account for any significant variation in fertility when body weight was included in the model (Figures 3 and 4). There were no two-factor interactions that affected fertility (Table 5).

Line affected fertility at first service only (Table 5). Low, H, and C ewes had first service fertility rates of 73.8 ± 3.7, 66.9 ± 3.8 and 81.5 ± 3.6 percent respectively, though the difference between the L and H lines was not significant (Table 6). To determine the influence that sire of mating may have had on fertility, another analysis was conducted that included sire of mating within line and

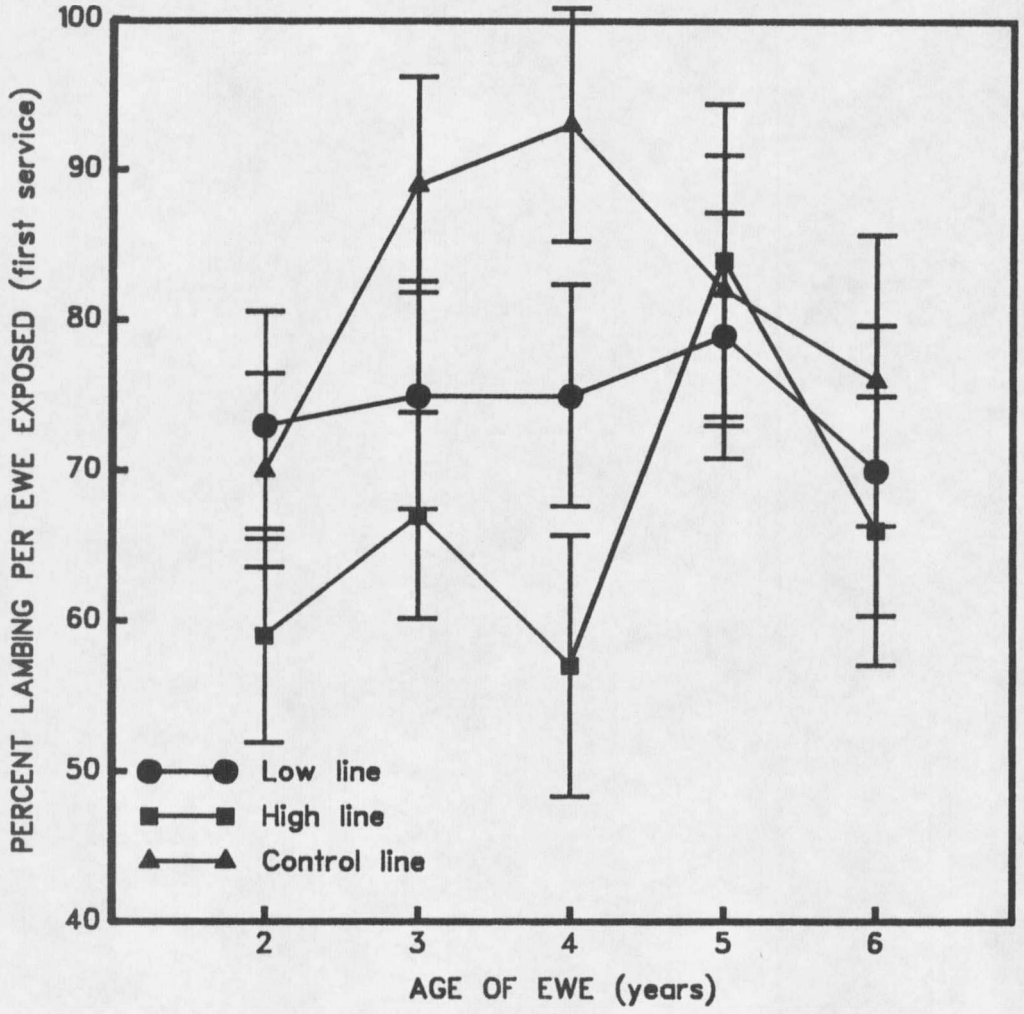


FIGURE 3. EFFECT OF LINE AND AGE ON FERTILITY (FIRST SERVICE).

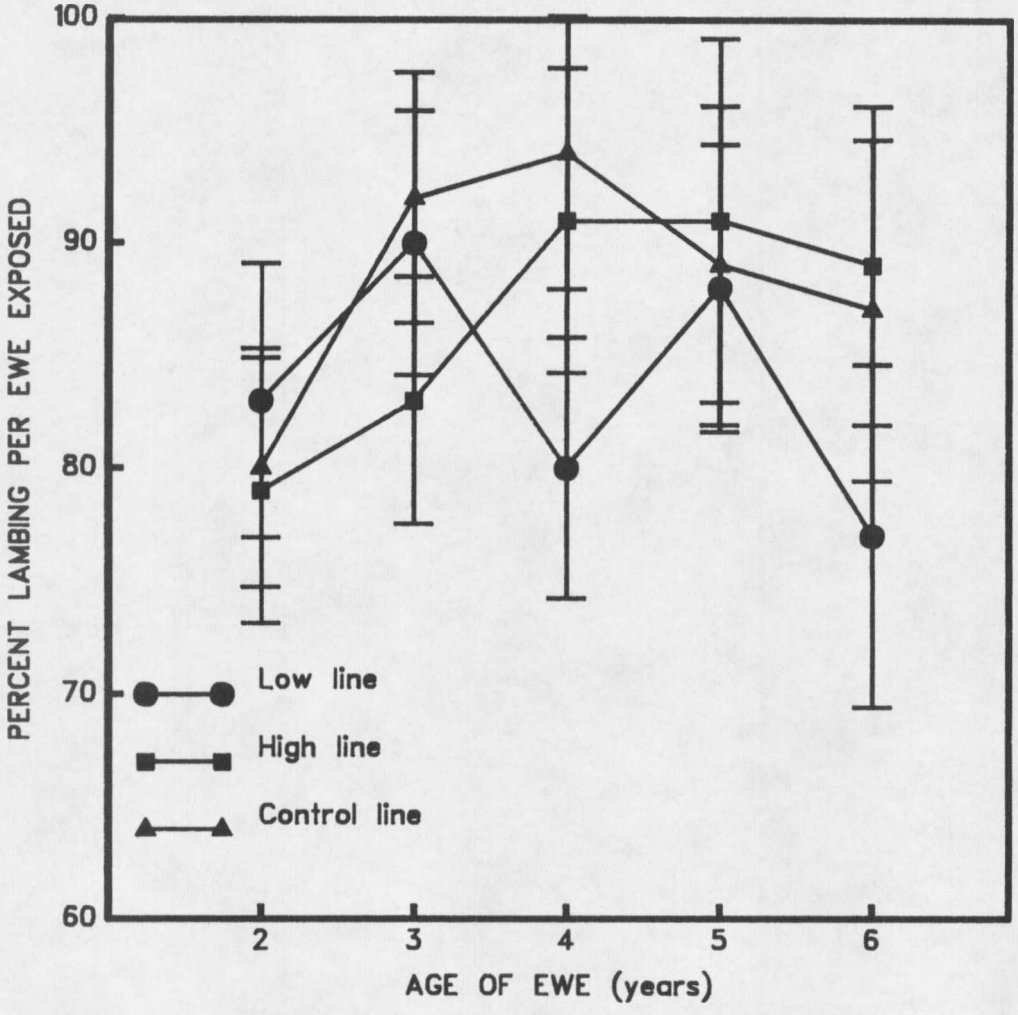


FIGURE 4. EFFECT OF LINE AND AGE ON FERTILITY (ALL SERVICES).

year. While individual rams did have an effect (P<.01) on fertility, it did not change the differences between lines, therefore, ram was left out of the model. There were no differences in fertility observed in the three lines when the trait was assessed for the entire 35-day breeding season (Table 5). Thus, selection for reproductive rate did not produced a correlated response in fertility. If anything, the selected lines have decreased in fertility when compared to the control line. Other studies have reported higher conception rates for sheep selected for multiple births (Wallace, 1964; Clarke, 1972, Turner, 1978; McGuirk, 1976 and Bradford et al., 1986).

TABLE 5. LEAST SQUARES ANALYSIS OF VARIANCE FOR FERTILITY (PERCENT EWES LAMBING PER EWE EXPOSED)

Source of variation	df	Mean squares	
		First service	All services
Line	2	7281*	796
Year	1	1243	10392**
Age	4	1545	1065
Line x year	2	939	457
Line x age	8	1436	673
Year x age	4	2547	1238
Regression Weight	1	5564+	4839*
Error	427	1860	1128

+(P<.10) *(P<.05) **(P<.01)

Litter Size

Litter size data were subdivided into first service and all services. Line, weight and line x age interaction were all significant sources of variation for both traits (Table 7). Age was significant

for all services (P<.10) and it approached significance for first service (P = .15). In general, litter size increased with age of ewe until 5 years old, then a slight decline was observed in 6 year old ewes (Figures 5 and 6). As body weight increased, first service litter size decreased (b = -.0014 ±.0007) When assessed over all services, litter size increased following an increase in pre-breeding body weight (b = +.0083 ±.0019).

TABLE 6. LEAST SQUARES MEANS AND STANDARD ERRORS FOR FERTILITY (PERCENT EWES LAMBING PER EWE EXPOSED)

Line	No. of ewes	First service	All services
Low	147	$73.8^{a} \pm 3.7$	$83.6^{a} \pm 2.9$
High	149	$66.9^{a} \pm 3.8$	$86.7^{a} \pm 2.9$
Control	154	$81.5^{b} \pm 3.6$	$88.3^{a} \pm 2.9$

^{a,b,c}Means within the same column with different superscripts are significantly different (P<.05).

TABLE 7. LEAST SQUARES ANALYSIS OF VARIANCE FOR LITTER SIZE (NUMBER OF LAMBS BORN PER EWE LAMBING)

Source of variation	df	Mean squares	
		First service	All services
Line	2	5.02**	5.55**
Year	1	0.05	0.00
Age	4	0.31	0.40+
Line x year	2	0.04	0.05
Line x age	8	0.48**	0.39*
Year x age	4	0.22	0.27
Regression Wt.	1	3.83**	3.53**
Error	311[a]	0.19	0.19

+(P<.10) *(P<.05) **(P<.01)

[a]Error df for all services is 366.

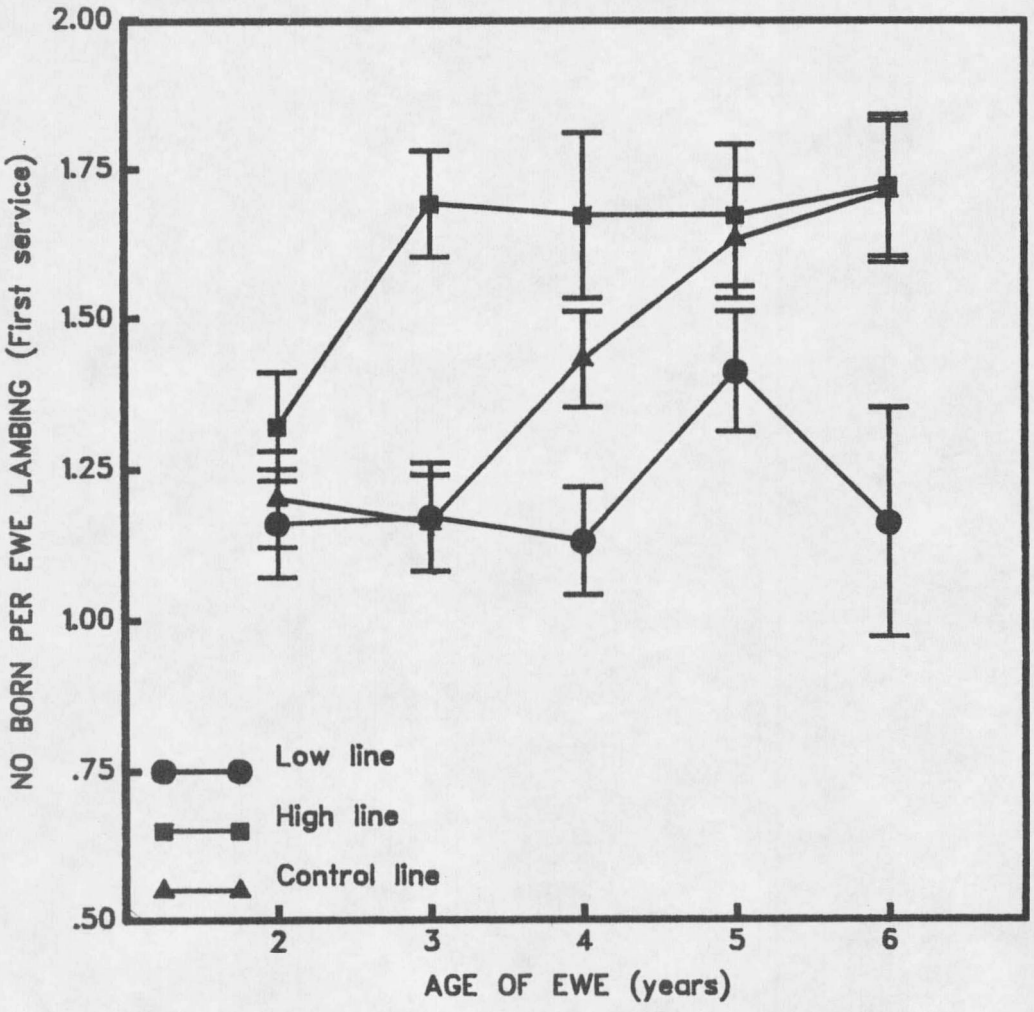


FIGURE 5. EFFECT OF LINE AND AGE ON LITTER SIZE (FIRST SERVICE).

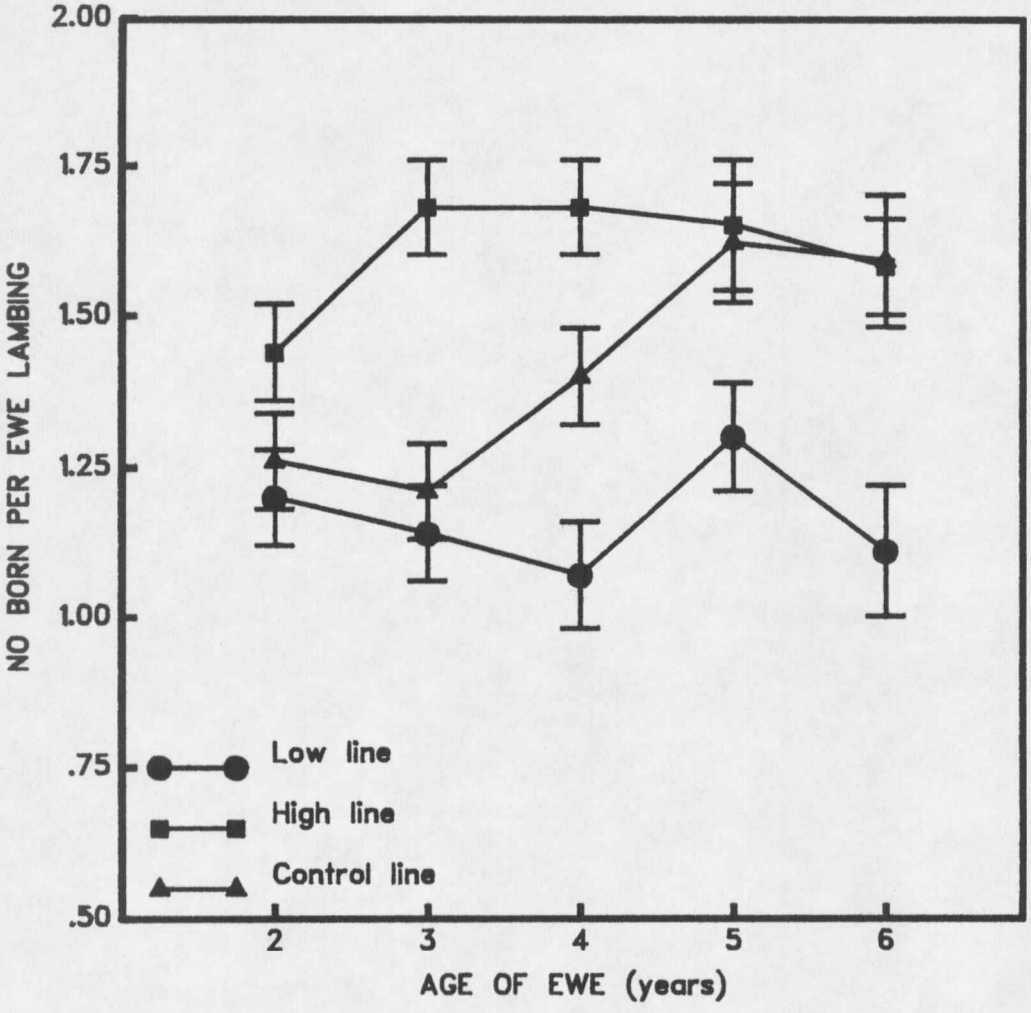


FIGURE 6. EFFECT OF LINE AND AGE ON LITTER SIZE (ALL SERVICES).

As would be expected the three lines differentiated and line proved to be the major source of variation for litter size. High line ewes were superior to L line ewes, with a mean litter size of 1.64 ±.05 compared to 1.17 ±.04 lambs in the L line. The control line averaged 1.42 ±.04 lambs born per ewe lambing, and were slightly closer to the H line. Examining the data for all services (Table 8) reveals the same trends, with means of the same magnitude. In general, the H line maintained its superiority at all ages (Figure 5 and 6). In addition, Figures 5 and 6 show that while the C line shows the expected increase in litter size with age, the L and H lines appear to have leveled off in litter size following their first parity. The relatively flat curve observed for 3-6 year old ewes in the L and H lines reflects the selection imposed in this experiment.

Our data are in general agreement with other selection studies which generally report results in terms of changes in litter size. In the New Zealand experiment, Clarke (1972) reported litter sizes of 1.13, 1.62 and 1.22 for the low, high and control lines, respectively. Clarke (1972) reports greater change in the high line. In the Australian study, (Turner, 1978) litter size was 1.18 and 1.70 for the 0 and T lines respectively. Greater progress has been made in the downward direction as in our study. It should be noted, however, that selection in these experiments has occurred for a longer period of time, 24 and 18 years, respectively. The response in other studies has been less, but they have been of shorter duration (Mann et al., 1978; Hanrahan and Timon, 1978; Atkins, 1980; and Bradford, 1985).

TABLE 8. LEAST SQUARES MEANS AND STANDARD ERRORS FOR LITTER SIZE (NO LAMBS BORN PER EWE LAMBING)

Line	First service		All services	
	No. of ewes	Litter size	No. of ewes	Litter size
Low	111	$1.17^{a} \pm .04$	125	$1.17^{a} \pm .04$
High	97	$1.64^{b} \pm .05$	128	$1.61^{b} \pm .04$
Control	126	$1.42^{c} \pm .04$	136	$1.42^{c} \pm .04$

^{a,b,c}Means within the same column with different superscripts are significantly different ($P<.05$).

Ovulation Rate

Ovulation rate was affected by line, age and weight (Table 9). There were no significant two-factor interactions (Table 9). Age was a significant source of variation in ovulation rate even following adjustment for body weight ($P<.01$). Ovulation rate was lowest for yearling ewes and it increased with age, but declined in 6 year old ewes (Figure 7). The linear regression of ovulation rate on body weight was $.0089 \pm .0014$ ($P<.01$).

Based on the results of this study, there is clear evidence for a correlated response in ovulation rate following selection for reproductive rate. The three selection lines differentiated in ovulation rate, as expected. High line ewes had a significantly higher mean ovulation rate than L ewes, $1.75 \pm .034$ versus $1.23 \pm .034$, with the control line intermediate between the two selection lines at $1.48 \pm .033$ (Table 10). The high line maintained their advantage at all ages (Figure 7).

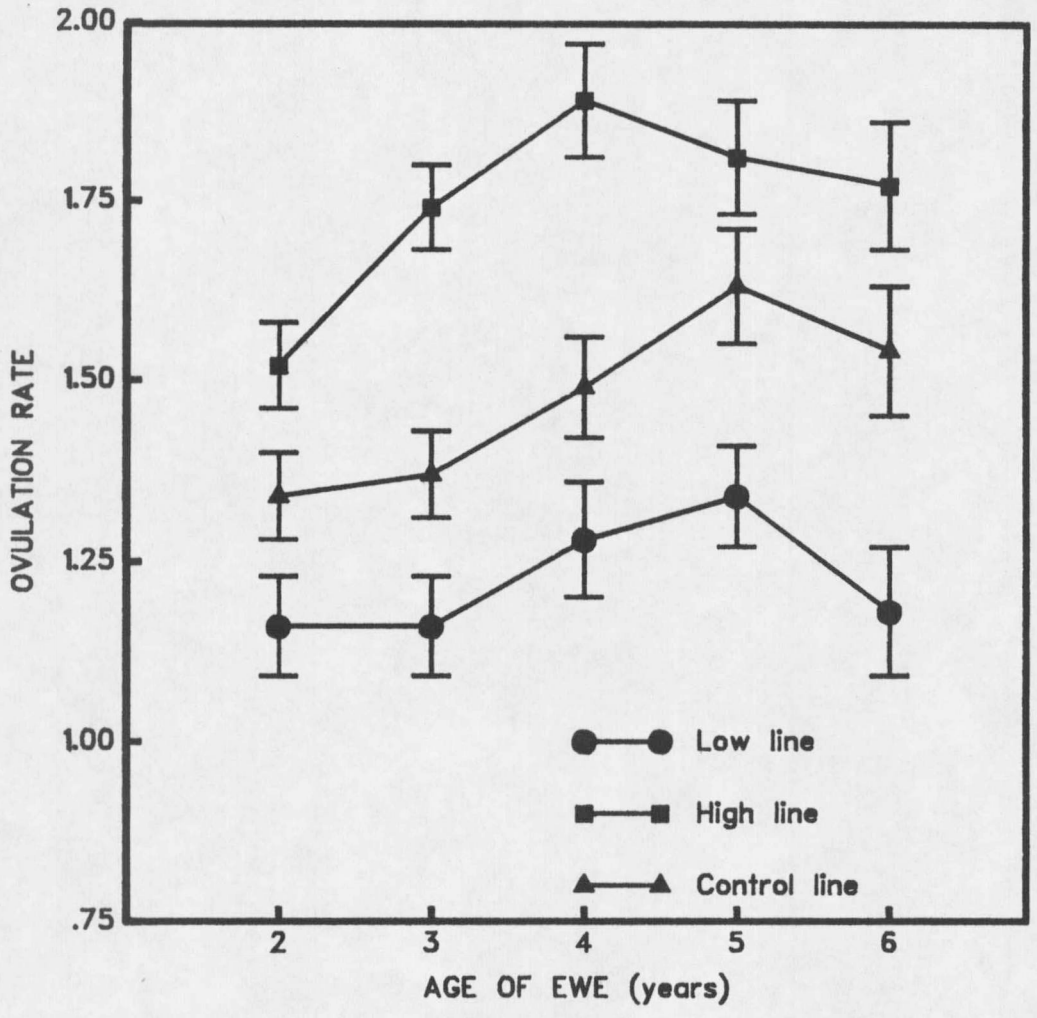


FIGURE 7. EFFECT OF LINE AND AGE ON OVULATION RATE.

TABLE 9. LEAST SQUARES ANALYSIS OF VARIANCE FOR OVULATION RATE

Source of variation	df	Mean squares
Line	2	14.08**
Year	2	0.15
Age	4	3.80**
Line x year	4	0.03
Line x age	8	0.22
Year x age	8	0.28
Regression Weight	1	8.70**
Error	670	0.23

*(P<.05) **(P<.01)

Repeatability was estimated to be .03 for ovulation rate. This is very low compared to published estimates of .20 for Galway ewes (Hanrahan and Quirke, 1985) and .38 for a mixed group of Rambouillet, Targhee and Columbia ewes (Hulet and Foote, 1967). Quirke et al. (1985) gave a repeatability estimate for CL count of .27 and .25 for mature and yearling Targhee ewes respectively. Carrick et al. (1980) reported a repeatability coefficient of .50 for Merino ewes, but this was within the same breeding season. Higher estimates have been reported for the more prolific breed types, such as the Finnish Landrace and Booroola Merino, but the relative magnitude of these estimates may be the result of greater variation in ovulation rate or in the case of the Booroola, the action of a single gene for high ovulation rate.

TABLE 10. LEAST SQUARES MEANS AND STANDARD ERRORS FOR OVULATION RATE

Line	No. of ewes	Ovulation rate
Low	226	$1.23^{a} \pm .034$
High	241	$1.75^{b} \pm .034$
Control	233	$1.48^{c} \pm .033$

^{a,b,c}Means with different superscripts are significantly different (P<.05).

TABLE 11. COMBINED LEAST SQUARES OF ANALYSIS OF VARIANCE

Source of variation	df	Mean squares
Yearline	17	1.85**
Sire/yearline	72	0.30
Ewe/sire yearline	244	0.24
Age	4	0.49+
Regressions		
wt/B linear	1	2.66**
Error	277	0.23

+(P<.10) *(P<.05) **(P<.01)

Sire within line was not a significant source of variation for ovulation rate (Table 11). Heritability for ovulation rate was estimated to be .15 ±.16. Published information on the heritability of ovulation rate is rather limited. Hanrahan and Quirke (1985) reported heritability estimates of .50 ±.09 and .32 ±.16 for Finn and Galway breeds respectively. This compares with heritability estimates of .05 ±.07 and .16 ±.07 for 18 month old Merino ewes (Piper et al., 1980). Our data give a very low estimate for both the repeatability and

heritability of ovulation rate. The low magnitude of our estimates is probably the result of the small variation in ovulation rate found in this selected population. Ovulation rate varied from one to three with a distribution of 56.0 percent single ovulations, 42.8 percent twins and only 2.2 percent triplets. The distribution of ovulation rates for the L, H, and C lines was 77.0, 21.7, 1.3; 33.9, 61.5, 4.6; and 57.1, 40.8, 2.1, singles, twins and triplets respectively.

Finnish Landrace is the only breed in which the effects of selection on ovulation rate have been assessed (Hanrahan and Quirke, 1982). A difference of 1 ovulation between high and low lines and a realized heritability of .50 $\pm$.07 was reported after eight years of selection by Hanrahan (1982). The correlation between ovulation rate and litter size is high, and the regression is almost linear at ovulation rates up to four (Hanrahan, 1982). Thus, it appears that selection for ovulation rate rather than litter size would enhance the rate of genetic improvement.

Embryo Survival

Selection for embryo survival may be necessary to realize the benefits from increased ovulation rates. In contrast to the effects of increased ovulation rates, an increase in embryo survival will decrease variability in litter size (Hanrahan, 1980) thus, improvement in embryo survival can contribute to achieving uniformity in litter size.

Embryo survival data were considered for all ewes ovulating and for pregnant ewes. Percent embryo survival was estimated by dividing the number of lambs born into the number of CL's counted during laparoscopy. Ewes which ovulated, but failed to lamb to whiteface

rams, were assessed as having 100 percent embryo mortality. This was easily determined, as the birth of a crossbred lamb indicated that the mating by the whiteface ram did not result in a viable pregnancy. The data from blackface sires were disregarded when assessing embryo survival for pregnant ewes.

TABLE 12. LEAST SQUARES ANALYSIS OF VARIANCE FOR PERCENT EMBRYO SURVIVAL

Source of variation	df	Mean squares	
		All ewes	Pregnant ewes
Line	2	8127*	763*
Year	1	1202	21
Age	4	1560	123
Line x year	2	817	82
Line x age	8	1607	223
Year x age	4	1730	408
Regression Weight	1	2710	885
Error	427[a]	1845	243

+(P<.10) *(P<.05) **(P<.01)

[a]Error df for pregnant ewes is 311.

TABLE 13. LEAST SQUARES MEANS AND STANDARD ERRORS FOR PERCENT EMBRYO SURVIVAL

Line	Pregnant ewes		All ewes	
	No. of ewes	% Embryo survival	No. of ewes	% Embryo survival
Low	111	$97.0^{a} \pm 1.6$	147	$71.6^{a} \pm 3.7$
High	97	$92.1^{b} \pm 1.6$	149	$61.7^{b} \pm 3.8$
Control	126	$94.6^{ab} \pm 1.5$	154	$77.0^{a} \pm 3.6$

[a,b]Means within the same column with different superscripts are significantly different (P<.05).

TABLE 14. LEAST SQUARES ANALYSIS OF VARIANCE FOR PERCENT EMBRYO SURVIVAL DUE TO EFFECTS OF SITE OF OVULATION

Source of variation	df	Mean squares	
		all ewes	pregnant ewes
Line	2	5393+	56
Year	1	1665	1466+
Age	4	1051	500
Site	2	3022	315
Line x site	4	937	784
Age x site	8	1693	387
Error	418[a]	1874	492

+(P<.10)

[a]Error df for pregnant ewes is 98.

The analyses of variance for all ewes and pregnant ewes are given in Table 12. Line was the only main effect that was significant. There were no important two-factor interactions (P>.10). High line ewes had the lowest percent embryo survival, 61.4 ± 3.8, for pregnant ewes. This can be the result of many things. First of all, because data on fertilization rate are often unavailable, the difference between ovulation rate and the number of lambs born is typically referred to as "embryo" or "prenatal" loss, but it is important to realize that this loss may reflect variation in other factors in addition to embryonic death. Further, as the number of eggs entering the uterus increases, embryo survival declines in a linear fashion (Hanrahan, 1986; Fogarty, 1984), and H line ewes because of their higher ovulation rate would be expected to have lower embryo survival. Nonetheless, fertilizaton failure may have also contributed to the low

value observed in the H line. Percent embryo survival for the L and C line was 72.2 ± 3.7 and 77.3 ± 3.6 respectively, though the differences were not significant. Percent embryo survival for pregnant ewes was highest in the L line, 97.0 ± 1.6, which can be explained by the high percentage of single ovulations. High line ewes, characterized by a higher percentage of multiple ovulations, again exhibited the lowest embryo survival value, 92.1 ± 1.6. But, here too, fertilization failure may possibly have contributed to the lower value. Percent embryo survival for the control line was 94.6 ± 1.5, intermediate between the two selected lines, but not significantly different from L or H (Table 13).

Embryo survival was not affected by site of ovulation ($P<.01$) (Table 15). Embryo survival in pregnant ewes was 88.6 ± 2.0 and 84.7 ± 2.0 percent (Table 15) for unilateral (both ovulations on one ovary) and bilateral (ovulations on both ovaries) ovulating ewes, respectively. Though the differences were not significant, the 4 percent advantage of unilateral ovulating ewes was not expected. This relates to the question of the migration of embryos between uterine horns (Sittman, 1972; Doney et al., 1973; Scanlon, 1972). It is thought that transuterine migration is routine in ewes with two ovulations on one ovary, but while migration decreases uterine crowding effects, failure to successfully complete the migration may result in embryo mortality (Scanlon, 1973). The effect of site of ovulation on embryo survival has been studied on many occasions. Several experiments report little if any effect of site of ovulation in twin ovulating ewes (Sittman, 1972; Kelly and Johnstone, 1983; Meyer, 1985;

Bradford et al., 1986). On the other hand, results of some studies (Casida et al., 1966; Doney et al., 1973; White et al., 1981) indicated an effect of site of ovulation. The reverse trend was observed when embryo survival was calculated for all ewes. Unilateral and bilateral twin ovulating ewes had survival values of 63.8 ± 5.0 and 66.2 ± 6.0 (Table 15), respectively. While the values were not significantly different, the tendency of bilateral twin ovulators to be superior would be expected.

TABLE 15. PERCENT EMBRYO SURVIVAL AS AFFECTED BY OVULATION PATTERN

	All ewes		Pregnant ewes	
Type of ovulation	No. of ewes	% Embryo survival	No. of ewes	% Embryo survival
Single	289	73.5[a] ± 3.0		
Unilateral twin	83	63.8[a] ± 5.0	59	88.7[a] ± 3.3
Bilateral twin	68	66.2[a] ± 6.0	54	84.9[a] ± 3.4

[a]Means within the same column with the same superscripts are not significantly different (P<.05).

Correlated Responses in Production Traits

Lamb Birth Weight

Lamb birth weight was affected by year, line or breed, sex of lamb, type of birth and rearing, and date of birth (Table 16). A year x line interaction was observed for 3, 4 and 5 year old dams (Table 16). Birth weights were lowest for lambs from 2 year old dams (Tables 17 and 18). Ram lambs exhibited heavier birth weights than ewe lambs

TABLE 16. LEAST SQUARES ANALYSIS OF VARIANCE FOR BIRTH WEIGHT

Source of variation	df	Mean squares for ewes age 2 to 6 (kg^2)				
		2	3	4	5	6
Year	15[a]	1.99**	1.73**	1.94**	1.01**	1.05**
Line	3	3.25**	3.67**	8.20**	4.63**	2.78**
Sex	1	10.96**	33.98**	18.23**	31.78**	15.87**
Type of birth and rearing	2	94.16**	132.57**	101.73**	62.25**	63.71**
Year x line	41[b]	0.41	0.57+	0.59*	0.66**	0.50
Regression						
Date of birth	1	7.16**	0.72**	6.46**	6.73**	4.85**
Error	1153[c]	0.38	0.41	0.38	0.37	0.45

**(P<.01) *(P<.05) +(P<.10)

[a]Year df for ewes age 3 to 6 were 14, 13, 12 and 11 respectively.
[b]Year x line df for ewes age 3 to 6 were 38, 35, 32, and 25 respectively.
[c]Error df for ewes age 3 to 6 were 1153, 979, 732 and 553 respectively.

TABLE 17. LEAST SQUARES MEANS AND STANDARD ERRORS FOR LAMB BIRTH WEIGHTS (KG)

Line	Age of dam				
	2	3	4	5	6
Low	$4.06^{a} \pm .15$	$4.58^{a} \pm .05$	$4.62^{a} \pm .05$	$4.71^{a} \pm .05$	$4.70^{ab} \pm .08$
High	$4.06^{a} \pm .15$	$4.44^{b} \pm .04$	$4.50^{b} \pm .04$	$4.60^{a} \pm .05$	$4.53^{a} \pm .07$
Control	$4.12^{a} \pm .16$	$4.60^{a} \pm .05$	$4.55^{ab} \pm .05$	$4.71^{a} \pm .06$	$4.84^{b} \pm .09$
Targhee	$4.27^{b} \pm .15$	$4.69^{c} \pm .03$	$4.88^{c} \pm .03$	$4.94^{b} \pm .04$	$4.87^{c} \pm .04$

[a,b,c]Means within the same column with different superscripts are significantly different (P<.05).

(P<.01). Single born lambs weighed approximately 1.0 kg more (P<.01) than twin-born lambs, across all ages of dam. Birth weight increased later in the season. This would be expected as ewes that lambed later in the season were on a high plane of nutrition for a longer period of time, and this was reflected in the birth of heavier lambs.

Examining least squares means for age of dam (Table 18) shows that there was a tendency for H line lambs to have lighter birth weights than both L and C line lambs, although the differences are probably not biologically important. Targhee lambs had heavier (P<.05) birth weights than Rambouillet lambs for all ages of dam.

TABLE 18. ESTIMATED REGRESSION COEFFICIENTS FOR LAMB BIRTH WEIGHTS (KG)

Age of dam	Low		High		Control		Targhee	
	a	b±se	a	b±se	a	b±se	a	b±se
2	4.91	-.011±.012	6.03	-.025±.012	5.00	-.012±.014	5.24	-.013±.012
3	6.02	-.018±.013	5.74	-.016±.008	4.79	-.003±.020	6.84	-.022±.014
4	6.62	-.025±.016	6.77	-.029±.015	6.47	.024±.025	4.31	.007±.015
5	6.67	-.024±.015	6.87	-.028±.013	1.99	.036±.041	3.41	.019±.015
6	2.88	-.022±.029	4.24	.004±.029	1.04	.046±.025	2.76	.026±.018

The regression coefficients for birth weight on year of birth are given in Table 19. No clear pattern can be established. Figures 8 and 9 show the phenotypic time trend for birth weight for 2 and 4 year old dams. In general, birth weight has declined over time, however the data points appear to be erratic and probably signify the fluctuations in management and environment that can occur from year to year in a range sheep operation.

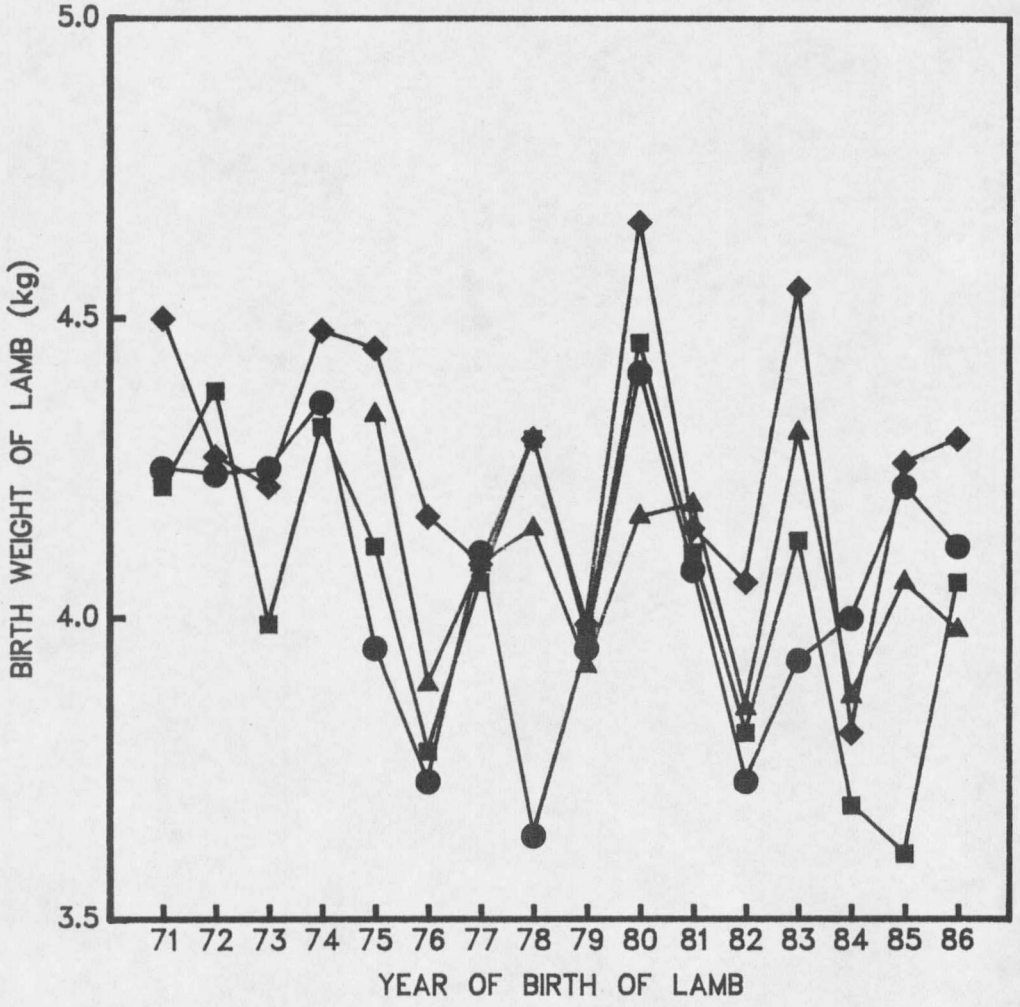


FIGURE 8. EFFECT OF LINE AND YEAR ON BIRTH WEIGHT - 2 YR OLD DAMS.

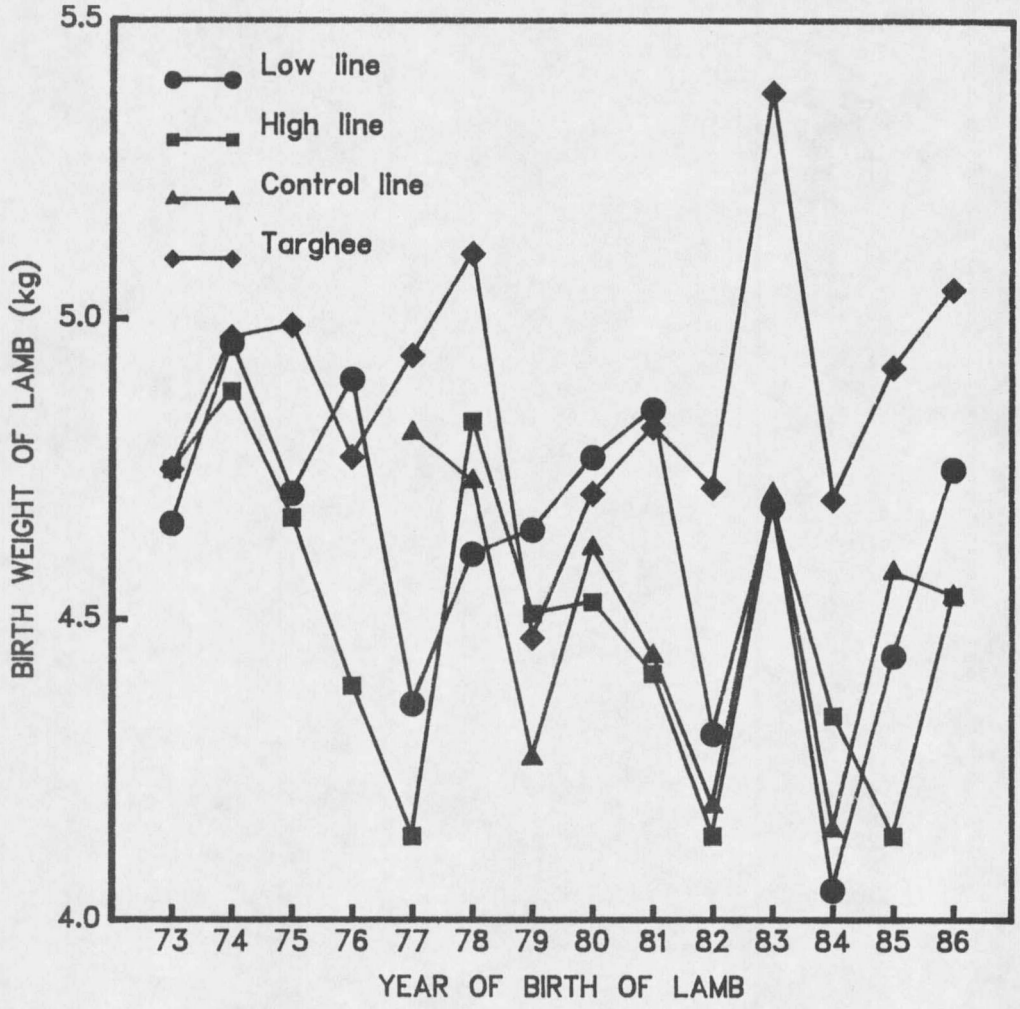


FIGURE 9. EFFECT OF LINE AND YEAR ON BIRTH WEIGHT - 4 YR OLD DAMS.

Lamb Weaning Weight

Weights of the lambs were taken at weaning when the lambs returned from high mountain Forest Service grazing allotments (prior to 1977), around August 15, or after 1977, around the end of August. Weaning occurred at approximately 130 days of age.

All main effects were significant for weaning weight (Table 19). Ram lambs were heavier ($P<.01$) at weaning than ewe lambs. Single lambs grew faster than both twin lambs that were raised as twins and twin lambs that were raised as singles ($P<.01$), although not tested statistically. Lambs from dams age 3 through 5 grew faster than lambs from 2 year old dams (Tables 20 and 21). Greater variation was also observed in lambs from 2 year old ewes, and a slight decline in production was noted for 6 year old dams (Tables 20 and 21). Lambs born earlier in the year were heavier at weaning ($P<.01$). No clear trend in line associated with weaning weight can be revealed by examining the least squares means (Table 20). There may be a tendency for L lambs to be lighter at weaning, though the reason is unclear. Further, the differences, although statistically significant in some age of dam groups, are probably not biologically important. The data are in general agreement with the literature which reports no detectable correlation between selection for reproductive rate and weaning weight (Land et al, 1983). Targhee ewes weaned heavier lambs than Rambouillet ewes ($P<,01$) in all age of dam groups.

The regression coefficients for weaning weight on year of birth (Table 21) show no important differences between the four lines. Each has steadily decreased over the duration of the experiment, at approximately the same rate. As indicated by a positive b value, lambs from 6 year old dams (except the L line) have increased over time. Figures 10 and 11 show the downward trend for the phenotypic time trend for the Rambouillets and Targhees. The four lines, in general, have followed the same pattern over time.

The general fall in weaning weights during the experiment may be due to a variety of factors. Prior to 1977, the ewes and lambs spent from early July to the last week in August grazing high mountain Forest Service grazing allotments. However, after 1977, they spent the entire summer grazing season on the research ranch. This decrease in the quality of summer range is probably responsible for much of the decline in weaning weight. The Targhees, which have been selected for post-weaning gain, have also suffered a decline in weaning weight. Their decrease in production parallels that of the three Rambouillet lines, indicating that it is primarily environment that has contributed to the long downward trend in lamb growth. The effect of inbreeding on the productive characteristics of the studied population is worthy of consideration, as well. It was not taken into account in these analyses.

TABLE 19. LEAST SQUARES ANALYSIS OF VARIANCE FOR WEANING WEIGHTS

Source of variation	df	Means squares for ewes age 2 to 6 (kg^2)				
		2	3	4	5	6
Year	15[a]	3109.2**	2987.4**	2622.2**	1778.6**	1030.9**
Line	3	777.7**	534.2**	470.2**	383.7**	168.5**
Sex	1	1187.4**	2269.4**	1244.1**	1882.7**	809.2**
Type of birth and rearing	2	2066.8**	6548.0**	5761.3**	3876.9**	2817.6**
Year x line	41[b]	20.2	16.8	13.1	17.6	23.6
Regression date of birth	1	1159.7**	1143.1**	1220.5**	661.5**	244.5**
Error	1153[c]	17.5	18.6	18.0	20.5	20.7

**(P<.01)

[a]Year df for ewes age 3 to 6 were 14, 13, 12 and 11 respectively.
[b]Year x line df for ewes age 3 to 6 were 38, 35, 32, and 25 respectively.
[c]Error df for ewes age 3 to 6 were 1153, 979, 732 and 553 respectively.

TABLE 20. LEAST SQUARES MEANS AND STANDARD ERRORS FOR LAMB WEANING WEIGHTS (KG)

Line	Age of dam				
	2	3	4	5	6
Low	$27.65^{a} \pm 1.05$	$32.30^{a} \pm .33$	$31.59^{a} \pm .33$	$32.10^{a} \pm .41$	$30.54^{a} \pm .56$
High	$28.79^{b} \pm 1.03$	$33.03^{a} \pm .27$	$32.77^{b} \pm .30$	$32.70^{a} \pm .34$	$32.32^{b} \pm .50$
Control	$28.86^{ab} \pm 1.05$	$32.28^{a} \pm .35$	$32.45^{ab} \pm .38$	$32.65^{a} \pm .47$	$32.09^{ab} \pm .59$
Targhee	$31.35^{c} \pm 1.01$	$35.01^{b} \pm .22$	$34.69^{c} \pm .23$	$35.12^{b} \pm .29$	$33.46^{c} \pm .28$

^{a,b,c}Means within the same column with different superscripts are significantly different ($P<.05$).

TABLE 21. ESTIMATED REGRESSION COEFFICIENTS FOR LAMB WEANING WEIGHTS (KG)

Age of dam	Low		High		Control		Targhee	
	a	b±se	a	b±se	a	b±se	a	b±se
2	131.7	-1.32 ±.15	146.7	-1.50 ±.12	149.0	-1.52 ± .21	140.9	-1.39 ±.13
3	143.7	-1.41 ±.13	143.8	-1.40 ±.16	155.8	-1.56 ± .23	155.9	-1.53 ±.15
4	149.4	-1.48 ±.19	154.2	-1.53 ±.19	138.8	-1.35 ± .29	159.7	-1.57 ±.19
5	151.0	-1.48 ±.23	147.6	-1.43 ±.20	124.4	-1.16 ± .33	152.8	-1.47 ±.18
6	40.7	-0.13 ±.24	22.2	.074 ±.23	26.3	.045±1.18	62.7	.34 ±.55

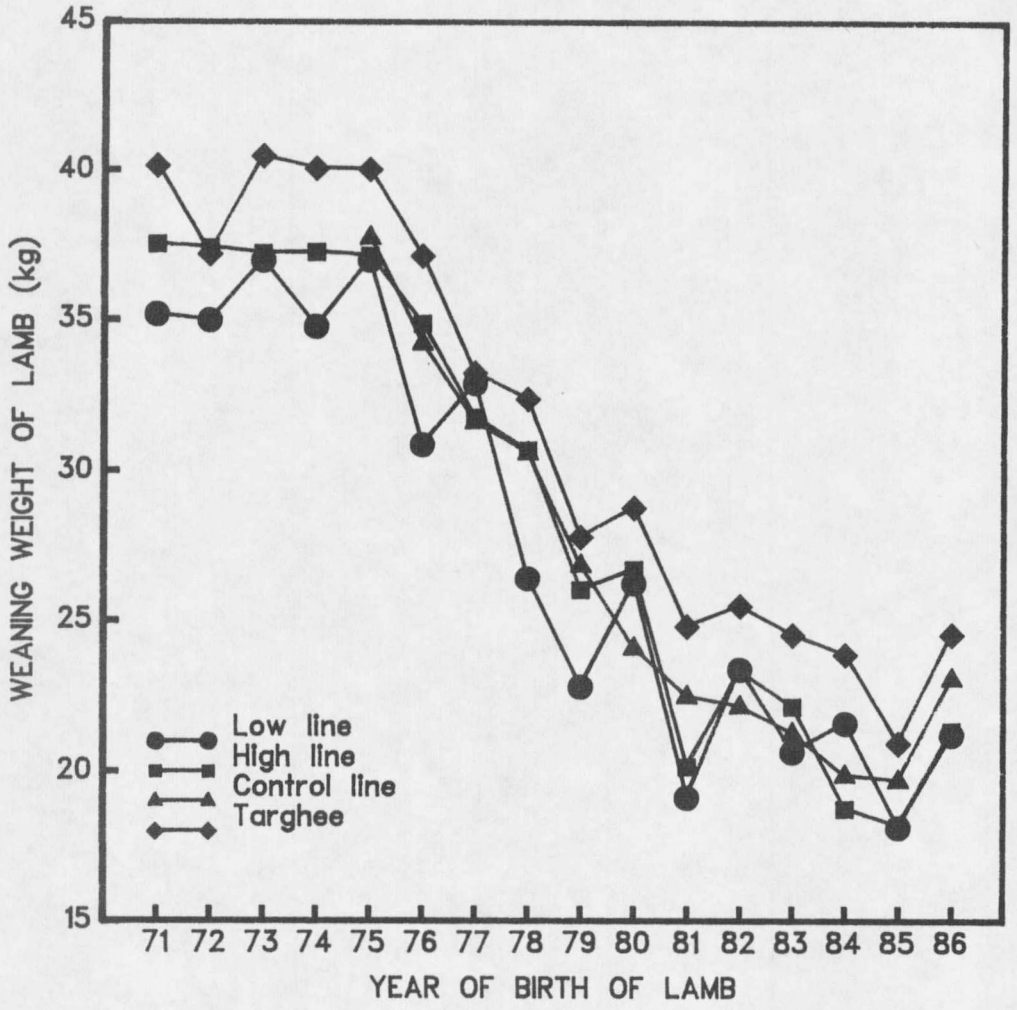


FIGURE 10. EFFECT OF LINE AND YEAR ON WEANING WEIGHT - 2 YR OLD DAMS.

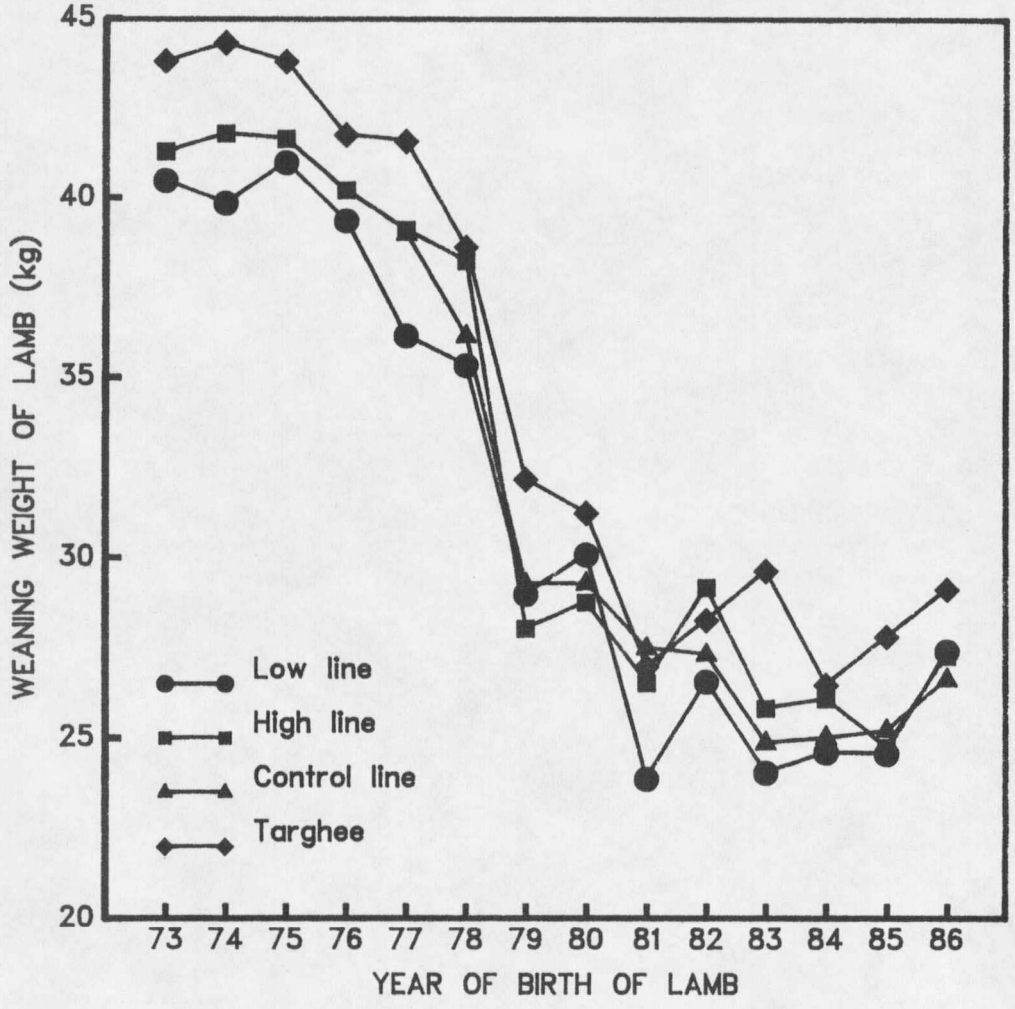


FIGURE 11. EFFECT OF LINE AND YEAR ON WEANING WEIGHT - 2 YR OLD DAMS.

Ewe Body Weight Prior to Mating

Body weight was affected by line, year of birth, and lactation status, and a significant year of birth x line interaction was observed for 5.5 year old ewes (Table 22). Ewes which failed to raise a lamb, an indication of lactation status, had heavier pre-breeding weights. However, means were not adjusted for the number of lambs a ewe raised because this adjustment may remove some of the genetic differences of interest. Body weight increased with age (Table 23 and 24).

At ages 1.5, 2.5 and 3.5, H line ewes were lighter, although the differences would not appear to be biologically important. Low and C ewes were not statistically different. At ages 4.5 and 5.5, there was no significant differences between the three lines. Targhee ewes were heavier ($P<.05$) than Rambouillet ewes (Table 24). Further, the difference between the Targhee and Rambouillets appears to be getting larger (Figures 12 and 13).

Body weight of the T line decreased at a slower rate than the Rambouillet lines (Table 24), which were not different ($P>.05$) (Table 24), probably indicating that selection for post-weaning gain in the Targhees has influenced ewe body weight. However, the four lines seemed to follow the same general pattern (Figures 12 and 13).

Land et al. (1983) reported a positive genetic correlation between adult body weight and reproduction and Clarke (1972) reported a small correlated response in the same direction. Hanrahan (1976) reported no change in body weight as a result of selection for increased lambing rate and Bradford (1985) found no significant differences in live weight at the yearling stage. The data from this study do not

TABLE 22. LEAST SQUARES ANALYSIS OF VARIANCE FOR EWE BODY WEIGHT

Source of variation	df	Mean squares for ewes age 1.5 to 5.5 (kg^2)				
		1.5	2.5	3.5	4.5	5.5
Line	3	3572.0**	2403.5**	2101.2**	1514.9**	1137.5**
Year	17[a]	1614.6**	2128.8**	1742.2**	1157.8**	805.4**
Lactation status	1	357.9**	1155.1**	884.7**	804.7**	1402.0**
Line x year	47[b]	38.6	49.9	35.0	39.8	47.2+
Error	2029[c]	23.3	29.6	29.5	32.2	33.6

*(P<.05) **(P<.01)

[a]Year df for ewes age 2 to 6 are 17, 16, 15, 14 and 13.
[b]Line x year df for ewes age 2 to 6 are 47, 44, 41, 38 and 31.
[c]Error df for ewes age 2 to b are 2029, 1540, 1194, 886 and 757.

TABLE 23. LEAST SQUARES MEANS AND STANDARD ERRORS FOR EWE BODY WEIGHTS (KG)

Line	Age of ewe				
	1.5	2.5	3.5	4.5	5.5
Low	$54.96^{a} \pm .40$	$62.77^{a} \pm .36$	$66.27^{a} \pm .46$	$67.84^{a} \pm .55$	$68.36^{a} \pm .63$
High	$53.88^{b} \pm .39$	$61.41^{b} \pm .36$	$64.78^{b} \pm .46$	$66.72^{a} \pm .58$	$67.72^{a} \pm .67$
Control	$54.49^{ab} \pm .43$	$62.34^{ab} \pm .42$	$65.67^{ab} \pm .52$	$66.89^{a} \pm .64$	$67.76^{a} \pm .68$
Targhee	$59.09^{c} \pm .35$	$66.49^{c} \pm .30$	$70.15^{c} \pm .40$	$71.80^{b} \pm .52$	$72.62^{b} \pm .50$

^{a,b,c}Means within the same column with different superscripts are significantly different ($P<.05$).

TABLE 24. ESTIMATED REGRESSION COEFFICIENTS FOR EWE BODY WEIGHT (KG)

Age of ewe	Low		High		Control		Targhee	
	a	b±se	a	b±se	a	b±se	a	b±se
1.5	97.9	-0.55±.15	91.7	-0.62±.14	104.2	-0.64±.20	90.7	-0.41±.14
2.5	125.3	-0.81±.15	135.2	-0.96±.12	139.6	-1.00±.21	122.9	-0.73±.17
3.5	136.3	-0.92±.16	139.2	-0.97±.16	136.2	-0.92±.27	121.3	-0.67±.17
4.5	141.2	-0.97±.14	139.9	-0.96±.14	119.9	-0.70±.21	126.1	-0.72±.17
5.5	154.2	-1.14±.14	135.9	-0.91±.16	121.5	-0.73±.25	144.5	-0.95±.20

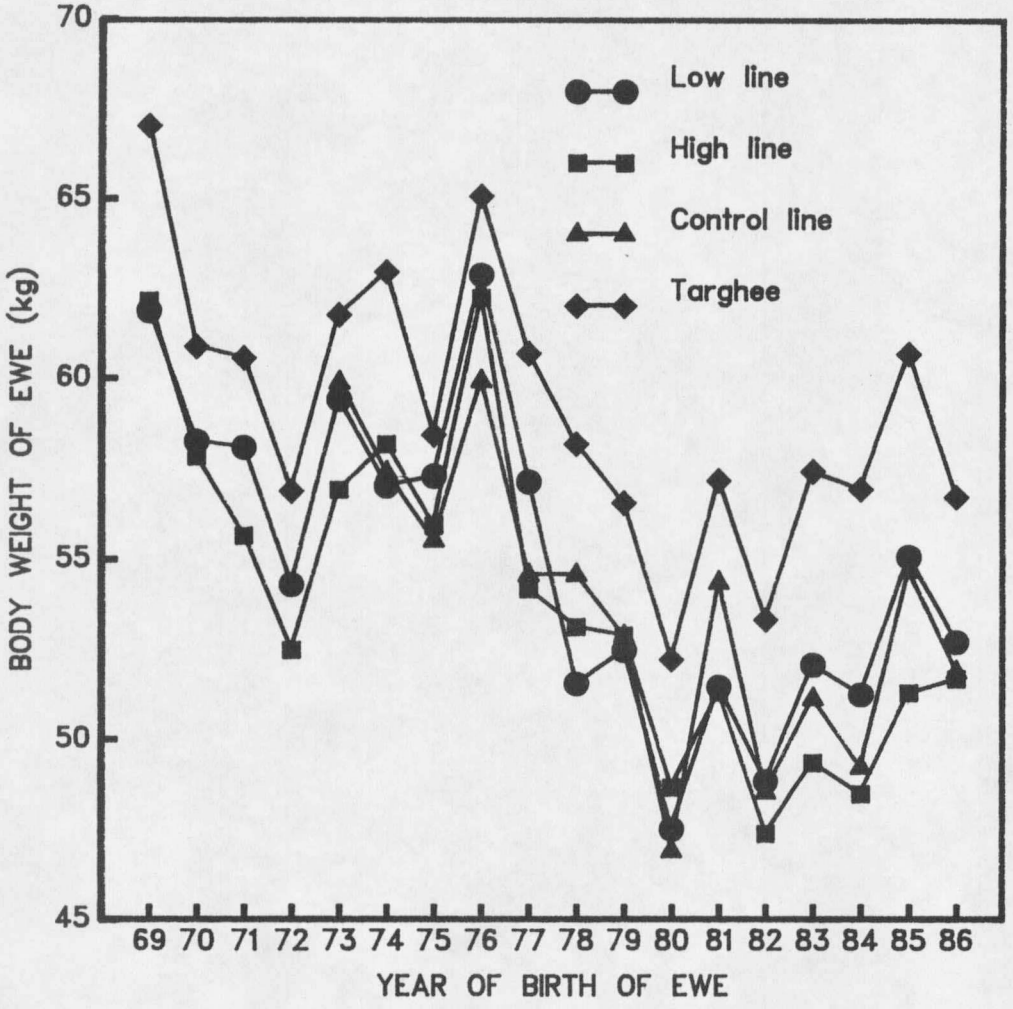


FIGURE 12. EFFECT OF LINE AND YEAR ON BODY WEIGHT - 1.5 YR OLD EWES.

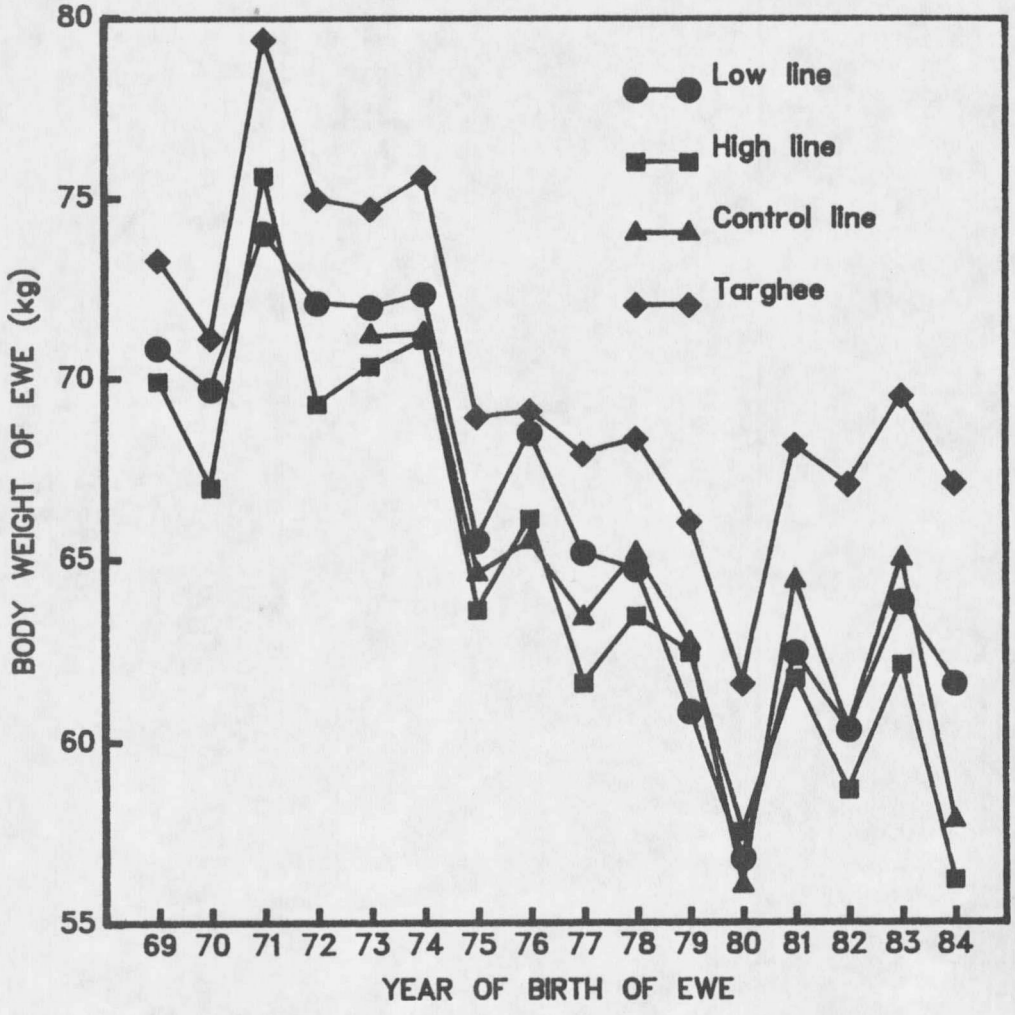


FIGURE 13. EFFECT OF LINE AND YEAR ON BODY WEIGHT - 3.5 YR OLD EWES.

substantiate the positive correlation between adult body weight and reproduction that was observed in many studies.

The long downward trend observed in ewe body weight is probably the result of the change in summer range described previously. Further, ewe body weight appears to be increasing over the past few years.

Ewe Fleece Weight

Fleece weight was affected by line or breed, year of birth, and lactation status (Table 25). A significant line x year of birth interaction was observed for yearling ($P<.01$) and 2 year old ($P<.05$) ewes. Ewes which failed to rear a lamb had heavier fleeces. Fleece weight increased with age up to 4 years of age (Tables 26 and 27). After 4, a slight decline was observed in fleece production.

Selection for reproductive rate has not adversely affected grease fleece weight. The least squares means indicate that there were no significant differences in fleece weight between L, H and C ewes at any age (Table 27). Land et al. (1983) reports a negative correlation between reproduction and fleece weight, giving an estimate of -.1. Clarke (1972) also reported a small negative estimate. Turner (1978), on the other hand, reports no change in average clean wool weight in the T and 0 groups, which agrees with our data.

The Targhee ewes had heavier fleeces, as would be expected. Further, the difference between the Targhees and Rambouillets appears to be getting larger (Figures 12 and 13). This can be explained by the fact that the Targhees have been selected for fleece production.

The regression coefficients indicate that there was a downward phenotypic time trend for all four lines. This is shown graphically for the yearling and 3 year old ewes in Figures 14 and 15. It should be noted that the high data point in 1978 and the low data point in 1979 are due to inconsistent shearing dates. The data entry for 1978 represents approximately 14 months growth, whereas the entry for 1979 represents approximately 10 months growth. All other records represent 12 months of wool growth. While the C and T lines declined at a slower rate than the two selected Rambouillet lines, the overall pattern for the four lines was the same.

Fleece weight has declined over the duration of the experiment. The change in summer range is considered to be a major cause of this reduction. It should also be noted that the decline in fleece weight has been paralleled by a steady decline in body weight. Further, as with body weight, fleece weights appear to be increasing over the past several years.

TABLE 25. LEAST SQUARES ANALYSIS OF VARIANCE FOR EWE FLEECE WEIGHTS

Source of variation	df	Mean squares for ewes age 1 to 5 (kg^2)				
		1	2	3	4	5
Line	3	3.6**	5.1**	2.9**	2.5**	2.5**
Year	15[a]	31.9**	34.5**	23.7**	17.6**	13.9**
Lactation status	1	2.1**	6.6**	6.5**	5.8**	3.6**
Line x year	41[b]	0.5**	0.5*	0.2	0.2	0.4
Error	1577[c]	0.3	0.3	0.3	0.3	0.4

*(P<.05) **(P<.01)

[a]Year df for ewes age 2 to 6 are 15, 14, 13, 12 and 11.
[b]Line x year df for ewes age 2 to 6 are 41, 38, 35, 32 and 25.
[c]Error df for ewes age 2 to 6 are 1577, 1206, 809, 663 and 531.

TABLE 26. LEAST-SQUARES MEANS AND STANDARD ERRORS FOR EWE FLEECE WEIGHTS (KG)

Line	Age of ewe				
	1	2	3	4	5
Low	4.11a ±.06	4.32[a] ±.04	4.45[a] ±.06	4.43[a] ±.07	4.20[a] ±.08
High	4.09[a] ±.06	4.37[a] ±.04	4.43[a] ±.06	4.46[a] ±.07	4.18[a] ±.08
Control	4.13[a] ±.06	4.37[a] ±.05	4.45[a] ±.07	4.48[a] ±.08	4.23[a] ±.09
Targhee	4.28[b] ±.05	4.59[b] ±.04	4.64[b] ±.05	4.67[b] ±.07	4.45[b] ±.06

[a,b]Means within the same column with different superscripts are significantly different ($P<.05$).

TABLE 27. ESTIMATED REGRESSION COEFFICIENTS FOR EWE FLEECE WEIGHT (KG)

Age of ewe	Low		High		Control		Targhee	
	a	b±se	a	b±se	a	b±se	a	b±se
1	10.5	-.084 ±.028	11.2	-.093 ±.023	7.80	-.049 ±.048	8.44	-.054 ±.029
2	13.5	-.121 ±.021	13.2	-.116 ±.028	9.55	-.069 ±.059	12.10	-.099 ±.034
3	13.1	-.115 ±.032	12.2	-.102 ±.030	9.13	-.063 ±.072	11.79	-.094 ±.034
4	13.1	-.116 ±.042	11.9	-.100 ±.035	8.60	-.056 ±.087	11.96	-.097 ±.044
5	13.2	-.122 ±.055	9.9	-.077 ±.056	9.09	-.066 ±.091	9.75	-.071 ±.047

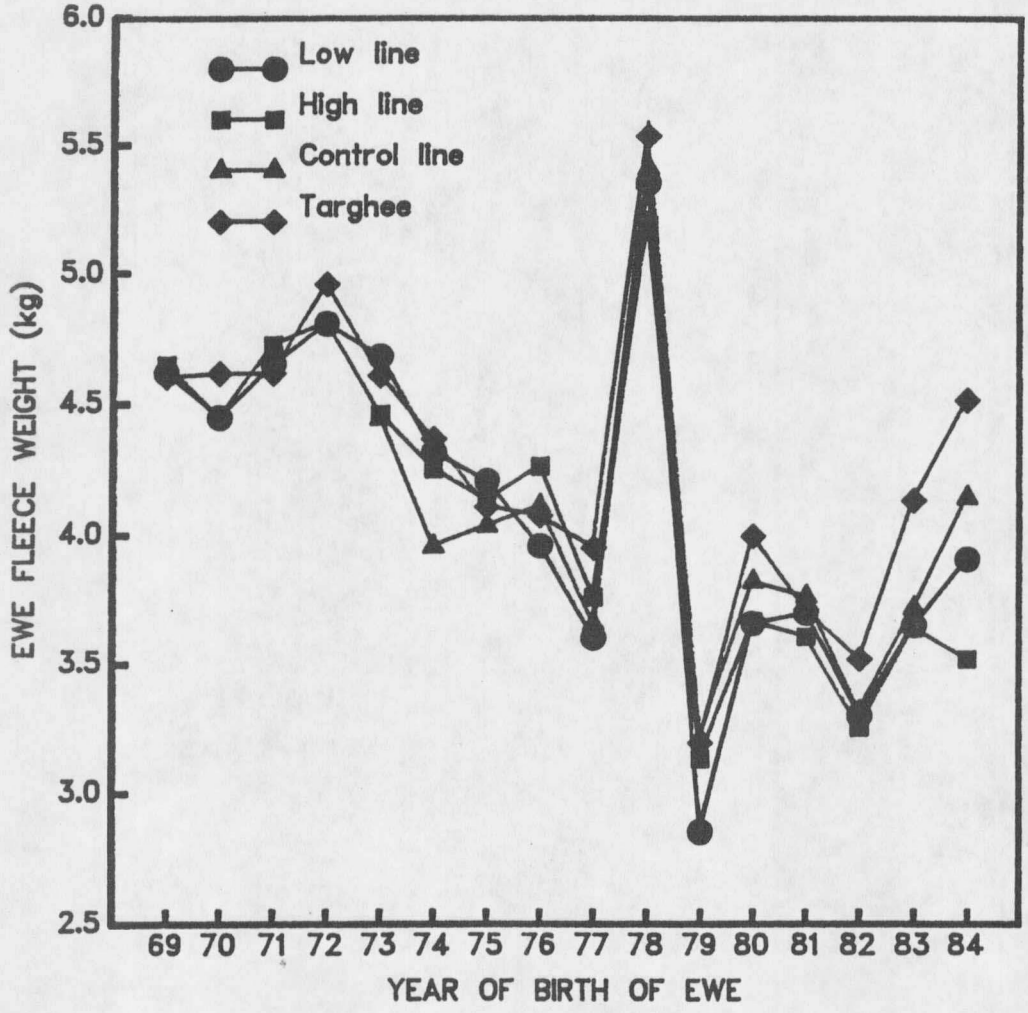


FIGURE 14. EFFECT OF LINE AND YEAR ON FLEECE WEIGHT - 1 YR OLD EWES.

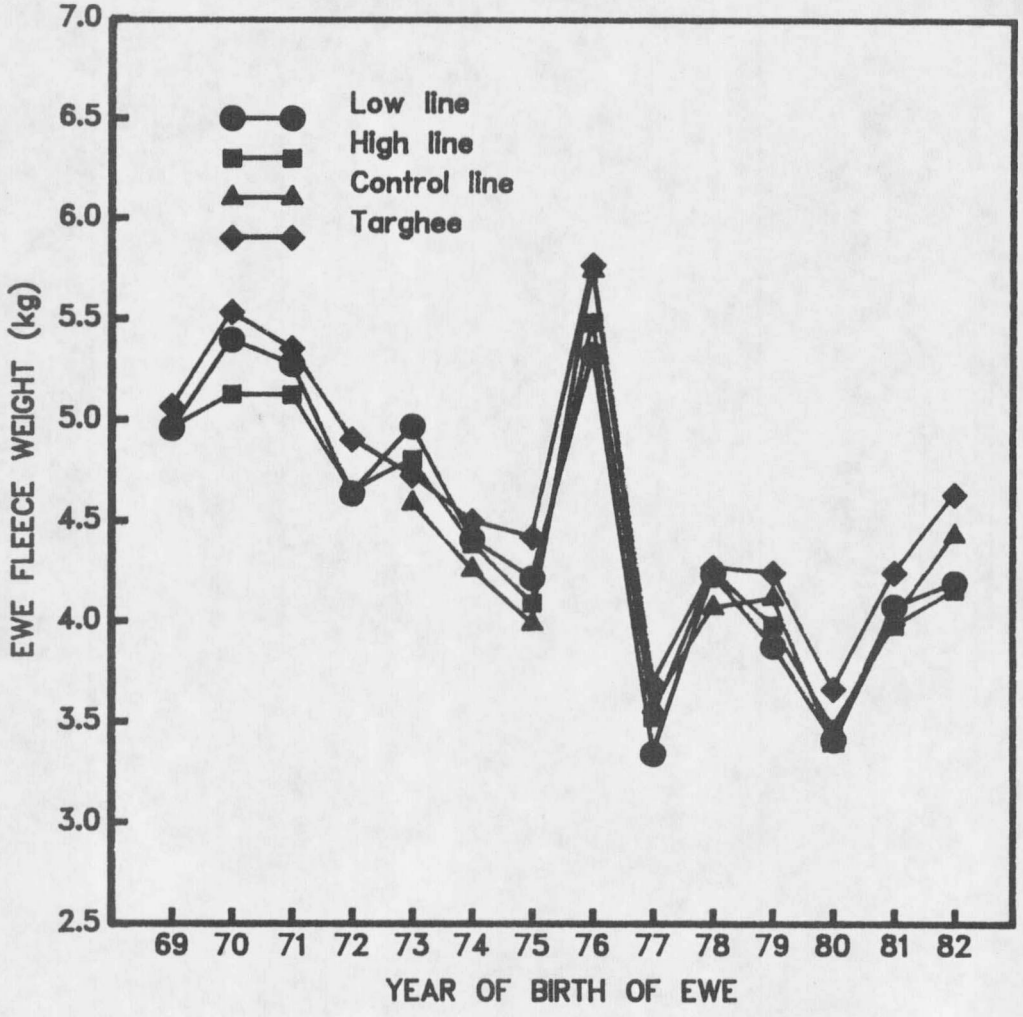


FIGURE 15. EFFECT OF LINE AND YEAR ON FLEECE WEIGHT - 3 YR OLD EWES.

Fleece Grade

Fleece grade was affected by line or breed and year of birth ($P<.01$) (Table 28). A significant lactation effect was noted in yearling ($P<.01$) and 4 year old ewes ($P<.10$) and a line x year of birth interaction was observed for yearling ewes (Table 28). Yearling ewes had the lowest grade codes. Grade code increased to age 3 and then fiber diameter decreased (Tables 29 and 30). It should be noted that for this trait the lowest value is the most desirable. In other words a low grade code signifies a higher quality fleece (higher spinning count).

The regression coefficients for fleece grade on year of birth of ewe are given in Table 30. They indicate that the Rambouillets and Targhees have both suffered a decline in fleece quality. This is shown graphically for yearling and 3 year old ewes in Figures 16 and 17. The phenotypic time trend for the four lines indicates an increase in fleece grade code. In other words, fleece quality has declined over the duration of the experiment. Further, the decline has been much more pronounced in the second half of the experiment. While the changes observed in the three Rambouillet lines are relatively the same, grade code has increased at a slower rate in the Targhee line. The slower rate may be the result of some selection pressure on fleece quality in the Targhee flock.

The decline in fleece quality in the Rambouillets is of great concern and the reasons for its decline are uncertain. The observed changes in fleece grade in the Targhees indicate that selection for reproductive rate in the Rambouillet lines may have adversely affected

fleece quality. Unfortunately, there is nothing in the literature that these results can be compared to.

TABLE 28. LEAST SQUARES ANALYSIS OF VARIANCE FOR EWE FLEECE GRADE

Source of variation	df	Mean squares for ewes age 1 to 5 (kg^2)				
		1	2	3	4	5
Line	3	26.9**	24.2**	18.4**	11.8**	10.2**
Year	15[a]	4.4**	2.0**	1.5**	1.9**	1.3**
Lactation status	1	1.9*	0.9	6.1**	0.2	0.3
Line x year	41[b]	0.6**	0.3	0.4	0.5+	0.5
Error	1577[c]	0.4	0.3	0.4	0.4	0.4

+(P<.10) **(P<.01) *(P<.05)

[a]Year df for ewes age 2 to 6 are 15, 14, 13, 12 and 11.
[b]Line x year df for ewes age 2 to 6 are 41, 38, 35, 32 and 25.
[c]Error df for ewes age 2 to 6 are 1577, 1206, 809, 663 and 531.

TABLE 29. LEAST SQUARES MEANS AND STANDARD ERRORS FOR EWE FLEECE GRADE[1]

Line	Age of ewe				
	1	2	3	4	5
Low	$1.3^a \pm .07$	$1.4^a \pm .05$	$1.7^a \pm .06$	$1.5^a \pm .07$	$1.5^a \pm .09$
High	$1.3^a \pm .07$	$1.4^a \pm .05$	$1.6^a \pm .07$	$1.4^a \pm .08$	$1.5^a \pm .09$
Control	$1.2^a \pm .07$	$1.4^a \pm .06$	$1.6^a \pm .07$	$1.6^a \pm .08$	$1.5^a \pm .09$
Targhee	$1.8^b \pm .06$	$1.9^b \pm .04$	$2.1^b \pm .06$	$2.0^b \pm .07$	$2.0^b \pm .07$

[1]1 = fine, 2 = 1/2 blood, 3 = 3/8 blood and 4 = 1/4 blood

[a,b]Means within the same column with different superscripts are significantly different (P<.05)

TABLE 30. ESTIMATED REGRESSION COEFFICIENTS FOR FLEECE GRADE CODE[a]

Age of ewe	Low		High		Control		Targhee	
	a	b±se	a	b±se	a	b±se	a	b±se
1	-2.67	.052±.011	-0.98	.029±.012	-3.26	.058±.015	-.088	.024±.008
2	-0.70	.028±.008	-0.68	.027±.010	-2.72	.053±.021	.618	.017±.006
3	-1.11	.036±.012	-0.45	.027±.011	-1.08	.034±.026	1.41	.009±.006
4	-1.70	.042±.015	-1.50	.039±.011	-2.33	.051±.052	1.42	.007±.011
5	-0.18	.023±.026	.083	.019±.020	-0.74	.030±.053	1.39	.008±.017

[a]1 = fine, 2 = 1/2 blood, 3 = 3/8 blood and 4 = 1/4 blood.

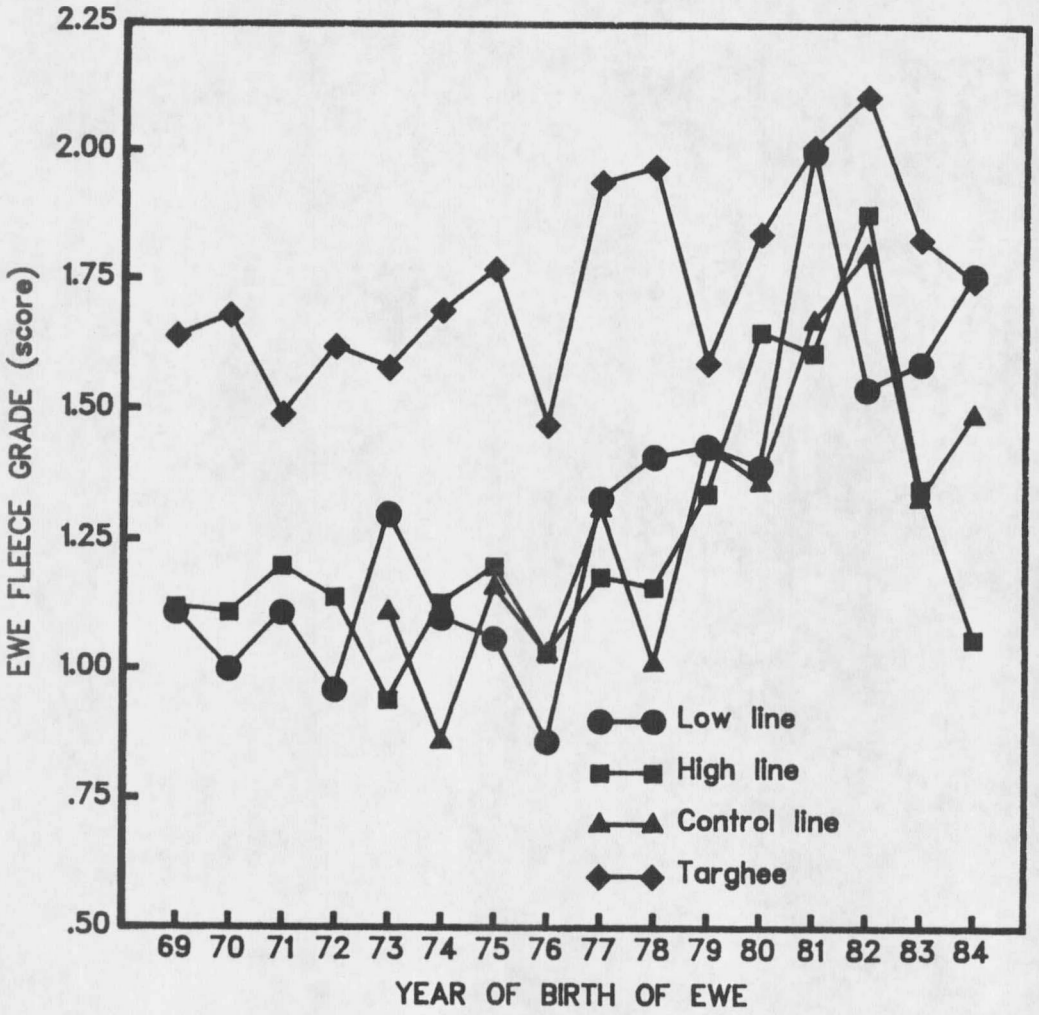


FIGURE 16. EFFECT OF LINE AND YEAR ON FLEECE GRADE -1 YR.

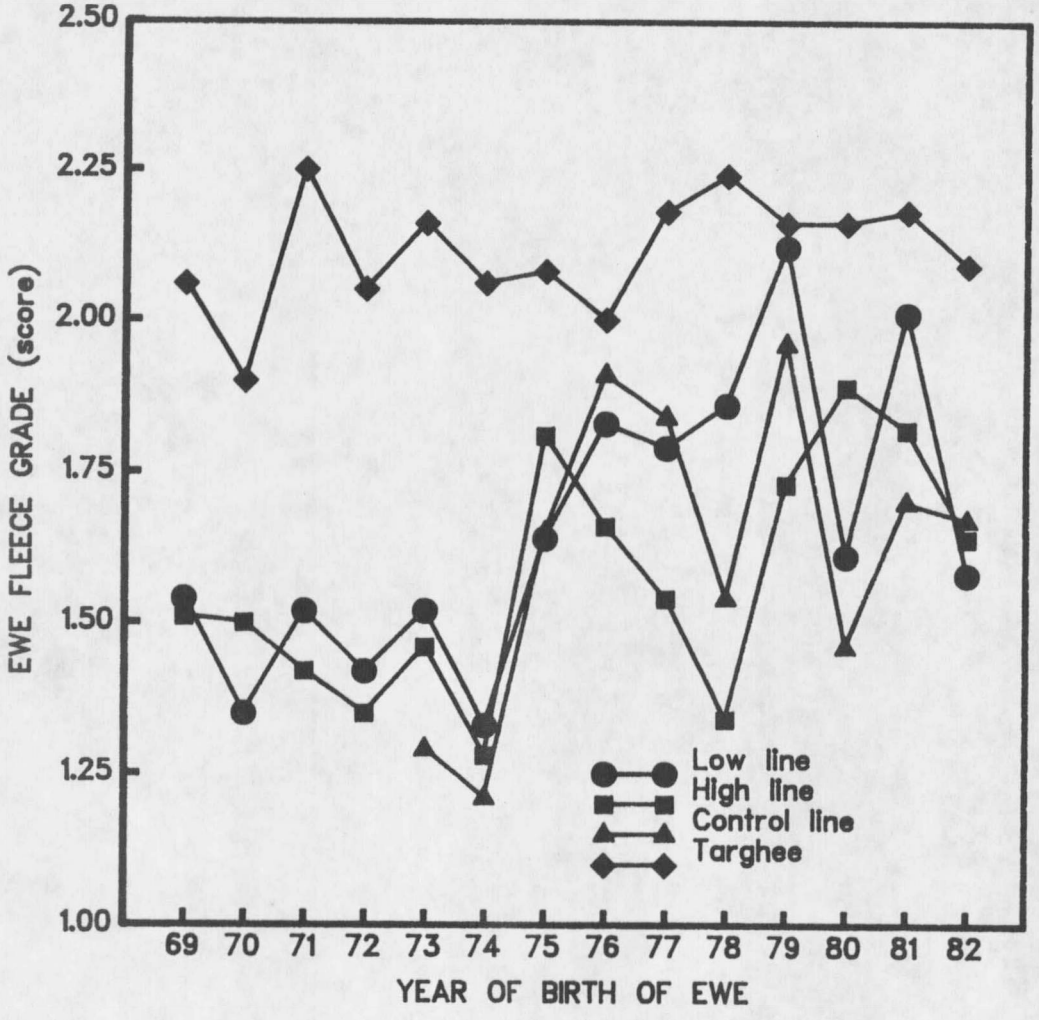


FIGURE 17. EFFECT OF LINE AND YEAR ON FLEECE GRADE -3 YR.

SUMMARY AND CONCLUSION

The number of lambs weaned per ewe exposed is the most important factor influencing the productivity of sheep and the net returns from a sheep enterprise. Of all the possible components of reproductive performance, the most profitable criterion of selection to raise reproductive rate is the high incidence of mulitiple births.

This study presents some of the results from selection for reproductive rate in Rambouillet sheep at the Montana Agricultural Experiment Station. The selection experiment began in 1968 and three populations of Rambouillet sheep have been developed: a High (H) line selected for high reproductive rate, a Low (L) line selected for low reproductive rate and a random bred control (C) line. These three distinct populations offer a tremendous opportunity to study the changes that have occurred over a period of many years (1969-1986), as a result of selection for reproductive rate. The experiment station's registered Targhee flock has been included in some of the analyses to help assess the phenotypic time trends for various measures of lamb and ewe performance over the duration of the experiment.

Any time selection for a particular trait is practiced, the major objective is to determine the direct responses to selection. In this particular study, lambing rate is the trait of primary importance. Lambing rate is reported for two years (1986 and 1987). It represents a minimum of 16 years of selection. As would be expected the three lines have differentiated in lambing rate. There is a significant difference in the number of lambs born per ewe exposed for the two

selected lines, H and L. High line ewes show an average rate of 1.40 lambs born per ewe exposed. This compares to a lambing rate of .98 for the low line. The control line had a lambing rate of 1.25 for the two years presented, thus it appears that greater progress has been made in the downward direction. Turner (1978) also reported greater progress in the downward direction in an Australian experiment. The difference between the high and control lines is only .15. This is consistent with other studies reporting a 1-2 percent increase in the number of lambs born per year (Land, 1979; Bradford, 1985), but considerably less than many selection experiments (Turner, 1978; Atkins, 1980; Hanrahan, 1982). The small response in this experiment may be the result of many factors. No initial screening of the ewe population was practiced. Further, the variation in lambing rate in this population is small and thus, accounts for a selection differential of small magnitude. Thus, direct selection for lambing rate has resulted in a positive change in lambing rate, however, the progress has been very slow and reflects the low heritability of the trait.

Selection for lambing rate has produced correlated changes in other components of reproduction. While first service fertility was lowest in the high line, there were no differences in fertility during the entire 35 day breeding season. Thus, unlike other studies, our data do not yield a correlated response in fertility following selection for reproductive rate. Litter size in the high line was 1.61 compared to 1.17 for the low line. The control line was intermediate between the two selected lines at 1.42. Greater progress was made in the downward direction. Further, it appears that differences in

lambing rate in the H and L lines are primarily a result of differences in litter size.

The change in ovulation rate has been greater than the change in lambing rate, although it should be noted that ovulation rate data have been reported for three years whereas, the third lambing season has yet to occur. Mean ovulation rate for the low, high and control lines is 1.23, 1.78 and 1.48 respectively. Further, while the high line ewes ovulated more eggs they were characterized by higher embryo mortality. What proportion of this higher mortality can be attibuted to embryonic loss or fertilization failure, is unknown. Percent embryo survival for pregnant ewes was 97.0, 92.1, and 94.6 for the L, H, and C lines respectively. For all ewes, percent embryo survival was 72.2, 61.4 and 77.3 for the L, H, and C lines. No significant differences in embryo survival were noted when ovulatory pattern was considered.

As in all traits in all species, selection for reproductive rate in sheep can lead to correlated responses in other traits. Birth weight and weaning weight were studied to assess the effect of selection for reproductive rate on lamb growth. Body weight, fleece weight and fleece grade were studied to determine the effect of selection on measures of ewe productivity. Selection for reproductive rate did not adversely affect any of these traits. There were no important differences between the L, H, and C lines for birth weight, weaning weight, body weight, fleece weight and fleece grade. During the duration of the experiment, however, each of these traits has steadily declined. This decline was paralleled by a similar decrease in the Targhee line. The fact that the Targhees have been selected for

post-weaning gain and fleece weight would indicate that the decline is primarily the result of environmental time trends. The change in summer range, from high mountain Forest Service grazing allotments to the research ranch, appears to be the major cause. The only trend that cannot be explained is the steady decline in fleece grade, and because the decline observed in the Targhee line is not of the same magnitude, this observed change in the Rambouillet selection lines may be a result of the experiment and the selection imposed. In general, selection for reproductive rate should not be expected to adversely affect other production traits.

The results of this study present little new information, but merely substantiate the findings of other studies. But, perhaps these distinct populations should be valued for the future knowledge that may be gained from them. Each line differs in reproductive level and has segregated in various measures of reproductive performance. Future efforts will enhance our understanding of reproduction in sheep and perhaps, may expose a more effective way of improving the reproductive rate in sheep and other multiparous farm animals.

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APPENDIX

TABLE 31. LEAST SQUARES MEANS AND STANDARD ERRORS FOR BIRTH WEIGHT AS AFFECTED BY LAMB YEAR OF BIRTH AND AGE OF DAM (KG)

Year	Age of dam									
	2		3		4		5		6	
	n	mean	n	mean	n	mean	n	mean	n	mean
1971	107	4.32 ±.16								
1972	105	4.29 ±.16	118	4.71 ±.06						
1973	104	4.15 ±.16	102	4.60 ±.07	93	4.69 ±.07				
1974	87	4.38 ±.16	89	4.89 ±.08	98	4.91 ±.07	55	5.06 ±.10		
1975	73	4.21 ±.17	87	4.84 ±.08	77	4.76 ±.07	78	4.64 ±.08	55	4.66 ±.10
1976	74	3.89 ±.16	82	4.49 ±.08	72	4.66 ±.08	78	4.76 ±.08	32	4.58 ±.13
1977	49	4.09 ±.18	89	4.60 ±.08	78	4.56 ±.07	56	4.83 ±.09	23	4.73 ±.16
1978	65	4.10 ±.17	68	4.59 ±.09	87	4.82 ±.07	67	4.74 ±.08	44	4.88 ±.11
1979	70	3.96 ±.17	64	4.40 ±.09	56	4.47 ±.09	68	4.60 ±.08	67	4.54 ±.09
1980	69	4.42 ±.17	69	4.49 ±.09	71	4.66 ±.09	46	4.60 ±.10	59	4.66 ±.09
1981	84	4.13 ±.16	56	4.56 ±.09	57	4.63 ±.09	53	4.76 ±.09	33	4.83 ±.14
1982	66	3.86 ±.17	80	4.31 ±.07	56	4.34 ±.09	50	4.59 ±.10	50	4.49 ±.11
1983	67	4.23 ±.17	77	4.64 ±.08	74	4.87 ±.08	40	4.91 ±.10	63	5.00 ±.10
1984	47	3.84 ±.18	65	4.49 ±.09	64	4.31 ±.09	64	4.62 ±.08	46	4.74 ±.13
1985	87	4.04 ±.16	79	4.36 ±.08	97	4.52 ±.07	66	4.62 ±.08	71	4.88 ±.11
1986	64	4.12 ±.17	88	4.65 ±.07	55	4.72 ±.09	63	4.88 ±.08	54	4.85 ±.11

TABLE 32. LEAST SQUARES MEANS AND STANDARD ERRORS FOR WEANING WEIGHT AS AFFECTED BY LAMB YEAR OF BIRTH AND AGE OF DAM (KG)

Year	Age of dam									
	2		3		4		5		6	
	n	mean	n	mean	n	mean	n	mean	n	mean
1971	107	37.53 ± 1.09								
1972	105	36.43 ± 1.09	118	40.68 ±.42						
1973	104	38.13 + 1.09	102	41.16 ±.47	93	41.73 ±.48				
1974	87	37.27 ± 1.12	89	43.22 ±.52	98	41.86 ±.49	55	42.73 ±.71		
1975	73	37.98 ± 1.13	87	40.77 ±.52	77	42.01 ±.51	78	41.16 ±.58	55	40.97 ±.67
1976	74	34.28 ± 1.12	82	39.75 ±.52	72	40.30 ±.58	78	41.67 ±.57	32	41.65 ±.91
1977	49	32.40 ± 1.26	89	38.65 ±.50	78	38.96 ±.51	56	38.88 ±.69	23	36.91±1.07
1978	65	30.03 ± 1.16	68	35.69 ±.62	87	37.08 ±.49	67	37.63 ±.59	44	36.76 ±.75
1979	70	25.87 ± 1.15	64	30.52 ±.63	56	29.61 ±.63	68	31.18 ±.60	67	31.41 ±.62
1980	69	26.46 ± 1.14	69	29.32 ±.57	71	29.84 ±.58	46	31.22 ±.77	59	30.78 ±.65
1981	84	21.65 ± 1.11	56	26.99 ±.61	57	26.21 ±.61	53	28.42 ±.64	33	27.74 ±.95
1982	66	23.59 ± 1.14	80	27.12 ±.50	56	27.83 ±.59	50	27.17 ±.77	50	29.13 ±.75
1983	67	22.16 ± 1.14	77	25.61 ±.53	74	26.09 ±.52	40	27.86 ±.75	63	27.07 ±.66
1984	47	21.03 ± 1.20	65	26.68 ±.57	64	25.55 ±.62	64	28.41 ±.60	46	28.31 ±.87
1985	87	19.25 ± 1.10	79	24.48 ±.52	97	25.59 ±.46	66	25.85 ±.60	71	25.99 ±.74
1986	64	22.56 ± 1.18	88	26.68 ±.49	55	27.61 ±.64	63	28.69 ±.58	54	28.51 ±.74

TABLE 33. LEAST SQUARES MEANS AND STANDARD ERRORS FOR EWE BODY WEIGHT AS AFFECTED BY YEAR OF BIRTH AND AGE (KG)

Year	Age of ewe 1.5		2.5		3.5		4.5		5.5	
	n	mean	n	mean	n	mean	n	mean	n	mean
1969	132	63.32 ±.56	106	71.32 ±.59	83	70.99 ±.70	53	70.94 ± .88	44	77.74 ± 1.00
1970	119	58.62 ±.57	94	65.62 ±.65	68	68.90 ±.78	62	76.37 ± .88	25	74.04 ± 1.28
1971	128	57.74 ±.57	81	65.99 ±.69	72	76.00 ±.74	59	75.54 ± .89	17	77.23 ± 1.51
1972	96	54.19 ±.65	80	69.85 ±.71	70	71.76 ±.81	47	71.77 ± .99	56	72.60 ± 1.01
1973	98	59.50 ±.62	81	69.28 ±.70	66	72.03 ±.77	51	73.47 ± .90	47	68.68 ± .93
1974	114	58.89 ±.59	91	69.55 ±.63	80	72.55 ±.70	72	68.98 ± .79	62	71.40 ± .84
1975	76	56.80 ±.72	63	67.74 ±.78	55	65.65 ±.85	44	68.94 ± 1.05	64	68.06 ± 1.06
1976	86	62.53 ±.66	76	62.40 ±.68	64	67.28 ±.78	60	66.31 ± .84	77	67.51 ± .84
1977	91	56.64 ±.64	83	63.71 ±.67	69	64.51 ±.74	63	67.12 ± .85	78	66.06 ± .83
1978	114	54.36 ±.58	82	59.28 ±.64	71	65.40 ±.71	48	64.68 ± .96	47	64.10 ± 1.03
1979	131	53.70 ±.54	120	60.13 ±.54	102	62.98 ±.63	87	61.97 ± .74	63	67.10 ± .91
1980	123	48.82 ±.57	110	56.85 ±.59	100	57.97 ±.67	67	64.60 ± .86	81	64.30 ± .87
1981	139	53.58 ±.50	115	56.21 ±.57	88	64.17 ±.66	74	65.83 ± .80	97	65.56 ± .69
1982	138	49.51 ±.52	90	59.77 ±.67	69	61.58 ±.78	65	64.60 ± .80	48	63.22 ± .94
1983	127	52.50 ±.53	108	59.22 ±.58	107	65.09 ±.60	91	63.59 ± .72		
1984	103	51.47 ±.55	96	60.60 ±.60	91	60.65 ±.67				
1985	134	55.43 ±.49	129	57.80 ±.53						
1986	149	53.25 ±.55								

TABLE 34. LEAST SQUARES AND STANDARD ERRORS FOR FLEECE WEIGHT AS AFFECTED BY YEAR OF BIRTH AND AGE (KG)

Year	Age of ewe									
	1.5		2.5		3.5		4.5		5.5	
	n	mean	n	mean	n	mean	n	mean	n	mean
1969	118	4.62 ±.07	101	5.05 ±.07	80	4.98 ±.08	46	5.41 ±.10	40	4.94 ±.12
1970	112	4.50 ±.07	84	4.86 ±.08	65	5.34 ±.09	51	5.17 ±.10	24	4.68 ±.15
1971	122	4.66 ±.07	79	5.51 ±.08	65	5.24 ±.08	56	4.86 ±.10	16	4.59 ±.17
1972	92	4.85 ±.08	66	4.89 ±.09	65	4.71 ±.09	43	4.56 ±.11	47	4.07 ±.12
1973	76	4.55 ±.08	75	4.83 ±.08	57	4.77 ±.09	37	4.55 ±.11	45	4.03 ±.11
1974	104	4.23 ±.07	78	4.63 ±.07	53	4.39 ±.09	72	4.21 ±.09	51	5.54 ±.10
1975	60	4.12 ±.09	42	4.42 ±.11	54	4.18 ±.09	34	5.77 ±.13	60	3.70 ±.12
1976	42	4.10 ±.10	74	3.90 ±.07	49	5.58 ±.10	52	3.60 ±.09	69	4.10 ±.10
1977	90	3.74 ±.08	69	5.42 ±.08	63	3.53 ±.08	59	4.28 ±.09	68	3.75 ±.10
1978	98	5.37 ±.08	75	3.34 ±.07	61	4.21 ±.08	43	3.92 ±.11	41	3.59 ±.12
1979	122	3.10 ±.07	113	4.11 ±.06	98	4.06 ±.07	85	3.75 ±.08	61	4.02 ±.10
1980	118	3.79 ±.07	107	3.60 ±.06	95	3.48 ±.08	66	3.94 ±.09	50	4.16 ±.10
1981	133	3.69 ±.06	113	3.46 ±.06	87	4.08 ±.07	68	4.57 ±.09		
1982	137	3.35 ±.06	87	3.91 ±.07	60	4.35 ±.09				
1983	126	3.79 ±.06	100	4.26 ±.06						
1984	88	4.02 ±.08								

TABLE 35. LEAST SQUARES MEANS AND STANDARD ERRORS FOR FLEECE GRADE AS AFFECTED BY YEAR OF BIRTH AND AGE (CODE[1])

Year	Age of ewe									
	1.5		2.5		3.5		4.5		5.5	
	n	mean	n	mean	n	mean	n	mean	n	mean
1969	118	1.2 ±.08	101	1.5 ±.07	80	1.7 ±.09	46	1.4 ±.11	40	1.6 ±.12
1970	112	1.2 ±.08	84	1.4 ±.08	65	1.5 ±.10	51	1.6 ±.11	24	1.7 ±.15
1971	122	1.2 ±.08	79	1.4 ±.08	65	1.7 ±.09	56	1.5 ±.10	16	1.4 ±.18
1972	92	1.2 ±.09	66	1.4 ±.09	65	1.6 ±.10	43	1.4 ±.11	47	1.3 ±.13
1973	76	1.2 ±.10	75	1.4 ±.08	57	1.6 ±.10	37	1.3 ±.11	45	1.5 ±.11
1974	104	1.2 ±.09	78	1.4 ±.07	53	1.5 ±.10	72	1.5 ±.09	51	1.6 ±.11
1975	60	1.3 ±.11	42	1.5 ±.11	54	1.8 ±.10	34	1.8 ±.14	60	1.8 ±.12
1976	42	1.1 ±.12	74	1.4 ±.07	49	1.8 ±.11	52	1.5 ±.10	69	1.9 ±.10
1977	90	1.4 ±.09	69	1.7 ±.08	63	1.8 ±.09	59	1.9 ±.10	68	1.9 ±.10
1978	98	1.4 ±.09	75	1.4 ±.07	61	1.7 ±.09	43	1.7 ±.11	41	1.8 ±.12
1979	122	1.4 ±.08	113	1.7 ±.06	98	2.0 ±.07	85	1.9 ±.09	61	1.7 ±.11
1980	118	1.6 ±.08	107	1.6 ±.07	95	1.8 ±.08	66	1.6 ±.10	50	1.5 ±.11
1981	133	1.8 ±.07	113	1.8 ±.06	87	1.9 ±.08	68	1.7 ±.09		
1982	137	1.8 ±.07	87	1.8 ±.07	60	1.7 ±.10				
1984	88	1.5 ±.09								

[a]1 = fine, 2 = 1/2 blood, 3 = 3/8 blood and 4 = 1/4 blood

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