



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: $I = \text{no. lambs born} / (\text{age of ewe} - 1)$ 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.

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KILOGRAMS OF LAMB WEANED PER EWE IN RAMBOUILLET SHEEP

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Lisa Praharani

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This thesis has been read by each member of the thesis committee and has been found to be satisfactory regarding content, English usage, format, citations, bibliographic style, and consistency, and is ready for submission to the College of Graduate Studies.

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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: $I = \text{no. lambs born} / (\text{age of ewe} - 1)$ 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 (lambled or not lambled), 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 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).

McGuirk (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, 1996). 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 N_e 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:

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

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 decrease 1.6 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 Ozkutuk (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 (Ricoardeau 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 anestrus 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 (Burfenig 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 (UK)		High	1.86	1-2%	Anderson and Curran(1990)
		Control	1.63		
Romney (NZ)	1948-1972	High	1.62	1.5%	Clarke (1976) Wallace (1964)
		Control	1.22		
		Low	1.13		
Merino (AU)	1954-1972	High	1.70	2%	Turner (1978)
		Low	1.18		
Merino (AU)	1965-1975	High	1.22	0.4%	Mann et al. (1978)
		Low	1.20		
Merino (AU)	1959-1973	High	1.52	1.3%	McGuirk (1976) Atkins (1980)
		Control	1.32		
Galway (IR)	1963-1981	High	1.67	1.8%	Hanrahan (1982) and Timon (1978)
		Control	1.32		
Targhee (US)	1963-1981	High	1.39	1.5%	Bradford (1981)
		Control	1.24		
Rambouillet (US)	1968-1986	High	1.43	1.3%	Schoenian and Burfening (1990) Burfening et al. (1993)
		Low	1.04		
		Control	1.33		

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

