Effect of selection for high and low reproductive rate on kilograms of lamb weaned per ewe in Rambouillet sheep
by Lisa Praharani

A thesis submitted in partial fulfillment Of the requirements for the degree of Master of Science in Animal Science
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Abstract:
This study presents some of the results from selection for reproductive rate based on their dam's reproduction performance by using the following index: I=no. lambs born/(age of ewe-1) in Rambouillet sheep at the Montana Agricultural Experiment Station. This study evaluated the phenotypic and genetic effects of selection for reproductive rate on total kilograms of weaning weight per ewe exposed and per ewe lambing, number of lambs born per ewe exposed and per ewe lambing, and number of lambs weaned per ewe exposed and per ewe lambing. The selection began in 1968 when two populations of Rambouillet sheep were developed: a high line (HL) selected for high reproductive rate; a low line (LL) selected for low reproductive rate. No initial screening was practiced for ewes. A random control line (CL) was established in 1972. There were 10035 animal records from 1969 through 1996. Traits measured were number of lambs born, number of lambs weaned and total kilograms of weaning weight. The three lines have differentiated ($P<0.0l$) both phenotypic and genetic effects for total kilograms of weaning weight, number of lambs born and weaned either per ewe exposed or lambing. Estimated Breeding Values (EBV) was estimated by using MTDFREML using the full animal model and permanent environmental effect was included. For overall traits measured both phenotypic and genetic effect, the HL had the highest ($P<0.01$) means, the LL had the lowest ($P<0.01$) means while the CL had intermediate ($P<0.01$) means between HL and LL. The mean EBV for total kilograms of weaning weight were -1.76, 3.37 and 2.28 kg per ewe exposed for LL, HL and CL, respectively. The mean EBV for total kilograms of weaning weight were -1.36, 3.28 and 2.5 kg per ewe lambing for LL, HL and CL, respectively. Estimated heritability for total kilograms of weaning weight per ewe exposed and lambing was 0.0525 and 0.0763 respectively. Estimated heritability for number of lambs born per ewe exposed and lambing was 0.083 and 0.136, respectively. Estimated heritability for number of lambs weaned per ewe exposed and per ewe lambing was 0.046 and 0.06 respectively. Genetic change estimated as regression coefficients of EBV for kilograms of weaning weight per ewe exposed on year of birth of dam was 0.005, 0.170 and 0.190 kilograms per year for the LL, HL and CL, respectively. Genetic change for kilograms of weaning weight per ewe lambing on year of birth of dam was 0.034, 0.130 and 0.210 for the LL, HL and CL, respectively. Greater progress has been achieved in the upward direction (HL) than downward direction (LL) for genetic effects of all traits. It was not easy to explain the response to selection by taking the difference between HL and CL. These results concluded that selection for reproductive rate has improved EBV for total kilograms of weaning weight per ewe exposed and lambing.

EFFECT OF SELECTION FOR HIGH AND LOW REPRODUCTIVE RATE ON KILOGRAMS OF LAMB WEANED PER EWE IN RAMBOUILLET SHEEP

by

Lisa Praharani

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8-24-98
Date

Peter Burfening
Chairperson, Graduate Committee

Approved for the Department of Animal and Range Sciences

8-24-98
Date

Peter Burfening
Head, Major Department

Approved for the College of Graduate Studies

8/25/98
Date

Joseph J. Fedock
Graduate Dean

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ABSTRACT

This study presents some of the results from selection for reproductive rate based on their dam's reproduction performance by using the following index: I=no. lambs born/(age of ewe-1) in Rambouillet sheep at the Montana Agricultural Experiment Station. This study evaluated the phenotypic and genetic effects of selection for reproductive rate on total kilograms of weaning weight per ewe exposed and per ewe lambing, number of lambs born per ewe exposed and per ewe lambing, and number of lambs weaned per ewe exposed and per ewe lambing. The selection began in 1968 when two populations of Rambouillet sheep were developed: a high line (HL) selected for high reproductive rate; a low line (LL) selected for low reproductive rate. No initial screening was practiced for ewes. A random control line (CL) was established in 1972. There were 10035 animal records from 1969 through 1996. Traits measured were number of lambs born, number of lambs weaned and total kilograms of weaning weight. The three lines have differentiated ($P<0.01$) both phenotypic and genetic effects for total kilograms of weaning weight, number of lambs born and weaned either per ewe exposed or lambing. Estimated Breeding Values (EBV) was estimated by using MTDFREML using the full animal model and permanent environmental effect was included. For overall traits measured both phenotypic and genetic effect, the HL had the highest ($P<0.01$) means, the LL had the lowest ($P<0.01$) means while the CL had intermediate ($P<0.01$) means between HL and LL. The mean EBV for total kilograms of weaning weight were –1.76, 3.37 and 2.28 kg per ewe exposed for LL, HL and CL, respectively. The mean EBV for total kilograms of weaning weight were –1.36, 3.28 and 2.5 kg per ewe lambing for LL, HL and CL, respectively. Estimated heritability for total kilograms of weaning weight per ewe exposed and lambing was 0.0525 and 0.0763 respectively. Estimated heritability for number of lambs born per ewe exposed and lambing was 0.083 and 0.136, respectively. Estimated heritability for number of lambs weaned per ewe exposed and per ewe lambing was 0.046 and 0.06 respectively. Genetic change estimated as regression coefficients of EBV for kilograms of weaning weight per ewe exposed on year of birth of dam was 0.005, 0.170 and 0.190 kilograms per year for the LL, HL and CL, respectively. Genetic change for kilograms of weaning weight per ewe lambing on year of birth of dam was 0.034, 0.130 and 0.210 for the LL, HL and CL, respectively. Greater progress has been achieved in the upward direction (HL) than downward direction (LL) for genetic effects of all traits. It was not easy to explain the response to selection by taking the difference between HL and CL. These results concluded that selection for reproductive rate has improved EBV for total kilograms of weaning weight per ewe exposed and lambing.

CHAPTER 1

INTRODUCTION

Total ewe productivity or kilograms lamb weaned per ewe exposed per year is the single most important factor influencing the profitability of sheep production. This trait is a composite trait that depends on several component traits. The factors affecting this trait are ewe reproduction (fertility and litter size), ewe viability, offspring growth rate (influenced by mothering ability, milk production), and lamb survival.

Meat production is increased by the number of lambs produced per ewe and lamb growth. The first objective can be reached by increasing lambing rate and lambing frequency. The second requires improvement in growth potential and survival of lambs.

Litter size, defined as number of lambs born per ewe lambing is the major factor affecting ewe productivity and contributes much more to the total kilograms of lamb weight weaned than other factors. As a result, an increase in the number of lambs marketed per ewe per year offers the greatest single opportunity for increasing the efficiency of sheep production, because it is the most influential trait affecting the total kilograms of lambs marketed per ewe per year. More lambs per ewe lambing can spread ewe maintain costs over more lambs born and can reduce total ewe costs per lamb, especially feed costs. Furthermore, a heavier market weight of lambs weaned would reduce costs per unit of meat. Therefore, it is obvious that improvement of reproductive rate can increase not only biological efficiency of animals but also economic efficiency of meat production.

Generally, two methods of increasing animal production are by improved environment including management and feeding, and by genetics. Reproductive rate can be increased by several methods such as better nutrition, use of high fertility breeds, crossbreeding, immunization and hormonal stimulation, and selection. However, most of these methods, except for genetics, give one time or temporary gains.

There are two main avenues of genetic improvement, selection and crossbreeding. Selection, especially for purebred animals, has the advantage of giving genetic gains permanently, which in the long term can make a greater improvement. In addition, the products of selection within a breed have no adaptation problem and are more uniform.

Selection for improved reproductive rate has not been considered to be practical because of low heritability. However, the high coefficient of variation permits annual rates of response to selection.

Effect of selection for reproductive rate on total kilograms of weaning weight per ewe has not been reported for most of the selection experiments in the literature. Furthermore, there are some questions whether selection for reproductive rate can increase total weaning weight per ewe, because multiple births have lower birth and weaning weight and lower survival and growth rate.

The objectives of this study are to evaluate the phenotypic and genetic effects of selection for reproductive rate in Rambouillet sheep on: total kilograms of weaning weight per ewe exposed and per ewe lambing and number lambs born and weaned per ewe exposed and per ewe lambing.

CHAPTER 2

LITERATURE REVIEW

Reproductive rate

Reproduction rate can be expressed in a number way, but generally, the most practical method of determining reproduction rate is by the number of lambs weaned per ewe as exposed for breeding (Fogarty, 1984). This trait is a complex trait and varies between breeds. It is a function of several components, such as fertility (lambed or not lambed), litter size (fecundity), and lamb survival which is mainly a function of the ewe and the lamb (Bindon and Piper, 1980). Therefore, reproductive rate may be increased by increasing the number of ewes lambing, numbers lambs born per ewe lambing and or lamb survival leading to increase lambs weaned per ewe exposed for breeding (Turner, 1966). Piper (1982) noted that increases in lifetime reproductive rate of females may be achieved by increasing the opportunities for conception through reductions in age of puberty, the incidence of seasonal and lactinal anestrous and by increasing the proportion of cycling females that become pregnant. In addition to fertility changes, ovulation rate and embryo survival led to increase litter size (Piper, 1982). A more complex definition, from producer's standpoint, is weight of lamb weaned per ewe per year, which involves number of lambs weaned and lamb weaning weight per ewe per year (Fogarty, 1984).

Reproduction performance is influenced by environmental, management system within and between years such as nutrition, age and genetic variation between and within breeds (Turner, 1978; Gunn, 1983; Doney and Gunn, 1981; Fogarty, 1984; Purvis et al., 1987).

Increased Reproductive Rate

Improving reproductive performance is likely to increase both the biological and economic efficiency of animal production enterprises (Large, 1970; Dickerson, 1970, 1978). Biological efficiency, normally defined as the product output per unit of food input, involves a complex of relationship between input, maintenance requirements and output (Bowman, 1973). One of the major costs in most production systems is that of high maintenance requirements of the breeding female which limit biological efficiency (Dickerson, 1996).

It is generally desirable to maximize the output from the most limiting resources, such as feed. In most cases, the primary factors affecting nutritional efficiency of lamb production are percent lamb crop raised and weight of lamb marketed (SID, 1992). Therefore, increasing reproductive rate will often be a more efficient way to increase income compared to increasing the number of ewes, because it spreads out the fixed costs associated with ewe maintenance cost over more lambs sold (Dickerson, 1996).

The other advantages of improving reproductive rate are a greater number of surplus stocks for sale, maximizing pasture management, and a greater possibility of improvement through constant size (Turner, 1962). Furthermore, a higher reproductive rate also provides more ewes and rams to select from allowing greater selection intensity and leading to higher rate of genetic improvement in the breeding objective of the flock (Turner, 1962; Brash et al., 1994).

The importance of reproductive rate in determining weight of lamb weaned per ewe is illustrated by 54% greater average litter weight of ewes weaning twins vs those weaning singles (Nawaz and Meyer, 1992). Black (1982) observed in dollar terms, triplet rearing ewes produce 13% higher returns per hectare than twin rearing ewes and 49% higher return than single rearing ewes and twinning ewes produce 32% higher returns than singles in Coopworth ewes under NZ intensive grazing condition. In addition, multiple-born ewes had a significantly better index value for weight of lambs weaned per ewe they also weaned 0.07 more lambs which was 2.5 kg heavier than singles. Lambourne (1955), Wallace (1955), and Large (1972) showed two lambs per ewe are 20-35% more efficient than one per ewe. Schoeman et al. (1995) noted ewe producing twins were 43% more efficient than singles.

There is considerable evidence that increasing reproductive performance will reduce the performance of individual breeding females, such as ewe body weight (Russel et al., 1992). In addition, it can reduce and their offspring performance as a direct environmental effect on performance. However it can increase marginal feed requirements with litter size (Large, 1970) because the breeding female has a higher feed requirement than one which is not pregnant (Weston and Hogan, 1973).

It has to be considered that the greater the number of lambs produced, the more feed the ewe will consume for pregnancy and lactation. However, the output is higher than the additional input resulting in increased efficiency as was shown in the case of twins vs singles (Schoeman et al., 1995).

McGuirck (1976) reported producers relate the production costs of producing twins to the individual animal and are not aware of the possible benefits of increased reproductive performance to the biological and economic efficiency of their flocks. Dickerson (1970) stated there might be costs associated with increasing reproductive performance, such as higher feed costs during gestation and lactation, or increased post-weaning costs per offspring, because of their smaller size at weaning. Also, it is needed an extra labor requirement for flock with more ewes giving birth to triplets.

Some breeders would prefer higher reproduction rates, in order to increase income from the sale of surplus stock and enable more intense selection of replacement breeding stock (Baillie et al., 1980). However many would choose to achieve this with a minimum of twins and they do not see increased twinning as an important breeding objective (Baillie et al., 1980). They claim that twins have lower survival rates than singles, particularly in dry seasons, and grow more slowly, and that pregnant ewes carrying twins tend more have pregnancy toxemia (Baillie et al., 1980). Many producers do not realize that twins are necessary to achieve a high lambing percentage (McGuirk,1976).

Increasing reproductive rate in term of lambs born per ewe lambing is dependent upon the production environment (Bradford, 1985). Twin or multiple births are more desirable in intensive systems with good quality pasture for 6 or more months of the year, when ewes were fed to meet nutrient requirements. However, generally, in extensive system, when forage scarce and more variables between seasons and supplements are unavailable, singles are more desirable (Bradford, 1985).

Genetic Improvement of Reproduction Rate

There are some possible ways to improve reproductive rate and efficiency such as flushing, use of high fertility breeds, crossbreeding, immunization techniques, single gene effect on ovulation rate, multiple lambing, control of reproduction, hormonal stimulation and use of milk replacers for excess lambs over the mother capacity. (Terril,1984; Dickerson, 1970; Speeding et al., 1976; Marshal et al., 1984; Roux and Scholtz, 1992). Of these methods, selection within populations (or breeds), and crossbreeding, development and use of new synthetic or composite breeds to improve reproductive rate seem to be the most effective programs (Bowman, 1973; Large, 1972;).

Genetic improvement of reproduction rate in sheep is being sought in many countries, by means of both selection and crossbreeding. Several breeds with exceptionally high performance such as Romanov, Finnish Landrace, Barbados and Merino have been reported having a high incidence of multiple births, with litter sizes often above two, and frequently twice-yearly lambing (Fahmy, 1996). Crossing with these breeds has been shown to raise the reproduction rate.

The use of sheep such as the Booroola with a major gene for high ovulation rate is to increase prolificacy (Piper et al., 1985). Other examples of these breeds are Barbados blackbelly (Rastogi, 1996), and Javanese sheep (Bradford and Inounu, 1996). The disadvantage of using sheep with a major gene for ovulation rate such as Booroola, is that the litter size increase above the desire level and increase in variability of litter size as well. Turner (1978) reported coefficients of variation for number of lambs born are 32%, 29% and 44% for O (dropped singles), T (dropped twins) and B (Booroola) group respectively.

Crossbreeding between prolific breed and less prolific breed can also increase reproductive rate (Bradford, 1985). That implies introduction of inheritance from a prolific breed to less prolific breeds. The reasons of crossbreeding are to add hybrid vigor or heterosis and to take advantage of breed complementary. However, the effect of crossbreeding, hybrid vigor, is only for F1 (100%) and might diminish or either decline or remain at 50% in later generation (Bourdon, 1997). Furthermore, there are some international restrictions on the movement of genotypes between countries. In addition, in some cases, the problem in importing the prolific breed is the adaptability to the local environments. A more general constraint is that prolific breeds available are lacking in a number of important traits for some environments, such as 50% Finn crosses are susceptible to Pneumonia (Bradford, 1985) have a high attrition rate (Dickerson, 1977).

Selection

Selection is the method used to make long-term genetic change in animals. Selection is also a process that determines which individuals become parents, how many offspring they may produce, and how long they remain in the breeding population (Bourdon, 1997). In selecting for polygenic traits, it is very important to choose individual as parent based upon breeding values defined as parental value or the value of individual as a contributor of genes to the next generation (Bourdon, 1997).

Selection has the advantage of giving both phenotypic and genetic gains, which is permanent for the indefinite future (Turner, 1969). Especially in purebreds, selection is the best way to improve genetics of animals (Turner, 1966). Selection acts primarily on genes which have additive effects, the gains achieved being permanent and cumulative (Bourdon, 1997). Crossbreeding in addition to utilizing the additive genetic differences between breeds which are permanent, but it is not cumulative (Bourdon, 1997).

Selection for Reproductive Rate

Selection for reproductive rate can be studied directly and indirectly. The direct selection means selecting the ewes which weaned the most lambs, culling dry ewes, selecting ewes, which bore the highest numbers of lambs, or whose lambs had the highest survival rate (Turner, 1966). The indirect selection means selecting for characteristics known to be strongly associated with reproduction rate, but more easily observed on the ram himself, such as selection for scrotal circumference. One of the difficulties in selecting for increased reproductive performance is that it is a sex-limited characteristic and male-breeding values can only be estimated from the performance of their female relatives (Turner, 1969).

There are some advantages of selection, particularly in reproductive rate. One of the advantages of selection within breeds is that litter size can be increase without changing in environment, management, and more net return by increasing number of lambs born but the breeding females are constant (Bradford, 1985). Another advantage of selection within breeds is that there is no adaptation problem like crossbreeding using prolific breeds particularly imported breeds. The consequences of selection for reproductive rate affect the number, value and cost of production of animals reared to marketable age, and the productivity of the breeding female (McQuirk, 1976). In addition, the product of selection is more uniform.

Response to Selection for Reproductive Rate

Response to selection can be examined by measuring the rate of genetic change resulting from selection (Falconer and Mackay, 1996). More specifically, it is the rate of change in the mean breeding value of a population caused by selection. Breeding value is the value of individual as a parent and passed from parent to offspring, so that change due to selection of parents is really change in breeding value. There are three main factors affecting the rate of genetic change which are heritability (genetic variation), generation interval, and selection differential (Bourdon, 1997).

Heritability is a measure of the strength of the relationship between performance (phenotypic values) and breeding values for a trait in a population, and ranges from zero to one or 0% to 100% (Bourdon, 1997). However, traits related to fertility or reproduction tends to be lowly heritable (0 – 20%), ranging from –0.15 to 0.35 with a mean 0.1 (summarized by Bradford, 1985 and Land et al, 1984). Table 1 shows estimated heritability for reproductive trait and weaning weight of some breeds and demonstrates that heritability for reproductive traits are low. Although the heritability of one trait is low, selection response can still reach the maximum rate, if the two other factors (phenotypic variation and selection differential) are large.

Table 1. Summary of Heritability for Reproductive Traits in Sheep

Heritability	Breed	Source
Lambs born:		
0.12	Rambouillet	Shelton and Menzies (1970)
0.17		Burfening et al. (1993)
0.11	Merino	Mann et al. (1978)
0.05	Romney	Anderson and Curran (1990)
	Targhee	Abdulkhaliq et al. (1989)
	Columbia	Abdulkhaliq et al. (1989)
	Suffolk	Abdulkhaliq et al. (1989)
0.15	UK Hill	Purser (1965)
0.08	Galway	Hanrahan (1976)
	Dorset	Hall et al. (1994)
		Brash et al. (1994)
0.18	Galway	More O'Ferrall (1976)
0.19	Hyfer	Fogarty et al. (1994)
Lambs weaned:		
0.38 (exposed)	Rambouillet	Burfening (1993)
0.43 (lambing)	Rambouillet	Burfening (1993)
0.19	Targhee	Abdulkhaliq et al. (1989)
0.26	Columbia	Abdulkhaliq et al. (1989)
0.12	Suffolk	Abdulkhaliq et al. (1989)
0.03	Corriedale	Brash et al. (1994)
0.04	Dorset	Brash et al. (1984)
0.04	Hyfer	Fogarty et al. (1994)
0.24	Galway	More O'Ferrall (1976)
Weaning weight:		
0.13	Rambouillet	Vesely, et al. (1970)
0.28	Targhee	Abdulkhaliq et al. (1989)
0.25	Columbia	Abdulkhaliq et al. (1989)
	Suffolk	Abdulkhaliq et al. (1989)
0.14	Galway	More O'Ferrall (1976)
0.10	Composites	Martin (1981)
0.06	Merino	Hall et al. (1995)
	Hyfer	Fogarty et al. (1994)

born per ewe made up of 50% of ewes with singles and 50% with twins, the standard deviation was 0.5 and the coefficient of variation 33%. Forrest and Bichard (1974) reported a coefficient of variation of 30% for number born alive, That means the low heritability is counterbalanced by relatively large variance of number born and permits annual rates of response to selection.

Variation is important source of genetic change in selection program. Selection will be easier, if there is variation in breeding values for the trait among individuals. Variation is measured by variance or standard deviation. Large variation permits more selection differential. The coefficient of variation of litter size is large, for example in French breeds, the coefficient of variation of litter size is 36.5 % in natural condition (Bodin and Elsen, 1989). Bradford (1985) reported in a flock with a mean of 1.5 lambs

Effect of Population Size

According to Bourdon (1997) selection can increase the gene frequency of favorable alleles. The change in gene frequency is influenced by population size (Falconer and Mackay, 19960. Population size is defined by the number of breeding individuals in each line and generation (Falconer and Mackay, 1996). It is a crucial variable in the design of animal breeding. First of all, it will influence the selection intensity. Most experiments on selection are made with populations not very large in size. The small populations can lead to inbreeding (Franklin, 1982). One effect of inbreeding is inbreeding depression defined by a decrease in performance of inbreeds that is noticeable (fitness traits), such as survivability and fertility (Bourdon, 1997). If the character selected is one subject to inbreeding depression, there will be a tendency for the mean to decline through inbreeding (Falconer and Mackay, 1996). The rate of inbreeding can be measured by using Falconer and Mackay (1996) equation :

$$\Delta F = 1/2N_e$$

where ΔF is the rate of inbreeding and Ne is effective number of breeding individuals. N_e is influenced by the proportion of numbers of males and females that can be estimated by using following equation:

$$N_e = (4N_mN_f)/(N_m+N_f)$$

Where N_f is numbers of females and N_m is number of males.

The rate of inbreeding depends mainly on the numbers of the less numerous sex (Falconer and Mackay, 1996).

Selection for Litter Size

There have been several experiments in mice on selection for some aspect of reproductive performance. Falconer (1960) reported that after 20 generations selection for 1 litter size increase 1.6 pups with heritability 0.15 in the high line and decrease1.6 pups in the low line. Luxford and Beilharz (1990) also reported selection for increased litter size response was 0.13 per generation with heritability 0.10. Direct selection for increasing litter size by Gion et al. (1990) and Kirby and Nielsen (1992), after 13 generations averaged 1.7 pups with heritability 0.09. Some studies initiated selection for small litter size, after 17 generations, the litter size dropped by 2.3 pups (Bradford,1979), and 3 pups (Joakimsen and Baker, 1977).

There have been many studies and reviews of genetic variation in litter size in cattle. Piper and Bindon (1979) reported calving records were too few to give a reliable estimate of genetic gain. Bichard and Ozkütuk (1977) observed the average calf crop almost never exceeds one and is usually less than 0.9. Maijala and Syvajarvi (1977) found estimates of the heritability of twinning rate an average of 0.03.

There have been few attempts to select for litter size in pigs The literature estimates for the heritability of litter size in pigs with average 0.10 as summarized by Young et al. (1978). Selection for increased litter size in the Large white breed was initiated by Oliver and Bolet (1981) in France, with a little response (no response after 10 generations).

Sheep

It is well recognized that the number of lambs born per ewe has a genetic basis however the heritability estimates for this trait is low as given in Table 1. Reeve and Robertson (1953) reviewed factors influencing multiple births in sheep which are age of dam, time of mating, flushing, body weight of ewe, and there was breed differences in the incidence of multiple births, but the genetic variation of individual was small

There is considerable genetic variation between and within sheep breeds for ewe reproduction rate (Fogarty, 1984; Purvis et al., 1987) with a continuous range from the highly fecund breeds such as Finnsheep with a mean litter size of 2.6 (Bradford et al., 1971; Maijala, 1996); Romanov, with a mean litter size of 2.6 (Ricordeau et al., 1982; Fahmy, 1996); D'man, with a mean litter size of 2.1 (Lahloukassi and Marie, 1985; Boujenane, 1996) to lowly fecund types such as Merino and other fine wool breeds. In addition there are differences between breeds for all reproductive traits such as age puberty, length of the breeding season and anestus period, ovulation rate, litter size and lamb survival (Hanrahan, 1982).

Since the genetic variation (heritability) of this trait is very low, studies of selection for litter size in sheep were not considered. Therefore, crossbreeding with the prolific breeds, such as Finnish Landrace and Romanov, is a more desirable way to increase litter size until Turner et al. (1962) and Wlace (1964) showed there was a considerable response to selection for litter size.

Many selection experiments aimed at increasing number lambs born have been reported and are summarized in Table 2. However, methods and specific selection criteria have varied between experiments. For example, some studies maintained control line (Wallace, 1964; Clarke, 1972; Hanrahan, 1976, 1982; Atkins 1980; Bradford, 1981; Schoenian and Burfening, 1990; Burfening et al., 1993; Anderson and Curran, 1990). Some studies did not practice initial screening (Hanrahan, 1976; Atkins 1980; Schoenian and Burfening, 1990; Burfening et al., 1993). Land et al. (1984) and Bradford (1985) summarized that the selection response of number lambs born is about 1-2%, with a mean of 1.5% per year except Mann et al. (1978) in which selection applied only in the ram, more limited selection pressure and the shortest duration. The responses are all linear and no one showed any sign of falling off or indication of declining with time.

As we know, environmental differences between generations can arise from many causes, climatic, nutritional and general management. In order to eliminate environmental fluctuations from the rate of selection response, control line is maintained (Falconer and Mackay, 1996). Based on a assumption that environmental differences may affect both selected and control line, therefore, the difference between selected and control line was the genetic improvement due to selection (Falconer and Mackay, 1996). However, the difference between selected and control line did not sometimes improve the precision of selection response by measuring the difference between selected and control (Falconer and Mackay, 1996). Thus, another way to measure the selection response is by divergent selection, or by taking differences between two selected line (Falconer and Mackay, 1996). Turner (1972, 1978) and Mann et al. (1978) did not maintained control line and measured the response to selection between two selected lines or by divergence.

Initial screening makes an important contribution to the response realized (Clarke, 1972; Turner, 1978; Hanrahan and Timon, 1978; Bradford, 1982). In the Ruakura flock, it contributed about one quarter of the total response. In the California Targhee line, it contributed about two-thirds of total response. In Ireland, initial screening almost certainly contributed importantly to the development of highly prolific stock (Bradford, 1985). However, some studies (Atkins, 1980) in Trangie Merino, Galway (Hanrahan and Timon, 1978) and Rambouillet (Burfening et al. 1993) did not involve initial screening indicating that this phase is not necessary to achievement of good response.

Table 2. Results of Selecting for Litter Size in Sheep.

Breed	Duration	Lines	Litter size	Annual response	Source
Romney		High	1.86	1-2%	Anderson and
(UK)		Control	1.63		Curran(1990)
Romney	1948-1972	High	1.62	1.5%	Clarke (1976)
(NZ)		Control	1.22		Wallace (1964)
		Low	1.13		
Merino	1954-1972	High	1.70	2%	Turner (1978)
(AU)		Low	1.18		
Merino	1965-1975	High	1.22	0.4%	Mann et al. (1978)
(AU)		Low	1.20		
Merino	1959-1973	High	1.52	1.3%	McGuirk (1976)
(AU)		Control	1.32		Atkins (1980)
Galway	1963-1981	High	1.67	1.8%	Hanrahan (1982) and
(IR)		Control	1.32		Timon (1978)
Targhee	1963-1981	High	1.39	1.5%	Bradford (1981)
(US)		Control	1.24		
Rambou-	1968-1986	High	1.43	1.3%	Schoenian and
illet (US)		Low	1.04		Burfening (1990)
		Control	1.33		Burfening et al. (1993)

In Ruakura, New Zealand, Wallace (1964) initiated study with Romney sheep in 1948. His study practiced initial screening of the ewes population and selection criterion of ewes and rams was based on incidence of multiple birth. Clarke (1972) observed the greater change was in the high line, with the linear regression or divergence of the high line and control was 1.75 lambs born per 100 ewes lambing per year, and little divergence was achieved in the low line over 24 years. In Deniliquin and Armidale, Australia, Turner (1978) studied divergence selection with Merino sheep begun in 1954. Initial flocks made up of ewes producing twins (T) or multiple birth and the other producing singles (O). She found the greater progress has been made in the downward direction (b=-2.55) than upward direction over 18 years of experiments and a continuing response equivalent to 0.02 lamb born per ewe annually. In England, Bhuiyan and Curran (1993) initiated a study with Romney sheep as a source of high merit breeding stock in 1980. The regression of overall averaged breeding values on year of birth increased 0.14 lambs born per ewe exposed which was higher than litter size because of direct selection pressure on prolificacy.

Atkins (1980) practiced no initial screening in Merino sheep at Trangie, Australia, and reported 1.8% annual increase in litter size based on selection of rams and ewes born from multiple births over 14 years of experiment. Another study, in Ireland with Galway sheep, practiced no initial screening and found an increase of 1.5% per year in litter size in response to selection over about 19 years for litter size of dam and sire's dam Hanrahan (1982). Some studies (McGuirk, 1976; Hanrahan and Timon, 1978; Bradford 1985, Atkins, 1980) with shorter duration of experiments demonstrated positive response to selection for reproductive rate. Bradford (1985) reported little or no direct response in litter size after initial screening of ewes in 1963. Ercanbrack and Knight (1998) found annual increases in prolificacy based on selection for litter weight weaned in Rambouillet, Polypay, Targhee and Columbia line, were 1.84 lambs per 100 ewe phenotypically and 1.44 lambs per 100 ewes genetically.

In Montana, USA, Burfening et al. (1993) studied with Rambouillet sheep over 20 years. No initial screening was practiced and selection criterion was based on the dam's past reproduction performance. Annual increasing of breeding value on year of birth was 1.63 lambs born per 100 ewe exposed and 1.64 lambs born per 100 ewes lambing for the high reproductive rate line. The greater progress has been achieved in the upward direction. Our study is a continuation of the work by Burfening et al. (1993).

Correlated Response

The correlation coefficient is a measure of the strength of the relationship between two variables and ranges from –1 to 1. A correlation either near –1 or 1 indicates very strong association, and a zero indicates no correlation.

Selection of one trait usually affects other traits which are mostly dependent upon the degree of correlation between traits (Bourdon, 1997). Genetic and phenotypic change in one or more traits resulting from selection for another is called correlated response to selection. Some changes in other aspects of production will come about as a result of a genetic antagonism between reproductive performance and other traits (Bourdon, 1997). For example, there may be a negative correlation between fleece weight and lambs born per ewe joined (Turner, 1972; Barlow, 1974; Mullaney et al., 1969; Rose, 1974). Shelton and Menzies (1968) and More O'Ferrall (1976) noted increasing reproductive rate are possibly a lower fleece weight per head in the ewes born as multiple births, because there is a negative genetic correlation between reproduction and fleece weight However, the correlation between fleece weight and litter traits has generally been low. Hullet et al. (1969) reported a slight negative correlation and Eikje (1975) reported genetic correlation of –0.06 to 0.09. Purser (1965) and Jonmundsson et al. (1977) reported low positive genetic and phenotypic correlation between fleece weight and litter size.

There is considerable evidence that increasing reproductive performance will reduce the performance of individual breeding females and their offspring as a direct environmental effect on performance (McGuirk, 1976). For example, as a litter size increases, there is a decrease in the birth weight of individual lambs, lamb survival, weaning weight, and growth rate. A number of studies found singles has higher birth weight (Dickinson et al., 1962; Bradford, 1985; Bhuiyan and Curran, 1995; Peeters et al., 1996; Hall et al., 1995) lamb survival rate (Purser and Young, 1964; Shelton, 1964; Maund et al., 1980; Bradford, 1985; Subandryo, 1984; Nawaz et al., 1992), growth rate (Peeters et al., 1996;Mavrogenis, 1996; Hall et al., 1995), and weaning weight (Mavrogenis et al., 1996; Buvanendran et al., 1992; Bradford, 1985) than twins.

Type of birth has negative phenotypic correlation with individual birth weight. The ratio of mean birth weight of single, twins and triplets are 1.0:0.78:0.62 (Dickinson et al., 1962); 1.0:0.77:0.64 (Maund et al., 1980); 1:0.77-0.78 (Bradford, 1985). Birth weight of single, twin and triplet were 5.99, 4.95 and 4.00 kg respectively (Bhuiyan and Curran, 1995. Peeters et al. (1996) observed birth weight was 4.9 kg and 4.1 kg for singles and twins respectively. Single lambs were 0.62 kg heavier than twin lambs, which were 0.44 kg heavier than triplet lambs at birth (Hall et al., 1995).

Survival of lambs to weaning is a major factor affecting number of lambs weaned. Non-genetic factors associated with increased lamb mortality include type of birth (single or twins), age of ewe and lamb birth weight (Turner and Young, 1965). Birth weight had a highly significant effect on lamb survival and negative phenotypic correlation. High and Jury (1970) indicated a small difference in lamb birth weight could have a large effect on lamb survival and particularly upon the differential survival values of singles and multiple born to dams of different age. Lambs born in larger litters have higher mortality rates than singles, associated with lighter birth weights. Other author have shown that there is strong genetic correlation between weight of lambs weaned per ewe lambing and lamb survival. (Fogarty, 1985). The mean survival for single, twins and triplets are 87.6, 81.9 and 70.2% respectively (Purser and Young, 1964; Shelton, 1964; Maund et al., 1980, Bradford, 1985). Subandryo (1984) reported the mean survival to weaning for Rambouillet sheep were 87% and 75.3% for single and twin born lambs. Turner (1966) reported at Cunamulla, the survival rate of O group (singles) was 82% and 64% for T group (twins) on native pasture. Nawaz and Meyer (1992) reported lamb survival was 94 and 85% for singles and twins respectively. Lambs survival of multiple births or twins indicates 50% more lambs weaned compared to singles. That implies although singles-born lambs have a higher survival rate than twin-born lambs, but the differences have never great enough to wipe out the advantage of the extra lambs born (Turner, 1966). For this to happen, the survival rate would need to fall half that of the singles or lower. The higher mortality in multiple births is generally due to lower birth weight, low milk production and poor maternal behavior. The survival rate may be increased by improvement in environment such as pasture improvement.

Litter size influenced postnatal growth rate by having a negative correlation (Peeters et al., 1996). His study reported lambs suckling as twins have a significantly lower growth at 7 and 11 kg body. Singles lambs were heavier and had a faster growth than twins or other multiples (Mavrogenis, 1996). Hall et al. (1995) observed singles have 37 gram per day faster growth rate than twins. Buvanendran et al. (1992) found weaning weight ratio twins and singles was 1:1.2. Bradford (1985) reported lamb weight weaned was 30 kg (single rearing as single), 27.9 kg (twin as single), 26.4 kg (twin as twins). Mavrogenis (1996) noted weaning weight of singles, twins and multiples were 17.1, 14.5 and 12.9 kg respectively.

The effect of selection for litter size on total kilograms of lamb weight weaned per ewe exposed and per ewe lambing has not been reported for most of the experiments, but available evidence on numbers weaned indicates a positive response (Bradford, 1985). However, there might be little reason to doubt that selection for multiple births increases production of lamb meat per ewe, because twin lambs have lower birth weight, less survival rate, slower growth rate and lower weaning weight.

Table 3 shows correlation coefficient between reproductive rate and weaning weight. In general, there is negative correlation between reproductive rate (litter size) and individual weaning weight, because of lower birth weight and growth rate of lamb born twins (Shelton and Menzies, 1968; Gjederm, 1966). However, some studies (Abdulkhalig, 1989; Russel et al., 1992; Fogarty, 19894; Martin et al., 1981) reported that correlation coefficients between reproductive rate (litter size) and lambs weight weaned per ewe were positive and quite large. That indicates reproductive rate (litter size) permits increasing in total lambs weight weaned per ewe.

Table 3. Correlation between Litter Size and Weaning weight

Genetic correlation	Phenotypic Correlation	References
0.24		Chang and Rae (1972)
0.06		Eikje (1975)
-0.03		Shelton and Menzies (1968)
-0.12		Gjedrem (1966)
	0.37 (per ewe)	Abdulkhaliq (1989)
	0.50 (per ewe)	Russel, et al. (1992)
0.41 (per ewe)	0.57 (per ewe)	Fogarty et al. (1994)
	0.47	Martin et al. (1981)
0.837 (lambs weaned per ewe)		Snyman et al. (1996)
-0.11		Snyman et al. (1996)

Bradford et al. (1994) reported total weight of lamb weaned per ewe, over 30 years, of experiment increased in selected line for multiple birth. Atkins (1980) noted genetic gains was also achieved in weaning weight per ewe by selection for increased fleece weight and weaning weight in fertility flock. The estimated rates of improvement for weaning weight per ewe was 0.3 kg or 0.8% per year (Atkins, 1980).

It is clear that although lambs born as singles have better performance (birth weight, lamb survival, weaning weight, growth rate) than twins whose performance is more than half of singles. However, the differences have never great enough to wipe out the advantage of extra lambs weaned (Turner, 1966). Turner (1962) reported T (dropped twins or multiple births) group weaned an average of 0.96 lambs per ewe and had 13 more lambs weaned per 100 ewes mating than O (dropped singles) group which weaned an average of 0.83 lambs per ewe. Total kilograms of weaning weight per ewe were 47.3 kg and 42.0 kg for the T and O group, respectively. Kilograms of total weaning weight in T were greater than O, because the T group weaned more lambs.

CHAPTER 3

MATERIAL AND METHODS

Animals and Management

This study was initiated in the fall 1968 at Montana Agricultural Experiment Station's, Red Bluff Research Ranch located at Norris, Montana. Elevations range from 1280 m at the ranch headquarters to 1900 m in the Cottonwood pasture. Precipitation ranges from 25 to 48 cm, with an average of 42 cm. There were 10035 animal records from 1969 through 1996.

Sheep

Rambouillet ewes were assigned at random within age to one of two selected lines: HL (high reproductive rate line) and LL (low reproductive rate line). No initial screening was practiced for ewes. Rams were selected from the foundation ewes on the basis of their dam's reproductive index (I). The four highest-ranking indexes rams were assigned to the ewes in HL and the lowest ranking index rams were assigned to ewes in LL. The first progeny were born in the spring 1969 and after this time both HL and LL were closed. A control (CL) line was established in the fall 1972. All remaining foundation ewes were pooled together and eight male offspring from HL and LL selected randomly.

Selection Procedures

Rams and ewes were selected within line based on a simple index of their dam's past reproductive performance. The index is the average number of lambs born in a ewe's lifetime up until the time she gave birth to the lamb under consideration.

I = total lifetime lamb production / (age of ewe – 1).

All years that a ewe was exposed to breeding, whether ewes lambed or not were included in the index. The four highest reproductive indexing rams within the HL and four rams with the lowest reproductive indexes within the LL and a random sample of eight rams within the CL were selected. Furthermore, four reserve rams were also selected within each line. There was the restriction that rams selected within line could not be paternal half sibs. In addition, the rams could not have horns or wool blind. Rams were used only for one breeding season to reduce inbreeding depression at 18 months of age.

Ewes in the HL, LL and CL were selected on similar basis as rams at 16 months of age. Ewes were bred to lamb at first 2-year-olds and were removed from the flock at 6 years of age. The only other restrictions were no physical problems such as horns, woolblindness or mastitis. Each line was maintained at approximately 100 ewes.

Management

Ewes were brought to the ranch headquarters for breeding, shearing, lambing, weaning, and data collection. The breeding season was from mid November-December. Ewes were assigned to single sire breeding pens and stayed in the pen for about 20 days.

After that time the ewes were removed from the pens and herded on the range and exposed to blackface rams for 15 days.

Ewes were managed as one group on winter range composed of blue-bunch wheat grass and Idaho fescue. Ewes were supplemented with 0.15 kg of a 20% protein pellet which contained 48% barley, 5% wheat millrun, 27% soybean meal, 5% dehydrated alfalfa, 6% molasses, 7.5% dicalcium phosphate and salt. When the snow cover was too deep for grazing, ewes were given mixed alfalfa and grass hay. This was usually 5 to 7 days per winter.

Ewes were shorn prior to lambing in March. Grease fleece weights were recorded and graded at the Montana Wool Laboratory.

Lambing season was in April and May and shed lambing was practiced. Prior to lambing, ewes were moved to a large pen and observed 24 hours per day. Upon lambing ewes and lambs were placed in individual pens for one to three days. Lambs were eartagged and weighed within 24 hours of birth and the data recorded. Ewes and lambs were moved to larger pens with other 6 to 8 ewes and their lambs for 3 days. Ewes nursing twins were separated from ewes nursing single and given extra grain.

Ewes and lambs were managed as one group on a fenced area of the research ranch until early-June. Before 1977, ewes were taken to high mountain Forest Service grazing allotments for the remaining summer grazing until the last week of August. After 1977, ewes and lambs remained on the research ranch and not taken to high mountain Forest service allotments.

Lambs were weighed at turn out (30 days of age) and weaning (120 days of age). Replacement ewe lambs were maintained as one group at Red Bluff and supplemented 0.3 kg of a 20% protein pellet and grazing hay meadow aftermath until November. During the winter, ewe lambs were given a mixed alfalfa grass hay. After weaning, ram lambs were moved to Fort Ellis and the initial selection was done. The selected ram lambs were fed one pound of barley and free choice mix grass-alfalfa hay through the winter and grazed cultivated pasture during the summer grazing.

Data

Phenotypic effects

Total kilograms of weaning weight. Data for this study were collected from three selected lines of Rambouillet sheep, which are low (LL), high (HL) and control (CL) line from 1969 until 1996. Traits measured were birth weight and weaning weight.

Individual lamb weaning weight was corrected to 125 days of age by using the equation:

$$\text{Corrected WW} = \left[\frac{(\text{WW} - \text{BW})}{\text{age at weaning}} \times 125\right] + \text{BW}$$

where: BW is birth weight and WW is weaning weight.

The individual 125-d weaning weight were analyzed by using GLM (General Linear Model) procedure (SAS, 1988). Preliminary analysis showed that age of dam (2, 3, 4 to 6), year of lamb birth (1971 through 1996) and lamb's sex (ewe and ram lambs) were significant (P<0.01) sources of variation for 125-d weaning weight. Therefore, in order to remove non-genetic environment effects, the 125-d weaning weight data were adjusted for age of dam, year of birth of lamb, lambs' sex, so that a large proportion of the remaining variation within the line would be due to genetics. Additive factors (Table 4) to adjust for year of birth of lamb, age of dam and lamb sex were derived from the entire data set because the flock size was sufficiently large. The 4 to 6 years old dams and ram lambs were used as the base class for comparison. The overall means were used as the base adjustment for year of lamb birth. Then, the additive factors were added to individual 125-d lamb weight weaned. The weight of lamb weaned for each ewe (kilograms weaned per ewe) was then determined by summing the adjusted weights for each lamb weaned. This composite trait total kilogram of weaning weight also includes ewes that failed to lamb or ewes that lost their lambs. Thus, for some ewes the total kilograms of weaning weight was zero. The orphaned lambs were not included. However, their mothers were still taken into account in selection.

Table 4. Additive Factors of Adjusted Weaning Weight

Year	additive	year	additive	year	additive	year	additive
1971	–9.53	1977	-6.41	1983	4.59	1989	2.48
1972	–6.79	1978	-2.68	1984	3.92	1991	2.17
1973	–7.96	1979	3.49	1985	5.55	1992	4.37
1974	–8.53	1980	2.94	1986	2.83	1993	0.90
1975	–7.85	1981	4.20	1987	5.38	1994	2.28
1976	–5.46	1982	3.88	1988	2.10	1995	-0.99
						1996	3.37

Age of dam	additive
2	2.80
3	0.83

Sex	additive
Ewe lambs	2.06

The data were analyzed using the General Linear Model procedure of SAS (1988). Independent variables in the analyses were line, year of birth of dam and two factor interactions. Dependent variables are total kilograms of weaning weight per ewe exposed and total kilograms of weaning weight per ewe lambing.

Number of lambs born and lambs weaned. The data of number of lambs born per ewe exposed, number of lambs born per ewe lambing, number of lambs weaned per ewe exposed and number of lambs weaned per ewe lambing were collected from the three selected lines (L, H, and C) of Rambouillet sheep from 1969 until 1996.

The data were analyzed using the General Linear Model procedure of SAS (1988). Independent variables in the analyses were line, year of birth of dam, age of dam, year of birth of dam by line interaction and year of birth of dam by age of dam interaction. Dependent variables were number of lambs born per ewe exposed, number of lambs per ewe lambing, number of lambs weaned per ewe exposed and number of lambs per ewe lambing.

Genetic effects

A number of identifiable non-genetic or environmental effects are known to influence the productive traits in sheep. The non-genetic effects which can usually be identified are sex, age of dam. To reduce the environmental variation in the trait is by adjustment for these known effects so that animals are compared on a similar basis. This can result in increasing of heritability. In addition, estimate of breeding values becomes more accurate. As a result, the selection response becomes greater as well. Therefore, the adjusted data of total kilograms weaning weight per ewe exposed and lambing were used to estimate breeding value and heritability of total weaning weight per ewe exposed and lambing.

Variance components which were used to calculate heritability and breeding value were estimated by using MTDFREML (Multiple Trait Derivative-Free Restricted Maximum Likelihood) using the full animal model (Boldman et al., 1993). Variance components estimated were genetic variance, environmental variance and permanent environmental variance. Permanent environmental effect obtained in all animals in each line were included in estimating direct breeding value and heritability, because permanent environmental effects influence an animal's performance for a repeated trait when individual has more than one performance record (Bourdon, 1997). Genetic maternal effects were originally included but were very close to zero, so they were deleted from the model. Year of dam birth is a fixed effect in running MTDFREML for breeding value of total kilograms weaning weight and lambs born and weaned. In addition, age of dam was included as fixed effect in estimating number of lambs born per ewe exposed and lambing, and number of lambs weaned per ewe exposed and lambing.

Heritability (h^2) was estimated from MTDFREML analysis using the following equation:

$$h^2 = \frac{V_G}{(V_G + V_E + V_P)}$$

where V_G is the estimated variance of additive, V_E is the estimated variance of environment and V_P is the estimated variance of permanent environmental effect. MTDFREML estimated V_A by calculating all possibility relationship among the animals, including paternal half sib, offspring-parents, and relatives.

Individual Estimated Breeding values (EBV) were then analyzed using the General Linear Model procedure of SAS (1988). Independent variables in the analyses were line, year of birth of dam and two factor interactions. Dependent variables were estimated breeding values (EBV) for total kilograms of weaning weight per ewe exposed and lambing, number of lambs born per ewe exposed and lambing, and number of lambs weaned per ewe exposed and lambing,

Genetic changes in response to selection for all traits for each line were measured as the regression coefficients of the ewe's EBV on year of dam birth. The regression of the ewe's EBV were then analyzed by using the GLM procedure of SAS (1988) in order to test the regression coefficients between lines whether they were different from zero or not and whether they were different from each other or not.

CHAPTER 4

RESULTS AND DISCUSSION

Total Kilograms of Weaning Weight

Phenotypic Effects

Analyses of variance for total kilograms of weaning weight per ewe exposed and lambing are presented in Table 5. Year of dam birth and selection line affected (P<0.01) total kilograms of weaning weight per ewe exposed and lambing. Two factor interaction between year of birth of dam and line had an effect (P<0.01) only on total kilogram of weaning weight per ewe lambing. The variation between and within year of birth of dam could be caused by many factors including management, feeding and environment.

Table 5. Least Squares Analysis of Variance for Total Kilograms of Weaning Weight per Ewe Exposed and Lambing.

	Exposed		Lambing	
Source of variation	df	MS	df	MS
Line	24	4151.921*	24	1889.343*
Year of dam of birth	2	18098.417*	2	16015.939*
Line x year of dam of birth	44	534.514	44	504.105*
Error	5994	428.123	4955	292.770

*(P < 0.01) df (degree of freedom) MS (Means Square)

Total kilograms of weaning weight per ewe exposed and lambing differed (P<0.01) between lines (Table 6). The HL had greater (P<0.01) total kilograms of weaning weight per ewe exposed and lambing than the L. The CL means was intermediate between HL and LL, however the estimated mean of CL was close to HL.

Turner (1972) observed total kilograms of weaning weight per ewe were 47.3 kg and 42.0 kg for the T (dropped twins or multiple births) and O (dropped singles) group, respectively. The T group weaned average 0.96 lambs per ewe or 13 more lambs weaned per 100 ewes mating than O group which weaned an average 0.83 lambs per ewe. Kilograms of total weaning weight in T were greater than O group, because the T group weaned more number of lambs. This is similar to our study in which total kilograms of weaning weight per ewe exposed and lambing in the HL was greater (P<0.01) than the LL and CL line because of a greater number of lambs weaned in the HL due to greater number of lambs born. Turner (1972) proved that although lambs born as twins have a lighter average weaning weight and slower growth rate than lambs born as singles, the total weight of lamb weaned per ewe was higher for the T group ewes, because of the greater number of lambs.

Table 6. Least Squares Means and Standard Error of Total Kilograms of Weaning Weight per Ewe Exposed and L.ambing

	Exposed	Lambing
LL	27.59 ± 0.46^{a}	33.53 ± 0.42^{a}
HL	33.11 ± 0.46^{b}	39.46 ± 0.41^{b}
CL	32.22 ± 0.51^{c}	38.12 ± 0.47^{c}

^{a,b,c}Means within the same column with different superscripts are different (P<0.01).

Figure 1 and 2 show the phenotypic trend for total kilogram of weaning weight per ewe exposed and per ewe lambing over 25 years of experiments. These figures

Figure 1. Total Kilograms of Weaning Weight per Ewe Exposed.

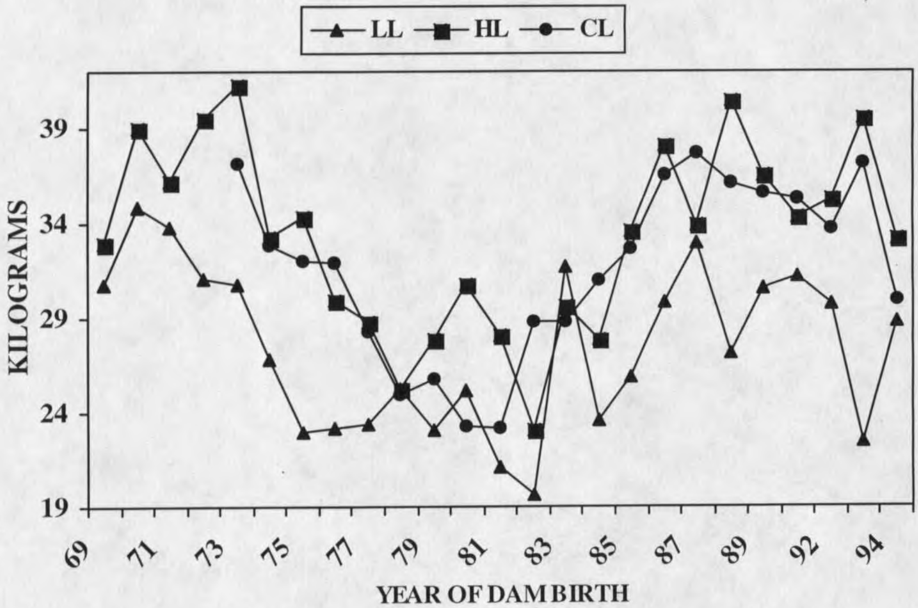
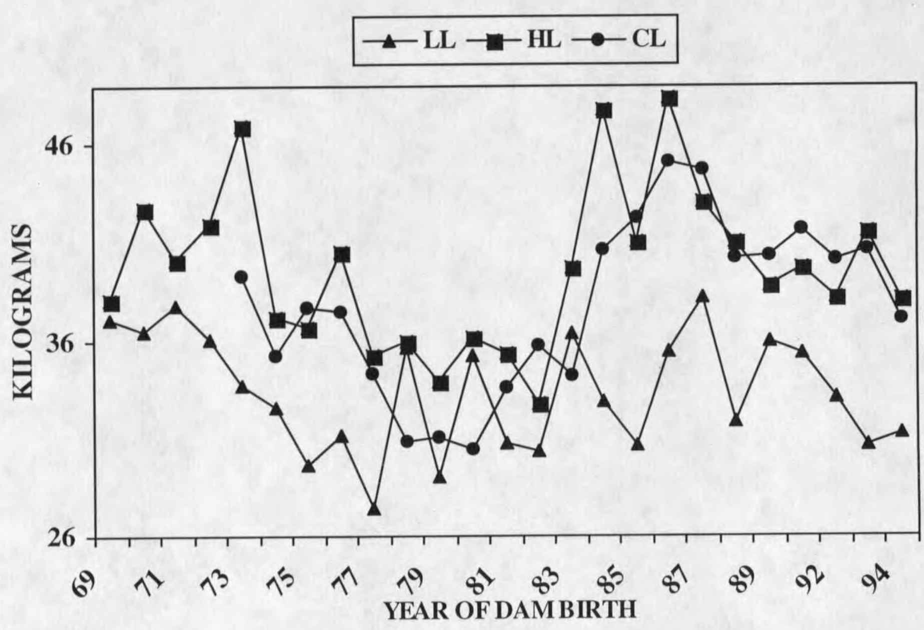


Figure 2. Total Kilograms of Weaning Weight per Ewe Lambing.



demonstrate that the total kilograms of weaning weight per ewe exposed and lambing for all lines decreased up until 1977 and then began to increase after 1977. Thus, the difference of management and environment might play a major cause of the difference of total kilograms of weaning weight within and between line over the years of experiment.

As described previously, there was different management in feeding and environment during the experiment. The ewes and lambs were herded on unfenced areas of the research ranch and then they were taken by truck to high mountain Forest Service grazing allotments for the remaining summer grazing. However, after 1977, ewes and lambs were remained on the research ranch for the entire summer grazing. The summer grazing on the Forest Service Allotments provide much better forage than did Red Bluff Ranch during this grazing period.

The main cause in which selection reproductive rate might not change total kilograms of weaning weight is that twin performance is lower than singles. Several literatures stated that individual lamb of multiple birth or twins have lower birth weight (Maund et al, 1980; Peeters et al, 1996) that causes lower survival compared to singles (Nawaz and Meyer, 1992) and a lower weaning weight (Buvanendran et al, 1992). In addition, twins have lower growth rate than singles (Hall et al, 1995). According to Subandryo (1984) the lamb survival of Rambouillet sheep up until 120-d was 71%, which was quite low.

Besides the number of lambs weaned, the total weaning weight was influenced by growth rate of lambs. However, the HL weaned more lambs due to more number of lambs born. Thus, lamb growth rate might be a major cause of slow response to selection for reproductive rate in total kilograms of weaning weight per ewe. Further study of lamb growth rate in this population is needed. Lower birth weight and lack of feeding or milk might affect twin's survival and growth rate.

Genetic Effects

Table 7 presents a summary of variance component and percentage of the total variation. There was 92.3% of total variation in total kilograms weaning weight influenced by environment. Estimated heritability of total weaning weight per ewe exposed and lambing were 0.053 and 0.076. These results were similar to the estimates of 0.06 reported by Fogarty et al, (1994) for Hyfer sheep. Hall et al (1995) estimated heritability of this trait for Merino sheep was 0.10. Heritabilities for weaning litter weight published in the literature ranged between –0.05 (Clark and Hohenboken, 1983) to 0.50 (Basuthakur et al, 1973). Other estimates for weaning litter weight from purebred populations (Targhee and Columbia) include 0.12 (Eikje, 1975), 0.17 (Gjedrem, 1967), 0.21 (Shelton and Menzies, 1968; Parker, 1969). 0.24 (Jonmundsson, 1976) and 0.25 (More O'Ferrall, 1976). There was close agreement between the results obtained in this study and those reported in the literature.

Table 7. Summary of Variance Component Estimates and Percentage of the Total Variation for Total Kilograms of Weaning Weight.

	Exposed (%)	Lambing (%)
Genetic	22.75 (5.25)	22.81 (7.630)
Permanent environment	17.54 (4.05)	0.12 (0.004)
Environment	393.01 (90.70)	276.11 (92.330)
Total	433.30	299.04

Table 8 shows the analyses of variance for EBV of total weaning weight per ewe exposed and lambing. EBV of total kilogram per ewe exposed and lambing were affected by line, year of birth of dam, line x year of birth of dam interaction (P < 0.01). Line was the main major source of variation in EBV of the total kilograms of weaning weight. The variation of EBV for total kilograms of weaning weight was undoubtedly affected by selection for reproductive rate.

Table 8. Least Squares Analysis of Variance of EBV for Total Kilograms of Weaning Weight per Ewe Exposed and Lambing.

	Exposed		Lambing	
Source of variation	df	MS	df	MS
Line	2	4130.433*	2	3888.512*
Year of dam of birth	24	129.619*	24	29.865*
Line x year of birth of dam	44	34.360*	44	29.623*
Error	1773	8.382	1607	5.454

*(P < 0.01) df (degree of freedom) MS (Mean Squares)

Table 9 shows the EBV of total weaning weight per ewe for each line. The estimated means between lines were different (P<0.01). Thus, ewes were genetically different among line. The HL ewes had a greater (P<0.01) mean EBV than LL. The CL was intermediate between HL and LL (P<0.01). These results indicate that selection for reproductive rate has also resulted in genetic change in total kilogram of weaning weight per ewe exposed and lambing.

Table 10 presents regression coefficient of total kilograms per ewe exposed and lambing. Regression coefficients for each line were all different (P<0.01) from zero, except total weaning weight per ewe exposed in LL (P>0.01). The regression coefficients were all different from each other between line (P<0.01), except for total weaning weight per ewe exposed between HL and CL (P>0.01).

Table 9. Least Square Means and Standard Error of EBV for Total Weaning Weight per Ewe Exposed and Lambing.

Lines	Exposed	Lambing
LL	-1.76±0.09[a]	-1.36±0.09[a]
HL	3.37±0.09[b]	3.28±0.09[b]
CL	2.28±0.11[c]	2.50±0.10[c]

[a,b,c]Means within the same column with different superscripts are significantly different (P<0.01).

Table 10. Regression Coefficients of EBV for Total Kilograms of Weaning Weight per Ewe Exposed and Lambing on Year of Dam Birth.

Lines	Exposed		Lambing	
	Intercept	Reg. Coefficient	Intercept	Reg.coefficient
LL	-1.35	0.005±0.0001[d]	-1.31	0.034±0.0001[d,g]
HL	1.20	0.170±0.0001[e,g]	1.91	0.130±0.0001[e,g]
CL	0.61	0.190±0.0001[e,g]	0.16	0.210±0.0002[f,g]

[d,e,f]Regression coefficients with different superscripts within column differ (P<0.01)
[g]Regression coefficients differ from zero (P<0.01).

Figure 3 and 4 illustrate the genetic change of total kilograms of weaning weight per ewe exposed and lambing over 25 years. The HL steadily increased (P<0.01) over the duration of the experiment, as indicated by a positive of regression coefficient. Genetic improvement in the HL increase at a rate of 0.17 kg per ewe exposed (17 kg per 100 ewes) and 0.13 kg per ewe lambing (13 kg per 100 ewes lambing). There is no genetic change in LL, because the regression coefficient was not different (P<0.01) from zero.

There are two ways to estimate the genetic improvement made by selection. These are by taking the differences between selected and control line or by taking the

Figure 3. Genetic Change of Total Kilogram of Weaning Weight per Ewe Exposed.

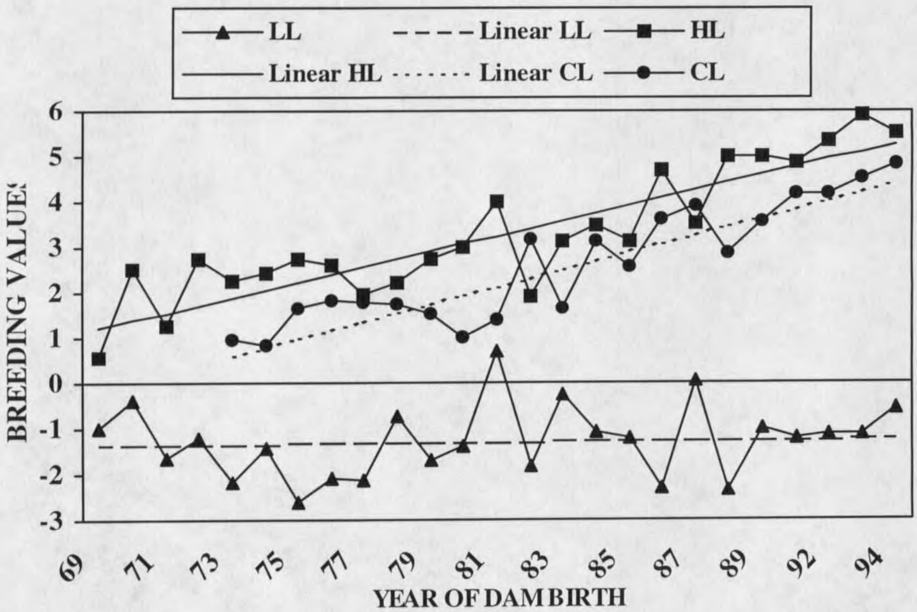
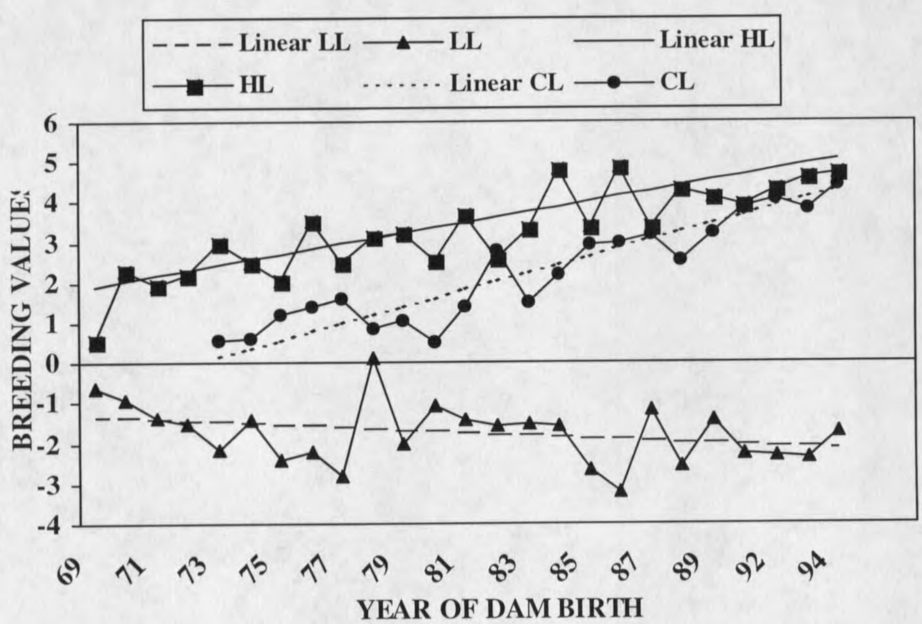


Figure 4. Genetic Change of Total Kilograms of Weaning Weight per Ewe Lambing.



difference between two selected lines (Falconer and Mackay, 1996). The annual response to selection of total weaning weight per ewe measured as the divergence between two lines (HL-LL) were 0.1635 kg per ewe exposed per year (16.35 kg per 100 ewes) and 0.158 kg per ewe lambing (15.8 kg per 100 ewes) per year. However, response to selection as difference between selected line and control line was smaller.

The annual response to selection in EBV of total kilograms of weaning weight (HL-CL) was –0.02 kg per ewe exposed and –0.07 kg per ewe lambing. These negative results were effects of a greater increase of genetic change in the CL than the HL.

The positive change in the CL line was one of the unexpected results of this study. The CL was used to eliminate environmental fluctuations from the rate of selection response. Based on an assumption that environmental differences may affect both selected and control line, therefore, the difference between selected and control line was the genetic differences due to selection. As a result, it is not easy to explain that selection for reproductive rate affect total kilograms of weaning weight per ewe exposed and lambing, because the response CL increased at a rate similar to HL .

There was a greater ($P<0.01$) response to selection in the HL compared to LL, based on regression coefficients. According to Falconer and Mackay (1996) there are several possible causes of asymmetrical responses, such as random drift, selection differential, inbreeding depression, maternal effects. As we know that response to selection is dependent upon selection differential, heritability and generation interval.

Selection differential may differ between selected lines for several reasons such as natural selection, changing in fertility and variance. Natural selection will be useful in one selected line, but it will be useless in other selected line. Changing in fertility may affect more to the selected line that has higher intensity of selection so that greater response is achieved in that selected line. Changing in variance resulted from the change of mean so that can increase selection differential as the variance increase. Changing in variance can decrease selection differential as the variance decrease (Falconer and Mackay, 1996). In a previous study, Burfening (1993) reported regression of cumulative selection differential on year of birth was negative in LL and positive in HL.

Another cause of asymmetry is different heritability in each line (Falconer and Mackay, 1996). Although all animals were maintained together in the same flock that might reduce the variance phenotypic, the variance genetics between line might be different due to selection differential. The heritability between line was not tested in this study, hoewever Burfening (1993) reported heritability for lambs born and weaned between lines were different.

Due to only one selection line in each direction (HL and LL), the main causes of asymmetrical responses is random drift. In other words, without replication of selected lines, it is hard to prove the reality of asymmetry. Because of no replication, the asymmetry is doubtful.

Effect of Population Size

According to Falconer and Mackay (1996), response to selection is affected by effective population size that can influence the rate of inbreeding. In our study the effective population size and the rate of inbreeding was measured by using equation from Falconer and Mackay (1996) given in Table 11.

Table 11. Effective Population Size and Rate of Inbreeding.

Line	N_f	N_m	Population size	Rate of inbreeding
LL	100	4	15.385	0.032
HL	100	4	15.385	0.032
CL	100	8	29.630	0.017

N_f (Number of females) N_m (Number of males)

The rate of inbreeding is associated to inbreeding depression that can change the fitness traits, such as survivability and fertility of the next generation. There will be a tendency for the mean to decline through inbreeding. Table 11 shows that the rate of inbreeding in CL is smaller than in HL and LL because of greater population size due to greater number of males. The rate of inbreeding in HL and LL were almost doubled to CL. Therefore, the survivability and fertility in HL and LL were smaller than CL. The greater fitness traits in CL might lead increasing the rate of response in the CL and the lower fitness in HL might lead decreasing the rate of response in HL. Therefore the rate of response for CL will be close to HL. There was no question that kilograms of weaning weight either per ewe exposed or per ewe lambing in CL increase at similar rate to HL.

To further evaluate the effect that selection had on the total kilogram of lamb weaned, the number of lambs born and number of lambs weaned per ewe were studied further.

Number of Lambs Born

Phenotypic Effects

Analyses of variance for number of lambs born per ewe exposed and lambing are presented in Table 12. Year of dam birth, lines of reproductive rate, age of dam, age of dam x year of dam birth interaction and line x year of dam birth were all significant source of variation (P<0.01) for number of lambs born per ewe exposed and lambing. Age of dam was the major source of variation for lambs born either per ewe exposed or lambing.

Table 12. Least Squares Analysis of Variance for Number of Lambs Born per Ewe Exposed and Lambing.

	Exposed		Lambing	
Source of variation	df	MS	df	MS
Line	24	3.681*	24	0.823*
Year of dam of birth	2	31.044*	2	28.962*
Age of dam	4	35.035*	4	23.278*
Line x year of dam of birth	44	0.884*	44	0.512*
Age of dam x year of dam birth	79	1.464*	79	0.496*
Error	5907	0.424	4871	0.202

*(P < 0.01) df (degree of freedom) MS (Mean Squares)

The estimated means of number of lambs born per ewe exposed and lambing differed (P<0.01) among lines (Table 13). HL ewes were superior (P<0.01) to the other selection lines, than LL. While CL ewes were intermediate between LL and HL.

Table 13. Least Square Means and Standard Error of Number of Lambs Born per Ewe Exposed and Lambing.

Lines	Exposed	Lambing
LL	1.079 ± 0.015^{a}	1.301 ± 0.011^{a}
HL	1.323 ± 0.015^{b}	1.563 ± 0.011^{b}
CL	1.229 ± 0.017^{c}	1.440 ± 0.012^{c}

^{a,b,c}Means within the same column with different superscripts are significantly different ($P<0.01$)

These results agree with those published for selection experiments in sheep for reproductive rate in several countries with different breeds (Bradford, 1985; Land et al, 1984). In Ruakura, New Zealand, Wallace (1964) initiated a study with Romney sheep in 1948. This study practiced initial screening of the ewe population and selection criterion of ewes and rams was based on incidence of multiple birth. Clarke (1972) observed after 18 years, liter sizes of 1.13, 1.62 and 1.22 for the low, high, and control lines, respectively. In Deniliquin and Armidale, Australia, Turner's (1978) study with Merino sheep begun in 1954. Initial flocks were made up of ewes producing or multiple birth (T) and producing singles (O). After 18 years the mean litter size was 1.18 for O line and 1.70 for T line. In Hopland, California, Targhee sheep have been selected since 1963 Bradford (1981). The study selected rams and ewes on the basis of dam's lifetime multiple birth record initial screening was also practiced. Litter size averaged 1.39 and 1.24 for HL and CL respectively at the end of study. In England, Bhuiyan and Curran (1994) initiated a study with Romney sheep as a source of high merit breeding stock in 1980. Litter size was 1.86 and 1.63 for the selected and control line, respectively. Number of lambs born per ewe exposed (prolificacy) was 1.54 and 1.33 for the selected and control line, respectively. Atkins (1980) practiced no initial screening in Merino sheep at Trangie, Australia. Litter size achieved was 1.52 and 1.32 for the HL and CL over 21 years of experiment. Other study, in Ireland with Galway sheep, Hanrahan (1982) practiced no initial screening resulting in litter size averaging 1.67 for HL and 1.44 for LL and found an increase of 1.5% per year in litter size in response to selection over about 19 years for litter size of the dam and sire's dam.

In Montana, USA, Schoenian (1988) studied Rambouillet sheep over 20 years. No initial screening was practiced and selection criterion was based on dam's past reproduction performance. Lambing rate (lambs born per ewe exposed) was 1.40, 0.98 and 1.25 for the HL, LL and CL respectively less than our study. HL ewes were superior to LL ewes in litter size 1.61 compared to 1.17 and 1.42 for the CL, higher than our study.

The effect of initial screening makes an important contribution to the response realized (Clarke, 1972; Turner, 1978; Hanrahan and Timon, 1978; Bradford, 1981). In the Ruakura (Clarke, 1972), it contributed about one quarter of the total response. In California Targhee (Bradford, 1981) line, it contributed about two-thirds. In Ireland (Hanrahan, 1982), initial screening almost certainly contributed importantly to the development of highly prolific stock. However, some studies in Trangie Merino (Atkins, 1980), Galway (Hanrahan and Timon, 1978) and Rambouillet (Burfening et al, 1993) did not involve initial screening indicating that this phase is not necessary to achievement of good response.

Figures 5 and 6 illustrate phenotypic trend for number of lambs born per ewe exposed and per ewe lambing over 25 years of experiments. It was not easy to describe the trends for the number of lambs born either per ewe exposed or per ewe lambing.

Genetic Effects

Table 14 presents a summary of variance component estimates and percentage of the total variation. Estimates of heritability for number of lambs born were 0.083 (exposed) and 0.136 (lambing). Estimated heritability of lambs born lambing was higher than lambs born exposed similar to those reported by Burfening et al (1993) that the estimated of genetic variance for lambs born was in Rambouillet sheep over 18 years. In previous study, Burfening (1993) found that heritability for number of lambs born per ewe exposed and lambing by taking average within each line were 0.117 and 0.125 These results were a little different from our study which might be due to different methods in calculation and duration of experiment that may change either the variance of genetics or variance of phenotypic in short term of selection .

Table 14. Summary of Variance Component Estimates and Percentage of the Total Variation for Number of Lambs Born.

	Exposed (%)	Lambing (%)
Genetic	0.036 (8.30)	0.028 (13.60)
Permanent environment	0.004 (0.96)	0.0016 (0.78)
Environment	0.392 (90.7)	0.176 (85.60)
Total	0.432	0.2056

These estimates were less than the estimates of 0.23 (Targhee), 0.35 (Columbia) and 0.18 (Suffolk) based on sire-of-ewe variance component by Abdulkhaliq (1989).

Figure 5. Number of Lambs Born per Ewe Exposed.

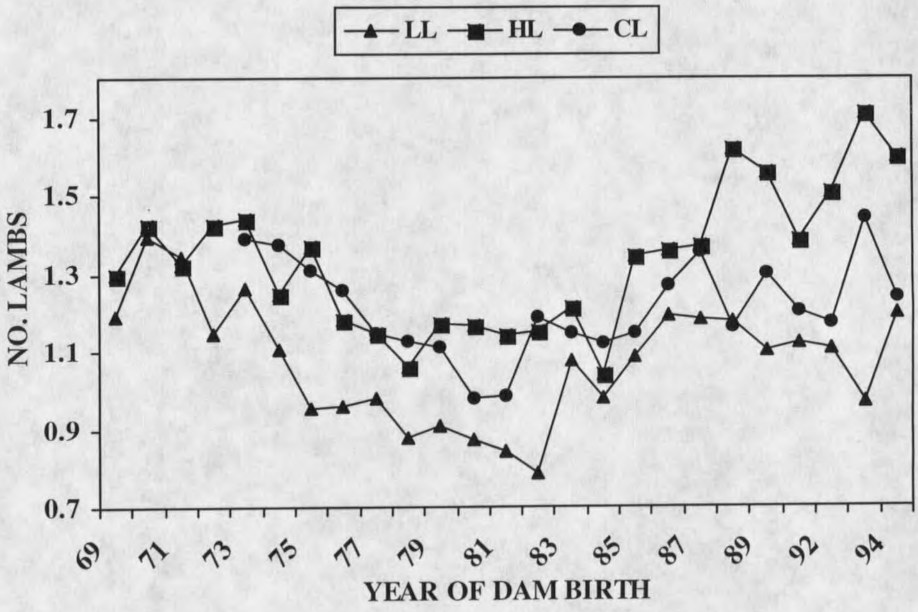
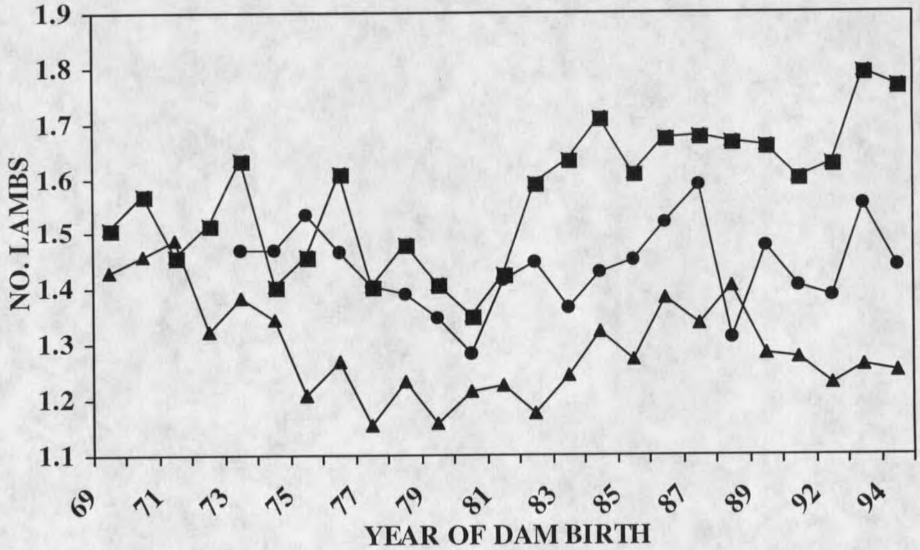


Figure 6. Number of Lambs Born per Ewe Lambing.



Other estimates for purebreds include 0.03 (Ch'ang and Rae, 1961), 0.08 (Forest and Bichard, 1974; Eikje, 1975), 0.10 (Mann et al, 1978), 0.19 (Jonmundsson, 1977) 0.20 (Kennedy, 1967) and 0.26 (Shelton and Menzies, 1968). In general, these estimates were similar to the average heritability estimate summarized from the literature by Bradford (1985) that estimated heritability of litter size in sheep ranged from –0.15 to 0.35 and a mean of 0.10. More than eighty five percent of total variation in lambs born per ewe is influenced by environment.

EBV for number of lambs born per ewe exposed and per ewe lambing were affected ($P < 0.01$) by year of birth of dam, line and line x year of birth of dam interaction (Table 15). Line proved to be the major source of variation for EBV of number of lambs born per ewe exposed and per ewe lambing

Table 15. Least Squares Analysis of Variance of EBV for Number of Lambs Born per Ewe Exposed and Lambing.

	Exposed		Lambing	
Source of variation	df	MS	df	MS
Line	2	8.639*	2	9.172*
Year of dam of birth	24	0.142*	24	0.054*
Line x year of dam	44	0.099*	44	0.100*
Error	1773	0.0094	1607	0.0104

*(P<0.01) df (degree of freedom) MS(Mean Squares)

Table 16 shows the least square means and standard error of EBV for lambs born per ewe exposed and lambing. HL ewes had superior ($P<0.01$) mean EBV compared to LL ewes, with mean EBV of 0.165 ±0.004 lambs per exposed and 0.153±0.005 lambs per ewe lambing versus –0.075±0.004 lambs per ewe exposed and –0.11±0.005 lambs per ewe lambing respectively. CL was intermediate and different ($P<0.01$) than the two selection lines at 0.05±0.005 lambs per ewe exposed and 0.02±0.005 lambs per ewe lambing. It was clear that each line was genetically different. Ewes in the HL had superior EBV's genetically than CL which were superior to LL.

Table 16. Least Squares Means and Standard Error of EBV for Number of Lambs Born per Ewe Exposed and Lambing.

Lines	Exposed	Lambing
LL	-0.075±0.004[a]	-0.106±0.005[a]
HL	0.165±0.004[b]	0.153±0.005[b]
CL	0.055±0.005[c]	0.017±0.005[c]

[a,b,c]Means within the same column with different superscripts are significantly different (P<0.01)

The regression coefficients for the number of lambs born on year of birth of dam by selection line are given in Table 17. Regression coefficient for EBV of number of lambs born per ewe exposed and lambing for each line were all different (P<0.01) from zero, except the regression coefficient of lambs born per ewe exposed within the LL, and the regression coefficient of lambs born per ewe lambing within the CL. Regression coefficient were different (P<0.01) among lines. Thus, EBV between the line and within the line were changing during the study.

Table 17. Regression Coefficients of EBV for Number of Lambs Born per Ewe Exposed and Lambing on Year of Dam Birth.

Lines	Exposed		Lambing	
	Intercept	Reg.coefficient	Intercept	Reg.coefficient
LL	-0.07	-0.00008±0.00000[d]	-0.07	-0.003±0.00000[d,g]
HL	0.002	0.013±0.0005[e,g]	0.01	0.012±0.0000[e,g]
CL	0.04	0.003±0.0007[f,g]	0.02	0.0006±0.0000[f]

[d,e,f]Regression coefficients with different superscripts within column differ (P<0.01)
[g]Regression coefficients differ from zero (P<0.01).

Figures 7 and 8, and regression coefficients in Table 17 show that genetic change, as estimated by EBV, for number of lambs born per ewe exposed and lambing was achieved. The figure shows the differences between the three lines. The HL has steadily increased over the duration of the experiment, as indicated by a positive of regression coefficient (b = 0.013 lambs born per ewe exposed and b= 0.012 for lambs born per ewe lambing) and magnitude of the response of the HL in number of lambs born either per ewe exposed or lambing was greater ($P < 0.01$) than in the LL (b = -0.00008). The CL in per ewe exposed tended to increased over time ($P <0.01$), but not in per ewe lambing ($P > 0.01$). The negative results from LL showed that negative selection on reproductive rate will result in a decrease in reproductive rate. Burfening et al (1986) reported the regression of cummulative selection differential on year of birth for ewes were –0.065, 0.048 and –0.014 for LL, HL and CL respectively.

The annual genetic improvement as a response to selection for reproductive rate (HL-CL) was 0.011 lambs per ewe exposed (1.1 lambs per 100 ewes) and 0.0114 lambs per ewe lambing (1.14 lambs per 100 ewes) per year. In a previous study, Burfening et al (1993) reported estimated average annual EBV for number of lambs born for upward selection (HL) were 1.63 lambs per 100 ewes exposed and 1.64 lambs per 100 ewes. The annual EBV for number of lambs born in downward (LL) were -0.74 lambs per 100 ewes exposed and –0.73 lambs per 100 ewes lambing (Burfening et al, 1993). The annual EBV for number of lambs born in CL were 0.46 lambs per 100 ewes exposed and 0.5 lambs per 100 ewes lambing (Burfening et al, 1993). The greater progress was achieved in the upward direction which is similar to the results from our study.

Figure 7. Genetic Change of Number of Lambs Born per Ewe Exposed.

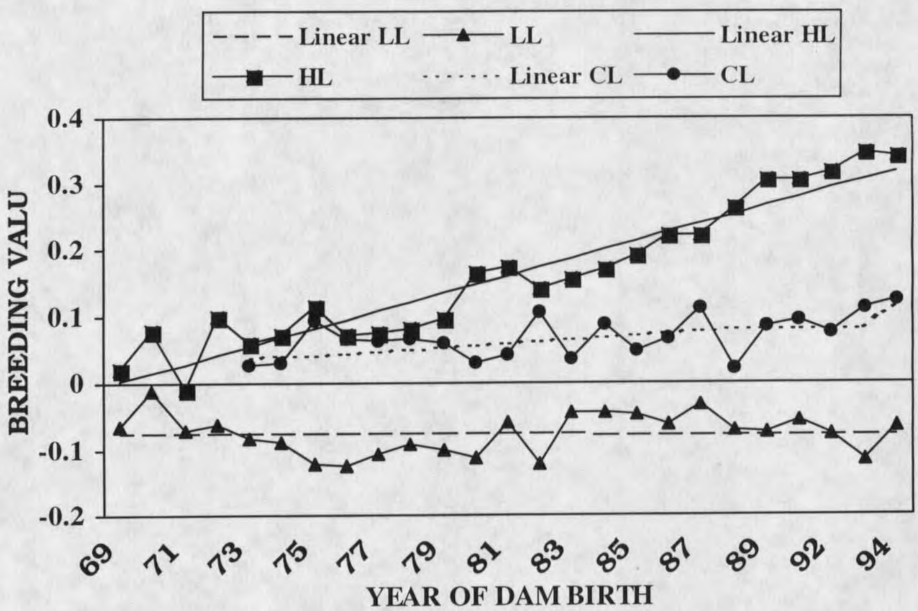
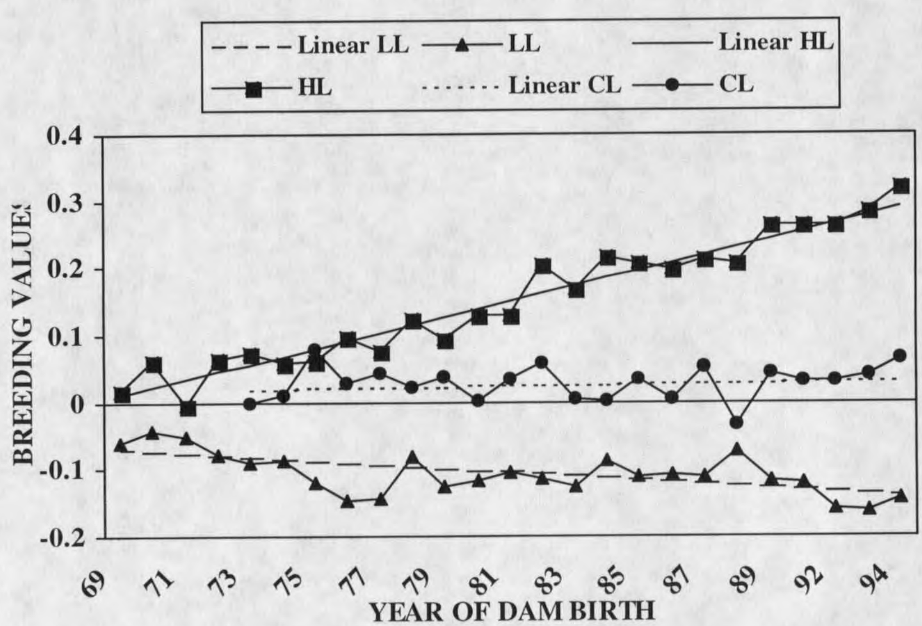


Figure 8 . Genetic Change of Number of Lambs per Ewe Lambing.



The regression of EBV was lower, particularly within the HL. The duration of the experiment for our study which might be a major cause of differences was longer. Years of dam birth affected the number of lambs born per ewe exposed and lambing. This can change the EBV due to changing heritability over the years (Falconer, 1996). Ercanbrack and Knight, 1998. found that average annual increase in prolificacy, based on selection for litter weight weaned in four lines (Rambouillet, Polypay, Targhee and Columbia) were 0.0144 lambs genetically. The regression of overall averaged EBVs on year of birth increased 0.0014 for number of lambs born per ewe exposed which was higher than litter size because of direct selection pressure on prolificacy (Bhuiyan and Curran, 1994).

The annual genetic improvement on number of lambs born per ewe, as the divergence between two selected lines (HL-LL) was 0.01 lambs per ewe exposed and 0.02 lambs per ewe lambing. Turner (1978) noted a continuing response after initial screening of ewes equivalent to 0.02 lambs born per ewe annually between T (dropped twins) group and O (dropped singles) group in Merino underselection for 18 years.

Generally, the estimated number of lambs born per ewe lambing either genotypic (EBV) or phenotypic (actual number) within lines was greater than lambs born per ewe exposed. A major cause was ewes that mated but failed to lamb. In estimating lambs born per ewe lambing, only ewes lambed were calculated. However in estimating lambs born per ewe exposed, either ewes lambed or fail to lambed were included in calculating.

Number of Lambs Weaned

Phenotypic Effects

The analyses of variances for number of lambs weaned per ewe exposed and lambing are given in Table 18. The number of lambs weaned per ewe exposed and lambing was affected ($P<0.01$) by line, year of dam birth, age of dam, and age of dam x year of birth of dam interaction. Year of dam birth x line interaction affected ($P<0.05$) lambs weaned per ewe exposed. However, year of dam birth x line interaction was not an important in affecting lambs weaned per ewe lambing. Age of dam was a main source of variation in lambs weaned.

Table 18. Least Squares Analysis of Variance for Number of Lambs Weaned per Ewe Exposed and Lambing.

	Exposed		Lambing	
Source of variation	df	MS	df	MS
Line	24	3.719*	24	1.872*
Year of dam of birth	2	19.961*	2	18.779*
Age of dam	4	31.733*	4	24.184*
Line x year of dam of birth	44	0.443	44	0.433**
Age of dam x year of dam birth	79	1.445*	79	0.754*
Error	5907	0.394	4871	0.288

*($P < 0.01$) **($P<0.05$) df(degree of freedom) MS(Mean Squares)

Table 19 shows least square means of lambs weaned per ewe exposed and lambing. The three lines differed ($P<0.01$) in number of lambs weaned per ewe exposed and lambing. The HL ewes were superior to LL and CL, because the HL had more lambs born than the LL, with CL intermediate between HL and CL. Turner (1966) reported average difference between T and O line was 0.17 lambs weaned per ewe exposed which was similar to our study (0.19 lambs difference between HL and LL). Clarke (1972) showed that lambs weaned per ewe lambing was 1.19, 0.85 and 0.86 for the HL, LL and CL, respectively, lower than our study.

Table 19. Least Squares Means and Standard Error of Number of Lambs Weaned per Ewe Exposed and Lambing.

Lines	Exposed	Lambing
LL	0.87 ± 0.015^{a}	1.04 ± 0.014^{a}
HL	1.06 ± 0.014^{b}	1.25 ± 0.013^{b}
CL	1.01 ± 0.016^{c}	1.18 ± 0.015^{c}

[a,b,c]Means within the same column with different superscripts are significantly different ($P<0.01$)

Figures 9 and 10 demonstrate phenotypic trends for number of lambs weaned per ewe exposed and per ewe lambing over 25 years of experimant. It is not easy to explained the trends for number of lambs weaned either per ewe exposed or per ewe lambing.

Genetic Effects

Table 20 shows a summary of variance component estimates and percentage of the total variation for number of lambs weaned. Estimates of genetic variances (heritability) for number of lambs weaned per ewe was 0.046 (exposed) and 0.06 (lambing) which were somewhat higher than those reported by Burfening et al (1993).

Figure 9. Number of Lambs Weaned per Ewe Exposed.

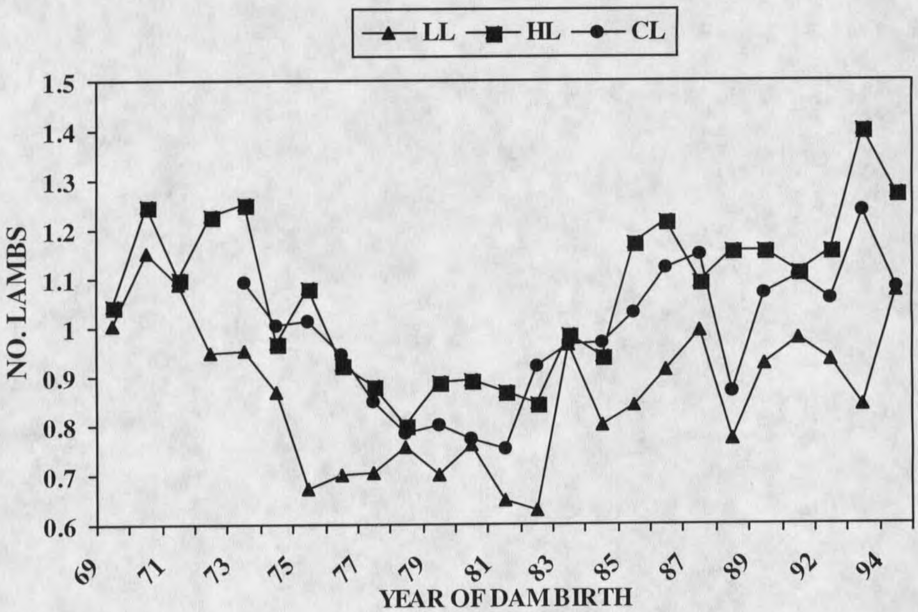
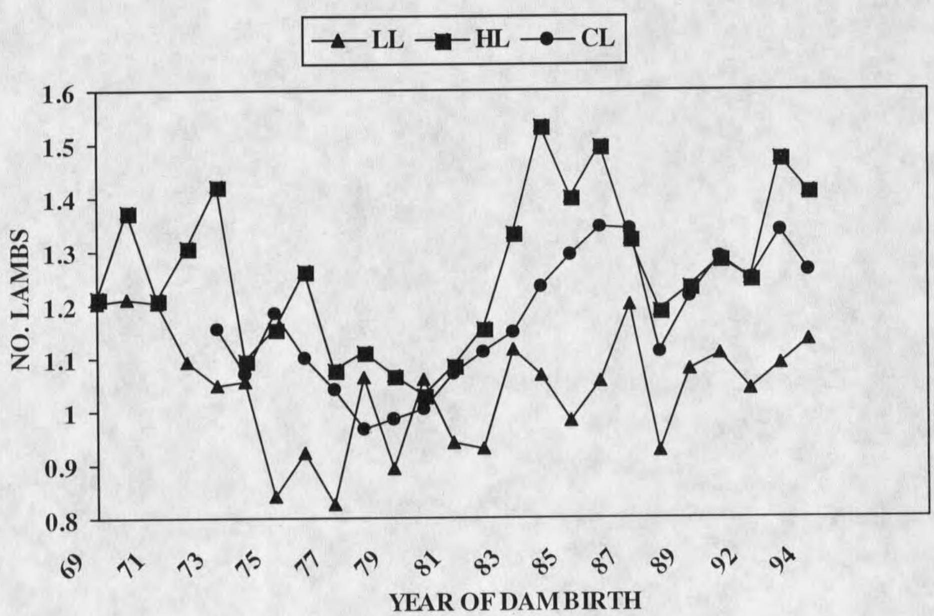


Figure 10. Number of Lambs Weaned per Ewe Lambing.



The estimated genetic variance for number of lambs weaned averaged from three lines (HL, LL and CL) were 0.043 (exposed) and 0.038 (lambing). The estimated heritability of our study was higher than the estimates of 0.06 (Kennedy, 1967), 0.03 (Eikje, 1975) and 0.02 (Martin et al, 1981) and less than the 0.15 (Young et al, 1963), 0.43 (Basuthakur et al, 1973). The findings of genetic variance in this study generally agree with most published estimates that heritability of reproductive rate whether measured as number of lambs born or weaned per ewe exposed or per ewe lambing is low and will respond very slowly to selection. Table 20 illustrates that the number of lambs weaned per ewe was influenced 93.8% by environment.

Table 20. Summary of Variance Component Estimates and Percentage of the Total Variation for Number of Lambs Weaned.

	Exposed (%)	Lambing(%)
Genetic	0.019 (4.6)	0.18 (6.0)
Permanent Environment	0.007 (1.7)	0.0006 (0.2)
Environment	0.386 (93.7)	0.28 (93.8)
Total	0.412	0.298

Sources of variation in EBV of number of lambs weaned per ewe exposed and lambing were line, year of birth of dam, and line x year of birth of dam interaction (Table 21). These variables affected EBV for number of lambs weaned (P < 0.01). Line was the main source of variation for EBV of number of lambs weaned per ewe exposed and lambing.

Table 21. Least Squares Analysis of variance for EBV of Number of Lambs Weaned per Ewe Exposed and Lambing.

	Exposed		Lambing	
Source of variation	df	MS	df	MS
Line	2	4.388*	2	4.701*
Year of dam of birth	24	0.038*	24	0.015*
Line x year of dam	44	0.032*	44	0.035*
Error	1773	0.004	1607	0.005

*(P < 0.01) df (degree of freedom) MS(Mean Squares)

Table 22 presents the least square means of EBV for number of lambs weaned per ewe exposed and lambing. The HL ewes had the highest (P<0.01) EBV of number of lambs weaned per ewe exposed and lambing compared to the LL and the CL.

Table 22. Least squares Means and Standard Error for EBV of Number of Lambs Weaned per Ewe Exposed and Lambing.

Lines	Exposed	Lambing
LL	-0.066±0.003[a]	-0.083±0.003[a]
HL	0.102±0.003[b]	0.100±0.003[b]
CL	0.052±0.003[c]	0.038±0.003[c]

[a,b,c]Means within the same column with different superscripts are significantly different (P<0.01)

Table 23 presents regression coefficients of EBV for number of lambs weaned per ewe exposed and lambing. Regression coefficients for each line were all different (P<0.01) from zero, and were all different (P<0.01) among lines. Figures 11 and 12 demonstrate genetic change of mean EBV within and between lines for lambs weaned on the year of dam birth. The HL increased (P<0.01) at a rate of 0.006 lambs weaned per ewe exposed and 0.005 lambs weaned per ewe lambing and the LL decreased (P<0.01) at a rate of 0.001 lambs weaned per ewe exposed and 0.003 lambs weaned per ewe lambing. Burfening et al. (1993) reported that the regression coefficient for HL was 0.0075 (exposed and lambing) and –0.0041 (exposed) and –0.0046 (lambing) for the LL over 16 years. These results were higher than, those observed in this study. It might be caused by changes of EBV due to changing in heritability. The CL trend tended to increase (P<0.01) at a similar rate as the HL. There was greater response to selection in the HL compare to LL. Ercanbrack and Knight (1998) observed annual genetic increase of 0.018 lambs weaned per year averaged over four lines (Rambouillet, Targhee, Polypay and Columbia) selected for litter weight weaned.

Table 23. Regression Coefficients for EBVof Number of Lambs Weaned per Ewe Exposed and Lambing on Year of Dam Birth.

	Exposed		Lambing	
Line	Intercept	Reg.coefficient	Intercept	Reg.coefficient
LL	-0.05	$-0.001\pm0.000^{d,g}$	-0.05	$-0.003\pm0.000^{d,g}$
HL	0.02	$0.006\pm0.000^{e,g}$	0.03	$0.005\pm0.000^{e,g}$
CL	0.01	$0.004\pm0.000^{f,g}$	-0.0004	$0.004\pm0.000^{f,g}$

^{d,e,f}Regression coefficients with different superscripts within column differ (P<0.01)
^{g}Regression coefficients differ from zero (P<0.01).

The annual genetic improvement of the number of lambs weaned per ewe, as the divergence between two selected lines (HL-LL) were 0.007 lambs per ewe exposed and 0.008 lambs per ewe lambing. Burfening et al (1993) found the differences between the HL and LL was 0.0116 lambs weaned per ewe exposed higher than our study. The annual increasing of response to selection by taking the difference between the HL and CL line (HL-CL) was 0.002 lambs per ewe exposed and 0.001 lambs per ewe lambing lower than those reported by Burfening et al (1993). They reported the average for number of lambs weaned per ewe exposed and lambing was 0.0048.

Figure 11. Genetic Change for Number of Lambs Weaned per Ewe Exposed.

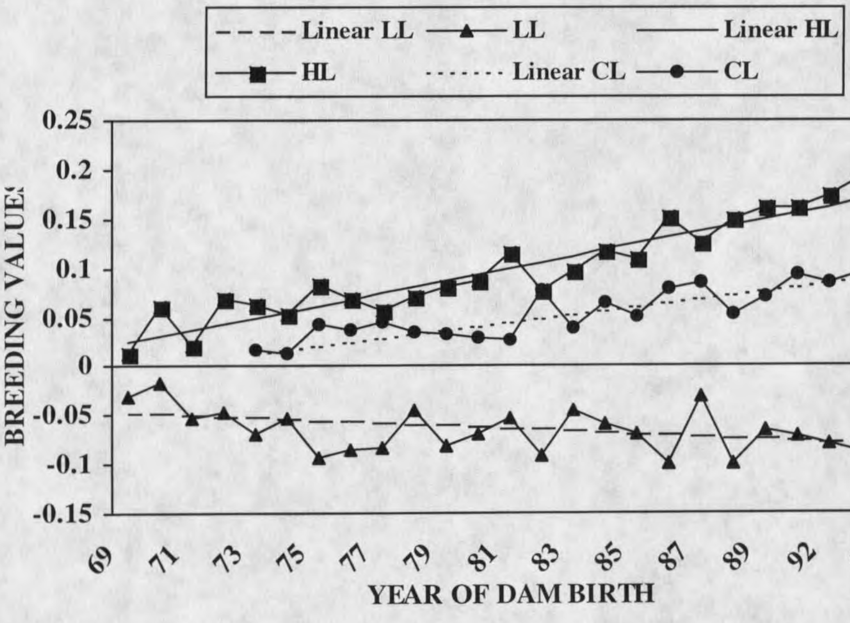
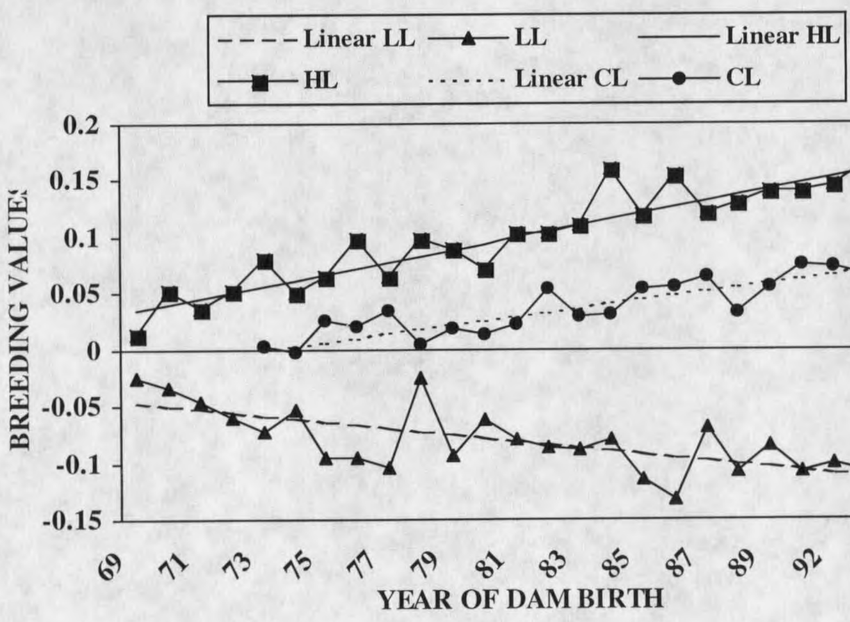


Figure 12. Genetic Change for Number of Lambs Weaned per Ewe Lambing.



Generally, lambs weaned both for EBV and for phenotypic either per ewe exposed or lambing within lines was less than lambs born per ewe exposed and lambing. A major cause that influenced the number of lambs weaned was lamb mortality, mother ability and predation

CHAPTER 5

SUMMARY AND CONCLUSION

Total weight of lamb marketed per ewe exposed per year is generally the single most important factor influencing the profitability of sheep production. Total weight of lamb weaned is determined by litter size, lamb survival, mother ability and offspring growth rate. Litter size defined, as number of lambs born per ewe lambing is a major factor affecting ewe productivity and contributing much more to the kilograms of lamb weaned than growth rate. More lambs marketed economically spreads ewe maintenance costs over greater number of lambs born. Therefore, increasing the number of lambs marketed per ewe offers the greatest single opportunity for increasing the profitability of sheep enterprises.

Reproductive rate as determined by the number of lambs weaned per ewe exposed is influenced by environment, management and genetics. Genetic improvement of reproductive rate gives more permanent gains than those by environment. Selection is the best way to improve reproductive rate for purebred, because it gives both phenotypic and genetic gains permanently and cumulatively.

Response to selection is affected by heritability, selection differential and generation interval. Although heritability of reproductive traits is low, the high coefficient of variation influencing selection differential permits annual rates of response to selection.

Effects of selection for reproductive rate on total kilograms of weaning weight per ewe have not been reported for most of the selection experiments. Therefore, the objectives of this study are to evaluate the phenotypic and genetic effects of selection for reproductive rate in Rambouillet sheep on total kilograms of weaning weight per ewe exposed and number of lambs born and weaned per ewe exposed and lambing.

This study presents some of the results from selection for reproductive rate based on their dam's reproduction performance in Rambouillet sheep at the Montana Agricultural Experiment Station. The selection began in 1968 when two populations of Rambouillet sheep were developed: a high line (HL) selected for high reproductive rate; a low line (LL) selected for low reproductive rate. A random control line (CL) was established in 1972. These three distinct populations offer a great opportunity to study the changes of response to selection for reproductive rate that have occurred from 1968 through 1996.

The three lines have significantly differentiated both phenotypic and genetic effects for total kilograms of weaning weight, number of lambs born and weaned either per ewe exposed or lambing. The HL always had the highest means ($P<0.01$), the LL had the lowest means ($P<0.01$) while the CL had intermediate means ($P<0.01$) between HL and LL. The means of total kilograms lamb weight weaned for HL is higher than CL which is higher than LL, because of greater number of lambs weaned due to more number of lambs born per ewe in agreement with Turner (1962).

The mean EBV for total kilograms of weaning weight were –1.76, 3.37 and 2.28 kg per ewe exposed for LL, HL and CL, respectively. The mean EBV for total kilograms of weaning weight were –1.36, 3.28 and 2.5 kg per ewe lambing for LL, HL and CL, respectively.

Estimated heritability for total kilograms of weaning weight per ewe exposed and lambing were 0.0525 and 0.0763 respectively. Estimated heritability for number of lambs born per ewe exposed and lambing were 0.083 and 0.136, respectively. Estimated heritability for the number of lambs weaned per ewe exposed and per ewe lambing were 0.046 and 0.06 respectively. Genetic variance (heritability) for all traits are generally small, in consistent with those summarized by Bradford (1985) ranging from –0.15 to 0.5 with a mean 0.1. This study shows total kilograms lamb weaned per ewe, number of lambs born and weaned per ewe are more influenced by environment (90%).

A greater progress has been achieved in the upward direction (HL) in genetic effects of all traits than downward direction (LL). The greater progress in HL has been shown by magnitude of regression on year of dam birth.

Response to selection per year for both phenotypic and genetic effects of total kilograms lamb weight weaned per ewe should be measured by taking difference between selected lines and control line. However, to remove non genetic effects from selected lines was not easy, because the CL changed and tended to increase at a rate similar to HL due to a changing number of lambs weaned in CL as well. Therefore, it was not easy to explain the response to selection by taking the difference between HL and CL. Response to selection for number of lambs born is easier to measure because the CL was more constant.

Selection for reproduction rate resulted in genetic increase of 1.0 lambs born per 100 ewes exposed per year and 1.14 lambs born per 100 ewes lambing per year . Selection for reproduction rate resulted in genetically increase of 0.2 lambs weaned per 100 ewes exposed per year and 0.01 lambs weaned per 100 ewes lambing per year . These results were in reasonably agreement with those summarized by Bradford (1985) that an in increase of 1-2 lambs born per ewe exposed and lambing.

Line is the major source of variation for total kilograms lamb weight weaned per ewe exposed and lambing for both genetic and phenotypic effects. The age of the dam is the major source of variation in phenotypic effects for both number of lambs born and weaned per ewe, but for in genetic effect is line.

A small increasing in total kilograms of lamb weaned per ewe resulted from selection for reproductive rate. Total kilograms of lambs weaned is mostly influenced by number of lambs weaned and lamb growth rate which is more affected by mother ability. Results show there is a greater number of lambs weaned resulting from selection for reproductive rate. However, it needs further study for lamb growth rate as correlated response to selection for reproductive rate in this Rambouillet population.

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