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Genetic improvement of overall reproductive success in sheep: A review

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ABSTRACT. Reproduction is an economically important complex composite trait in sheep. Genetic improvement of composite traits can occur by selection for individual components traits, some combination of individual component traits, or by direct selection for the composite trait. This review discusses the responses of selecting directly for litter weight weaned compared to selection responses for one of its component traits. Litter weight weaned is concluded to be a biological selection index determined by environmental factors under which it is selected for. Selection for litter weight weaned can result in a balanced biological composite trait with favorable responses in component traits such as fertility, number of lambs born, lamb survival, lactation, and lamb growth. It is concluded that selection to improve reproductive efficiency under most production and environmental systems would benefit from selection for a composite trait such as litter weight weaned rather than for a single component trait.

Key words: Selection, Litter Weight, Heritability, Genetic Correlation, Composite Trait

Mejoramiento genético de características indicadoras de éxito reproductivo en ovejas. Una Revisión.

RESUMEN. La eficiencia reproductiva es una característica compuesta y compleja de importancia económica en ganado ovino. El mejoramiento genético de caracteres compuestos puede realizarse por selección de un carácter individual que lo constituye, por la combinación de varias características que componen esa variable, o directamente por selección de la característica compuesta. Esta revisión presenta una discusión sobre las respuestas en la selección directa de una variable compuesta como peso de la camada al destete y su comparación con la respuesta de selección por uno de los caracteres que constituyen a esta variable. El peso de la camada al destete es reconocido como un índice de selección biológico determinado por factores ambientales bajo las cuales ha sido seleccionado. La selección para esta característica puede resultar en una mejora con balance biológico, expresado en respuestas favorables en caracteres individuales tales como: fertilidad, número de crías nacidos, numero de sobrevivientes, lactancia, y caracteres de crecimiento. Se concluye que la selección para mejorar eficiencia reproductiva bajo la mayoría de los sistemas de producción y ambiente podría ser mas eficiente sí se selecciona indirectamente utilizando una característica compuesta como peso de la camada al destete en lugar de realizarlo por una característica simple componente de la eficiencia reproductiva.

Palabras clave: Selección, Peso de la camada, Índice de herencia, Correlación genética, característica compuesta.

Introduction

Reproduction is a complex composite trait influenced by many components including puberty, ovulation, estrus, fertilization, embryo implantation, pregnancy, parturition, lactation, and mothering ability. The genetic effect on each component of reproduction varies (Safari *et al.*, 2005). Although component traits of reproduction are under the influence of many genes, a limited number of major

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genes associated with separate components of reproduction have been reported in sheep (Piper and Bindon, 1982; Bradford *et al*., 1986; Davis *et al*., 1991). Expressions of the genetic effects on reproduction are affected by numerous environmental factors such as season, climatic conditions, management, health, nutrition, ram to ewe breeding ratio, age of ewe, and ram libido and fertility. Because genetic and environmental factors interact, genetic improvement of reproduction is very complicated.

Selection for a single component of reproduction such as ovulation rate, litter size at birth or number of lambs weaned has commonly been practiced. However, selection for a single component of a composite trait does not always result in an overall improvement of a complex trait such as reproduction (Snowder, 2002). Improvement in a component trait may be offset by an antagonistic correlated response or a lack of response in a supporting trait such as a failure to increase lactation for larger litter sizes or faster growing lambs.

The objective of this review is to discuss the scientific basis of selecting for overall reproductive success rather than selecting for components of reproduction. Discussion of environmental factors and their association with genetic effects will be limited. The basic assumption is that the purpose of genetic improvement of reproduction is to increase profitability per ewe exposed at breeding.

Defining overall reproductive success.

Genetic improvement of livestock is generally motivated by economics. Economic and biological efficiency of animal production enterprises can generally be improved by increasing reproductive performance (Dickerson, 1970). The most common marketable product of reproduction occurs at weaning when maternal and lamb(s) effects are separated. The end product is a measure of lamb production valued on a weight basis, such as total weight of lambs weaned. Although, value is placed on individual lamb weight or the total weight of lambs, the production unit is the ewe (expressed as per breeding ewe or per ewe lambing). Profitability is strongly associated with genetic improvement of the production unit. Increasing the litter weight weaned per breeding ewe is one of the most important economic contributions that genetics can make to a sheep production system. An exception to this occurs in a few countries where the number of lambs weaned rather than their weight is the unit of monetary value. In this review, total litter weight of lamb(s) weaned is the assumed marketable product.

Although early literature suggested increasing litter size at birth or weaning as the single most useful criterion to improve reproductive efficiency (Clarke, 1972; Turner, 1978), in more recent years the total weight of lamb(s) weaned per breeding ewe has been a reproductive trait of interest (Ercanbrack and Knight, 1985; Lasslo *et al*., 1985, Abdulkhaliq *et al*., 1989). Litter weight weaned per breeding ewe is a convenient biological measure of overall ewe reproductive ability (Martin and Smith, 1980; Ercanbrack and Knight, 1998; Snowder, 2002). The trait is also an economically important composite trait for meat rabbit doe evaluation (Lukefahr and Hamilton, 1997). The trait is affected by the genetic expression of all the component traits of reproduction previously mentioned.

The phenotypic variation of a composite trait is influenced by the level of variability among its component traits and their interactions. Within a production or management system, variation in litter weight weaned among ewes is useful to estimate a ewe's overall reproductive success and her adaptation to that system. Litter weight weaned may be defined as a total life time trait or as a repeated measures trait. Total life time performance may be defined as a mean or sum over a fixed number of opportunities to lamb (Fogarty *et al*., 1994, Cloete *et al*., 2002). Analyzing litter weight weaned as a repeated measures trait is generally most appropriate because statistical adjustment of individual records can be made for age of ewe, year effects, and other significant effects which may include breeding pasture, ram to ewe ratio, etc. Because genotypic expression of litter weight weaned may differ across ages in some breeds, Okut *et al*. (1999) recommended that age of ewe be considered as a part of the trait rather than simply adjust for age of the ewe. When parity or age performance is analyzed over time, the permanent environmental effect of the ewe can be accounted for (Bromley *et al*., 2001, Hanford *et al*., 2003).

Another important statistical adjustment of total litter weight weaned is for gender of lamb(s). High fecundity breeds have large litter sizes varying in gender composition thus creating a significant statistical effect. For example, on average, one out of eight sets of triplets born will be all males or females. Without adjustment for gender, ewes rearing a triplet set of males will generally have significantly heavier litter weights than a ewe rearing a triplet set of all females because of the faster growth rate in male lambs. Since litter weight weaned is a composite trait of a lamb's individual weaning weight and litter size at weaning, it is necessary to adjust for the effect of gender of lambs weaned, without adjusting for the number of lambs weaned. Hanford *et al*. (2003)

addressed this problem by using three covariates that described the proportion of lambs of each gender weaned by the ewe. For example, if a ewe weaned a litter of three lambs, that included two ewe lambs and one intact ram lamb, covariates would be 0 for wethers, 0.33 for ram lambs, and 0.67 for ewe lambs.

Litter weight weaned may also be influenced by fostering of lambs. When the number of lambs born exceeds the number of lambs a ewe is capable of raising, a lamb(s) is often fostered to another ewe capable of rearing the lamb, or the lamb(s) is raised as an orphan, or sold shortly after birth. Most fostering of lambs occurs with first parity ewes lacking sufficient milk to rear twin lambs but such ewes at subsequent parities will usually rear large litters (Snowder *et al*., 2001a). Whether or not to adjust a ewe's litter weight weaned for giving birth to a live lamb that was fostered is a matter for debate. One argument is that litter weight weaned should be limited to lambs born and reared by the birth ewe. The other side of the debate is that the foster lamb is a contribution to the overall production system and the ewe should be given partial credit. Ercanbrack and Knight (1985) credited both the birth ewe and the ewe that reared the lamb with one-half of the weaning weight for a fostered lamb.

A significant variation in the definition of weight of lamb(s) weaned per ewe occurs when age at weaning varies, such as 40-d, 60-d, 90-d, 120-d, etc. Variation in age at weaning is an important consideration because ewes with genetic merit to rear a lamb to 120-d of age may not be genetically desirable as ewes with genetic merit to rear a lamb to 40-d. For example, production systems with ewes and lambs grazing mountain ranges often wean lambs at approximately 120 to 140 d of age; therefore, ewes with extended lactations generally rear heavier lambs (Snowder and Glimp, 1991; Snowder *et al*., 2001a, b). Ewes with extended lactations are not desirable in production systems weaning lambs at younger ages because of increased likelihood of post weaning mastitis and subsequent culling (Powell and Keisler, 1995).

Although weight of lamb(s) weaned per ewe is a sex limited trait, selection need not be limited to ewes. Breeding values of female linked traits for rams can be estimated from their female relatives (Fogarty, 1994; Hanford *et al*., 2002).

Component vs composite trait selection.

Selection for a component trait may be more efficient than direct selection for a composite trait when the component trait has a larger heritability estimate than the composite trait, a larger coefficient of variation, and when the traits are highly correlated. Smith (1967) proposed that differences in response to selection between a composite trait and a component trait can be determined by comparing the products of heritability estimates and coefficients of variation. Using data from Rosati *et al*. (2002), the product value for total litter weight weaned is 6.87 compared to 4.66 for fertility, 3.37 for number of lambs at weaning per ewe exposed, and 1.84 for number of lambs born. Therefore, selection response for litter weight weaned would be greater than the responses expected for its component traits. However, the comparison of economic values of component traits with the composite trait was not considered by Smith (1967). When economic values are considered, the economic advantage of selecting for litter weight weaned compared to one or many component traits is significant.

Predicted selection responses using formulas from Falconer (1989) for litter weight weaned compared to number of lambs weaned parameterized with values from Rosati *et al*. (2002) and an assumed selection intensity of 20% (i = 1.40) were 6.16 kg and 0.09 lambs, respectively. The average weight of lambs weaned in Rosati *et al*. (2002) was 13.5 kg, so the average increase in litter weight weaned after selecting for number lambs weaned is predicted as 1.22 kg, assuming no genetic correlation between litter weight weaned and number of lambs weaned. The overall difference of selecting for litter weight weaned compared to number of lambs weaned is 4.94 kg per generation.

Because of the complexity of reproduction and its many component traits, for some production systems it may be practical to select for a component trait directly influencing the selection objective. If a component trait is the most significant factor affecting profitability then the selection objective should be to improve that trait. For example, selecting ewes to breed out of season may be important to one management system, while selection for early puberty to increase the proportion of ewes lambing at 1-yr of age may be an important breeding objective in a different management system. Certainly, selection for a component trait in some environments or management systems may be more advantageous over selection for a composite trait. This review acknowledges such scenarios often exist and discusses the long term effect of selection for the component trait compared to the composite trait.

Long term selection for a composite trait may (but not necessarily) improve each individual component trait. Three general concepts need to be understood when selecting for any composite trait. First, component traits will not improve at the same rate because they are usually influenced by different genetic effects. Some component traits may not change at all. Second, component traits may not change equally or even similarly among individuals within a population. The more complex a composite trait is, the greater the opportunity for genetic diversity among individuals. Three, in theory, if one of the component traits becomes fixed, then continued selection may place emphasis on other component traits. The latter concept has yet to be investigated with litter weight weaned.

Litter weight weaned is a biological selection index determined by environmental factors under which it is selected for (Martin and Smith, 1980). Selection for a composite trait should result in a balance among the component traits and increase the adaptation of a ewe to the production system. In contrast, selection for an individual component trait may reduce adaptability because it can cause an imbalance among other component traits. For example, selection response for a component trait such as ovulation rate in sheep is positive but improvement in ovulation rate is offset by decreased embryo survival (Fogarty, 1984; Bradford, 1985; Schoenian and Burfening, 1990). Long term selection 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). Whereas, genetic improvement in 120 d litter weight weaned after 12 yr of direct selection was attributed to favorable changes in many component traits (Ercanbrack and Knight, 1998). In the latter study, the contribution of individual component traits attributed to the genetic improvement in litter weight weaned was 37% to prolificacy, 27% to preweaning survival, 17% to lamb weaning weight, 12% to fertility, and 7% to ewe viability. Fogarty *et al.* (1985) reported different contributions of component traits to the proportion of the phenotypic variance for 42 d litter weight weaned: 35% for fertility, 34% for preweaning survival, 14% for prolificacy, 10% for neonatal survival, and 7% for lamb weaning weight.

Often, adverse genetic correlations exist among important component traits. Selection for individual lamb 90-d weaning weight can result in a negative genetic correlated response in ewe fertility in the fall (-0.25, Fossceco and Notter, 1995) and spring (-0.31, Al-Shorepy and Notter, 1996). In mice, selection for litter size at birth increased the number of pups born but had a negative correlated effect on the dam's ability to reallocate body resources for lactation resulting in reduced pup development and increased preweaning mortality rates (Rauw *et al.*, 2003).

Selection for major genes can also create an imbalance among component traits. The Booroola (Fec^B) allele substantially increases ovine ovulation rate but is associated with decreases in lamb survival and weaning weight (Willingham and Waldron, 2000; Gootwine *et al.*, 2006).

Ideally, a selection index with reliable estimates of heritabilities, genetic correlations, and economic weights for all known component traits of reproduction would be a quantitative alternative to selection for total litter weight weaned (Martin and Smith, 1980). Such an index is not practical because it requires measurements on all component traits and, economic weights would have to be estimated for many different production systems. Also, genetic correlations among component traits are often lacking or poorly estimated. The advantage of a selection index approach to improve overall reproduction is that one can control selection to influence all component traits or a number of component traits. The disadvantage of this approach is that artificial control of a complex biological trait may not result in an adapted or robust animal (Knap, 2005). In contrast, single trait selection for litter weight weaned is much simpler because it can be easily measured and animals are selected within a production system.

Another alternative to direct selection for litter weight weaned is tandem trait selection. Tandem selection is generally recommended for selecting traits with adverse genetic relationships but can be applied to composite traits. Response to selection for a single component trait followed by selection for a different component trait can be favorable. No literature related to reproductive traits is available to support this conclusion, however; it is feasible that selection for increased litter size at birth may be followed by selection for increased lactation. Even so, if the overall breeding objective is to increase litter weight weaned, then response to direct selection for the litter weight weaned would be expected to be greater than tandem selection under most environments.

Few studies have directly compared selection for litter weight weaned with its component traits. Selection for litter weight weaned was the most efficient protocol for genetically improving litter weight weaned in four sheep breeds (Ercanbrack and Knight, 1998). They reported that ram selection based on an independent culling level for 15 mo weight coupled with the dam's value for litter weight weaned was only 85% as effective as selection based solely on litter weight weaned. Similarly, selection for early puberty was only 59% as effective and selection on body weight only 67% as effective. In mice, direct selection for litter weight weaned was three times as effective as selection for litter size to increase litter weight weaned (Luxford and Beilharz, 1990).

Heritability of litter weight weaned.

Heritability estimates of most reproductive traits are negligible to low. From the literature, most heritability estimates for litter weight weaned in sheep are low, ranging from 0.00 to 0.29 (Table 1). Average heritability estimates for litter weight weaned from the literature are 0.14 (Fogarty, 1995) and 0.11 (Safari *et al*., 2005). Even when breeds share management and production environments estimates of heritability for litter weight weaned vary among breeds, but are still low ranging from 0.02 to 0.11 (Bromley *et al*., 2001). Similarly, estimates of heritability for litter weight weaned are low to moderate in rabbits (ranging from 0.03 to 0.20, Lukefahr and Hamilton, 1997; Sorenson *et al*., 2001; Iraqi *et al*., 2006) and low in mice (0.08 to 0.09, Eisen *et al*., 1970; Robinson *et al*., 1974).

It has long been established that age and/or parity of the ewe significantly affects reproductive traits, most notably litter size (Haresign, 1985; Waldron and Thomas, 1992), lactation (Torres-Hernandez and Hohenboken, 1980; Snowder and Glimp, 1991; Snowder *et al*., 2001a; Sawalha *et al*., 2005), and litter weight weaned (Ercanbrack and Knight, 1985; Okut *et al*., 1999). A study by Fogarty *et al*., (1985) reported the phenotypic variation in litter weight weaned increased across parities and was accompanied by a greater increase in the variation due to direct genetic effects which resulted in an increase in the heritability estimate. This is in contrast to the findings by Okut *et al*., (1999) who reported heritability estimates for litter weight weaned decreased with age of ewe due to increases in the phenotypic variance. Genetic correlations among age of ewe classes for litter weight weaned were generally greater than 0.80 (Okut *et al*., 1999) inferring similar genetic effects are involved in the expression of litter weight weaned at different ages. Further investigation of the genetic relationships across ages of ewe for litter weight weaned in other prolific breeds may be warranted.

The permanent environmental effect of the ewe for repeated reproductive records across years for litter weight weaned, when expressed as a fraction of the phenotypic variance, is a small but significant effect (Table 1). Safari *et al*., (2005) reported a weighted mean literature estimate of 0.08 for this effect. The small permanent environmental effect of the ewe is likely related to the effect of age of ewe on fertility, litter size, lactation, and mothering ability.

Response of litter weight weaned to selection.

The marketable litter weight per breeding ewe can be increased through genetic selection. Crossbreeding with prolific breeds or the use of purebred prolific breeds are two genetic alternatives. However, genetic progress from crossbreeding and use of purebreds can be constrained unless such breeding schemes are accompanied by selection for genetically superior individuals. The relative response to selection for litter weight weaned has been favorable.

Intensive selection studies for litter weight weaned were conducted for over 20 years at the U.S. Sheep Experiment Station at Dubois, Idaho, USA. The average annual genetic response to selection for litter weight weaned at 120-d postpartum in four breeds (Columbia, Polypay, Rambouillet, and Targhee) over the first 12 years or approximately 5 generations was 0.69 kg per breeding ewe (Ercanbrack and Knight, 1998). Annual response to selection varied among breeds, from 0.43 kg for the prolific Polypay breed to 1.06 kg for the larger and faster growing, less prolific Columbia breed.

After only two generations of selection for litter weight weaned in Hyfer sheep, an Australian composite breed, total litter weight weaned at 6 to 12 wk postpartum was 15% heavier compared to the randomly bred flock (Fogarty, 1994).

Predicted responses to selection for litter weight weaned have been reported. Annual genetic improvement to selection for litter weight weaned was predicted at 0.32 kg of lamb weaned (a 2.9% annual increase) by Fogarty *et al*., (1985) using a heritability estimate of 0.15, a phenotypic standard deviation of 6.3 kg of litter weight weaned per breeding ewe, and a generation interval of 1.75 yr. Greater genetic responses to selection ranging from 10 to 50% were predicted by Martin and Smith (1980). Although heritability estimates for litter weight weaned are low, response to selection can be enhanced by the trait's large phenotypic variation accompanied by intense selection for sire and dams. Selection for number of lambs reared, rather than total weight weaned, in the South African Merino over a 16 yr period resulted in annual increases in breeding values of 1.3% for lambs born per ewe, 1.8% for lambs weaned per ewe, and 1.8% for litter weight weaned (Cloete *et al*., 2004).

In economic terms, an annual response of 0.35 kg to selection for litter weight weaned for a flock of 300 breeding ewes results in a gross increase of 525 kg after 5 yr.

Genetic correlations with litter weight weaned.

The genetic relationships of litter weight weaned with other production traits should be known before litter weight weaned can be recommended as a selection trait. Some of these genetic relationships have been previously estimated (Table 2). The breeds from which these estimates were derived include the Australian Hyfer (a three breed cross of Booroola Merino, Trangie Merino, Dorset; Fogarty *et al*., 1994), the Australian Merino (Cloete *et al*., 2002), a grouping of American

Table 1. Estimates of heritability and permanent environmental effects of the ewe for litter weight weaned

h^2	pe^2	Breed	Lamb age, d	Source
0.29		Rambouillet		Shelton and Menzies, 1970
0.06 ± 0.02		5 pure / 2 composites	42	Fogarty *et al*., 1985
0.27 ± 0.13		Rambouillet		Bunge *et al*., 1990
0.13		Hyfer	42 – 84	Fogarty *et al*., 1994
0.15 ± 0.05		Polled Dorset		Hall *et al*., 1994
0.00 to 0.21	0.03 to 0.26	Columbia	105 - 160	Okut *et al*., 1999
0.05 to 0.08	0.00 to 0.01	Polypay	105 - 160	Okut *et al*., 1999
0.12 to 0.15	0.02 to 0.26	Rambouillet	105 - 160	Okut *et al*., 1999
0.18 to 0.29	0.06 to 0.14	Targhee	105 - 160	Okut *et al*., 1999
0.02	0.10	Columbia	105 - 160	Bromley *et al*., 2001
0.10	0.00	Polypay	105 - 160	Bromley *et al*., 2001
0.11	0.05	Rambouillet	105 - 160	Bromley *et al*., 2001
0.08	0.07	Targhee	105 - 160	Bromley *et al*., 2001
0.05 ± 0.01	0.13 ± 0.02	Merino	100	Cloete *et al*., 2002
0.11	0.05	5 pure / 2 composites	35 - 70	Rosati *et al*., 2002
0.04 ± 0.02	0.11 ± 0.03	Merino	100 - 120	Cloete *et al*., 2004

[a] h^2 = heritability estimate; pe^2 = variance of permanent environmental effects of the ewe as a fraction of total variance.

Dorset, Finnsheep, Rambouillet, Suffolk, Targhee, and two composite lines (Rosati *et al*., 2002) and four American breeds independently: Columbia, Polypay (a four breed cross including Finnish Landrace), Rambouillet, and Targhee (Bromley *et al*., 2001).

Reproductive traits were favorably genetically correlated with litter weight weaned, ranging from 0.41 to 0.99, with the exception of lower estimates (0.10 to 0.19) reported by Rosati *et al*., (2002). Weighted mean genetic correlations from the literature for litter weight weaned with reproductive traits were high: 0.54 for fertility, 0.60 for litter size at birth, and 0.80 litter size at weaning (Safari and Fogarty, 2003; Safari *et al*., 2005). Birth weight was slightly adversely associated with litter weight weaned (-0.22) in the Columbia breed but positive for the three other breeds, ranging from 0.11 to 0.28 (Bromley *et al*., 2001). The genetic relationship between preweaning average daily gain and litter weight weaned was negligible for three American breeds, ranging from -0.07 to 0.07, and slightly positive (0.23) in the Polypay breed.

Subjective milk scores recorded within 24 hr of parturition have high genetic correlations with litter weight weaned at 120 d in four breeds of sheep, ranging from 0.77 to 1.00 (Snowder *et al*., 2001b). However, Sawalha *et al*., (2005) estimated lower

Table 2. Estimates of genetic correlations for litter weight weaned with production traits[a]

Production trait	Fogarty *et al*., 1994	Bromley *et al*., 2001	Rosati *et al*., 2002	Cloete *et al*., 2002
Fertility of ewe	0.92		0.19	
Litter size at birth	0.41	0.42 to 0.65	0.14	0.84 ± 0.06
Litter size at weaning	0.94	0.80 to 0.99	0.10	0.93 ± 0.02
Birth weight		-0.22 to 0.28		
Average daily gain		-0.07 to 0.23		
Grease fleece weight	0.29	-0.56 to 0.19		0.30
Fleece grade[b]		-0.15 to 0.02		
Fiber diameter				0.17
Staple length		-0.11 to 0.08		

[a] All traits measured on the ewe except for the lamb's birth weight and average daily gain.[b] Fleece grade is a subjective visual measure based on the English Worsted Yarn Spinning Count System. Higher spinning counts are associated with finer fiber diameters.

genetic correlations between milk score and litter weight weaned at a younger age of 70 d, ranging from 0.15 to 0.68 for lifetime performance. Nonetheless, the genetic relationship between subjective milk scores and litter weight weaned is favorable.

Generally, wool traits should not be adversely affected by selection for litter weight weaned. Fogarty *et al*., (1994) and Cloete *et al*. (2002) reported a positive genetic association between litter weight weaned and 15 mo grease fleece weight (0.29 and 0.30, respectively). In the American breeds reported by Bromley *et al*. (2001), this relationship with mature ewe grease fleece weight was minor in three breeds, ranging from -0.07 to 0.19, but adverse in the Columbia breed (-0.56). The accuracy of the estimated negative genetic correlation between these two traits in the Columbia breed was questioned by the authors and explained as a possible artifact associated with the small heritability estimate for litter weight weaned in the Columbia (0.02). Weighted means of literature estimates of genetic correlations between litter weight weaned and wool traits were not large: 0.16 for fleece weight and 0.15 for fiber diameter (Safari *et al*., 2005). Estimates of genetic correlation of litter weight weaned with measures of fiber fineness (grade and diameter) and staple length were of minor importance.

Correlated responses of production traits to direct selection for litter weight weaned were reported by Ercanbrack and Knight (1998). After 12 yr of direct selection, the annual genetic change for prolificacy was 0.014 lambs, 0.031 for milk score, 0.018 for number of lambs weaned, 0.124 kg for lamb weaning weight, 0.527 kg for ewe body weight, and -0.005 kg for ewe fleece weight. Overall, correlated responses of long term selection for litter weight weaned were favorable with a negligible effect on fleece weight.

Selection for number of lambs reared rather than total weight weaned over a 16 yr period resulted in a greater vigor in lamb suckling behavior (Cloete and Scholtz, 1998), a significant increase in lamb survival to rearing, improved maternal behavior, and stronger dam-offspring bonding (Cloete *et al*., 2005).

Limitations to increasing litter weight weaned.

Genetic change in animal production results in biological change of the animal. Such biological changes often require corresponding changes in nutritional and management inputs for optimal genetic expression. The upper limits for genetic improvement of production traits are generally determined by the nutritional and management constraints within a production system. Selection for increased weaning weight in Targhee sheep in two different environments (range vs. irrigated pasture-feedlot) resulted in significantly greater genetic improvement 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, litter weight weaned may be greatly improved by multiple births, increased milk production, and improved lamb growth. Thus, it is important for managers 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.

The upper limit for selection response to litter weight weaned in sheep is unknown. In mice, after 17 generations of selection for 12-d litter weight a plateaued response was observed (Eisen, 1972). The plateau in selection response could not be explained by a decrease in fitness or exhaustion of genetic variability. The cause was hypothesized to be due to a small negative genetic correlation between direct and maternal genetic effects.

Summary

Litter weight weaned is a composite trait that can be used as a biological index for selection to improve overall reproductive rate in sheep. Although the heritability of litter weight weaned is low, its large phenotypic variance when coupled with intense selection can result in favorable selection response. Long term selection for litter weight weaned should result in a balanced biological system within the environment and production system selected upon. Although a small negative genetic correlation may exist between litter weight weaned and grease fleece weight, no other antagonistic genetic correlations with litter weight weaned have been reported. Litter weight weaned is recommended as a major trait to select for to increase overall reproductive rate.

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