



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

A thesis submitted in partial fulfillment of the requirements for the degree of Master of Science in
Animal Science

Montana State University

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Abstract:

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

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

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

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

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

by

Susan Gail Schoenian

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ABSTRACT

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

INTRODUCTION

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

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

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

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

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

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

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

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

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

LITERATURE REVIEW

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

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

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

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

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

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

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

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

Components of Reproduction

Ovulation Rate

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

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

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

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

Embryo Survival

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

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

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

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

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

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

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

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

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

Methods of Effecting Genetic Change in Reproductive Rate

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

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

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

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

Selection for Reproductive Rate

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

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

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

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

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

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

