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Composite Trait Selection for Improving Lamb Production

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Introduction

When the value of wool is low, as at present, there is a greater potential for increasing both biological and economic efficiency of sheep production through improvement in meat production. It has been suggested that biological and economic efficiency can be increased more through genetic selection for improved reproductive rate than in growth rate or body composition (Fogarty et al., 1982). Reproductive rate is the most important component of total litter weight, which is clearly the single most important economic trait in American commercial sheep production. Loss of the Wool Incentive Program and lower wool prices in recent years have increased the economic importance of the total litter weight weaned per ewe. Current farm prices for wool and lamb indicate gross income from lamb exceeds that from wool by up to sixteen fold for most commercial producers of western white faced sheep. Hence, genetically increasing marketable litter weight per ewe is one of the most important contributions genetics can make to the economy of the sheep industry.

Increases in litter weight weaned can be made quickly through crossbreeding especially with prolific breeds. However, introduction of new breeds, often exotic, can result in unadapted genotypes with or without other desirable characteristics. Also, after crossbreeding has been thoroughly exploited, the only recourse for continued genetic progress is via selection for genetically superior individuals within breeds or crosses. It is important, therefore, to determine the relative effectiveness of alternative selection procedures for improving litter weight weaned.

The trait, litter weight weaned, is a composite trait affected by the expression of several genetically influenced traits. Variation in these component traits contributes to the phenotypic variation in the composite trait. Litter weight weaned is a combination of several different aspects of ewe reproduction (fertility, and litter size), ewe viability and offspring growth rate (mothering ability, milking performance, lamb survival, lamb growth rate). Thus, it is a convenient biological and economic measure of ewe productivity (Martin and Smith, 1980; Ercanbrack and Knight, 1985).

Long term selection for a composite trait may (but not necessarily) improve each individual component trait. Component traits within a composite trait should not be expected to improve at the same rate because they may differ in the genetic parameters involved. However, selecting for a composite trait should result in a balance among the component traits that produces an adapted animal, while selection for an individual trait can result in a reduction in adaptability. For example, selection response for a non-composite trait such as ovulation rate in sheep may be positive but gains in ovulation rate can be offset by decreased embryo survival (Bradford, 1985). Similarly, selection for increased litter size at birth may not be accompanied by increased milking performance and lamb growth rate. There may be limiting factors associated with favorable major genes such as the Booroola (FecB) allele which increases ovine ovulation rate substantially. While the FecB allele will increase litter size, there are associated decreases in lamb survival and weaning weight (Willingham and Waldron, 2000).

Direct selection for the composite trait of litter weight weaned in mice was three times as effective as selection for litter size for increasing litter weight weaned (Luxford and Beilharz, 1990). Long term selection in Targhee sheep for individual lamb weaning weight, rather than total litter weight weaned, resulted in decreases in lamb survival to weaning and ewe fertility (Bradford et al. 1999). From this last study, it is obvious that single trait selection for growth rate to weaning can improve weaning weight but it does not necessarily increase total lamb production per ewe. Thus, litter weight weaned per ewe exposed is the most appropriate composite trait to be used in selection for increasing total lamb production. The objective of this review is to characterize the composite trait litter weight weaned and its component traits.

Review

Limitations to increasing litter weight weaned. Breeders should be mindful that genetic change in animal production results in a biological change of the animal, often requiring a corresponding change in nutritional and management inputs. The upper limits for genetic improvement of a trait are generally determined by the nutritional and management constraints within a production system. In a selection study to increase weaning weight in Targhee sheep in two different environments (range vs irrigated pasture-feedlot) genetic improvement was significantly greater in the better environment (Lasslo et al., 1985).

In relation to litter weight weaned, consider the extensive production situations identified by Bradford (1985). An extensive production system may have limited forage availability with nutritional supplements being scarce or uneconomical and limited labor at lambing. Under a limited extensive system, the goal for increasing litter weight weaned may be restricted to production of only one lamb per ewe with satisfactory growth. However, under an improved extensive production system with better forage availability, especially in the early spring and summer, the litter weight weaned may be greatly improved with multiple births, increased milk production, and improved lamb growth. Thus, it is important for the sheep breeder to recognize environmental potentials and limitations for genetic improvement. In theory, selection response for the composite trait litter weight weaned under any production system should result in an adapted and biologically balanced ewe because she has been selected for her genetic potential to raise a lamb(s) to weaning in that environment, and the component traits of litter weight weaned have changed appropriately for the environmental conditions.

Selection Response for Litter Weight Weaned. A significant selection study for litter weight weaned was conducted at the U.S. Sheep Experiment Station in the years1976 to 1988 (Ercanbrack and Knight, 1998). Selection occurred under western range conditions that included shed-lambing, spring grazing of sagebrush-grass-forb pastures, and summer grazing of mountain range at elevations of 2,000 to 2,900 meters. Selection lines were established in four breeds of sheep (Rambouillet, Targhee, Columbia, and Polypay). Ewes were selected on their lifetime average litter weight weaned and rams were selected on the basis of their dam's record for this trait. Response was positive during the 12 years (1976 - 1988) of selection. Non-selected random bred Rambouillet and Targhee control lines were maintained during the study; the average of these two lines was used for estimating environmental trends. Tables 1 and 2 indicate the phenotypic and genetic responses, respectively, for reproduction and body weight.

Phenotypic trends (Table 1 and Figure 1) were positive for reproductive traits and body weight. Modest increases in phenotypic trends in the control lines indicate improvements in management and(or) environment over the time period. Genetic improvement (Table 2) was generally positive for all traits. Genetic improvement for litter weight weaned averaged 0.69 kg per year. For a flock of 100 ewes this represents an annual increase in marketable lamb of 69 kg. Over a 12 year period, selection for litter weight weaned resulted in a genetic improvement of 8.28 kg/ewe. The economic consequences of selecting for litter weight weaned during this period was a total annual increase in gross value of production per ewe of $21.51 for phenotypic improvement, which reflects the effects of environmental improvement, and $11.40 of which could be attributed directly to genetic gains through selection for litter weight weaned (Ercanbrack and Knight, 1998).

Selection responses for litter weight weaned in all four breeds in this study were positive and significant. However, breed differences in response to selection for litter weight weaned were observed (Ercanbrack and Knight, 1998). Improvements for reproductive traits were less in the Polypay than in the other breeds despite its outstanding superior means for litter weight weaned. The rate of response to selection in the Polypay was negligible during the early years of the experiment but increased after 1984 (Figure 1). At the beginning of this selection study in 1976, the Polypay breed was a newly created breed and several F2 and F3 generation ewes were still present in the flock. The delayed response to selection for litter weight weaned in early generations was examined by Snowder et al. (1996) who reported that at least three generations were necessary to overcome the loss of reproductive performance due to decreased heterosis and recombination loss. Thus, response may be lower in the early years of selection in a newly created composite.

Breed differences for litter weight weaned clearly exist. Shrestha et al. (1992) characterized litter weight weaned in five purebred and two crossbred Canadian breeds under intensive management systems. Litter weight weaned at 91-d postpartum ranged from 47 to 67 kg. The Rideau breed weaned the heaviest litters and the lightest litters were weaned in the Suffolk breed. Although the Finnsheep breed had the highest level of prolificacy (219%), average litter weight weaned (53 kg) was less because lamb growth rates to weaning were lower than for the other breeds. Because of the significant economic differences among breeds for litter weight weaned, individuals entering the commercial sheep production industry should consider breed differences for litter weight weaned when selecting a breed.

Breed specific heritability estimates for litter weight weaned per ewe exposed are low. Martin et al. (1981) reported heritability estimates for litter weight weaned for different ages at weaning in a composite breed in Scotland (0.07 at 4 wk, 0.10 at 8 wk, and 0.14 at 12 wk). Heritability estimates for litter weight weaned for four US breeds at 120-d postpartum varied (Rambouillet, 0.11; Targhee, 0.08; Columbia, 0.02; and Polypay, 0.00; Bromley et al., 2001). Low heritability estimates for a complex trait such as litter weight weaned are expected because the trait is subjected to numerous environmental influences from breeding to weaning. The repeatability for litter weight weaned at 120-d postpartum in four breeds ranged from 0.10 to 0.16 suggesting significant temporary environmental influences on this trait (Bromley et al., 2001). Although the heritability for litter weight weaned is low, the genetic improvement observed in the flocks at the U.S. Sheep Experiment Station indicates the trait responds positively to selection and at a level of economic significance (Ercanbrack and Knight, 1998).

The reason for the positive selection response of this low heritability trait can be explained by examining the three factors influencing selection response: heritability, selection differential and phenotypic variation. The product of these three factors determines selection response. Response to selection for low heritability traits can be significant if the trait has a large phenotypic variation and(or) the selection differential is large. The phenotypic variation for litter weight weaned is large. The coefficient of variation is a statistical value (standard deviation divided by the mean) used to compare variation among different traits. The coefficient of variation for litter weight weaned at the U.S. Sheep Experiment

Station is approximately 50% (Bromley et al., 2001). The coefficients of variation are lower for fertility (35%), prolificacy (36%), weaning weight (19%), and grease fleece weight (23%) in the same population (Bromley et al., 2000). Consequently, the selection response for litter weight weaned can be significant even with a low heritability. More importantly, the greater economic value for each unit increase in litter weight weaned justifies selection for this trait (Ercanbrack and Knight, 1998).

As previously discussed, selection for a component trait of litter weight weaned may or may not result in a favorable correlated response in litter weight weaned. After 30 yr of selection for 120-d weaning weight in Targhee sheep in California, total phenotypic improvement of litter weight weaned was 6.5 to 7.1 kg but less when selection emphasized multiple births (4.5 kg; Bradford et al., 1999), while direct selection for 120-d litter weight weaned in four breeds in Idaho had an average phenotypic improvement of 15.8 kg in only 12 yr (Ercanbrack and Knight, 1998).

Improving selection response for litter weight weaned. Because litter weight weaned is a sex-limited trait with a low heritability, the accuracy of selection can be improved by considering more information on breeding individuals. This can include records on relatives and multiple observations on a single individual. Martin and Smith (1980) reported that by adding records on the dam and paternal half sibs to those of the ewe increases the rate of genetic response by 10 to 50% for litter weight in sheep. The genetic analyses used in the National Sheep Improvement Program utilize modern statistical approaches that could optimize selection response for litter weight weaned. Another approach to enhance selection response for low heritability traits is to increase the selection differential by maximizing the number of offspring from high performing ewes with multiple ovulation and embryo transfer in a nucleus breeding scheme (Teepker and Smith, 1990).

A potential difficulty in selecting for litter weight weaned is the level of record keeping necessary to optimize selection. This requires proper identification of pedigree relationships and weighing of lambs at weaning. This is not possible in most commercial production systems. However, commercial producers may be able to identify and select rams from ewes that have a history of weaning heavy multiple birth lambs. Another alternative would be to purchase purebred rams with high breeding values for litter weight weaned as reported by the National Sheep Improvement Program.

Although the purpose of this review is to discuss the advantages of using selection to improve the litter weight weaned per ewe, crossbreeding can be an effective breeding tool and should also be considered. It is well established that crossbred ewes exhibit heterosis for fertility and prolificacy rates which contribute to litter weight weaned. However, no studies on crossbred ewes were found which directly report litter weight weaned. Another consideration would be the production of terminal crossbred lambs that are known to exhibit heterosis for lamb survival and pre- and post-weaning growth (Mavrogenis and Louca, 1979; Malik et al., 1980; Sheridan, 1981; Young et al., 1986). Crossbreeding does not result in permanent genetic improvement in litter weight weaned unless direct selection for retained heterosis is practiced following crossbreeding.

Maternal genetic effects on litter weight weaned. Maternal behavior or maternal genetic effects have long been known to influence the pre-weaning growth of their offspring. Improvement of maternal behavior should be associated with an increase in litter weight weaned. Alexander (1988) in a review of maternal behavior described how maternal effects influence lamb survival and growth as observed in the dam's nesting, parturition, grooming of the newborn, suckling behavior, bonding, spatial association with the offspring, defense against predators, and care of multiple births.

The maternal genetic component of a trait is described by the estimate of maternal heritability. The 40-d weaning weight of crossbred Romanov lambs has an estimated 0.25 maternal heritability (Maria et al., 1993). Maternal genetic effects on lamb growth rates tend to diminish with increasing age of the lamb as evidenced with decreasing maternal heritabilities from birth to increasing weaning age (0.22 to 0.01, Maria et al.,1993; 0.30 to 0.07, Nasholm and Danell, 1996). Some negative genetic correlations between maternal and additive effects for weaning weight have been reported but these varied greatly with the statistical models used in their prediction (Burfening and Kress, 1993).

The correlation between additive genetic and maternal effects for weaning weight can be large (r_g = 0.76, Nasholm and Danell, 1996). Also, the correlation between the additive genetic effect for rate of gain from birth to 120-d weaning with the maternal effect for litter size at weaning can be significant in some breeds (r_g = 0.51 for Columbia, r_g = 0.95 for Rambouillet, and r_g = 0.36 for Targhee; Bromley et al., 2000) but not all (r_g = 0.03 for Polypay). Therefore, increases in lamb weaning weight and total litter weight weaned may be associated with genetic improvements in maternal behavior.

The positive relationship of maternal behavior and litter weight weaned has also been observed in mice selection studies. Postnatal maternal performance in mice did improve significantly when lines were selected solely on litter weight weaned (Wilkinson,1986). Selection only for litter size at birth in mice was not accompanied by improvement of postnatal maternal performance, resulting in a negative estimated phenotypic relationship between numbers born and mouse pup weaning weight (Luxford and Bielharz, 1990).

Contribution of component traits to litter weight weaned. Ercanbrack and Knight (1998) estimated the average annual relative contributions of component traits to genetic change in litter weight weaned over 12 yr for four breeds (Table 3). They found that 37% of the genetic improvement in litter weight weaned was attributed to prolificacy, 27% to number of lambs weaned, 17% to lamb weaning weight, 12% to fertility, and 7% to ewe viability. Improvements in these traits occurred simultaneously during selection for litter weight weaned, both phenotypically (Table 1) and genetically (Table 2). These approximations of component relative contributions have also been confirmed by other studies of the biological differences between the Targhee line selected for litter weight weaned and the Targhee non-selected randomly bred control line at the U.S. Sheep Experiment Station. Improvement in litter weight weaned occurred through at least three biological events: 1) increased ovulation rate and number of live lambs born (Stellflug et al., 1994), 2) heavier lamb weaning weights (Head et al., 1995), and 3) increased pregnancy rate in ewe lambs (Westman, 1993).

Correlated and biological changes in sheep selected for litter weight weaned. Comparative studies of Targhees selected for litter weight weaned compared to a random bred control line have identified significant biological differences (Head et al., 1995, 1996a, 1996b). As previously described, Ercanbrack and Knight (1998) reported increases in fertility, prolificacy, number of lambs weaned, and lamb growth in sheep selected for litter weight weaned compared to control lines. In the selected line, daily milk production increased 13% and lamb weaning weights increased 7% compared to the control line (Head et al., 1995). Similar increases in milk production (10%, Pattie and Trimmer, 1964; 12%, Hinch et al., 1989) were observed when selecting Merino sheep for increased individual lamb weaning weights. Brown et al. (1987), reported increases in peak milk yield of 10 and 29% in two lines of Targhees selected for individual weaning weight. Increases in milk production from the Targhee selected lines at the U. S. Sheep Experiment Station were associated with higher concentrations of growth hormone than control ewes (Head et al., 1996a). The major functions of growth hormone are increased lipolysis, diabetogenesis, protein accretion, bone growth, gluconeogenesis, mammogenesis and galactopoiesis (Bauman and McCrutcheon, 1986). Therefore, the higher growth hormone concentration in the selected line infers the potential presence of other biological differences yet to be identified.

Lamb survival rates may also increase as a result of selecting for litter weight weaned. Litter weight weaned is moderately genetically correlated with neonatal survival rate (r_g = 0.49) but this correlation is large for postnatal survival to weaning at 42 d postpartum (r_g = 0.91; Fogarty et al., 1982). Twin lambs from a Targhee line selected for litter weight weaned had faster growth rates to weaning when compared to twin lambs from a control line (Head et al., 1995). The faster growth rates of the lambs from the litter weight weaned selection line were partially attributed to higher milk consumption and increased levels of dry matter intake (forage). However, post-weaning performance for gain, feed intake and carcass characteristics were similar among lambs from selected and control lines (Head et al., 1996b). The effects of selection for litter weight weaned do not appear to influence post-weaning gain or carcass characteristics. Similar observations were made in Australian Merino sheep selected for high and low weaning weight where selection had no effect on mature muscle-weight distribution (Perry et al., 1988) or adipose volume (Thompson et al., 1988).

Selection for litter weight weaned should also increase ewe fertility. The genetic correlation between litter weight weaned and ewe fertility is positive and large (rg = 0.58; Fogarty et al., 1982). Genetic improvement in litter weight weaned was associated with genetic improvement in ewe fertility rates (Ercanbrack and Knight, 1998). Ewe lamb fertility in the Targhee lines selected for litter weight weaned was 40% (21 percentage units) higher compared to the control line (Hatfield and Stellflug, 1996). It is not known if selection for litter weight weaned will decrease the age at puberty. Selection solely for litter size in Targhee sheep did not decrease age at puberty (Li et al., 1992).

Mature size should be expected to increase with selection for increased lambing performance. Genetic correlations between ewe body weight and lamb weaning weight are positive (Shelton and Menzies, 1968; Stobart et al.,1987; Nasholm and Danell, 1996). Large genetic correlations between ewe mature size and lamb weaning weight (r_g = 0.85, Nasholm and Danell, 1996) or total litter weight (r_g = 0.58 to 0.88, Martin et al., 1981) have been reported.

In the selection study of Ercanbrack and Knight (1998), they observed phenotypic and genetic increases for ewe mature size in all breeds selected for litter weight weaned (Table 1 and 2). This positive correlated response infers selection favored larger ewes more adapted to the nutritional environment under which they were selected. A positive relationship between litter weight weaned and body weight was also reported in mice (Luxford and Beilharz, 1990). Mature ewes selected for litter weight weaned were heavier at breeding and during lactation than control ewes. This was also observed for the body weights of selected ewe lambs which were 4.5 kg or 14% heavier at breeding than control ewe lambs. This increase in body weight does not appear to be related to forage intake expressed as a percent of body weight because this did not differ between Targhee selected and control lines (Head et al., 1995).

Increasing mature body size may have some disadvantages. Although increases in body weight that occur during selection for increased litter weight weaned may be related to adaptability to a production system, ewes of larger mature size will have greater requirements for nutrients and therefore, be more sensitive to environmental factors affecting nutrition such as drought or increased feed costs. Larger ewes are also harder to handle at shearing and lambing.

Increasing litter weight weaned will affect wool production. Pregnancy and lactation have a negative phenotypic effect on wool growth (Corbett, 1979; Shelton, 1998). Increases in litter size and lactation will positively affect litter weight weaned. Twin pregnancies reduce grease fleece weight by 4% compared to a single lamb pregnancy (Ray and Sidwell, 1964) and suckling of twins for 20 wk reduces grease fleece weight by 5 - 8% compared to suckling single lambs (Corbett, 1979). The general cause for the negative phenotypic relationship between lamb and wool production has been attributed to competition for nutrients (Shelton, 1998). The genetic correlation between wool and reproduction tend to be small and negative (Fogarty, 1984). However, these values range from negative to significant positive values (Shelton, 1998). Significant negative genetic correlations between reproduction and wool, ranging from -0.25 to -0.78, have been associated with environments limiting in feed resources and variation in age of ewe at lambing (Shelton, 1998). In more favorable environments, the genetic correlation may be negligible. Ercanbrack and Knight (1998) reported negligible changes in wool production (grease fleece weight and wool grade) after 12 yr of selection for litter weight weaned. Also, the genetic correlations of litter weight weaned with wool traits in this same flock were low (r_g = -0.07 for fleece weight, r_g = 0.02 for fleece grade score, and r_g =0.03 for staple length; Bromley et al., 2001). Other studies have reported small negative genetic correlations between the number of lambs weaned and grease fleece weight, approximately -0.30 (Shelton and Menzies, 1968; Snowder and Shelton, 1988). The effect of selection on litter weight weaned should have little effect on wool production.

Conclusions

Increasing profitability of a sheep enterprise can be accomplished by several means including genetic improvement of the breeding stock. When selection is practiced to increase profitability, it must focus on the most economically important trait for that production system. Typically, many commercial sheep producers sell lambs by their live weight shortly after weaning; thus, litter weight weaned is the most important economic trait. Direct selection for litter weight weaned will result in significant genetic improvement in most breeds. During selection, component traits contributing to litter weight weaned should favorably respond, with an appropriate balance among components.

Indirect selection for litter weight weaned by selecting for a component trait such as litter size born or lamb weaning weight will increase litter weight weaned but at a slower rate compared to direct selection. Also, component trait selection may not be accompanied with improvements in all other component traits related to litter weight weaned; therefore, indirect selection response for litter weight weaned is expected to be less.

It should be noted that the conclusion of relative effectiveness of selection for litter weight or for its components is based on the results of two experiments using each approach. These two experiments were carried out with different stocks and under quite different feeding, management and environmental conditions (Idaho vs California). While the general conclusion on the advantages of selecting for total litter weight seems clear, the limited number of selection experiments infers that the expected magnitude of the difference in response to direct selection for litter weight compared to selection for a component trait is not well estimated.

Implications

Litter weight weaned is the most economically important trait in most lamb production systems in the USA at the present time. Selection for litter weight weaned may result in increase profitability when the environment and management system favor increased reproductive efficiency. It is possible to achieve genetic improvement for litter weight weaned per ewe exposed in excess of 0.5 kg annually. At present market values for feeder lambs, this results in an annual increase of over $1.00 per ewe.

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Table 1. Linear regression coefficients (annual rates of phenotypic improvement) for reproductive traits and body weight

Breed/Line	Fertility, %	Prolificacy, %	Born live, %	Lambs weaned, %	Ewe viability[a], %	Body weight, kg	Net rate[b], %	Litter wt weaned[c], kg
Rambouillet	.84	2.54	.00	.36	.27	.82	2.77	1.24
Targhee	1.49	1.84	.65	.53	.15	.51	3.68	1.38
Columbia	1.81	1.84	.41	1.17	.25	.82	4.08	1.73
Polypay	.46	1.16	.00	.45	.20	1.03	2.19	1.10
Control[d]	.92	.41	.26	.18	.07	.27	1.37	.67

[a] Ewe viability = percent ewes alive at lambing per ewe into breeding
[b] Net rate = net reproductive rate, lambs weaned per ewes into breeding
[c] Litter weight weaned = total litter weight of lambs weaned (120 d) per ewe into breeding
[d] Control is average of non-selected randomly bred Rambouillet and Targhee lines
Source: Ercanbrack and Knight, 1998.

Table 2. Annual genetic improvement[a] among lines selected for litter weight weaned.

Breed	Fertility, %	Prolificacy, %	Born live, %	Lambs weaned, %	Ewe viability[b], %	Body weight, kg	Net rate[c], %	Litter wt weaned[d], kg
Rambouillet	.00	2.14	-.29	.18	.20	.55	1.40	.57
Targhee	.57	1.43	.39	.35	.08	.24	2.31	.71
Columbia	.89	1.43	.15	.99	.18	.56	2.71	1.06
Polypay	-.46	.75	-.26	.27	.13	.77	.82	.43

[a] Genetic improvement estimated by the difference in regression coefficients between selected and control lines.
[b] Ewe viability = percent ewes alive at lambing per ewe into breeding
[c] Net rate = net reproductive rate, lambs weaned per ewes into breeding
[d] Litter weight weaned = total litter weight of lambs weaned (120 d) per ewe into breeding
Source: Ercanbrack and Knight, 1998.

Table 3. Estimated percentage contribution of component traits for genetic improvement in litter weight weaned

Component trait	Percentage
Fertility	12
Prolificacy	37
Percentage lambs weaned	27
Lamb weaning weight	17
Ewe viability	7

Source: Ercanbrack and Knight, 1998.

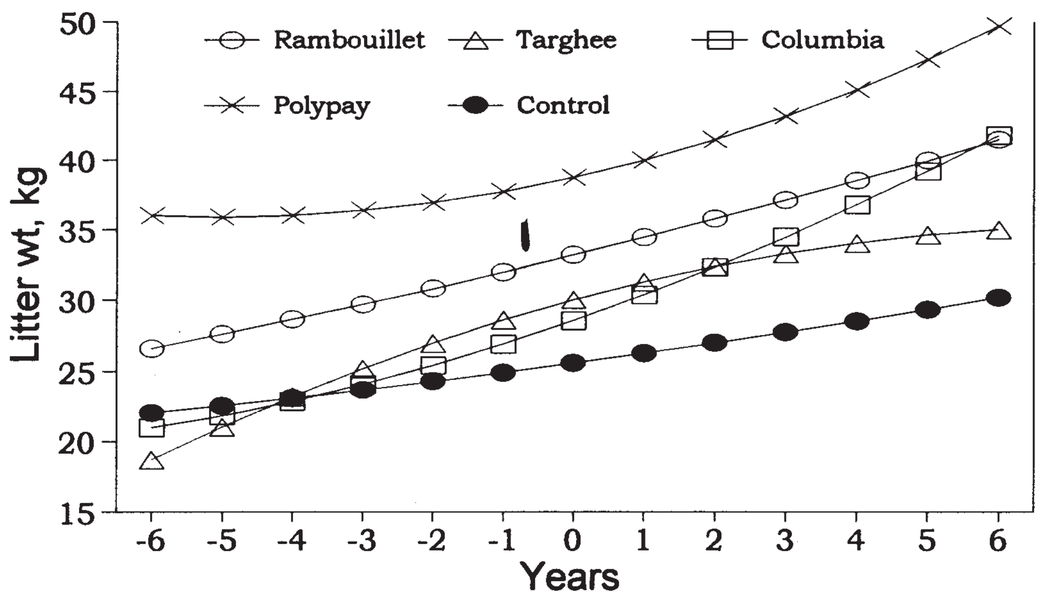

Figure 1. Breed direct response to selection for litter weight weaned expressed as a deviation from the median year (1976 - 1988). Control populations were non-selected randomly bred Rambouillet and Targhee ewes.