Phenotypic and genetic evaluation of fitness characteristics in sheep under a range environment

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Dissertation submitted to the faculty of the Virginia Polytechnic Institute and State
University in partial fulfillment of the requirements for the degree of

Doctor of Philosophy
In
Animal and Poultry Sciences

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April 23rd, 2007
Blacksburg, Virginia

Keywords: Ewe Size, Stayability, Heritability, Survival Analysis, Sheep

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ABSTRACT

The objectives of this dissertation were to evaluate genetic and environmental relationships between lamb and ewe traits including body weight, fleece weight and quality, prolificacy, body condition, ewe stayability and lamb survival. Average heritability estimates for lamb birth weight (BWT), weaning weight (WW), maternal weaning weight, yearling body weight, fleece weight, spinning count and staple length were 0.19, 0.09, 0.08, 0.35, 0.38, 0.25, and 0.31 respectively. Heritability estimates for adult traits averaged 0.43 for body weight (AW), 0.13 for body condition (AC), and 0.12 for number of lambs born per ewe lambing (NLB). Correlations between direct additive AW and direct additive and maternal lamb weights ranged from 0.21 to 0.96 ($P < 0.05$) and 0.29 to 0.53 ($P < 0.05$), respectively, with residual correlations ranging from 0.05 to 0.95. Correlations of lamb traits with adult body condition and NLB were generally not different from zero; genetic and residual correlations ranged from -0.52 to 0.69 and -.39 to 0.31, respectively.

Ewe stayability was analyzed as overall stayability (STAYn|2) which indicated the presence or absence of a ewe at n yrs of age, given that she was present at 2 yrs of age, and marginal stayability (STAYn|1-n) recording the presences of a ewe at n yrs of age, given that she was in the flock the previous year. Additive variance in ewe stayability was only found in stayability at 5 and 6 yr of age ($P < 0.05$). Heritability estimates for STAY5|4 and STAY6|2 from multiple trait analyses with other traits averaged 0.08 and 0.10, respectively. Phenotypic correlations between STAY and all other traits were near zero, ranging from -0.04 to 0.03. The estimated correlations between additive effects on STAY5|4 and STAY6|2 and additive maternal effects on WW were positive (both 0.46; $P < 0.05$). Genetic correlations between STAY5|4 and WW, adult weight, and NLB were 0.06, 0.13 and -0.06 ($P > 0.10$), respectively. However, genetic correlations between STAY6|2 and WW, adult weight, and NLB were negative (-0.17, -0.32 ($P < 0.05$) and -0.03, respectively). Significant genetic variation was thus present in stayability, with nonzero genetic correlations present between STAY, maternal milk, WW, and adult weight.

Survival analysis was performed using a proportional hazards model to measure the probability of lamb death before weaning. Lamb survival was recorded as the day of age at death. Records were censored if a live lamb was artificially removed from their litter before death. Fixed effects on survival included ewe age, litter size, sex, and linear and quadratic BWT. Average age of death was 13.7 d. Censoring of records before weaning occurred in 12.9% of the total lambs born. Risk ratios indicated lambs from yearlings and ewes older than 5 yr had the greater risk of death, as did triplet and quadruplet lambs. Linear and quadratic BWT effects on lamb survival were found ($P < 0.05$) and accounted for most of the litter size effects in large litters. The influence of informative censoring was considered by assuming that lambs censored by 3 d of age had died at the time of censoring. Heritability of lamb survival at 3 d of age (estimated using an animal model in MTDFREML) was near zero, ranging from 0.00 to 0.01. The lack of additive variance suggests that improvement in lamb survival should be made through changes in management practices.

ACKNOWLEDGMENTS

I would like to extend a thank you to my advisor, Dr. David Notter. Not only were you a great mentor but your support and respect for me provided encouragement throughout my graduate studies. I value your comprehension of both livestock production and research. I am grateful for all the opportunities you offered, from working with researchers and livestock producer groups throughout the country, to making professional contacts. Thank you for the opportunities to learn from, and work with you.

I wish to acknowledge Dr. Rodney Kott for his involvement in my committee. The data you offered and your knowledge of western sheep production was invaluable toward achieving the goals of my project. I truly appreciated the chance to work with you and your staff as a research associate. You offered a unique opportunity for me to gain a different perspective of the sheep industry and provided many chances to work with producers in Montana.

I would like to thank Drs. Ronald Lewis and Scott Greiner for their willingness to provide thoughtful suggestions and beneficial critiques throughout my graduate work. Both of you were always easy to approach and willing to help with any problem. I thank Dr. Lewis for your dedication to graduate education through the development of specialized courses. I wish to thank Dr. Greiner for support you offered in traveling to meetings and working with both beef and sheep producers in Virginia.

Special thanks go out to my fellow graduate students and friends: Kathryn, Smitha, Scott, and Joe. Your friendship brought a tremendous amount of enjoyment to my time at Virginia Tech. I especially would like to thank past graduate students Larry and Bindu. Both were instrumental in helping achieve my goals throughout graduate school. I would also like to thank the entire APSC faculty, staff, and fellow graduate students for their relations during by time as a student.

I wish to thank my family for the unending encouragement that they have offered during my colligate studies and for always standing behind regardless of how far away I may travel. Finally, I thank my beautiful wife, Kara. Without her sustained support and love, none of this would have been possible.

DEDICATION

To those killed at Virginia Tech on April 16, 2007 and their families, we will not forget.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

Introduction

Fitness characteristics are difficult to measure in practice because they encompass all phenotypic expressions that influence an individual's ability to contribute offspring to the next generation. Falconer and MacKay (1996) discuss the component traits that may influence the overall fitness of an individual with the primary characteristics including survival, reproduction, and maternal ability of the breeding female. Any differences in fitness that are associated with genetic variation in the component traits of fitness are influenced by selection.

In commercial sheep production systems, the importance of fitness relates to the attrition of both lambs and breeding ewes. Therefore, components of fitness that may be recorded include mortality rates, reproductive traits such as fertility, litter size, and number of lambs weaned, or maternal traits like milk production or body size, as they relate to lamb and breeding ewe performance. Both mortality and producer selection decisions are influenced by phenotypic expressions of fitness component traits. Lamb mortality can be attributed to factors that contribute to losses associated with diseases, predation, or competition for postnatal nutrition. Differences in breeding ewe fitness are expressed by early removal from the flock for reasons such as illness, injury, or death, or for producer-imposed reasons that include reproductive failure, poor milking ability, or unthrifty body weight characteristics that may lead to culling prior to the next lamb crop.

When selection of breeding animals takes place, economic factors associated with both market lamb and breeding ewe performance should be considered. Selection decisions that improve the characteristics associated with fitness would add economic returns to the production system by generating more market value through both improved lamb survival and reduced replacement rates for breeding ewes. However, to incorporate aspects of fitness into a breeding objective, data must be available to measure the length of time a sheep stays in the flock in order to obtain estimates of genetic parameters for fitness. Furthermore, any genetic or environmental relationships that exist between sheep fitness and performance should be incorporated into a multiple-trait evaluation program for optimal response to selection for economically important traits in a breeding program.

The purpose of this research is to evaluate those aspects of sheep fitness that are associated with the length of time a sheep stays in the flock. The first objective was to evaluate the phenotypic and genetic relationships between lamb and ewe traits involving body weight, fleece characteristics, prolificacy and body condition to determine what influence selection on lamb traits has on the mature ewe. The second objective was to estimate genetic parameters of different ewe longevity traits and evaluate the relationships between lamb growth, ewe performance and longevity. The third objective was to evaluate environmental and genetic components of lamb morality from birth to weaning using a proportional hazards model to incorporate the cumulative affects of environmental factors on lamb survival.

Chapter 1 Literature Review

1.1 INTRODUCTION

In most livestock breeds, selection has emphasized growth and production characteristics associated with economic gains for the producer and as a result, on-farm data collection programs have been developed for these traits. Although fitness characteristics are also of great economic importance, they typically receive less consideration in breeding decisions because of their strong affiliation with management practices and local environmental conditions. Inconsistent disposal data from on-farm recording schemes, deferred expression of fitness and longevity traits until late in life, and difficulty in clearly separating voluntary versus involuntary culling create challenges for evaluating genetic aspects of fitness. Furthermore, unlike production traits such as weight gain, weaning weight, or prolificacy measures, recording of dead or removed animals does not result in measures directly related to the value of market animals and therefore producers are likely to inconsistently record measures of longevity.

Most survival data in livestock is accessed indirectly from records of production traits. For female breeding stock, the presence of an individual at mating, parturition, or weaning of offspring provides evidence that an animal is still in production. In dairy cattle, survival can be indirectly inferred using frequent milk production records (VanRaden and Klaaskate, 1993); other livestock species have utilized the number of parities (Martinez et al., 2004) or age at last breeding (Brash et al., 1994) to assess fitness. In young animals, survival can be measured more consistently in association with recording of body weights. However, information of the specific age and reason for removal of an individual is rarely available. Additionally, the time required to obtain survival data restricts the use of these measures in most evaluations. Indirect selection for survival requires a careful evaluation of relationships between animal performance and fitness (Cundiff et al., 1982).

The following includes a review of different types of survival data, modeling procedures used for genetic evaluation of survival in livestock, and the relationship between animal performance and survival. Most survival studies have evaluated either the probability of survival of offspring from birth to weaning, slaughter or first parturition, or time intervals between first parturition and the point at which the animal is removed from the system. The first approach includes survival associated with animal and maternal effects on mortality, while the second includes animal effects on mortality or disposal of breeding females.

1.2 MEASURES OF LIVESTOCK SURVIVAL

1.2.1 Discrete data

Conditional measures of stayability have been used to evaluate survival and are recorded as binary variables indicating whether or not an individual is in the system at a fixed point in time (e.g., a fixed age). Stayability measures the probability that an animal stays productive until the fixed point, provided an animal had the opportunity to reach that point. Early genetic evaluations of dairy cow survival used binary measures of stayability to estimate the probability that a cow would stay in the herd for a given number of months (Everett et al., 1976; Van Vleck, 1980). Snelling et al. (1995) evaluated stayability in beef cows as the probability a cow would achieve two, five, eight or 11 calvings before being removed from the herd. Genetic evaluations of swine stayability to a given number of parities have also been presented (Tholen et al., 1996a; Lopez-Serrano et al., 2000; Serenius and Stalder, 2004).

Use of binary data for survival is beneficial if more continuous measures of time of removal are not available (i.e., when information on other recorded traits is used to identify the presence of an individual at a limited number of points in each production cycle). However, this approach may exclude a considerable amount of data from stayability evaluations because censored records are not included. Censored survival data includes records from individuals that have not yet been removed from the system at the time of evaluation. Conversely, uncensored survival data refers to records from those individuals that have been removed for reasons associated with poor fitness prior to the date of evaluation. Hudson and Van Vleck (1981) suggested that early stayability measures (i.e. at 36 or 48 mo of age) could be used to avoid exclusion of large amounts of data and to obtain survival records earlier in life for genetic evaluation. In that study, stayability was evaluated at 36, 48, 56, 72 and 84 mo of age, and genetic correlations among stayability traits measured at different ages ranged from 0.70 to 1.00. Madgwick and Goddard (1989) considered marginal measures of stayability as $S_i = 1$ if the cow survived from i to i +1 yr after first calving, or $S_i = 0$ if the cow did not survive. This approach accounts for marginal effects on survival at specific ages.

Measures of lifetime production can also be used to evaluate the fitness of breeding females. Discrete measures of numbers of lactations or parities by an individual before culling can be used to evaluate the productive life characteristics of an individual. Genetic analyses of productive life measures, such as lifetime number of lactations in dairy cattle (Sewalem et al., 2005), total number of calvings in beef cows (Tanida et al., 1988), or age at last breeding in sheep (Brash et al., 1994) have been used to evaluate survival. However, similar to binary data, discrete traits typically do not include censored survival data.

Discrete survival data has been evaluated with linear models (Hudson and Van Vleck, 1981; Tandia et al., 1988; Brash et al., 1994; Tholen et al., 1996a) even though linear methods ignore the discrete nature of the trait. Hudson and VanVleck (1981) suggested that stayability traits measured later in life may estimate additive variance better because as the frequency of surviving females decreases with age the variance of the binomial trait increases with more equal proportions of each category. However, Thompson (1979) suggested that linear models may not be adequate for discrete data evaluations because unequal incidences of culling among subgroups may violate the assumption of normality. To account for this violation, threshold models have been suggested for genetic evaluation of discrete traits (Gianola and Foulley, 1983) where discrete survival values were assumed to follow an unobserved normal distribution with liability thresholds on the underlying scale that distinguish between categorical groups (Falconer and Mackay, 1996). Heritability estimates from threshold models are expressed on the underlying normal scale, whereas estimates from linear models are expressed on the observed scale. Heritability estimates derived from binary data are a function of the heritability on the underlying scale and the incidence of categorical expression can therefore be transformed to the underlying scale for comparison with estimates from threshold models (Robertson and Lerner, 1949; Dempster and Lerner, 1950).

Mantysaari et al. (1991) created a simulated data set to evaluate genetic parameters of binary traits with linear and threshold models. True parameters were calculated for binary traits in the simulation using underlying continuous variables that were associated with the categorically expressed traits. True parameters were compared with parameters estimated from the linear and threshold models. Bias was measured as the difference between true and estimated variance components, summed over all replicates. Heritability estimates from the observed binary scale were transformed to the underlying normal scale based on equations from Dempster and Lerner (1950). Threshold models showed a slight advantage when data structure was highly unbalanced, meaning that some fixed effect subgroups did not express all categories of the trait when the incidence of expression was assumed to be low (5%). Heritability and correlation estimates between linear and threshold models were similar when compared on the underlying scale if the incidence of trait expression was between 25 and 75%. Discrepancies between true and estimated parameters existed for both linear and threshold models indicating that accurate estimation of genetic parameters is inherently more difficult for binary traits than for continuous variables, but these differences became trivial as the incidence of trait expression increased from very low to intermediate values. Jairath et al.

(1998) found similar results in an evaluation of Canadian Holstein stayability, determining that the less computationally demanding linear model was adequate for estimation of breeding values for survival.

1.2.2 Continuous data

The age or time when an animal leaves the production system can be used to evaluate survival. Continuous measures of time, such as days between birth and death (longevity) or days between first parturition and disposal or death (length of productive life) can be included in genetic evaluations for survival. Continuous measures of longevity have been evaluated in beef (Martinez et al., 2004b), sheep (Conington et al., 2001), and swine (Serenius and Stalder, 2004), and length of productive life of dairy cattle assessed as days in milk or days between first parturition and culling (VanRaden and Klaaskate, 1993; Tsuruta et al., 2005; VanRaden et al., 2006).

The loss of information from censored data can be overcome by projecting measures of productive life for censored individuals. VanRaden and Klaaskate (1993) estimated partial regression coefficients for length of productive life on cumulative months in milk, months in milk for the current lactation, age at first calving, and lactation status to project the number of months a Holstein cow will have milked at 84 mo of age. An additional coefficient was included for the current month of the dry period for cows that were pregnant and not milking at the time of evaluation. With this procedure, all animals were included in the evaluation for productive life. However, projected data is less variable than completed data and received less weight in the genetic evaluations. Projected months in milk at 84 mo of age was adjusted by expanding error variance based on phenotypic variance ratios between completed and projected data and weighted by a factor equal to $(1-h^2)/(x-h^2)$, where x is the expansion factor. This adjustment of projected data was similar to the procedure used for adjusting projected 305-d milk yield for genetic evaluations (VanRaden et al., 1991). More recently, multiple trait evaluation procedures have been implemented to more appropriately account for relationships between productive life and production traits (Weigel et al., 1998; VanRaden, 2001).

Survival analysis models, such as proportional hazard models (Cox 1972), are useful for evaluating non-normally distributed survival time data. Along with incorporating time-dependent variables, survival analysis techniques utilize all censored records to account for the lower bound of survival at a given time of censoring (Kalbfleisch and Prentice, 1980; Allison, 1995; Klein and Moeschberger, 1997). The use of hazard models was adapted to include frailty terms (random variables) for estimation of random effects for livestock evaluation (Smith and Quass, 1984). Ducrocq et al. (1988a,b) demonstrated a procedure for incorporated censored records in a non-parameteric Weibull hazard function that included fixed and random effects to estimate sire variance in length of productive life for daughters of Holstein bulls that were located in New York. When all records within a contemporary grouping were censored, the records did not contribute to the evaluation. However, when both censored and uncensored records were included within fixed effect groupings, the censored records provided useful information on the lower bound of survival for estimation of scale parameters for more precise modeling of the Weibull distribution (Ducrocq, 1997). Censoring was treated as a time-dependent variable along with stage of lactation, herd by birth year grouping, and lactation number in a model similar to:

$$\lambda(t) = \lambda_0(t) \exp\{\mathbf{x}\beta + \mathbf{z}u\}$$

where $\lambda(t)$ is the hazard of a cow being culled at time t given she is alive just before t; $\lambda_0(t)= \lambda\rho(\lambda t)^{\rho-1}$ is the Weibull baseline hazard function with scale parameter λ and shape parameter ρ; t is number of days from first calving until removal from the herd; β contains fixed effects on the hazard with **x** being the corresponding design vectors and **u** the vector of random variables with associated incidence vector **z**. Multivariate frailty models incorporate random effects to account for the association between individual survival times within a subgroup (Klein and Moeschberger, 1997). Procedures for estimating random effects from survival analysis models have been presented (Kalbfleisch and Prentice, 1980; Klein and Moeschberger, 1997; Durcroq and Casella, 1996). Ducrocq and Casella (1996) described Bayesian procedures from Kalbfleisch and Prentice (1980) for estimating sire variance from a frailty model assuming the additive genetic effects follow a log-normal distribution where heritability was calculated as $h^2 = 4$ (sire variance)/($\pi^2/6$ + sire variance).

Vukasinovic et al. (1999) used simulated and real survival data from dairy cows to evaluate the influence that number of daughters per sire and proportion of censored daughter records had on accuracy of breeding value estimates for productive life with a survival analysis sire model. Simulation of 1,000 sires with 10 daughters each resulted in rank correlations between true and estimated sire breeding values that never exceeded

0.50 regardless of the proportion of censored data. However, correlations increased to near 0.80 in scenarios with 200 sires and 50 daughters per bull and 60% censoring. The number of uncensored records directly influences the accuracy of estimated breeding values in a hazards model (Ducrocq, 1997). In survival analyses, accuracy is calculated as $n/(n + (4-h^2/h^2))$ where n is the number of uncensored records. Thus a greater number of uncensored records, or a higher heritability, will result in greater accuracy (Ducrocq, 1997). Vukasinovic et al. (1999) varied the number of daughters and percent censoring. Although a large portion of censored records did not improve accuracy, the authors concluded that high rates of censoring (> 50%) along with sufficient progeny records, did not reduce the accuracy of breeding value estimation.

Ducrocq and Solkner (2000) developed computational software ("The Survival Kit") similar to that described by Ducrocq et al. (1988b) to utilize time-dependent data in genetic evaluation. These time-dependent models have been used to estimate genetic parameters of survival for many livestock populations including dairy cattle (Vukasinovic et al., 2001; Caraviello et al., 2004; Sewalem et al., 2005), beef cattle (Rogers et al., 2004), swine (Serenius and Stalder, 2004), poultry (Ducrocq et al., 2000), and sheep (Southey et al., 2001; Sawalha et al., 2007) as well as to evaluate the incidence of clinical mastitis (Carlen et al., 2005) and fertility in dairy cattle (Schneider et al., 2005).

1.3 LINEAR AND SURVIVAL ANALYSIS MODELS

The computational demands to implement a survival analysis model are much greater than those required for traditional linear models. Sire and animal models can be fitted with available survival analysis software. Animal models may be preferred over sire models for genetic evaluations because of the opportunity to use more pedigree relationships, however, data structure and model assumptions should be considered (Ducrocq et al., 1996). Many dairy evaluations have preferred use of a sire model with survival analysis to avoid small fixed effect subgroups that potentially have no uncensored data. Vukasinovic et al. (1999) compared correlations between true and predicted breeding values in a simulation study were sire pedigree relationships were excluded from a sire-model survival analysis. The authors reported that rank correlations between true and predicted breeding values were similar if the occurrence of censoring was less than 20 percent. At higher levels of censoring, sire relationships were more informative in predicting genetic values for longevity.

Current limitations of survival analysis models include restriction to single-trait evaluations and difficulty in incorporating the relationship matrix for multiple random additive genetic effects (i.e. additive and maternal) (Ducrcoq and Solkner, 2000). Linear models, on the other hand, can easily be used to simultaneously estimate variance and covariance components for multiple traits.

Theoretically, survival analyses with proportional hazards models are superior for estimating variance parameters for survival because they account for non-normal distributions and appropriately incorporate censored data and time-dependent effects on survival to better account for environmental factors (Kalbfleisch and Prentice, 1980; Parmar and Machin, 1995; Klien and Moeschberger, 1997). However, analyses of field data that clearly support these theoretical assumptions are very limited. Breeding values for Jersey bulls for the risk of culling (risk ratio) were estimated with survival analysis and compared to breeding values for productive life (months in milk at 84 mo of age) estimated with a linear model to asses the predictive value of each model (Caraviello et al., 2004a). Risk ratio for predicted transmitting ability (PTA) were expressed as the risk of a sire's daughters being removed from the herd relative to the risk of removal for daughters of an average sire. A risk ratio PTA of 0.95 was interpreted to indicate that the bull's daughters had a 5% lower risk of leaving the herd early compared the daughters of a bull with a PTA of 1.0. Observed heritability estimates were larger for risk ratio estimates (0.18) compared to the linear model (0.07). Correlations between risk ratio and productive life PTA of sires ranged from -0.35 to -0.60 among different data sets, indicating that sires would re-rank with different evaluations. However the superiority of one procedure over the other was not determined.

Caraviello et al. (2004b) concluded that use of both censored and uncensored data in survival analysis provided an advantage for calculating more accurate longevity PTA for young sires, provided enough daughters were tested. Vollema and Groen (1998) likewise concluded that higher accuracy values for PTA of longevity traits were achieved with survival analysis compared to a linear model. Heritability estimates for the scenario with no censored data were not presented, but in the presence of censored data, higher heritability estimates and higher accuracies resulted from more precise modeling of environmental effects associated with longevity traits. Use of censored records only influences estimation of shape parameters which provide inferences about the rate of death for the baseline distribution in the survival analysis. Differences in accuracy from including censored data would only be expected if sire variance was markedly influenced by different shape parameters. For example, if long-lived animals were preferentially censored late in life the inclusion of their records may decrease the expectation of early death (i.e. increase shape parameter). Without including the censored records the baseline hazard function would less accurately fit the true survival function and estimation of individual sire effects would be correspondingly less accurate.

1.4 EFFECTS ON SHEEP SURVIVAL

Survival of sheep is primarily the result of poor health, predation or producer-imposed criteria for removing an individual from the system, although health may also be influenced by management. Lambs are removed because of death, poor health or environmental conditions that put them at a high risk of death if they remain in the system, such as light body weight, large litter size, or poor maternal environment. Decisions to retain breeding sheep in the flock are likewise based on health as well as performance. Livestock survival traits are typically partitioned into early life and adult traits to account for the different environmental and genetic effects on these aspects of survival. Lamb survival from birth to weaning has been analyzed in a number of different populations (Safari et al., 2005), however, the adult ewe survival literature is much more limited.

1.4.1 Early survival

Environment. Mortality at an early age is a major cause of involuntary removal from a flock. Most lamb deaths occur within 10 d of birth (Safford and Hoverland, 1960, Matos et al., 2005; Southey et al., 2001; Sawalha et al., 2007) at a time when environmental changes are extreme for both ewe and lamb. Management practices that provide adequate care, protection from predation, and avoid the spread of disease tend to promote higher survival rates between birth and weaning. Iman and Slyter (1996) presented overall lamb survival rate until weaning for range and farm flocks and suggested that range flocks avoided disease better than farm flocks with resulting survival rates of 88.2% and 78.2%, respectively. Similarly, Southey et al. (2001) showed that lambs reared in a nursery environment had a higher risk of death prior to weaning.

Ewe age. Yearling ewes tend to be less likely to maintain their litter to weaning. Although they have reached sexual maturity, young ewes have not reached physiological maturity and are still growing. Smith (1977) reported that yearling ewes had lambs with smaller birth weight, lower vigor, and higher mortality rates than lambs from older ewes in both purebred and crossbred populations. Ewe age effects on lamb survival have been shown to improve survival with increasing ewe age (Southey et al., 2001; Sawalha et al., 2007), although Brush (1994) and Morris et al. (2000) showed slight decreases in survival of lambs born to ewes greater than 5 yr of age. However, other studies have reported no specific pattern of ewe age effects on lamb survival in ewes that were at least 2 yr of age (Snyman et al., 1998; Cloete et al., 2001). In a subjective measure of maternal behavior at lambing in New Zealand Coopworth, Everett-Hincks et al. (2005) showed a slight increase among ewe age groups in maternal nurturing and litter survival.

Birth type. Ewe prolificacy impacts lamb mortality rates. Lambs born in triplet litters normally have a greater risk of death between birth and weaning compared to lambs born as singles or twins (Smith, 1977; Iniguez et al., 1986; Iman and Slyter, 1996; Morris et al., 2000, Southey et al, 2001; Everett-Hincks et al., 2005). Birth weights are normally less for lambs born in larger litters (Smith, 1977; Iman and Slyter, 1996; Morris et al., 2000; Sawalha et al., 2007) and therefore these lambs may be at a greater risk of succumbing to hypothermia, pneumonia, or other illnesses. Additionally, maternal effects on lamb survival are potentially compromised in large litters because more time is often required for ewes to attend to each of the newly born lambs. However, Everett-Hincks et al. (2005) found that ewes giving birth to triplets had a slight increase in maternal behavior, although most of the ewes with triple litters in that study were mature ewes. Sawalha et al. (2007) reported a higher risk of death at birth for single lambs compared to lambs born in multiple litters, but the risk of death was greater for multiple-born lambs after 1 d postpartum. The added risk for single lambs at birth was attributed to higher rates of dystocia for the larger single lambs. Lambs born to multiple litters may also have higher mortality due to limitations in milk production by the dam, either as a result of low genetic potential for milk production or restricted nutrient intake in limiting environments (Snowder and Knight, 1995; Snowder, 2001).

Lamb sex. Male lambs tend to be larger at birth and have more dystocia problems which can increase both lamb and ewe mortality (Smith, 1977). In survival analyses, Southey et al. (2001) and Sawalha et al. (2007) reported much higher risk of mortality for male lambs compared to female lambs. In a least-squares analysis with fixed effects of birth type included in the model, Iman and Slyter (1996) found no significant difference in lamb mortality between males and females.

Birth weight. Birth weight has been shown to have a quadratic relationship with lamb survival, with higher rates of survival initially associated with increases in birth weight until birth weight eventually reaches a level associated with increased dystocia. This intermediate optimum range for birth weight has been presented in many evaluations of lamb survival (Smith, 1977; Lopez-Villalobos and Garrick, 1999; Morris et al., 2000; Sawalha et al., 2007). Smith (1977) evaluated lamb mortality and concluded that birth weight had a large influence with most early deaths occurring in lambs with birth weights below the mean. Morris et al. (2000) found similar results with a larger portion of dead lambs with light birth weights. Shelton (2002) concluded in a review of lamb survival that underweight lambs were a more serious problem than excessively heavy lambs. Although lamb birth weight has an intermediate optimum, interactions between effects of birth weight and prolificacy on lamb survival may provide an incentive to increase genetic merit for birth weights as prolificacy levels increase.

Environmental effects such as weather and management, as well as other non-genetic effects like ewe age, birth type, litter size, and birth weight have a large impact on lamb survival. In practice, management strategies should be employed when possible to preferentially treat lambs that are born in these unfavorable non-genetic groups in order to reduce the risk of early mortality.

Genetic effects. The additive variance in lamb survival traits is typically small. Heritability estimates for lamb survival reviewed by Safari et al. (2005) ranged from 0.0 to 0.11 and maternal heritability estimates ranged from 0.0 to 0.19. In most evaluations, the maternal additive variance is higher than the direct additive variance, indicating a larger maternal genetic effect on lamb mortality. Everett-Hincks et al. (2005) reported similar results with heritability estimates for single, twin, and triple survival of 0.14, 0.00, and 0.08, respectively, and maternal heritability estimates of 0.11, 0.21, and 0.16, respectively. Variance components estimated with linear models tend to be smaller than those estimated with threshold, logistic, or time-dependent models (Southey et al., 2001; Matos et al., 2005; Sawalha et al., 2007). The assumption of normality in a binomial lamb survival trait is not met, and survival rates within different fixed effect classes may vary considerably. Therefore most evaluations have used link functions or threshold models to account for the distributional characteristics of lamb survival.

Sawalha et al. (2007) reported heritability estimates for survival from a survival analysis of 0.05, 0.20, 0.18, and 0.33 for survival at birth and between 1 and 14 d, 15 and 120 d, and 121 to 365 d postpartum, respectively. Maternal effects were only estimated for survival at birth (0.09) because of computational restrictions of the analyses. Southey et al. (2001) compared heritability estimates from a survival analysis with a sire model and logistic sire and animal models for lamb survival during different time periods. Maternal components were not considered in the sire models. Heritability estimates were nearly twice as large from a survival analysis versus from a logistic sire model; estimates from the survival analysis were 0.21 and 0.15 for survival to weaning age (60 d) and yearling age, respectively. For the logistic animal model, maternal effects were more important than direct effects for survival from birth to weaning.

1.4.2 Adult survival

Breed difference. Ewe survival under range environments was considered when Hohenboken and Clarke (1981) compared breed differences in ewe fitness characteristics in ewes in Oregon born between 1973 and 1974 out of Columbia or Suffolk ewes and sired by Cheviot, Dorset, Finnsheep, or Ronmey rams. The crossbred ewes were managed in either an irrigated pasture or an extensive hill pasture environment. Breed type by environmental interactions were presented for ewe longevity, measured as months of age at culling or death. Cheviot-sired ewes had the shortest longevity on irrigated pasture (51.3 mo); the other sire breeds did not differ. However, under extensive range conditions, Finnsheep-sired ewes had lower longevity (52.8 mo) while Dorset sired ewes had the highest longevity (59.1 mo). Dam breed also affected longevity differently in the different environments. In the more productive irrigated environment, ewes from Suffolk dams were only slightly older than ewes from Columbia dams at culling (56.8 versus 56.5 mo). Conversely, longevity in extensive range conditions was better for ewes from Columbia dams (59.6 mo) than from Suffolk dams (52.4 mo). The energy demand for high growth and milk production in Suffolk crossbred ewes may have contributed to differences in survival in the range environment. The authors hypothesized that differences between Suffolk and Columbia crossbred ewes in foraging activity on poorer quality range may have influenced ewe longevity and concluded that supplementation during late lactation (late summer or early fall) may decrease the difference in longevity between the Suffolk and white-faced ewe breeds.

Breed differences in longevity were also present in a study of reproductive performance of F_1 ewes sired by Dorset, Finnsheep, Montedale, Romanov, or Texel rams from Compsite III (½ Columbia, ¼ Suffolk, ¼ Hampshire) or whitefaced (Rambouillet influenced) ewes (Casas et al., 2004). Least-square means for the percentage of ewes remaining at 42 mo of age indicated that Romanov and Montadale crossbred ewes stayed in the flock longer (76.8 and 76.3 respectively; $P < 0.05$) than Dorset, Finnsheep, and Texel crosses (65.9, 70.5, and 68.7%, respectively). High prolificacy (2.20 lambs per ewe lambing) of Romanov crossbred ewes, along with relatively low lamb mortality, was assumed to be associated with a higher demand for intake energy. However, Romanov crossed ewes weighed less at breeding than the other breed types in the study ($P < 0.05$). Dorset and Montadale crosses were heaviest at breeding (67.9 and 67.7 kg, respectively) but were less prolific than Finnsheep and Romanov crosses. Ewes out of Composite III dams had higher survival rates than ewes out of whitefaced ewes (76.2% and 68.1%, respectively). Prolificacy was the same for the two dam breeds (1.71 lambs per ewe lambing), but Composite III crossbred ewes nursed more lambs per litter than the whitefaced crossbred ewes (1.24 and 1.18 lambs per ewe, respectively). Environmental conditions were the same for all ewes in this study, so issues of breed by environment interactions on survival were not considered. However, given the generally similar survival rates between prolific and less-prolific breeds, environmental restrictions were likely not a factor in this study.

Additive variance. Within-breed selection for ewe survival is only effective if additive genetic variation is present. Pedersen and Lauridsen (2003) estimated genetic parameters for ewe survival traits in a pooled analysis of ewes from 29 Danish sheep breeds as part of the development of a multiple-trait economic selection index. Ewe survival was measured as days in the flock at 1, 3, and 5 yr after birth. Survival was analyzed using a mixed linear model with fixed effects of breed x herd x year, breed x season, and breed x age (for survival at 3 and 5 years), and random animal additive and residual effects. Heritabilities at 1, 3, and 5 yr were 0.09, 0.14, and 0.05, respectively, with corresponding phenotypic standard deviations of 135.6, 429.2, and 676.8 d, respectively. Genetic correlations between survival traits were 0.93, 0.86, and 0.96 between survival at 1 and 3, 1 and 5, and 3 and 5 yr, respectively. Averages for survival times were not presented, but inclusion of all three survival traits in a sub-index for longevity (assuming no correlations between survival and other traits) was predicted to yield an improvement in survival time of 0.6 to 5.0 d per generation for different breeds. Other reported estimates of heritabilities for survival traits are similar to those for Danish sheep. Conington et al. (2001) obtained an estimate of heritability for days of age at the time of removal from the flock in UK hill sheep of 0.08 and Brash et al. (1994) reported a hertitability estimate for age (in years) at last breeding in Australian Dorset sheep of 0.06.

Correlations. Estimates of covariances between survival and other production traits from mixed linear models suggest that phenotypic correlations involving adult survival are typically low. Conington et al. (2001) reported phenotypic correlations between ewe survival and mature size, fleece weight, lamb weight, lamb survival, and five different carcass traits that ranged from -0.09 to 0.10. Brash et al. (1994) estimated phenotypic correlations between ewe survival and fertility and lamb survival traits that were all positive but small, ranging from 0.07 to 0.15 ($P < 0.05$). Genetic correlations involving ewe survival tend to be slightly larger, ranging from -0.35 to 0.35. The authors concluded that index selection would result in improvements in all traits, with an expected improvement in ewe survival of 7.1 d/yr. Brash et al. (1994) reported that no genetic correlations involving ewe survival differed from zero ($P > 0.05$), with the exception of a -1.00 correlation between lamb survival to weaning and ewe survival. Fertility had a positive genetic correlation with ewe survival (0.29), but all genetic correlations between ewe and other lamb survival traits were negative.

Differences between genetic relationships involving ewe survival in different populations are not entirely unexpected. Given the strong environmental influence on culling rates in most production systems, it is reasonable to expect genotype by environment interactions to play a role in these evaluations. Additionally, the Australian Dorset evaluation used data from an elite breeding scheme versus the more extensive management system common for UK hill sheep production. Culling practices undoubtedly differ between these two populations, and genetic relationships between survival and production traits may not be comparable.

Relationships between production level and ewe survival are unclear. Many producers likely remove breeding ewes for a combination of different reasons associated with poor performance rather than establishing specific individual culling criteria. More research is needed in characterizing relationships between growth, fertility, milk production and other traits associated with both voluntary and involuntary culling of ewes.

1.5 CONCLUSIONS

Survival can be thought of as a composite trait that includes characteristics of health, production, and fertility along with other components that influence the decision to remove a ewe from the system. Given the challenges associated with genetic evaluation of survival data, it has been proposed that selection on components of survival may lead to greater genetic improvement of survival, especially if at least some of the component traits are continuously distributed (Cundiff et al., 1982). Additive variance in lamb survival has been detected in most populations that have been studied, and lamb survival data can be obtained relatively early in life, allowing relatively convenient estimation of breeding values for lamb survival. However, indirect selection on component or correlated traits may be more appropriate for improvement of ewe survival given the generally limited availability of ewe culling information and limited documentation of additive genetic variation. However, relationships between ewe survival and other performance traits remain poorly documented, with more research required in order to better characterize these relationships.

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Chapter 2 Phenotypic and genetic associations between lamb growth traits and adult ewe body weights in western range sheep

2.1 INTRODUCTION

Progressive sheep producers use selection as a tool to improve flock profitability by increasing lamb crop value and reducing production costs. Traits of economic importance typically include lamb growth, ewe prolificacy and lamb and ewe wool characteristics, and genetic parameter estimates for these traits have been derived for many breeds (Safari et al., 2005). Selection for these traits can also have indirect effects on other aspects of flock performance. Lasslo et al. (1985) reported an increase in mature ewe size as a correlated response to selection for weaning weight in a western range environment. Herd et al. (1993) reported similar results in a Merino population selected for lamb weaning weight. Changes in mature ewe weight have a direct influence on feed intake and energy requirements for the flock and may also have indirect affects on lamb performance.

Sire selection based on EPD for economically important traits can improve the genetic potential for production, but the effects of such selection on the mature ewe are unclear, in part because of the strong environmental relationships between early growth and mature performance. Additionally, phenotypic selection of larger ewe lambs is common in most management systems, and therefore both environmental and genetic factors influencing the future performance of selected ewes are important. The objective of this study was to evaluate genetic and environmental relationships between lamb growth and adult ewe body weight, body condition and prolificacy to asses the potential impact of selection of replacement females on the mature ewe.

2.2 MATERIALS AND METHODS

The data set included records from 12,154 Targhee sheep born from 2,930 dams and 200 sires between 1960 and 2005 in the Montana State University flock. The flock has been primarily located at the Red Bluff Research Ranch near Norris, Montana and managed throughout the time period as a commercial western range flock. Ranch dynamics are described in Stobart et al. (1986). The annual production system was relatively consistent throughout years. However, forage quality differences from year to year accounted for some of the variation in lamb weight performance. Ewes were bred in Mid-October and November and lambs were typically born in early spring and weaned in fall at an average age of 120 d. The breeding flock was moved to summer range when the average age of the lambs was approximately 45 d (Mid-June). Ewe lambs were bred to have their first lambing at 2 yr of age. Annual shearing occurred prior to the start of lambing in February or March. Ewe lamb selection was based primarily on phenotypic assessment of body weight and wool quality. Ewe lambs retained for breeding were assumed to be selected at the time of weaning and were identified within the data set only by the presence of a lambing record at 2 yr of age. Ewe lambs not selected for breeding were assumed to be sold for market after weaning, sold for breeding prior to their first lambing, or died between weaning and first lambing. Ewes were assumed to be removed from the flock at 6 yrs of age or an earlier age for failure to breed, poor production (i.e., poor body condition or light body weights), or illness and were identified within the data set as ewes with missing lambing records. Ewes that remained in the flock after a missing lambing record represented 1.5% of the lambing data and did not contribute to future data after their first missing record. Specific information about time or reason for removal or death of a ewe was not available.

Body weights, condition scores (**CS**) (1 to 5 point scale with a score of 5 denoting the fattest ewes), fleece characteristics and ewe prolificacy were recorded over the productive lifetime of the ewe. Annual records were collected between 1960 and 2005 for lambs including body weights at birth (**BWT**), approximately 45 d of age (**45W**) (when lambs were turned out to summer pasture), and weaning at approximately 120 d of age (**120W**) in mid-August. Adult traits included body weight at the time lambs were weaned ($\mathbf{PWT}_i$) and number of lambs born ($\mathbf{NLB}_i$). In addition, a subset of this data contained yearling records collected at 12 mo of age for body weight (**YWT**), fleece weight (**YFW**), staple length (**YSL**) and spinning count (**YSC**), 18-mo body weights (**18MW**), and annual adult measures of late-gestation body weights ($\mathbf{GWT}_i$) and condition scores ($\mathbf{GCS}_i$), early lactation (Mid-June) body weights ($\mathbf{LWT}_i$) and condition scores ($\mathbf{LCS}_i$), adult weaning condition scores in August ($\mathbf{PCS}_i$) and adult fleece weight ($\mathbf{AFW}_i$), staple length ($\mathbf{ASL}_i$) and spinning count ($\mathbf{ASC}_i$) (where *i* represents age of ewe at the time of data recording). Body condition scores were recorded by trained evaluators. Typically, more than one evaluator contributed to the recording of condition scores taken through the year. However, each condition score record was the result of one evaluator. Late-gestation body weights were recorded at shearing. When weights were recorded prior to the ewe being shorn the weight was adjusted by subtracting the weight of the fleece from the ewe body weight record. Table 2.1 summarizes the years that records were collected, number of observations and number of sires and dams included in the data set for each measure.

All lambs born were included for the NLB evaluation, however, only lambs carried to full term and > 2.0 kg were included in birth weight evaluations. Lambs aborted or born prematurely were discarded from the BWT evaluation. Lambs not nursing from their birth mother or born in litters of four or more lambs were removed for all evaluations. Age adjustments were made for lamb traits (45W, 120W, YWT and YFW) based on the procedures of Bradford (2003). Data recorded early in life (BWT, 45W, 120W, YWT, YFW, YSL, YSC and 18MW) were considered to be lamb traits while those recorded after 18 mo were treated as adult traits.

Changes in adult BW and CS were calculated as the difference between adjacent weight or body CS records. Changes in BW were calculated for early lactation (**WC1** = $LWT_i - GWT_i$), late lactation weight (**WC2** = $PWT_i - LWT_i$), and during breeding and gestation (**WC3** = $GWT_{i+1} - PWT_i$), and changes in body CS were calculated for early lactation (**BC1** = $LCS_i - GCS_i$), late lactation (**BC2** = $PCS_i - LCS_i$), and during breeding and gestation (**BC3** = $GCS_{i+1} - PCS_i$), where *i* represents the age of the ewe.

2.2.1 Phenotypic evaluation

Least squares means were calculated using procedures in SAS (SAS Inst., Inc., Cary, NC). Effects of year of birth, age of dam, lamb sex, litter size and number of lambs reared were included as fixed effects for all lamb traits. The analysis of adult traits considered fixed effects for year of birth, ewe age, and number of lambs born and nursed during the year of record collection. Day of lambing was additionally included as a linear covariate for GWT, GCS, WC1, WC3, BC1, and BC3 to account for extent of fetal development at the time of data collection.

2.2.2 Genetic evaluation

In the genetic evaluation, multiplicative adjustment factors were used to account for residual effects of age of dam, lamb sex and type of birth and rearing combinations for BWT, age adjusted 45W and 120W, and age of ewe effects for NLB. Lamb records were adjusted to a single ewe lambs basis from an adult (4- or 5-yr-old) dam, and NLB was adjusted to a 5-yr-old ewe base. Adjustment factors for BWT and 120W were obtained from Bradford (2003) for the Targhee breed. Adjustments for 45W and NLB were obtained from the current data only and are listed in Table 2.2. Contemporary groupings for all traits included year of birth and flock management grouping with additional grouping by sex for YWT. Birth dates that were more than 45 d after the first lambing of the season were placed into a separate contemporary group for BWT. Lamb weights and wool records were additionally grouped by day of recording and shearing, respectively. Weight and CS changes during breeding and gestation (WC3 and SC3) were placed in contemporary groups by year of birth, and the number of fetuses carried during the interval was accounted for by including NLB at the next lambing in the model.

In preliminary analyzes, adult weight and CS measures recorded at younger ages were highly correlated with corresponding weights and CS from later years, so adult weights and CS were modeled as single traits with repeated records. Aside from NLB, no preliminary adjustments were made to adult traits, and contemporary groups were assigned based on year of birth. The number of lambs born or the joint effect of number of lambs born and reared was included as appropriate (Tables 2.4 and 2.5) in models of adult BW, CS, and their changes. Preliminary analyses of the covariance between adult traits and NLB included the type of birth and rearing effects on adult traits. However, NLB was adjusted for ewe age effects, and due to a lack of genetic variance within ewe age and birth/rearing groups for NLB the estimated genetic relationships were unreliable between NLB and adult BW, CS, and their changes. To estimate direct additive covariance, the type of birth and rearing effects were excluded from the two-trait evaluation between adult traits and NLB. This evaluation resulted in little change in additive variance estimation in adult traits compared to preliminary analyses.

An animal model was used to analyze all traits. The model included the same fixed effects as previously mentioned. A linear covariate for date of lambing was also included for GWT, GCS, WC1, SC1, WC3 and BC3 to account for fetal growth. All genetic analyses were conducted using multiple trait, derivative-free MTDFREML software (Boldman et al., 1993). Convergence of the solutions was assumed to have occurred when the variance of -2 times the log likelihoods across iterates was less than 1×10^{-9}. Once convergence was attained, analyses were re-started with converged estimates as priors to ensure global convergence. All lamb traits included random additive direct and additive maternal effects with a mean of 0 and variance of $\mathbf{A}\sigma^2_a$ and $\mathbf{A}\sigma^2_m$, respectively, where **A** is the additive numerator relationship matrix and σ^2_a and σ^2_m are additive direct and maternal variances, respectively. For all maternally influenced lamb traits, the additive direct and maternal covariance for trait *i*, as well as the covariance between additive direct effects on lamb trait *i* and additive maternal effects on lamb trait *j* were assumed to be zero ($r_{am} = 0$) (Notter and Hough, 1997; van Vleck et al., 2003). Random permanent environmental effects of the dam were included for BWT, 45W and 120W with mean 0 and variance $\mathbf{I_d}\sigma^2_{pe}$ where $\mathbf{I_d}$ is an identity matrix with order equal to the number of dams and σ^2_{pe} is the maternal permanent environmental variance. The analyses of yearling and 18-mo weights and fleece traits used a reduced model that excluded additive maternal and permanent environmental effects. Adult weight, body CS, changes in weight and condition, NLB, and fleece traits used a model that was similar to that used for yearling traits but with inclusion of a random permanent environmental variance of the animal to account for repeated measures of each trait. A random residual effect with mean 0 and variance $\mathbf{I_n}\,\boldsymbol{\sigma}^2_{\mathbf{e}}$ was assumed for all traits where $\mathbf{I_n}$ is an identity matrix with order equal to the number of records for each trait.

Single-trait analyses were initially conducted for each trait to asses the significance of each random effect. Two-trait analyses were then conducted using variance component estimates from the single-trait analysis as starting values. Each trait was initially analyzed in a two-trait evaluation with 120W to account for potential bias from selection of breeding ewes after weaning. Variance components estimated from the two-trait analyses with 120W were used as priors for additional multiple-trait analyses. Additive direct and residual covariances were calculated for all pairs of adult (*i*) and lamb (*j*) traits. Additive maternal and permanent environmental covariances between traits were also calculated if the final single-trait models for both traits included these effects.

Covariance for additive direct effects on adult trait *i* and direct maternal effects on lamb trait *j* were estimated, however, the software did not permit direct estimation of covariances between residual environmental effects on lamb and adult traits. In multiple-trait evaluations including lamb and adult traits, residual effects for lamb traits were estimated by fitting an independent permanent environmental effect of the lamb and forcing the residual variance of the lamb trait to be zero. The resulting covariances between independent random effects of the animal are equivalent to the covariances between residual effects on lamb traits and permanent environmental effects on repeated adult traits (Rao and Notter, 2000).

Significance of covariances in all two-trait analyses was determined by likelihood ratio tests after fixing each covariance to 0. Three-trait analyses were conduced when two-trait correlations were high or selection bias potentially influenced genetic parameter estimation.

2.3 RESULTS AND DISCUSSION

2.3.1 Phenotypic evaluation

Lamb traits. Least squares means of age-adjusted lamb and yearling traits are listed in Table 2.3. Residual effect of ewe age, type of birth and sex were observed for all lamb weight traits but ewe age had little influence on YWT or 18MW. Effects of birth type were significant for all lamb traits ($P < 0.01$). Single-born lambs were 22.6%, 32.3%, 23.6%, 6.2% and 5.1% heaver than twins for BWT, 45W, 120W, YWT, and 18MW, respectively. Relationships between early lamb growth and BWT were observed. The residual correlation between BWT and 45W was 0.47 ($P < 0.01$) and the regression of 45W on BWT was 1.71 kg/kg. Stobart et al. (1986) likewise reported positive correlations between birth weights and future lamb body weights. Ewe age effects on lamb weight were also significant ($P < 0.01$). Lambs born to 2 yr old ewes weighed less than lambs born to older ewes, with smaller effects of ewe age observed in the oldest ewes.

Phenotypic correlations between unadjusted weaning weight records and adult traits from preliminary analyses were similar to those obtained for fully adjusted 120W. Correlation between 120W and unadjusted weaning weights was not unity, but were high (0.86; $P < 0.05$). This strong relationship indicates that phenotypic correlations between the fully adjusted 120W and adult traits allow reasonable inferences about phenotypic relationships between lamb and adult traits.

Adult traits. Least-squares means for ewe BW and CS are presented in Table 2.4 for different fixed effect categories. In this flock, ewes less than 4 yr old had not yet reached a maximum mean body weight. Bradford et al. (1999) showed that ewe BW continued to increase until 5 yr of age in a group of mixed-breed white-faced ewes managed in a western range environment. Similar results were presented by Stobart et al. (1986) along with a positive phenotypic relationship between weight at 30 mo of age and mature weight of ewes (0.81; $P < 0.05$). In the current data, twin-born lambs weighted less than single-born lambs early in life but this effect was slight in adult ewes ($P > 0.05$). This result is in agreement with Lasslo et al. (1985) who found no effect of birth type on ewe weights after 12 mo of age. It was suggested in that study that lambs born and reared as twins could not express their growth potential early in life because of environmental restrictions associated with limited milk intake in an extensive range system but were able to compensate for that limited growth after a year of age. However, Stobart et al. (1986) reported differences in adult BW of single and twin born ewes and used partial regression analyses to suggest that these differences were attributed to early growth rates rather than dam age effects.

Adult body weights were expected to be higher during late gestation because of associated changes in weight of the developing fetus. Changes in body CS were small between production stages. Differences in body CS are a function of plane of nutrition and the ewe's ability to utilize both feed intake energy and body reserve energy to maintain production given her physiological status (i.e. age, number of lambs born). Least squares means for body condition (Table 2.4.) indicated little change in body fat composition from weaning to late gestation. However, ewes that left the flock after weaning their litter (and did not contribute future records) had significantly lower PCS (2.8 to 3.0) than ewes that remained in the flock for the next lambing (3.2 to 3.3) ($P < 0.05$). These differences corresponded with non-significant differences in PWT between ewes removed from the flock (70.4 kg) and ewes that stayed in the flock for at least one more production year (71.6 kg) ($P > 0.05$). These differences in condition indicate that PCS was a potential factor influencing a ewe's ability to remain productive in the flock.

Body CS were significantly lower ($P < 0.01$) during lactation, indicating that body energy reserves were being allocated for milk production, growth and maintenance of the ewe. Few studies have looked at changes in body condition over different physiological stages. Sanson et al. (1993) suggested that measures of body condition are good indicators of energy reserves based on comparisons of body CS and percent lipid of the carcass in a group of mature ovariectomized western ranges ewes. Ramsey et al. (1998) reported breed differences between Suffolk and Targhee for milk production and weight gain during lactation, with Suffolk's producing more milk and gaining less weight throughout lactation. In that study, ewes showed a decrease in milk production after 50 d postpartum, resulting in more energetically efficient weight gain during later stages of lactation. Results in Table 2.4 indicate higher body weights and condition during late lactation than during early lactation. Snowder and Glimp (1991) showed the same trend for weight gain during later stages of lactation and concluded that improvements in nutritional status may have a greater effect than diminishing milk production on changes in ewe weight prior to weaning.

Correlations between adult BW and CS taken at the same time, and after accounting for birth year, type of birth and rearing, and ewe age effects, ranged from 0.20 to 0.53 (average $r = 0.36$) ($P < 0.01$) resulting in an estimated average increase of 5.6 kg in ewe body weight for each 1-unit increase in body condition score. Sanson et al. (1993)

reported a strong correlation of 0.89 between CS and BW with a 5.06 kg change in weight for each 1-unit increase in body condition score using a 9-point scaling system. Although the condition score scales were different, both studies show a positive relationship between ewe weight and condition, likely associated with changes in energy reserves of the adult ewe.

After accounting for significant fixed effects of birth year, ewe age, and litter size born and reared, least square means for ewe body weight changes (Table 2.5) were –6.72 ±0.47 kg in early lactation (WC1), 4.88 ±0.44 kg in late lactation (WC2), and 0.69 ±0.48 kg during breeding and gestation (WC3). Weight loss in early lactation is a function of fetus weight lost at lambing, mobilization of lipid energy reserves in lactation, and continued structural growth of ewes that have not reached mature size. Two-yr-old ewes had a tendency to lose less weight during early lactation and gain more weight gain during other stages of production, but changes in body weight were more strongly associated with type of birth and rearing than ewe age (Table 2.5). Ramsey et al. (1998) recorded changes in weight from 33 d prepartum to 89 d postpartum and showed losses of -0.03 kg per d between 33 d prepartum and 6 d postpartum and gains of 0.05 kg per day between 6 d and 89 d postpartum for Targhee sheep in a range environment. More weight loss was observed in the current population of Targhee ewes, however, WC1 included a longer period of lactation. Body condition scores tended to decrease in early lactation, increase in late lactation, and remain relatively stable during breeding and gestation. Small differences ($P > 0.05$) in the magnitude of changes in body CS were observed among type of birth and rearing and ewe age categories and were generally consistent with the observed changes in body weights.

Least squares means for yearling and adult fleece characteristics are presented in Table 2.6. Yearling fleece weight and staple length were greater for single-born lambs and lambs born to older ewes. However, the correlation between yearling fleece weight and BW was 0.38 ($P < 0.05$) and after including body weight as a covariate in the yearling fleece analysis, effects of birth type and dam age were no longer significant ($P > 0.05$). Adult fleece weight and staple length were greater for 2-yr-old ewes, probably as a result of less physiological stress on younger ewes. The 2-yr-old ewe has not yet produced lambs and may therefore devote more energy to wool growth. However, in the current data, there were no significant differences in wool growth for ewes rearing fewer lambs.

Number of lambs born per ewe lambing increased with ewe age. Least-squares means for NLB for 2, 3, 4, 5 and 6 yr old ewes were 1.27, 1.42, 1.58, 1.64 and 1.68, respectively, and each differed significantly from the others ($P < 0.05$). The average lamb drop in the current data set was 1.46 which was similar to the 1.50 lambs per ewe for Targhee sheep reported by Hanford et al. (2003), but larger than the 1.22 and 1.37 lambs per ewe reported by Okut et al. (1999) for Targhee ewes.

2.3.2 Genetic evaluation

Variance component estimation. Variance component estimates for lamb traits from bivariate analyses including 120W are listed in Table 2.7. Heritability estimates for

BWT, 45W and 120W were 0.19, 0.07 and 0.12, respectively. Parameter estimates for early growth traits are similar to the pooled estimates reported by Safari et al. (2005) for dual-purpose sheep breeds. Lower estimates were reported for BWT in Romanov (0.07; Tosh and Kemp, 1994) and Swedish Finewool (0.07; Nasholm and Danell) sheep whereas slightly higher estimates were reported for Columbia (0.27; Hanford et al., 2002) and Targhee (0.24; van Vleck et al., 2003). Additive maternal heritability for lamb traits were similar to other reported estimates (Bromley et al., 2000; Rao and Notter, 2000), although much lower than the 0.30 reported for BWT in Swedish Finewool (Nasholm and Danell, 1996) and 0.25 reported for BWT in Columbia (Hanford et al., 2002).

Additive heritability estimates for lamb body weights were greater at 120 d (0.12) than at 45 d (0.07), although, maternal heritability and permanent environmental effects were similar for both traits. Similar trends for greater estimates of additive effects at older lamb ages have been reported (Notter and Hough, 1997; Tosh and Kemp, 1994). Parameter estimates for both pre-weaning and weaning weights are in agreement with other estimates for western range type breeds (Notter and Hough, 1997; Bromley et al., 2000; Rao and Notter, 2000; Hanford et al., 2002; van Vleck et al., 2003).

Moderate estimates for heritability for YWT and 18MW were 0.26 and 0.38, respectively. These estimates are within the range of estimates reported by Safari et al. (2005) for post-weaning weights or weights taken after 12 mo of age (0.29) for dual-purpose sheep breeds. Maternal components were not significant ($P > 0.10$) for YWT and 18MW and thus not included in the models. Notter and Hough (1997) reported a slightly lower estimate of heritability for YWT in Targhee (0.26) than that reported here. The heritability estimate for 18MW was similar to the 0.43 that was estimated for 18-mo BW in Rambouillet (Lee et al., 2000).

Variance component estimates for NLB are within the range of others presented for western white-faced sheep breeds (Okut et al., 1999). The heritability estimate of 0.12 for NLB was similar to the value of 0.11 reported for Targhee sheep at the US Sheep Experiment Station in Dubois, ID (Bromely et al., 2000) and for Targhee flocks participating in the Nation Sheep Improvement Programs (Rao and Notter, 2000). Slightly lower heritability estimates were reported for Columbia (0.07) and Rambouillet (0.08) breeds (Bromely et al., 2000). Permanent environmental effects associated with NLB accounted for 4% of phenotypic variance, which is higher than other estimates for the Targhee breed (0.01 by Bromley et al., 2000; 0.02 by Rao and Notter, 2000).

Few studies have estimated genetic parameters for adult traits. Adult size has been evaluated as a proportion of mature size (Fitzhuge and Taylor, 1972), as weight at a given age (Stobart et al., 1986), through prediction of mature size using a non-linear growth function (Nasholm and Danell, 1996), and as a repeated measure of adult BW (Kelley et al., 2006). In the current study, adult ewe weight was evaluated at three different stages of the annual production cycle (before lambing, early lactation and weaning). Adult body weight is a function of frame size, body composition, internal organ size, and fetal development at the time of weighing, whereas body CS is generally considered an indicator of body fat reserves relative to body size. Although body CS has been included in models for adult weight in sheep (Kelley et al., 2006) and beef cattle (Northcutt et al., 1992), this evaluation of adult weight did not include CS in the model because genetic relationships with CS were of interest.

Heritability estimates for adult weights in bivariate analyses with 120-d weaning weight were 0.38, 0.38 and 0.58 for PWT, LWT and GWT, respectively (Table 2.8) and were similar to estimates evaluated in trivariate evaluations that included all adult weight trait measurements of PWT, LWT and GWT (0.38, 0.38, and 0.48, respectively). These heritability values were similar to the pooled estimate of 0.40 reported for adult weight reported by Safari et al. (2005). Stobart et al. (1986) reported a heritability of 0.53 for mature weight from a parental half-sib regression analysis of Columbia, Rambouillet and Targhee ewes, while heritability estimates for ewe weight in Swedish Finewool ewe ranged from 0.29 to 0.55 (Nasholm and Danell, 1996). Lower estimates were reported by Hansen and Shrestha (1997), ranging from 0.17 to 0.33 for Canadian breeds of sheep. Heritability estimates for body weights in beef cattle are within the range of those presented here (0.52 by Bullock et al., 1993; 0.53 by Kaps et al., 1999).

Permanent environmental effects on adult body weight were similar at the different times, with estimates of 0.36, 0.34 and 0.21 for PWT, LWT and GWT, respectively. The resulting between-year repeatability estimates were thus 0.74, 0.72 and 0.79 for PWT, LWT and GWT, respectively.

Maternal effects on adult ewe body weight have been reported by Nasholm and Danell (1996) and Kelley et al. (2006). The inclusion of a maternal component for adult BW contradicts the diminishing impact maternal effects appear to have on lamb growth with increasing age (Robison, 1981). Nasholm and Danell (1996) reported a maternal component of variance for ewe body weight (0.22) that was not significantly different from zero; when this effect was removed from the model, most of the maternal portion was partitioned into the additive variance. Kelly et al. (2006) estimated a direct heritability of 0.59, a maternal heritability of 0.18, and an additive direct-maternal correlation of 0.10 for Rambouillet and Targhee sheep.

Heritability estimates for CS were all significant (0.15, 0.13 and 0.13 for PCS, LCS and GCS, respectively; Table 2.8) but were much lower than estimates for body weight. Permanent environmental effects of the animals were significant for PCS (0.12) and LCS (0.05) ($P < 0.05$) but not different from zero for GCS (0.02; $P > 0.10$). Repeatability estimates were lower for body CS than adult weight traits due to a greater environmental impact on within ewe variation of body condition across different years. The presence of additive variance in CS indicates that there is genetic variation in body fat composition and usage of body energy reserves during different physiological stages. However, coefficients of variation for body CS ranged from 14.3% to 15.4%, indicating that selection would result in only marginal changes in phenotype for CS.

Parameter estimates for changes in body weight and CS are listed in Table 2.9. Significant heritability estimates were observed for changes in body weight in early lactation (0.13) and late lactation (0.05) but not for the breeding and gestation phase (0.06). However, changes in body CS were not heritable and thus were not considered further. Smaller estimates of genetic variation may be expected for WC2 because changes in feed quality and decreasing milk production are both influencing changes in weight during this interval. Coefficients of variation were large for all BW changes, ranging from 86.3% to 240.3%. These parameter estimates indicate that selection could influence ewe body changes. These changes may also be useful as indicators of ewe productivity if they reflect changes in, and availability of, body energy reserves during the production year (Sanson et al., 1993).

Lamb and adult trait correlations. Two-trait analyses with NLB and lamb weight traits included environmental correlations between lamb traits and NLB that were positive, ranging from 0.27 to 0.99 (Table 2.10). The high residual correlations between NLB and YWT and 18MW contrast to the correlation between litter size and 18 month weights of 0.00 reported by Lee et al. (2000) in Rambouillet sheep. Genetic correlations involving NLB differed from zero ($P < 0.10$) only for 120W (0.31) and YWT (-0.53). The positive genetic correlation with 120W is slightly lower than the 0.48 reported by Rao and Notter (2000), however the negative correlations with YWT is in the opposite direction to the estimate of 0.35 reported by Lee et al. (2000). The negative genetic correlation between YWT and NLB may reflect an inverse relationship between body size and age at maturity, with larger animals tending to reach physiological maturity at older ages (Fitzhugh and Taylor 1972) which may influence lambing rates in younger ewes.

Genetic and residual correlations between lamb and adult body weights (Table 2.10) were all positive and within the range of other estimates (Stobart et al., 1986; Nasholm and Danell, 1996; Mousa et al., 1999). These correlations increased with lamb age. A similar relationship was reported in Swedish Finewool sheep (Nasholm and Danell, 1996) with genetic correlations between mature ewe size and birth and weaning weights of 0.36 and 0.85, respectively. Genetic correlations between lamb traits and ewe body CS ranged from -0.52 to 0.45 and were not different from zero ($P > 0.05$). Residual correlations between ewe body CS and lamb weights were generally not different from zero ($P > 0.10$) with the exception of the residual correlations between 120W and PCS (0.36), YWT and PCS (0.69) and YWT and LCS (0.42).

Relationships between changes in adult BW and lamb growth traits are presented in Table 2.10 and 2.11. Phenotypic correlations between changes in adult BW and lamb traits were all near zero, ranging from -0.04 to 0.04, with the exception of a phenotypic correlations of -0.16 ($P < 0.01$) between 120W and WC1. Negative genetic, maternal and residual correlations were generally observed between WC1 and lamb traits, with the exception of residual correlations of WC1 with BWT (0.30) and 45W (0.27). However, only genetic correlations of WC1 with 45W (-0.48) and 120W (-0.49) were significantly different from zero. Morgan et al. (2005) concluded that ewes producing more milk lost more weight during lactation which agrees with the negative correlations estimated in the present study. None of the correlation estimates involving WC2 were different from zero ($P > 0.10$), but a slight negative trend was observed between genetic effects on late lactation weight change and maternal effects on lamb growth. Although phenotypic relationships were not strong, the genetic and maternal correlations between lamb weights and WC3 were positive while environmental relationships tending to be negative. Direct-maternal correlations between early lamb weight traits and WC3 ranged from 0.51 to 0.57 ($P < 0.05$). These correlations suggest a significant relationship between maternal effects on lamb growth and ewe weight gain, independent of fetal growth, during breeding and gestation. An unrealistic genetic correlations of -0.99 was estimated for WC3 and 18MW, but the number of animals with both WC3 and 18MW records was limited and the estimates of the correlations between these traits is likely not reliable.

Our results confirm that selection for lamb weight will be accompanied by correlated increases in adult weight. This relationship likely reflects similar genetic effects influencing frame size and muscle development over time. Positive changes in ewe body weights and condition scores are also expected to accompany selection for maternal effects on lamb weight, although the association between maternal effects on lamb growth and body CS was only significant for 120-d weight (Table 2.11). Although daily milk yield was not measured, a positive relationship between milk production and body energy reserve would support this correlation, reflecting changes in body composition. Producers generally aim to achieve an intermediate optimum level for ewe body weight and CS. However, our results suggest that selection for either direct or maternal genetic effects on lamb growth will influence ewe BW changes in early lactation and during breeding and gestation.

Correlations among adult traits. Genetic and residual correlations involving adult traits are presented in Table 2.13 and permanent environment correlations are shown in Table 2.14. Uncorrelated random and residual effects involving adult body weights and CS were confounded with litter size effect in the two-trait analysis with NLB; therefore permanent environmental (-0.99) and residual correlations were difficult to interpret. Genetic effects on NLB were independent of those for other adult traits ($P > 0.10$).

Adult body weights and CS had strong genetic and permanent environmental correlations with other body weights and CS, respectively, reflecting the high repeatability of these traits. Phenotypic correlations between adult weights and CS were positive, ranging from 0.16 to 0.40. Adult body weights were genetically independent of CS ($P > 0.10$), however, residual and permanent environmental correlations were positive and often significant, indicating environmental effects influencing CS also influenced body weights. These correlations were expected because body fat associated with CS is a component of body weight.

Significant negative residual relationships between WC1 and WC2 (-0.46) and between WC2 and WC3 (-0.40) ($P < 0.001$) indicate a cyclical weight change pattern, such that greater weight loss in one interval is associated with greater weight gain during the next. However, genetic relationships between weight changes were not different from zero ($P > 0.10$). Genetic associations between adult body weight and WC1 were -0.41, -0.37 and -0.52 ($P < 0.05$) for PWT, LWT and GWT, respectively, and demonstrate that ewes with positive breeding values for body weight tend to also lose more weight during early lactation. Decreases in body weight during early lactation are not likely to be associated with losses in structural size (i.e. frame size; Fitzhugh and Taylor, 1972) so this decline in weight may be associated with use of more plentiful body energy reserves in larger ewes during a time of negative energy balance.

Other studies have reported and discussed a negative relationship between changes in body weight during lactation and milk yield (Snowder and Glimp, 1991; Morgan et al., 2005). The relationships presented here between ewe weight, body CS, and body weight changes suggest that genetic changes in ewe weight are anticipated to have little impact on other ewe performance traits except for WC1. However, environmental relationships with adult BW were stronger and may play a large role in ewe performance.

2.4 IMPLICATIONS

The relationships presented in this study indicate that continued selection for lamb growth traits will increase BW and milking ability of the adult breeding ewe. The impacts of these changes in performance are unclear with regards to breeding ewe fitness. Under a western range environment, additional milk production may compete with growth for intake energy and put an added strain on the ewe. Further study is needed to evaluate the relationships between selection for lamb growth and its effect on the length of productive life in the ewe flock. The inclusion of adult BW in a multiple-trait selection program would be beneficial if there were antagonistic relationships between adult size and ewe productivity; however, these relationships are not established.

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Table 2.1 Summary of data including years of recording, numbers of records, and numbers of sires and dams represented for each trait [1].

Trait Category	Trait	Years of evaluation	Number of: Records	Sires	Dams
Lamb Weight	BWT	1960 – 2005	12,154	200	2,930
	45W	1960 – 2005	10,280	199	2,782
	120W	1960 – 2005	10,099	199	2,764
Yearling Weight	YWT	1987 – 2005	1,122	48	578
	18MW	1960 – 1987	1,375	126	926
Yearling Ewe Fleece	YFW	1986 – 2004	2,319	43	465
	YSL	1986 – 2004	1,683	43	462
	YSC	1986 – 2004	2,171	43	462
Adult Body Weight	PWT	1960 – 2005	6,870	187	1,499
	LWT	1987 – 2005	3,496	86	777
	GWT	1996 – 2005	1,386	44	480
Adult Body Condition	PCS	1995 – 2005	1,806	52	523
	LCS	1995 – 2005	1,883	52	535
	GCS	1997 – 2005	1,166	44	426
Adult Fleece	AFW	1987 – 2005	3,643	86	801
	ASL	1987 – 2005	3,410	86	797
	ASC	1987 – 2005	3,404	86	797
Number Born	NLB	1960 – 2005	7,451	187	1,539

1. Abbreviations: BWT = Birth weight, 45W = 45d pre-weaning weight, 120W = 120d weaning weight, YWT = Yearling weight, 18MW = Eighteen month weight, YFW = Yearling fleece weight, YSL = Yearling staple length, YSC = Yearling spinning count, PWT = Adult body weight at post-weaning of lambs, LWT = Adult body weight during lactation, GWT = Adult body weight during late-gestation, PCS = Adult body condition score at post-weaning of lambs, LCS = Adult body condition score during lactation, GCS = Adult body condition score during late-gestation, AFW = Adult fleece weight, ASL = Adult staple length, ASC = Adult spinning count, NLB = Number of lambs born per litter.

Table 2.2 Multiplicative adjustment factors for lamb body weights and ewe litter sizes[1].

Category		NLB[2]	BWT[3]	45W[2]	120W[3]
Ewe age[4]	2	1.29	1.05	1.09	1.08
	3	1.15	1.00	1.00	1.00
	4	1.04	1.00	0.97	1.00
	5	1.00	1.00	0.96	1.00
	6	0.98	1.00	0.97	1.00
Lamb sex	Ewe		1.00	1.00	1.00
	Ram		0.94	0.95	0.91
	Wether			0.98	0.97
Number of lambs born	1		1.00		
	2		1.21		
	3		1.38		
Number of lambs born/reared	1/1			1.00	1.00
	2/1			1.17	1.12
	2/2			1.36	1.23
	3/1			1.20	1.20
	3/2			1.46	1.31
	3/3			1.40	1.36

1. See Table 1 for trait abbreviations.
2. Multiplicative adjustments derived from the current data.
3. Multiplicative adjustments obtained from Bradford (2003).
4. Age of ewe at the time of lambing for NLB; age of dam for BWT, 45W and 120W.

Table 2.3 Least square means of lamb weights by lamb sex, type of birth, and ewe age categories [1] [2].

	BWT (kg)			45W (kg)			120W (kg)			YWT (kg)			18MW (kg)		
	mean	*s.e.*	N	mean	*s.e.*	N	mean	*s.e.*	N	mean	*s.e.*	N	mean	*s.e.*	N
Gender															
Ewe	4.32	*0.02*	6,178	15.53	*0.08*	5,265	31.49	*0.13*	5,208	50.37	*0.72*	876	63.66	*0.46*	1,362
Ram	4.62	*0.02*	5,976	16.42	*0.08*	4,719	34.15	*0.13*	4,584	81.57	*0.90*	246			
Wether				15.75	*0.18*	294	32.19	*0.30*	307						
Type of Birth [3]															
1	5.36	*0.01*	4,523	19.30	*0.07*	4,098	37.80	*0.12*	4,055	68.46	*0.43*	535	65.78	*0.27*	607
2	4.37	*0.01*	7,322	14.59	*0.06*	6,011	30.59	*0.11*	5,860	64.47	*0.42*	571	62.61	*0.25*	738
3	3.68	*0.01*	306	13.81	*0.21*	169	29.44	*0.36*	184	64.97	*2.07*	16	62.58	*1.29*	17
Ewe age															
2	4.06	*0.02*	3,135	14.64	*0.10*	2,531	30.70	*0.17*	2,483	66.02	*0.86*	317	62.88	*0.55*	300
3	4.43	*0.02*	3,832	15.84	*0.10*	2,452	32.42	*0.17*	2,383	64.50	*0.87*	282	63.75	*0.53*	348
4	4.57	*0.02*	2,461	16.25	*0.10*	2,159	33.12	*0.18*	2,107	66.39	*0.91*	224	63.87	*0.53*	286
5	4.63	*0.02*	1,916	16.45	*0.11*	1,663	33.33	*0.18*	1,622	66.63	*0.90*	171	64.04	*0.56*	226
6	4.64	*0.02*	1,810	16.33	*0.11*	1,473	33.48	*0.18*	1,498	66.32	*0.98*	128	63.75	*0.56*	202

1. See Table 1 for trait abbreviation.
2. Standard errors are presented in italics.
3. Size of the litter in which the lamb was born.

Table 2.4 Least square means for adult weights and body condition scores of ewes for different litter size, type of birth and rearing, and ewe age groups [1].

		Post – weaning			Lactation			Late – Gestation		
		mean	*s.e.*	N	Mean	*s.e.*	N	Mean	*s.e.*	N
Adult Body Weight (kg)	Litter size [2]									
	1							65.49	*0.27*	748
	2							69.21	*0.28*	607
	3							73.84	*1.46*	20
	Birth/rearing type [3]									
	1/0	73.51	*0.40*	266	63.88	*0.63*	115			
	1/1	69.32	*0.12*	3,430	63.17	*0.22*	1,700			
	2/0	75.31	*0.65*	97	63.85	*0.94*	49			
	2/1	70.25	*0.24*	727	62.48	*0.37*	368			
	2/2	69.32	*0.14*	2,258	62.58	*0.24*	1,218			
	3/1	73.75	*1.40*	20	58.87	*2.46*	7			
	3/2	69.77	*0.91*	52	61.39	*1.24*	29			
	3/3	69.23	*1.73*	13	62.14	*2.30*	8			
	Ewe age									
	2	66.40	*0.97*	2,188	57.21	*1.02*	1,083	63.12	*1.66*	447
	3	70.04	*0.97*	1,706	61.62	*1.03*	886	67.96	*1.68*	361
	4	71.85	*0.98*	1,318	63.97	*1.03*	696	70.37	*1.69*	273
	5	72.66	*0.98*	950	65.00	*1.04*	487	71.77	*1.70*	184
	6	72.85	*0.99*	701	64.99	*1.05*	342	72.12	*1.77*	109
Body Condition Score	Litter size [2]									
	1							3.03	*0.02*	636
	2							3.05	*0.02*	515
	3							3.17	*0.13*	14
	Birth/rearing type [3]									
	1/0	3.24	*0.09*	35	2.94	*0.07*	36			
	1/1	2.92	*0.02*	888	2.78	*0.02*	920			
	2/0	3.29	*0.14*	15	2.76	*0.10*	20			
	2/1	2.85	*0.04*	202	2.63	*0.03*	209			
	2/2	2.82	*0.02*	641	2.58	*0.02*	670			
	3/1	3.05	*0.30*	3	2.55	*0.20*	5			
	3/2	2.81	*0.13*	16	2.63	*0.11*	17			
	3/3	2.97	*0.26*	4	2.62	*0.22*	4			
	Ewe age									
	2	3.06	*0.09*	600	2.53	*0.07*	614	3.00	*0.12*	376
	3	3.08	*0.09*	474	2.65	*0.07*	493	3.13	*0.13*	301
	4	3.09	*0.09*	355	2.69	*0.08*	372	3.07	*0.13*	234
	5	2.98	*0.09*	233	2.65	*0.08*	242	3.23	*0.13*	160
	6	2.78	*0.10*	142	2.54	*0.08*	160	3.12	*0.13*	93

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1. Standard errors are presented in italics
2. Number of lambs born after recording the late-gestation body weight.
3. Number of lambs born/number of lambs nursed by the ewe at the time of weighing.

Table 2.5 Least square means for changes in adult body weight and adult body condition score at different times in the annual production cycle [1][2].

		Early lactaion			Late lactation			Breeding and Gestation		
		mean	*s.e.*	N	Mean	*s.e.*	N	mean	*s.e.*	N
Adult Body Weight	Number of fetuses [3]									
	1							-0.19	*0.28*	419
	2							2.28	*0.28*	405
	3							5.51	*1.29*	15
	Birth/rearing type [4]									
	1/0	-2.58	*0.91*	39	7.33	*0.44*	131			
	1/1	-3.41	*0.25*	682	4.23	*0.17*	1616			
	2/0	-8.72	*1.17*	23	7.77	*0.72*	44			
	2/1	-6.50	*0.43*	185	5.68	*0.25*	449			
	2/2	-8.29	*0.30*	385	5.00	*0.19*	1068			
	3/1	-20.39	*2.79*	4	11.47	*1.87*	5			
	3/2	-9.98	*1.56*	13	6.98	*0.90*	31			
	3/3	-22.82	*5.60*	1	6.10	*2.02*	6			
	Ewe age									
	2	-9.53	*0.90*	432	7.72	*0.42*	1032	3.44	*0.55*	309
	3	-9.91	*0.90*	355	7.22	*0.43*	858	2.17	*0.55*	248
	4	-9.98	*0.91*	265	6.42	*0.43*	665	2.29	*0.58*	166
	5	-10.10	*0.01*	176	6.32	*0.45*	469	2.25	*0.68*	101
	6	-12.16	*1.01*	104	6.43	*0.46*	329	*	*	*
Body Condition Score	Number of fetuses [3]									
	1							0.15	*0.04*	312
	2							-0.03	*0.04*	288
	3							0.02	*0.20*	9
	Birth/rearing type [4]									
	1/0	-0.22	*0.11*	31	0.38	*0.09*	47			
	1/1	-0.29	*0.03*	583	0.13	*0.02*	852			
	2/0	-0.34	*0.15*	16	0.43	*0.13*	17			
	2/1	-0.45	*0.05*	155	0.23	*0.04*	238			
	2/2	-0.53	*0.04*	327	0.23	*0.03*	577			
	3/1	-0.36	*0.59*	1	0.52	*0.34*	2			
	3/2	-0.66	*0.18*	11	0.20	*0.14*	17			
	3/3	*	*	*	0.38	*0.34*	3			
	Ewe age									
	2	-0.48	*0.10*	364	0.46	*0.07*	566	-0.05	*0.08*	246
	3	-0.39	*0.10*	296	0.34	*0.07*	469	0.08	*0.08*	177
	4	-0.29	*0.10*	225	0.31	*0.07*	351	0.12	*0.08*	120
	5	-0.44	*0.10*	152	0.25	*0.08*	229	-0.10	*0.11*	66
	6	-0.44	*0.12*	87	0.20	*0.08*	138	*	*	*

1. Early lactation represents changes between 0d and 45 d post-parturition, late lactation represents changes between 45 and 120 d post-parturition, breeding and gestation represents changes between lamb weaning and the next parturition.
2. Standard errors are presented in italics
3. Number of fetuses carried during gestation.
4. Number of lambs born/number of lambs nursed by the ewe at the time of weighing.

Table 2.6 Least square means for lamb and adult fleece traits for different birth type and dam age groups for yearling ewe lambs and different ewe age groups for adults [1].

		Fleece weight (kg)			Staple length (cm)			Spinning count		
		mean	*s.e.*	N	mean	*s.e.*	N	mean	*s.e.*	N
Yearling	Type of birth [2]									
lamb	1	3.51	*0.02*	786	7.406	*0.04*	602	64.21	*0.10*	711
fleece	2	3.10	*0.02*	936	7.143	*0.04*	738	64.55	*0.08*	871
	3	3.03	*0.09*	36	6.923	*0.19*	28	63.93	*0.41*	34
	Dam age [3]									
	2	3.09	*0.04*	448	7.099	*0.08*	345	64.41	*0.18*	420
	3	3.17	*0.04*	425	7.147	*0.08*	334	64.20	*0.18*	400
	4	3.27	*0.04*	375	7.108	*0.09*	285	64.13	*0.18*	345
	5	3.25	*0.04*	285	7.226	*0.09*	227	64.20	*0.19*	258
	6	3.28	*0.05*	225	7.206	*0.10*	177	64.20	*0.22*	193
	Ewe age [4]									
Adult	2	4.21	*0.02*	1,093	8.346	*0.03*	1,033	62.33	*0.09*	1,031
fleece	3	3.88	*0.02*	904	7.919	*0.04*	844	63.00	*0.10*	839
	4	3.96	*0.03*	729	7.831	*0.04*	693	62.93	*0.10*	693
	5	3.67	*0.03*	531	7.796	*0.05*	499	62.85	*0.12*	499
	6	3.84	*0.03*	381	7.628	*0.05*	341	62.96	*0.14*	342

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1. Standard errors are presented in italics.
2. Size of the litter in which the yearling ewe was born.
3. Age of dam when the yearling ewe lamb was born.
4. Age of the adult ewe at the time of shearing.

Table 2.7 Variance components for lamb traits from bivariate analysis with 120 d weaning weights [1] [2].

Item[3]	BWT	45W	120W[4]	YWT	18MW	YFW	YSL	YSC
No. records	11818	10055	9736	1122	1375	2314	1681	2171
Mean	5.34	19.03	38.72	57.03	65.15	3.19	7.12	64.56
h^2	0.19	0.07	0.12	0.32	0.38	0.32	0.31	0.25
m^2	0.15	0.09	0.08	-	-	-	-	-
$pe_m{}^2$	0.09	0.06	0.04	-	-	-	-	-
e^2	0.57	0.79	0.76	0.68	0.62	0.68	0.69	0.75
σ^2_p	0.753	9.856	30.187	46.935	35.718	0.363	1.142	5.659

1. See Table 1 for trait abbreviations.
2. All variance component estimates were significantly greater than zero ($P < 0.05$).
3. h^2 = heritability, m^2 = maternal heritability, $pe_m{}^2$ = permanent environment of the dam, e^2 = residual, σ^2_p = phenotypic variation.
4. Variance components for 120 d weight were averaged over all bivariate analyses with lamb traits.

Table 2.8 Variance components for adult traits from bivariate analysis with 120 d weaning weight [1 2].

Item[3]	NLB	PWT	LWT	GWT	PCS	LCS	GCS	AFW	ASL	ASC
No. records	7451	6,870	3,496	1,376	1,806	1,883	1,166	3,643	3,410	3,404
Mean	1.61	69.21	62.52	66.63	2.86	2.70	3.06	4.01	8.07	62.80
h^2	0.12	0.38	0.38	0.53	0.15	0.13	0.13	0.44	0.37	0.25
pe^2	0.04	0.36	0.34	0.21	0.12	0.05	0.02†	0.25	0.01†	0.06†
e^2	0.85	0.26	0.28	0.26	0.73	0.82	0.85	0.32	0.62	0.69
σ^2_p	0.310	44.351	40.857	47.321	0.195	0.165	0.191	0.330	0.931	5.982

1. See Table 1 for trait abbreviations.
2. All variance components were significantly greater than zero ($P < 0.05$) in single trait analyses except those denoted with †.
3. h^2 = heritability, m^2 = maternal heritability, pe^2 = permanent environment of the animal, e^2 = residual, σ^2_p = phenotypic variation.

Table 2.9 Single-trait estimates of variance components for changes in adult body weight and condition scores[1].

	Body Weight Changes [3]			Body Condition Score Changes [4]		
Item[2]	WC1	WC2	WC3	BC1	BC2	BC3
# records	1342	3394	847	1133	1790	616
Mean	-5.37	4.94	1.95	-0.43	0.17	0.14
h^2	0.13^{**}	0.05^{**}	0.06	0.03	0.00	0.00
pe^2	$0.09^{\dagger}$	$0.04^{\dagger}$	0.25^{**}	0.00	0.03	0.08
e^2	0.78	0.91	0.70	0.97	0.97	0.92
σ^2_p	20.77	16.37	21.24	0.28	0.24	0.30

1. Significance values indicate if proportion of variance is different from zero: † = $P < 0.10$, * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$.
2. h^2 heritability, pe^2 = permanent environmental effects of the animal, e^2 = residual effects, σ^2_p = phenotypic variance.
3. Body weight changes during early lactation (WC1), late lactation (WC2), and breeding and gestation (WC3).
4. Changes in body condition scores during early lactation (BC1), late lactation (BC2), and breeding and gestation (BC3).

Table 2.10 Estimates of additive genetic and residual correlations between lamb and adult traits [1 2 3].

Adult Trait	Lamb trait BWT		45W		120W		YWT		18MW	
	r_a	r_e	r_a	r_e	r_a	r_e	r_a	r_e	r_a	r_e
NLB	-0.10	$0.27^{\dagger}$	0.25	0.35^{***}	0.31^{*}	0.53^{***}	-0.53^{***}	0.99^{***}	-0.08	0.93^{***}
PWT	0.36^{***}	0.27^{***}	0.72^{***}	0.34^{***}	0.74^{***}	0.57^{***}	0.85^{***}	0.65^{***}	0.96^{***}	0.95^{***}
LWT	$0.21^{\dagger}$	0.24^{***}	0.70^{***}	0.31^{***}	0.69^{***}	0.61^{***}	0.86^{***}	0.71^{***}	0.85^{***}	0.74^{***}
GWT	0.40^{**}	0.05^{***}	0.69^{***}	0.24^{**}	0.75^{***}	0.68^{***}	0.88^{***}	0.66^{***}	0.89^{***}	0.66^{***}
PCS	-0.01	$0.10^{\dagger}$	-0.07	0.13	$-0.13^{\dagger}$	0.36^{**}	$-0.39^{\dagger}$	0.69^{***}	-0.38	0.40
LCS	$0.07^{\dagger}$	$-0.12^{\dagger}$	0.14	-0.09	$0.14^{\dagger}$	$0.25^{\dagger}$	0.12	0.42^{*}	0.23	-0.09
GCS	$0.31^{\dagger}$	-0.49	0.45	-0.25	$0.18^{\dagger}$	$0.10^{\dagger}$	0.23	0.46	-0.52	0.62
WC1	-0.31	$0.30^{\dagger}$	-0.48^{*}	$0.27^{\dagger}$	-0.49^{*}	-0.23	$-0.39^{\dagger}$	-0.17	-0.37	-0.47
WC2	0.16	0.00	-0.05	0.02	0.44	0.04	0.07	-0.05	0.28	-0.26
WC3	0.32	-0.37^{**}	0.60^{*}	-0.36^{**}	$0.50^{\dagger}$	$-0.28^{\dagger}$	0.05	0.04	-0.99	0.21

1. See Tables 1 and 9 for trait abbreviations.
2. r_a = additive correlation between lamb trait and adult trait, r_e = residual correlation between lamb trait and adult trait.
3. Significance values indicate correlations are different from zero: † = $P < 0.10$, * = $P< 0.05$, ** = $P < 0.01$, *** = $P < 0.001$.

Table 2.11 Estimates of correlations between additive direct effects on adult traits and additive maternal effects on lamb traits [1,2].

Adult	Lamb trait		
Trait	BWT	45W	120W
NLB	$-0.17^{\dagger}$	-0.03	-0.26^{**}
PWT	0.40^{***}	0.31^{***}	0.29^{***}
LWT	0.45^{***}	0.44^{***}	0.36^{***}
GWT	0.53^{***}	0.59^{***}	0.48^{***}
PCS	$0.21^{\dagger}$	0.14	0.13^{*}
LCS	$0.07^{\dagger}$	$0.37^{\dagger}$	0.33^{*}
GCS	$0.31^{\dagger}$	$0.44^{\dagger}$	0.42^{*}
WC1	-0.46^{**}	-0.56^{***}	-0.57^{***}
WC2	-0.15	-0.32	-0.14
WC3	0.57^{**}	0.57^{**}	0.51^{*}

1. See Tables 1 and 9 for trait abbreviations.
2. Significance values indicate correlations are different from zero:
   † = $P < 0.10$, * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$.

Table 2.12. Estimates of additive genetic and residual correlations between yearling fleece and adult traits [1] [2].

	Lamb trait					
Adult Trait	YFW		YSL		YSC	
	r_a	r_e	r_a	r_e	r_a	r_e
NLB	-0.58^{***}	0.99^{***}	-0.24	0.27	0.34^{*}	-0.34^{*}
PWT	0.28^{*}	0.52^{***}	-0.22	0.24	0.16	-0.20^{**}
LWT	0.19^{*}	0.57^{***}	-0.26^{*}	0.27	0.17	-0.19^{**}
GWT	0.26^{*}	0.47^{***}	$-0.26^{\dagger}$	0.19	0.26	-0.20^{*}
PCS	-0.44^{*}	0.44^{**}	-0.07	0.12	-0.15	$-0.18^{\dagger}$
LCS	-0.46^{*}	0.32^{*}	-0.18	-0.02	-0.18	-0.07
GCS	$-0.40^{\dagger}$	0.34	-0.02	-0.05	-0.41	0.05
WC1	-0.09	0.12	0.07	0.20	0.37	-0.11
WC2	0.09	0.02	0.16	-0.08	-0.10	-0.22
WC3	-0.46	-0.17	-0.38	-0.04	-0.60	0.22^{*}

1. See Tables 1, 9, and 10 for trait abbreviations.
2. Significance values indicate correlations are different from zero: † = $P < 0.10$, * = $P< 0.05$, ** = $P < 0.01$, *** = $P < 0.001$.

Table 2.13 Additive direct and residual correlations among adult traits [1,2,3].

Trait		Adult Body Weight			Adult Body Condition Score			Adult Body Weight Change		
	NLB	PWT	LWT	GWT	PCS	LCS	GCG	WC1	WC2	WC3
NLB		0.12†	-0.11	0.09	-0.02	-0.07	-0.12	-0.09	0.47†	0.35
PWT	-0.15***		0.96***	0.93***	-0.04	0.33†	0.33	-0.41*	0.27	0.31
LWT	-0.19***	0.36***		0.94***	-0.24	0.26	0.28	-0.37*	-0.15	0.40
GWT	0.24***	0.28***	0.32***		-0.18	0.25	0.35	-0.52*	-0.03	0.45
PCS	-0.11***	0.35***	0.18***	0.10*		0.99***	0.99***	0.15	0.50†	0.25
LCS	-0.23***	0.23***	0.40***	0.19***	0.16***		0.93***	0.04	0.31	0.31
GCS	0.0	0.15***	0.07†	0.26***	0.03	0.08*		-0.09	0.41	0.96***
WC1	-0.36***	0.05	0.60***	-0.56***	0.03	0.17***	-0.13***		-0.07	-1.00*
WC2	0.07***	0.59***	-0.53***	0.01	0.18***	-0.11***	0.07*	-0.46***		-0.82
WC3	-0.01	-0.62***	-0.21***	-0.46***	-0.23***	-0.16***	0.05	0.10	-0.40***	

1. See Tables 1 and 9 for trait abbreviations.
2. Additive and residual correlations above and below the diagonal, respectively.
3. Significance values indicate correlations are different from zero:
   † = $P < 0.10$, * = $P < 0.05$, ** = $P < 0.01$, and *** = $P < 0.001$.

Table 2.14 Correlations of permanent environmental effects of the animal for adult traits[1,2].

Trait	Adult Body Weight			Adult Body Condition Score			Adult Body Weight Change		
	PWT	LWT	GWT	PCS	LCS	GCG	WC1	WC2	WC3
PWT									
LWT	0.97^{***}								
GWT	0.91^{***}	0.92^{***}							
PCS	0.94^{***}	0.92^{***}	0.90^{***}						
LCS	0.71^{***}	0.91^{***}	0.73^{**}	0.86^{***}					
GCS	0.37	0.73^{*}	$0.84^{\dagger}$	0.90^{***}	0.99^{**}				
WC1	0.35	0.35	-0.31	0.05	0.42	-0.63			
WC2	0.26	0.09	0.19	0.21	$-0.68^{\dagger}$	-0.99^{*}	0.17		
WC3	-0.21^{**}	0.12	0.99^{***}	0.30	0.63^{*}	-0.99	-1.00^{***}	0.08	

1. See Tables 1and 9 for trait abbreviations.
2. Significance values indicate correlations are different from zero:
   † = $P < 0.10$, * = $P < 0.05$, ** = $P < 0.01$, and ***= $P < 0.001$.

Chapter 3 Genetic analysis of ewe stayability and its association with lamb growth and adult production.

3.1 INTRODUCTION

Breeding ewes that stay in the flock for longer periods of time typically produce more lambs than ewes that leave the flock at younger ages. Therefore, the length of time a ewe remains productive influences profitability. Breeding ewes may be voluntarily removed from the flock if they fail to breed, have poor production, or reach a predetermined fixed culling age, or may necessarily be removed due to illness or death. However, consideration of the productive life of the breeding ewe in flock breeding objectives has been limited by the lack of information regarding genetic control of this trait.

Stayability is defined as the probability of survival to a specific age, given the opportunity to reach that age (Hudson and Van Vleck, 1981) and reflects the underlying fitness characteristics that contribute to the removal of a breeding animal from the production system. Genetic variation in stayability has been identified in dairy (Van Vleck, 1980) and beef cows (Snelling et al. 1995) and swine (Lopez-Serrano et al. 2000), however, evaluation of stayability in breeding ewes is limited. Stayability is typically measured as a binary trait and has been evaluated with both linear and threshold models. Results from these alternative models have usually been consistent so long as the observations are approximately equally distributed across fixed effects and not strongly associated with one category (Māntysaari et al., 1991). Similar results were obtained for genetic evaluation of stayability in Canadian Holstein cattle using linear and threshold models, and the less computationally demanding linear model was implemented (Jairath et al., 1998).

One of the challenges in evaluating stayability is the time required for assessment. Methods to incorporate censored stayability data have been used in dairy cattle (Vukasinovic et al., 2001; Van Raden et al., 2006) but these models require large data sets with either knowledge of time and reasons for removal, or covariance relationships between stayability and traits measured at an earlier age. In extensive sheep production systems, detailed information about ewe removal from the flock is often limited and incorporation of associations between stayability and other production traits in a multiple-trait evaluation could improve the accuracy of evaluation. The objective of this study was to estimate genetic parameters for alternative measures of ewe stayability and evaluate relationships between lamb growth, ewe performance and stayability.

3.2 MATERERIAL AND METHODS

3.2.1 Data

Data were available for 12,154 Targhee sheep born between 1960 and 2005 in the Montana State University flock. The flock was located mainly on the Red Bluff Research Ranch near Norris, Montana and managed as a commercial western range flock. Ranch dynamics and management practices were described in Stobart et al. (1986) and in Chapter 3 of this dissertation. Data included body weights of lambs at birth (**BWT**), approximately 45 d of age (**45W**), and weaning at approximately 120 d of age (**120W**) as well as adult ewe body weights at weaning (**PWT**$_i$), and the number of lamb born (**NLB**$_i$). In addition, subsets of the data contained body weights at 12 (**YWT**) and 18 mo of age (**18MW**), annual adult body weights in late gestation (**GWT**$_i$) and early lactation (**LWT**$_i$), annual adult condition scores in late gestation (**GCS**$_i$), early lactation (**LCS**$_i$), and at weaning (**PCS**$_i$), and annual adult fleece weights (**AFW**$_i$) staple lengths (**ASL**$_i$) and spinning counts (**ASC**$_i$), where *i* is the age of ewe at the time data was recorded. Table 3.1 shows the years when data were collected, numbers of observations, and numbers of sires and dams for each measure. Changes in adult body weight were calculated for early lactation (**WC1** = LWT_i - GWT_i), late lactation (**WC2** = PWT_i - LWT_i), and during breeding and gestation (**WC3** = GWT_{i+1} - PWT_i) where *i* is the age of the ewe. Further description of the adult body weight and condition traits and methods used to edit and adjust weight records are presented in Chapter 2.

Selection methods used to choose ewe lambs for breeding varied from year to year, but were primarily based on phenotypes for body weight and wool quality. Breeding ewes were identified in the data set as those that lambed at 2 yr of age. Specific information on the reason or exact date when a ewe left the flock was not available. Ewes were assumed to be removed from the flock for failure to lamb, poor production, illness, age, or death. Ewes were identified as being removed from the flock if a lambing record was present at n yrs of age but not at n + 1 yrs of age. All females were culled before reaching 7yr of age. Only 1.5% of the ewes apparently failed to lamb at age n but subsequently had lambing records at a later age. Reasons for these anomalous records were unknown, and these ewes were removed from the flock after the first missed lambing.

Stayability data were available for ewes born in the flock between 1960 and 2002 and included 2,525 ewes from 183 sires and 1,498 dams. Conditional stayability measures were recorded as binary indicators of a lambing record at a given age (failure = 0, success = 1). Eight different conditional stayability measures (Table 3.2) were evaluated in this study. Overall stayability traits (**STAY *n*|2**) were defined as the probability that a ewe that lambed at 2 yr of age also lambed at n yr of age for n equal to 3, 4, 5, and 6 yrs of age. Data for overall stayability only included individuals that had opportunity to express a lambing record at n yr of age. Therefore, ewes born after 1999, 2000, and 2001 did not have records for STAY 6|2, STAY5|2, and STAY4|2, respectively. Marginal stayability traits (**STAY *n*|*n*-1**) were defined as the probability that a ewe that lambed at n-1 yr of age also lambed at n yrs of age for n equal to 3, 4, 5, and 6 yrs of age. Marginal stayabilities were missing for ewes without lambing records at *n*-1 yrs of age. Years of productive life (**YPL**) was also considered as a stayability trait and was defined as age in years of the last known successful lambing. Missing values for YPL were assigned to ewes born after 1999 were not included in the analysis of YPL because they did not have the opportunity to remain in the flock until 6 yr of age.

3.2.2 Statistical Analysis

A linear animal model was used for all traits. Models included fixed and random effects as presented in Chapter 2 for lamb and adult traits. All genetic analyses were conducted using multiple-trait, derivative-free MTDFREML software (Boldman et al., 1995). Convergence of solutions was assumed to have occurred when the variance of -2 times the log likelihoods across iterates was less than 1 X 10^{-9}. Once convergence was attained, each run was re-started with the converged estimates used as priors to ensure global convergence. All stayability traits included random direct additive effects with mean of 0 and variance of $\mathbf{A}\sigma^2_a$, where **A** is the additive numerator relationship matrix and σ^2_a is the additive direct variance. Random residual effects were included with mean 0 and variance of $\mathbf{I_n}\sigma^2_e$, where $\mathbf{I_n}$ is an identity matrix with order equal to the number of individual records and σ^2_e is the residual variance.

Multiplicative factors were used to adjust BWT, 45W, and 120W for effects of age of dam, lamb sex and type of birth and rearing and to adjust NLB for effects of ewe age. Contemporary groupings for lamb body weights included year of birth and management group as well as sex of lamb for YWT. Methods for data adjustment and contemporary grouping are presented in Chapter 2 of this dissertation for lamb weight traits. Adult weight, condition score, and fleece measures were analyzed as traits of the ewe with yearly repeated records (Chapter 2) accounting for fixed effects of ewe age and number of lambs born and reared. Birth year contemporary groups were also included as fixed effects for all adult and stayability traits.

Variance component estimates for lamb traits and adult body weight, condition score, changes in weight, NLB, and fleece traits were previously discussed in Chapter 2 and used as prior estimates in two-trait evaluation of stayability. Models for BWT, 45W, and 120W included random direct additive, direct maternal, permanent environment of the dam and residual effects. Models for YWT and 18MW included only direct additive and residual random variances. Models for repeated observations of adult weights, body condition score, changes in weight, NLB, and fleece traits were similar to that used for yearling traits and also included a random permanent environmental effect of the animal.

Single-trait analyses were initially used for each stayability trait to evaluate the significance of each random effect. Variance components estimated from single-trait analyses were then used as priors for additional multiple-trait analyses. Additive direct and residual covariance was calculated between each stayability trait and all other lamb and adult traits. Covariances between additive direct effects on stayability and additive maternal effects on lamb traits were also estimated. The software did not permit direct estimation of covariances between residual environmental effects on stayability and repeated adult traits. In multiple-trait evaluations including stayability and adult traits, residual effects for stayability traits were estimated by fitting an independent permanent environmental effect of the ewe and forcing the residual variance of stayability to zero. The resulting covariances between independent random effects of the animal are equivalent to the covariance between residual effects on stayability traits and permanent environmental effects on repeated adult traits (Rao and Notter, 2000).

Significance of covariances in bivariate analyses was determined by likelihood ratio tests after fixing each covariance to 0. Trivariate analyses were conducted when selection bias potentially influenced genetic parameter estimates from bivariate analyses.

3.3 RESULTS AND DISCUSSION

Replacement rates of the breeding flock ranged from 21.5 to 33.9% per year, with an overall average of 30.7%, which was higher than the 20 to 25% replacement rate reported over a 9-yr period by Saboulard et al. (1995) for two flocks of white-faced range sheep in Wyoming. Table 3.3 lists numbers of ewes removed from the flock at different ages, including only ewes that had the opportunity to lamb at 6 yr of age. Nearly 66% of breeding ewes left the flock for reasons other than age. The marginal loss of young ewes was consistent, with 20% of the 2- and 3-yr-olds leaving the flock each year. Although the number of ewes removed from the flock decreased with age, the marginal loss of older ewes increased with a greater proportion of 5-yr-old ewes leaving the flock compared to younger age groups.

3.3.1 Single-trait analyses

Table 3.4 shows results of single-trait evaluations of stayability. More records were available for stayability traits expressed at earlier ages. Phenotypic variance ranged from 0.158 to 0.239 for conditional stayability traits with less phenotypic variance in marginal traits. The mean of YPL was 4.31 yrs with a coefficient of variation that was lower than other stayability traits. Heritability estimates for stayability ranged from 0.00 to 0.09 in single-trait evaluations with significant genetic variation only expressed in STAY 5|2, STAY 6|2, STAY 5|4, and STAY 6|5 ($P < 0.05$). Additive genetic variance for YPL approached significance with a heritability of 0.05 ($P < 0.10$). Hudson and Van Vleck (1981) suggested that an increasing additive variance may be expected as the frequency of surviving females decreases with age because the variance of a binomial trait increases with more equal proportions of each category. Those measures of stayability that expressed genetic variation had proportions of surviving females that ranged from 23% to 73%. Mantysaari et al. (1991) used simulated data to conclude that variance component estimation of binary traits were comparable between linear and threshold models when the incidence of a binary category was greater than 25% and the distribution of incidences across fixed effects groups was consistent. In the current data, the average incidence of ewes removed from the flock for most STAY3|2 contemporary groups were less than 20%, indicating that a threshold model may be superior to account for disproportional variance among fixed-effect classes. However, the average incidence across fixed effects for other stayability traits was within the range suggested by Māntysaari et al (1991) for estimating variance components of binary traits with a linear model.

3.3.2 Bivariate analyses

Heritability estimates for stayability traits from bivariate evaluations with lamb and adult traits are presented in Table 3.5. Proportion of additive variance in STAY3|2, STAY4|2, and STAY4|3 were not different from zero (P > 0.10) in all bivariate evaluations and therefore will not be discussed further. Significant heritability estimates for survival traits measured early in life have been reported in dairy (Boettcher et al., 1999; Vollema and Groen, 1996) and beef cattle (Snelling et al., 1995; Martinez et al., 2005), however, additive variance was not present in early measured stayability in these data. Estimates of additive variance for the remaining stayability traits were slightly higher than those estimated in single-trait analyses with heritability values of 0.06, 0.09, 0.10, 0.04, and 0.06 for STAY 5|2, STAY 6|2, STAY,5|4, STAY 6|5, and YPL, respectively, when averaged over all two-trait evaluations with lamb and adult traits. Heritability estimates from bivariate evaluations that included 120W and stayability traits resulted in the largest estimates of additive variance for stayability traits, with the exception of YPL which expressed the largest heritability when analyzed with BWT. Other estimates of stayability in sheep are limited. Conington et al. (2001) reported a heritability of 0.08 for time to death or removal from the flock in Scottish Blackface hill sheep. Brash et al. (1994) estimated a heritability of 0.06 for age at last breeding in an Australian Dorset flock.

Low estimates of heritability have been reported for stayability of breeding females in other species, with estimates increasing slightly for traits expressed later in life. Hudson and Van Vleck (1981) used a linear animal model in Holstein cows and obtained heritability estimates ranging from 0.02 to 0.05 for stayability untill 36 to 84 mo of age. Other literature shows similar estimates for stayability in dairy cattle (Boettcher et al., 1999; Vollema and Groen, 1996). Snelling et al. (1995) reported heritability estimates of 0.01 and 0.09 for the probability a beef cow would have two or eight calvings, respectively, before being removed from the herd. Stayability in Large White and Landrace sows was evaluated by Lopez-Serrano et al. (2000) with heritability estimates for 0.07 and 0.11 for removal prior to the second and third parities, respectively.

Phenotypic correlations between stayability and lamb traits were near zero, ranging from -0.07 to 0.06 (Table 3.6). Conington et al. (2001) reported phenotypic correlations of 0.04, 0.04, and 0.05 between ewe longevity and lamb weaning weight, muscle score and fat depth, respectively, in UK hill sheep. Direct additive correlations between stayability and lamb traits were generally not significantly different from zero ($P > 0.10$) in bivariate analyses. Genetic correlations between overall STAY, YPL and lamb body weights were generally negative, although the correlations between BWT and STAY6|2 and YPL were 0.19 and 0.05 ($P > 0.10$), respectively. Marginal stayability showed a slight trend for positive genetic correlation with lamb body weights. Genetic relationships involving overall stayability traits represent the impact of each lamb trait on the cumulative probability that a ewe will be removed from the flock prior to a given age, whereas marginal stayability relationships correspond to the impact of the lamb trait on the probability that a ewe will be removed from the flock at a given age. The differences between relationships involving overall and marginal stayability may reflect either different involuntary culling criteria imposed by the producer or different genetic influence on ewe stayability at different ages. Early marginal stayability traits could help differentiate genetic relationships involving ewe removals at different ages. However, early stayability traits did not express genetic variation, and therefore it was not possible to partition genetic differences between removal at early and late ages.

Correlations between additive effects on stayability and maternal effects on 120W were positive and ranged from 0.46 to 0.57 ($P < 0.05$) with the exception of a correlation of 0.09 ($P > 0.10$) between additive STAY6|5 and maternal 120W (Table 3.6). These relationships suggest that ewes providing a better maternal environment for lamb growth, perhaps through more milk production, are at a lower risk of being removed from the flock before 5 yrs of age. Mwansa et al. (2002) reported negative genetic relationships between calf growth and cow stayability in a Canadian Hereford population with stayability correlations of -0.52 and -0.01 for additive and maternal weaning weights, respectively.

Table 3.7 lists variance component estimates from bivariate analyses of stayability and adult traits. Variance components for adult traits are similar to those estimated in Chapter 2. Phenotypic correlations were weak between stayability and adult traits ranging from -0.01 to 0.16. Genetic correlations between NLB and stayability were not different from zero ($P > 0.10$) and ranged from -0.22 for STAY6|5 to 0.12 for YPL. Conington et al. (2001) reported a genetic correlation of 0.36 between longevity and number of lambs reared while Brash et al. (1994) presented a genetic correlation of -0.15 between ewe longevity and number of lambs born. Additive correlations between stayability and adult traits tended to be negative, however, the only significant correlations were between adult weight and STAY 6|2 and YPL. Negative relationships between stayability and adult traits were reported by Mwansa et al. (2002) with a genetic correlation of -0.48 between cow weight at weaning and the probability of having three calves prior to removal from the herd. Beckman et al. (2005) reported genetic correlations between cow body condition scores and stayability ranging from -0.12 to -0.22 in Red Angus cattle. In our data, environmental effects on adult weight and condition score were positively associated with ewe stayability. Residual correlations between stayability and adult traits were positive, with the exception of correlations of zero between STAY5|4 and adult weights. Correlations between adult fleece and stayability traits were never different from zero ($P > 0.10$) and therefore are not presented. In contrast, Conington et al. (2001) reported a genetic correlation of 0.26 between longevity and fleece weight.

Variance components from the bivariate analyses including stayability and adult weight changes are presented in Table 3.7. Ewes with genetic potential to lose less, or gain more, weight during lactation (WC1 and WC2) tended to have a lower risk of being culled. Genetic correlations involving WC1 approach significance ($P < 0.10$) for STAY 6|2 and YPL. However, environmental effects of greater weight loss during early lactation tended to have a negative affect on stayability with residual correlations between WC1 and stayability traits ranging from -0.35 to -0.11 ($P < 0.05$). Genetic correlations between WC3 and each stayability trait were -1.00. The estimation of this strong negative correlation was the result of limited WC3 records, as well as a dependency of one addition year of production for all ewes with a WC3 record (i.e., only ewes with measures of PWT at *n* yr of age and GWT at *n*+1 yr of age had WC3 measures and were therefore assumed to be in the flock at n+1 yr of age).

3.3.3 Trivariate analyses

Correlation estimates from selected trivariate analyses are presented in Table 3.8. Trivatiate evaluations included 120W as one of the traits to account for potential ewe lamb selection bias in estimation of correlations involving stayability and adult traits.

Trivariate analyses often did not reach convergence criterion set for univariate and bivariate analyses so a minimum convergence criterion of $1x10^{-6}$ was accepted for trivariate analyses.

Heritability estimates for STAY 6|2 ranged from 0.02 to 0.15 when evaluated with 120W and another stayability trait which was a larger range than that observed for estimates from bivariate analyses. However, correlation estimates between STAY6|2 and other traits were similar to those from bivariate analyses with genetic correlations between STAY6|2 and other stayability traits ranging from 0.92 to 0.98. For trivariate evaluations with adult traits, only STAY 6|2 and YPL were considered because of their high correlations with other stayability traits and the inclusion of all ewes removed for reasons other than age.

Parameter estimates that included 120W, STAY6|2, and adult weight or body condition were similar to those from bivariate evaluations. Correlations between 120W and STAY6|2 ranging from 0.32 to -0.36 in trivariate analyses. However, genetic correlations between STAY6|2 and adult weight traits were not significant in trivariate analyses, ranging from -0.07 to 0.01. A similar result was observed between YPL and adult weights in trivariate analysis indicating only a small additive relationship between adult weight and stayability. Residual relationships between stayability and adult weight were slightly smaller than those from bivariate analyses. Direct additive-maternal correlations were consistent with estimates in bivariate evaluations with positive correlations between maternal effects on 120W and stayability ranging from 0.38 to 0.63 ($P < 0.05$) and between maternal effects on 120W and adult weight ranging from 0.27 to 0.43 ($P < 0.05$).

3.3.4 Ewe performance and stayability

The genetic correlations between stayability and adult body weight may be more appropriately estimated in the three-trait model where the relationships between adult weight and 120W are included. Genetic effects involving stayability and body size are more strongly related to early lamb growth than to adult weight (Table 3.8). Stobart et al. (1986) concluded that phenotypic variation in adult weight was strongly associated with differences in lamb growth rates. Lamb growth and mature size have a strong genetic relationship, however, under extensive range environments, non-genetic factors influencing adult weight likely affect the rate of early flock removal. Negative correlations between WC1 and 120W presented in Chapter 2, along with the negative genetic relationships between stayability and growth presented here, indicate that ewes with higher genetic potential for growth may have lower stayability, possibly because attaining ewe growth potential is hindered due to limiting environmental conditions. Lasslo et al. (1985) suggested that ewes under extensive range environments may not express their maternal production potential due to limitations in feed intake. Greater energy requirements for adult growth and maintenance may not be met in the western range environment. Therefore ewes with high genetic value for growth and size may be voluntarily removed from the flock because they either phenotypically appear to be unfit for entering the breeding season or they are at greater risk of illness or death. Genetic correlation between 120W and stayability traits generally ranged from approximately -

0.20 to -0.40 and those with adult weights were generally not less then -0.20. Thus, selection to allow simultaneous improvement in growth potential and stayability is possible, provided a practical estimator of stayability can be identified and incorporated into the genetic evaluation.

3.4 IMPLICATIONS

Genetic variation in stayability implies that breeding objectives could incorporate selection for ewes that stay in the flock for a longer period of time. However, the genetic relationships between stayability and other production traits are unclear and currently do not provide a good indicator for early life traits for selection on stayability. Further study with more detailed information regarding time and reason for flock removal are needed to properly address genetic and environmental effects on early growth and ewe productivity to account for their influence on ewe stayability.

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Table 3.1 Summary of data including years of recording, numbers of records, and numbers of sires and dams represented for each trait [1].

Trait Category	Trait	Years of evaluation	Number of: Records	Animals	Sires	Dams
Lamb Weight	BWT	1960 – 2005	12,154	12,154	200	2,930
	45W	1960 – 2005	10,280	10,280	199	2,782
	120W	1960 – 2005	10,099	10,099	199	2,764
Yearling Weight	YWT	1987 – 2005	1,122	1,122	48	578
	18MW	1960 – 1987	1,375	1,375	126	926
Adult Body Weight	PWT	1960 – 2005	6,870	2,476	187	1,499
	LWT	1987 – 2005	3,496	1,270	86	777
	GWT	1996 – 2005	1,386	715	44	480
Adult Body Condition	PCS	1995 – 2005	1,806	621	52	523
	LCS	1995 – 2005	1,883	825	52	535
	GCS	1997 – 2005	1,166	803	44	426
Adult Fleece	AFW	1987 – 2005	3,643	1,325	86	801
	ASL	1987 – 2005	3,410	1,315	86	797
	ASC	1987 – 2005	3,404	1,313	86	797
Number Born	NLB	1960 – 2005	7,451	2,593	187	1,539

1. Abbreviations: BWT = Birth weight, 45W = 45d pre-weaning weight, 120W = 120d weaning weight, YWT = Yearling weight, 18MW = Eighteen month weight, YFW = Yearling fleece weight, YSL = Yearling staple length, YSC = Yearling spinning count, PWT = Adult body weight at post-weaning of lambs, LWT = Adult body weight during lactation, GWT = Adult body weight during late-gestation, PCS = Adult body condition score at post-weaning of lambs, LCS = Adult body condition score during lactation, GCS = Adult body condition score during late-gestation, AFW = Adult fleece weight, ASL = Adult staple length, ASC = Adult spinning count, NLB = Number of lambs born per litter.

Table 3.2 Definitions of each stayability trait.

Trait		Definition
Overall Stayability	STAY 3|2	Probability a ewe lambs at 3 yrs of age given that she lambed at 2 yrs of age.
	STAY 4|2	Probability a ewe lambs at 4 yrs of age given that she lambed at 2 yrs of age.
	STAY 5|2	Probability a ewe lambs at 5 yrs of age given that she lambed at 2 yrs of age.
	STAY 6|2	Probability a ewe lambs at 6 yrs of age given that she lambed at 2 yrs of age.
Marginal Stayability	STAY 4|3	Probability a ewe lambs at 4 yrs of age given that she lambed at 3 yrs of age.
	STAY 5|4	Probability a ewe lambs at 5 yrs of age given that she lambed at 4 yrs of age.
	STAY 6|5	Probability a ewe lambs at 6 yrs of age given that she lambed at 5 yrs of age.
Years of Productive Life	YPL	Number of yrs of age when ewe left the flock

Table 3.3 Number of ewes in each age group (2 through 6 years of age) [1].

Ewe Age, yr	No. ewes	Ewes removed from flock [2]	Frequency of ewes removed from flock	
			Marginal loss [3]	Cumulative loss [4]
2	2287	459	0.201	0.201
3	1828	374	0.205	0.364
4	1454	346	0.238	0.516
5	1108	329	0.297	0.659
6	779	779	1.000	1.000

1. A total of 2287 ewes lambed at 2 yrs of age and had opportunity to remain in the flock until 6 yrs of age.
2. Ewes that lambed at the given age but were removed from the flock before their next lambing opportunity.
3. Proportion of ewes within an age group that were removed from the flock.
4. Cumulative proportion of ewes removed from the flock after each year of production.

Table 3.4 Variance components for ewe stayability traits from univariate analyses[1 2].

	Overall Stayability				Marginal Stayability			
Item[3]	STAY 3|2	STAY 4|2	STAY 5|2	STAY 6|2	STAY 4|3	STAY 5|4	STAY 6|5	YPL
# records	2525	2450	2373	2287	1955	1500	1108	2287
Mean	0.791	0.628	0.499	0.341	0.787	0.752	0.703	4.314
h^2	0.00	0.01	0.05^{*}	0.08^{***}	0.01	0.09^{**}	0.03^{*}	$0.05^{\dagger}$
e^2	1.00	0.99	0.95	0.92	0.99	0.91	0.97	0.95
σ^2_p	0.158	0.222	0.239	0.218	0.158	0.182	0.189	2.492

1. See table 3 for trait abbreviations.
2. Significance values indicate if the heritability estimate is different from zero:
   † = P < 0.10, * = P < 0.05, ** = P < 0.01, *** = P < 0.001.
3. h^2 = heritability; e^2 = residual variation as a fraction of phenotypic variance; σ^2_p = phenotypic variance.

Table 3.5 Variance components averaged over all bivariate analyses for lamb, adult, and stayability traits[1].

Item		Phenotypic Variance	Proportion of variance[2]		
			h^2	m^2	pe^2
Lamb Traits	BWT	0.76	0.19	0.16	0.08
	45W	9.18	0.07	0.08	0.06
	120W	30.08	0.11	0.09	0.03
	YWT	40.48	0.31		
	18MW	30.05	0.34		
Litter Size	NLB	0.32	0.13		0.03
Ewe Weight	PWT	40.20	0.37		0.35
	LWT	36.79	0.34		0.34
	GWT	41.05	0.42		0.28
Ewe Condition	PCS	0.20	0.14		0.12
	LCS	0.16	0.10		0.07
	GCS	0.19	0.11		0.05
Weight Change[3]	WC1	20.82	0.14		0.09
	WC2	16.37	0.05		0.02
	WC3	21.53	0.06		0.25
Stayability	STAY5|2	0.24	0.06		
	STAY6|2	0.22	0.09		
	STAY5|4	0.18	0.10		
	STAY6|5	0.19	0.04		
	YPL	2.50	0.06		

1. See Table 1 and 2 for abbreviations.
2. h^2= heritability, m^2= maternal heritability, pe^2= permanent environment.
3. Body weight changes during early lactation (WC1), late gestation (WC2), and breeding and gestation (WC3).

Table 3.6 Phenotypic, genetic, additive-maternal, and residual correlations between stayability (i) and lamb (j) traits from bivariate analyses [1] [2].

		Item ^{j}				
Item ^{i}	Correlation [3]	BWT	45W	120W	YWT	18MW
STAY5|2	r_p	-0.02	0.02	0.02	-0.00	0.02
	r_g	-0.14	-0.35	-0.24	-0.73†	-0.21
	r_{am}	0.28†	0.29	0.57**		
	r_e	-0.07*	0.04	0.01	0.11†	0.06
STAY6|2	r_p	-0.01	0.03	0.02	-0.00	0.02
	r_g	0.19	-0.32	-0.17	-0.50	-0.17
	r_{am}	0.18	0.22	0.46*		
	r_e	-0.06†	0.06†	0.02	0.09	0.07
STAY5|4	r_p	-0.07**	-0.02	-0.04*	-0.07**	-0.03
	r_g	0.35	0.15	0.06	-0.20	0.17
	r_{am}	-0.17	0.12	0.46*		
	r_e	-0.09*	-0.04	-0.10*	-0.10	-0.07
STAY6|5	r_p	0.01	0.04*	0.02	0.06**	0.05*
	r_g	0.39	-0.22	0.05	-0.03	-0.20
	r_{am}	-0.07	-0.04	0.09		
	r_e	-0.02	0.06	0.02	0.07	0.08
YPL	r_p	-0.01	0.04*	0.04*	0.03	0.03
	r_g	0.05	-0.64†	-0.29	-0.99**	-0.29
	r_{am}	0.42**	0.24	0.54*		
	r_e	-0.06†	0.07*	0.06	0.21*	0.09*

1. See Tables 1 and 2 for abbreviations.
2. Significance values indicated correlations are different from zero: † = $P < 0.10$, * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$.
3. r_p = phenotypic, r_g = additive genetic, r_{am} = additive-maternal, and r_e = residual correlations between stayability and lamb traits.

Table 3.7 Phenotypic, genetic, and residual correlations between stayability (i) and adult (j) traits from bivariate analyses [1] [2].

Item ^{i}	Correlation ^{3}	Item ^{j}									
		NLB	PWT	LWT	GWT	PCS	LCS	GCS	WC1	WC2	WC3
STAY5|2	r_p	0.02	0.04^{*}	0.02	0.03	0.02	0.09^{***}	0.11^{***}	-0.02	0.06^{**}	0.14^{***}
	r_g	0.03	0.27	-0.41	-0.47	-0.13	-0.34	-0.57	$0.80^{\dagger}$	0.33	$-1.00^{\dagger}$
	r_e	0.10	0.12^{**}	0.12^{*}	0.22^{*}	0.36^{**}	0.43^{**}	0.37	$-0.30^{\dagger}$	0.19	0.45^{***}
STAY6|2	r_p	0.03	0.03	0.01	0.04^{*}	0.06^{**}	0.09^{***}	0.09^{***}	0.00	0.01	0.13^{***}
	r_g	-0.03	-0.32^{*}	$-0.41^{\dagger}$	-0.67^{*}	-0.24	-0.34	-0.56	$0.63^{\dagger}$	0.19	$-1.00^{\dagger}$
	r_e	0.23^{*}	0.16^{***}	0.14^{*}	0.31^{***}	0.36^{**}	0.46^{**}	0.66^{*}	-0.26	0.01	0.41^{***}
STAY5|4	r_p	-0.01	0.01	0.01	0.03	0.03	0.03	0.07^{**}	-0.01	0.05^{*}	0.10^{***}
	r_g	-0.06	0.13	0.03	-0.12	0.04	-0.15	-0.26	0.51	0.41	-1.00^{*}
	r_e	0.01	0.00	0.00	0.06	0.21	0.19	0.30	-0.22	0.10	0.43^{***}
STAY6|5	r_p	0.05^{*}	0.03	0.01	0.05^{*}	0.02	0.05^{*}	0.03	0.00	-0.02	0.07^{**}
	r_g	-0.22	-0.49^{*}	-0.33	-1.00^{*}	-0.20	-0.12	-0.49	0.43	0.62	$-1.00^{\dagger}$
	r_e	0.37^{*}	0.17^{**}	0.08	0.32^{**}	0.15	0.21	0.36	-0.11	-0.19	$0.22^{\dagger}$
YPL	r_p	0.03	0.07^{**}	0.03	0.04^{*}	0.05^{*}	0.16^{***}	0.16^{***}	-0.03	0.05^{*}	0.25^{***}
	r_g	0.12	-0.46^{*}	-0.74^{*}	-0.83^{*}	-0.36	-0.60	$-0.95^{\dagger}$	$0.79^{\dagger}$	0.23	$-1.00^{\dagger}$
	r_e	0.15	0.18^{***}	0.22^{**}	0.40^{**}	0.54^{**}	0.63^{***}	0.30^{*}	-0.35	0.21	0.58^{***}

1. See Tables 1, 2, and 5 for abbreviations.
2. Significance values indicated correlations are different from zero: † = $P < 0.10$, * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$.
3. r_p = phenotypic, r_g = additive genetic, r_{am} = additive-maternal, and r_e = residual correlations between stayability and lamb traits.

Table 3.8 Variance components from trivariate analyses of weaning weight, stayability traits, and adult weights or body condition scores [1] [2] [3] [4].

Item		Genetic Correlation			Maternal Correlation		Residual Correlation		
Trait ^{i}	Trait ^{j}	r_{120w*i}	r_{120w*j}	r_{i*j}	r_{120w*i}	r_{120w*j}	r_{120w*i}	r_{120w*j}	r_{i*j}
STAY 6|2	STAY 5|2	-0.10	-0.27	0.92	0.45	0.72	0.01	0.01	0.74
	STAY 5|4	0.32	0.22	0.98	-0.08	0.11	0.02	0.02	0.57
	YPL	-0.36	-0.63	0.94	0.59	0.59	0.02	0.06	0.82
	PWT[5]	-0.31	0.76	-0.07	0.55	0.27	0.02	0.57	0.11
	LWT[5]	-0.18	0.73	-0.07	0.45	0.31	0.03	0.60	0.10
	GWT[5]	-0.27	0.80	0.01	0.50	0.43	0.04	0.67	0.14
	PCS[5]	0.00	-0.09	-0.22	0.38	0.04	0.00	0.37	0.36
	LCS[5]	-0.11	0.21	-0.08	0.43	0.15	0.00	0.18	0.41
	GCS[5]	-0.14	0.18	-0.21	0.43	0.37	0.02	0.18	0.88
YPL	PWT[5]	-0.43	0.77	-0.10	0.63	0.27	0.07	0.57	0.13
	LWT[5]	-0.30	0.73	-0.17	0.51	0.32	0.06	0.60	0.15
	GWT[5]	-0.42	0.81	0.05	0.60	0.43	0.07	0.67	0.22
	PCS[5]	-0.26	-0.08	-0.36	0.48	-0.01	0.05	0.31	0.50
	LCS[5]	-0.24	0.22	-0.24	0.50	0.16	0.06	0.16	0.61
	GCS[5]	-0.26	0.17	-0.43	0.49	0.38	0.05	0.13	0.63

1. See Table 1 and 2 for trait abbreviations
2. All trivariate analyses included weaning weight
3. r = correlation between two traits.
4. Phenotypic variance and variance components were similar to bivariate analyses in Table 5.
5. Convergence level was 1 x 10^{-6}